Successions écologiques et potentiel de récupération des communautés coralliennes : structure, démographie et recrutement dans le sud-ouest de l'océan Indien

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THÈSE

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Successions écologiques et potentiel de récupération des communautés coralliennes : Structure, démographie et recrutement dans le sud-ouest de l'Océan Indien

Soutenue le 12 juillet 2019 devant le jury composé de :

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RÉSUMÉ

Les récifs coralliens subviennent aux besoins de millions de personnes à travers le monde. Toutefois, les effets du changement climatique et l'accentuation de la fréquence et de l'intensité des perturbations mènent à une accélération de leur dégradation et au déclin des communautés de coraux scléractiniaires. Les préoccupations actuelles portent sur les capacités de résilience de ces écosystèmes vulnérables. Dans ce contexte, il apparait essentiel d'améliorer la compréhension des mécanismes de maintien des communautés coralliennes dans l'optique d'aider à la conservation et à la gestion des récifs.

Ce travail de thèse vise à analyser les processus démographiques, y compris le recrutement, et la structure des assemblages coralliens à plusieurs échelles dans différents milieux insulaires de la zone sud-ouest de l'océan Indien. Ces descripteurs ont été abordés au travers de la succession écologique sur les récifs et coulées de lave sous-marines de La Réunion et par l'évaluation du potentiel de récupération des récifs de cinq systèmes insulaires de la zone.

Les résultats montrent que le recrutement corallien est faible dans les Mascareignes (La Réunion et Rodrigues) et très variable à toutes les échelles spatiales étudiées, de quelques centimètres à plusieurs centaines de kilomètres. Cette variabilité spatiale est également observée entre sites en termes de recouvrement benthique, de densité, de structure de taille, de mortalité ou encore de potentiel de récupération des communautés coralliennes. Cette variabilité spatiale n'est cependant pas clairement liée aux niveaux de protection des sites ni aux patrons théoriques de la succession écologique (étudiés à La Réunion). Un patron de succession est toutefois mis en évidence, au cours duquel la taille des coraux et la richesse spécifique augmentent avec le temps jusqu'à ce que les interactions interspécifiques (e.g. la compétition pour l'espace) conduisent à leur diminution. De plus, une forte dominance du genre *Pocillopora* est observée sur tous les sites de coulées de lave, confirmant sa nature pionnière et compétitive. L'indice de récupération (*RI*) développé suggère que le potentiel de récupération des récifs du canal du Mozambique est supérieur (notamment pour Europa) à celui des récifs des Mascareignes, soumis de manière plus générale aux pressions anthropiques directes. Ces résultats sont cohérents avec les observations passées de la récupération des récifs étudiés suite à des perturbations diverses. L'ajout des taux de recrutement au calcul des *RI* pour La Réunion et Rodrigues modifie nettement le potentiel de récupération des sites de ces îles : les sites ayant les taux de recrutement les plus forts sont également ceux dont le *RI* est le plus élevé.

Ce projet apporte ainsi des informations essentielles sur les communautés récifales de l'océan Indien qui permettront d'améliorer les plans de gestion pour la conservation des récifs coralliens.

Mots clés : Récifs coralliens ; Coulées de lave ; Coraux scléractiniaires ; Succession écologique ; Recrutement ; Potentiel de récupération ; Structure des communautés ; Démographie ; Océan Indien.

ABSTRACT

Coral reefs support millions of people's livelihood around the world. However, the effects of climate change and the increase in frequency and intensity of disturbances are leading to their accelerated degradation and to the decline of scleractinian coral communities. Current concerns relate to the resilience of these vulnerable ecosystems. In this context, it is essential to improve our understanding of the mechanisms underlying maintenance of coral communities, which may also improve conservation and management efforts that are urgently needed for these ecosystems.

This PhD work aims to analyze demographic processes, including recruitment, and the structure of coral assemblages at several scales in different island environments of the southwestern Indian Ocean region. These descriptors were addressed through ecological succession on reefs and underwater lava flows of Reunion Island, and through the assessment of the reef recovery potential of five island systems in the area.

Results show that coral recruitment in the Mascarene Islands (Reunion and Rodrigues) is low and highly variable at all spatial scales, from a few centimeters to several hundreds of kilometers. This spatial variability is also observed between sites in terms of benthic cover, density, size structure, mortality and recovery potential of coral communities. However, this spatial variability is not clearly linked to the protection levels of the sites, nor to the theoretical patterns of ecological succession (studied in Reunion Island). A succession pattern is yet highlighted through the increase in coral size and species richness over time until interspecific interactions (e.g. competition for space) lead to their decline. In addition, a strong dominance of the *Pocillopora* genus is recorded at all lava flow sites, confirming its pioneering and competitive nature. The recovery index (*RI*) that we developed suggests that the recovery potential of the reefs of the Mozambique Channel is higher (especially for Europa) than that of the reefs of the Mascarene Islands, which are more subject to direct anthropogenic pressures. These results are consistent with past observations of recovery trajectories of the studied reefs following various disturbances. The addition of recruitment rates to the calculation of *RI* for Reunion and Rodrigues islands clearly modifies the recovery potential of these islands sites: the sites with the highest recruitment rates are also those with the highest *RI*.

This project thus provides essential information on Indian Ocean reef communities that may improve management strategies for coral reef conservation.

Key words : Coral reefs; Lava flows; Scleractinian corals; Ecological successions; Recruitment; Recovery potential; Community structure; Demography; Indian Ocean.

À mon grand-père,

ma cousine Amandine,

et mon ami Geoffrey

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Voilà donc ce manuscrit, fruit du travail de plusieurs années, qui débarque enfin. Ceci a été rendu possible par l'intervention, l'aide ou le soutien de différentes personnes que je tiens à remercier.

Je remercie pour commencer les membres du jury, Henrich Bruggemann, Tarik Meziane, Eric Thiébaut, Laetitia Hédouin, et Lorenzo Bramanti qui ont accepté d'évaluer ce travail.

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Merci aux membres du comité de thèse : Lionel Bigot, Lola Massé, David Obura, Valeriano Parravicini et Jean-Pascal Quod qui, depuis la France hexagonale, le Kenya ou La Réunion, ont bien voulu assurer un suivi de cette thèse en me prodiguant de précieux conseils.

Merci aux membres d'ENTROPIE : Sophie, Lionel, Lucie, Mehdi, Patrick, Isabel et Simon, ainsi qu'aux stagiaires de Master : Arnaud et Louis, qui ont participé aux plongées effectuées dans le cadre de cette thèse à La Réunion et à Rodrigues. En particulier, merci à Sophie pour son implication et sa gestion d'une grande partie des sorties terrain, à Lionel pour toutes les données récoltées et ses nombreux conseils ainsi qu'à Patrick et Simon pour leur implication et participation au travail de terrain à Rodrigues. Je remercie également chaleureusement Patrick Durville pour l'acquisition des données « poissons » à Rodrigues.

Merci à Michel Guillemard et aux plongeurs de TSMOI pour leur aide logistique et technique lors des plongées à La Réunion. Merci particulièrement à Michel pour son professionnalisme et sa bonne humeur en mer comme sur terre.

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également la SEMPA et Jean-Rex Pierre Louis de nous avoir permis de plonger au sein de la réserve et la Rodrigues Regional Assembly pour les autorisations administratives. Merci enfin à Sheila et sa famille qui rendent les séjours sur ce joli caillou particulièrement agréables.

Un merci aux autorités mauriciennes d'avoir bien voulu me laisser voyager avec mes étranges paquets de plaques en terre-cuite !

Merci également à Pascale Chabanet, Lionel Bigot et David Obura pour leur collaboration afin de me fournir de précieuses données provenant des Îles Éparses, ainsi qu'à Henrich pour des données « poissons » de La Réunion.

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Enfin, un énorme merci à Anne pour m'avoir apporté un soutien sans égal, à distance puis à mes côtés, malgré la pression de son propre travail doctoral et de recherche.

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Si toutefois j'avais oublié de remercier quelqu'un, mille excuses.

AVANT-PROPOS

Ce travail doctoral a été effectué au sein de l'Unité Mixte de Recherche (UMR) ENTROPIE (Écologie mariNe TRopicale des Océans Pacifique et IndiEn) à l'Université de La Réunion.

ENTROPIE est une UMR à 3 tutelles (Université de La Réunion, IRD et CNRS) créée en 2015. Elle est issue du rapprochement des unités CoReUs (IRD) et ECOMAR (Université de La Réunion et CNRS) dont l'objectif vise à mieux comprendre le fonctionnement des écosystèmes marins et insulaires de l'Indo-Pacifique tropical dans le contexte du réchauffement climatique[1].

ENTROPIE regroupe des écologues, des écophysiologistes et des généticiens marins ainsi que des spécialistes de la télédétection et du traitement du signal afin de proposer des stratégies de conservation, de valorisation et de gestion durable[1].

L'originalité d'ENTROPIE est l'approche intégrative à différentes échelles spatio-temporelles des processus évolutifs et de résilience des écosystèmes récifaux et hauturiers à travers les interactions de l'homme avec les ressources et le milieu[1].

Ce travail doctoral a été réalisé grâce aux financements du LabEx CORAIL (EPHE UR n°2 AO 2014), de la Direction des Relations Internationales de l'Université de La Réunion (AAP DRI 2017 n°1 et AAP DRI 2018 n°1), de Fonds Européens de Développement Régional (FEDER) dans le cadre du projet CALIBIOME (PO FEDER 2014-2020) ainsi que de crédits récurrents de l'UMR ENTROPIE. J'ai également bénéficié d'une subvention de type MARG I (n°2015-19) du WIOMSA (Western Indian Ocean Marine Scientific Association) dont j'ai eu la charge.

Les données utilisées dans le cadre de cette thèse ont été acquises majoritairement pendant la période de la thèse par mes soins et avec l'aide de collaborateurs, et plus ponctuellement dans le cadre d'autres projets externes à cette thèse.

[1] Source : umr-entropie.ird.nc. Droits de reproduction réservés et limités.

J'ai procédé à l'échantillonnage des recrues sur substrats artificiels avec l'aide de plusieurs membres de l'UMR ENTROPIE et de SHOALS à La Réunion et à Rodrigues lors de 6 campagnes de terrain (espacées de 6 mois). L'analyse de près de 1000 plaques en terre-cuite faisant suite à cet échantillonnage a été réalisée par mes soins.

J'ai également réalisé l'intégralité du suivi des colonies adultes et juvéniles à La Réunion et à Rodrigues durant la période de la thèse (annulé à Rodrigues après 2 campagnes), représentant de 400 à 600 colonies suivies selon la campagne de terrain.

L'échantillonnage du recouvrement benthique ainsi que des photos transects pour l'étude des communautés coralliennes à La Réunion et à Rodrigues a été réalisé par Lionel Bigot (ENTROPIE) et par moi-même. J'ai ensuite procédé à l'analyse de l'intégralité des photos, ce qui représente plus de 10 000 colonies coralliennes enregistrées. La diversité corallienne a été évaluée *in situ* par Lionel Bigot (i) en 2013 sur les récifs de La Réunion, (ii) au cours de cette thèse sur les coulées de lave de La Réunion et les récifs de Rodrigues. Les données ichtyologiques des sites de La Réunion et de Rodrigues ont été récoltées durant cette thèse par Simon Elise (ENTROPIE) et Patrick Durville ou préalablement par Henrich Bruggemann (ENTROPIE) pour les sites au sein de la Réserve Naturelle Marine de La Réunion (2013). Les données provenant des îles Glorieuses, Europa et Mayotte ont été acquises pour certaines dans le cadre de la thèse et pour d'autres en partenariat avec les programmes BIORECIE (2011-2012) et SIREME (2015-2016) coordonnés par Pascale Chabanet (IRD Réunion). Ces programmes avaient pour objectifs de réaliser des inventaires de la biodiversité, d'établir une cartographie des habitats et de poursuivre le suivi de l'état de santé des récifs des Îles Éparses de l'Océan Indien et de Mayotte afin d'apporter des connaissances utiles pour la gestion des milieux et l'aide à la décision. Pour un site de Mayotte, les données de diversité en coraux sont issues d'une liste ZNIEFF de 2014 et ont été récoltées par Lionel Bigot.

L'ensemble des analyses de données a été réalisé par mes soins au cours de ce travail doctoral et m'ont permis de faire une présentation scientifique au congrès international du WIOSMA organisé en 2017 à Dar es Salam en Tanzanie.

En parallèle de mes activités de recherche, j'ai également dispensé des enseignements aux étudiants de licence de la faculté des Sciences et Technologies de l'Université de La

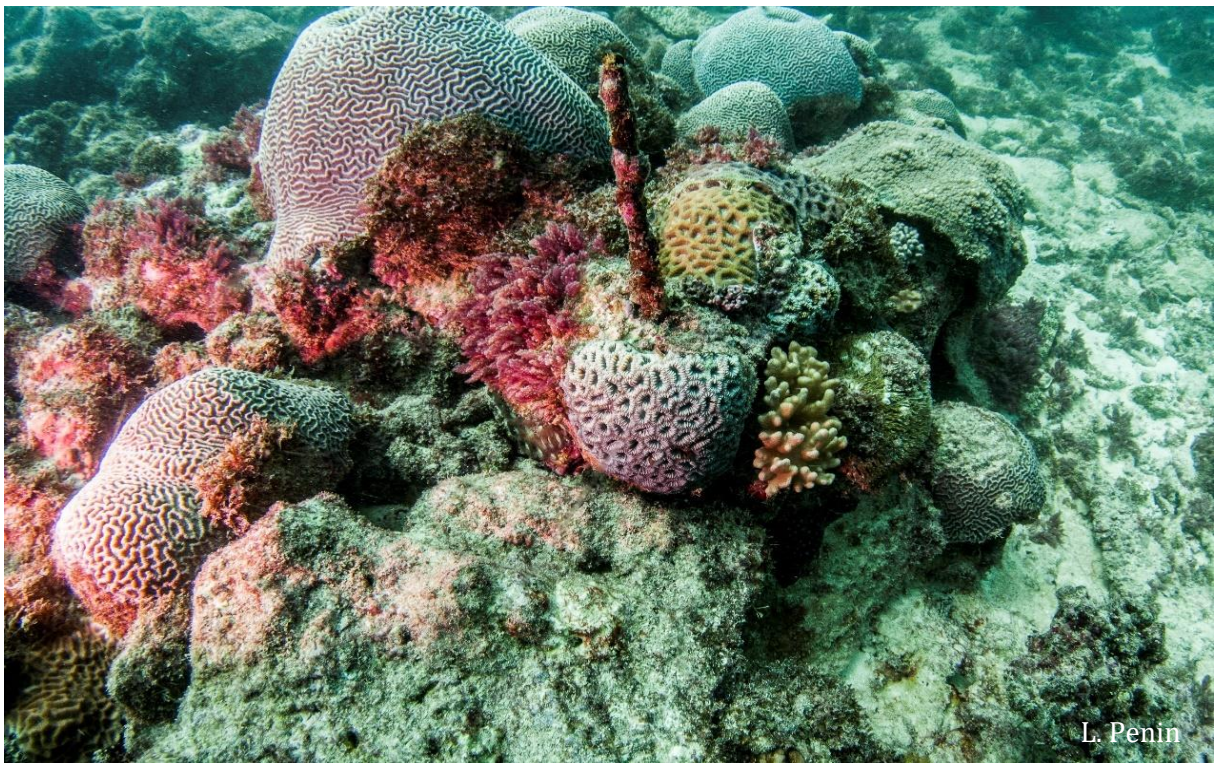
Réunion, qui se sont prolongés par le biais d'un contrat d'ATER pour l'année 2018-2019 représentant près de 330 heures d'enseignements (CM, TD et TP).

Enfin, j'ai participé à l'encadrement de deux binômes d'étudiants de Master I en écologie sur le thème du blanchissement corallien de masse de 2016 à Rodrigues (année universitaire 2016-2017) et sur le recrutement corallien sur les platiers récifaux dans la Réserve Naturelle Marine de La Réunion (année universitaire 2017-2018).

TABLE DES MATIÈRES

CHAPITRE 1.

INTRODUCTION GÉNÉRALE



1.1. Contexte scientifique

1.1.1. L'écosystème corallien

Le terme « récif corallien » traduit non seulement une structure tridimensionnelle océanique définissant un espace architectural bioconstruit mais aussi un environnement dans lequel les organismes associés interagissent et produisent une communauté complexe (Goldberg 2013). Ces écosystèmes marins abritent une biodiversité remarquable, notamment due à la complexité de l'habitat généré par des organismes hermatypiques, i.e. architectes des récifs, les coraux (Roberts et al. 2002, Holbrook et al. 2015). Les récifs coralliens sont présents dans une centaine de pays des zones tropicales et subtropicales et permettent de faire vivre de manière directe ou indirecte plusieurs centaines de millions de personnes à travers le monde (Figure 1 ; Moberg & Folke 1999, Wilkinson 2008, Kittinger et al. 2012, Harris et al. 2018). Les services écosystémiques qu'ils fournissent comprennent notamment les ressources halieutiques, la protection des côtes face à l'assaut des vagues ou encore un environnement favorable aux activités touristiques.

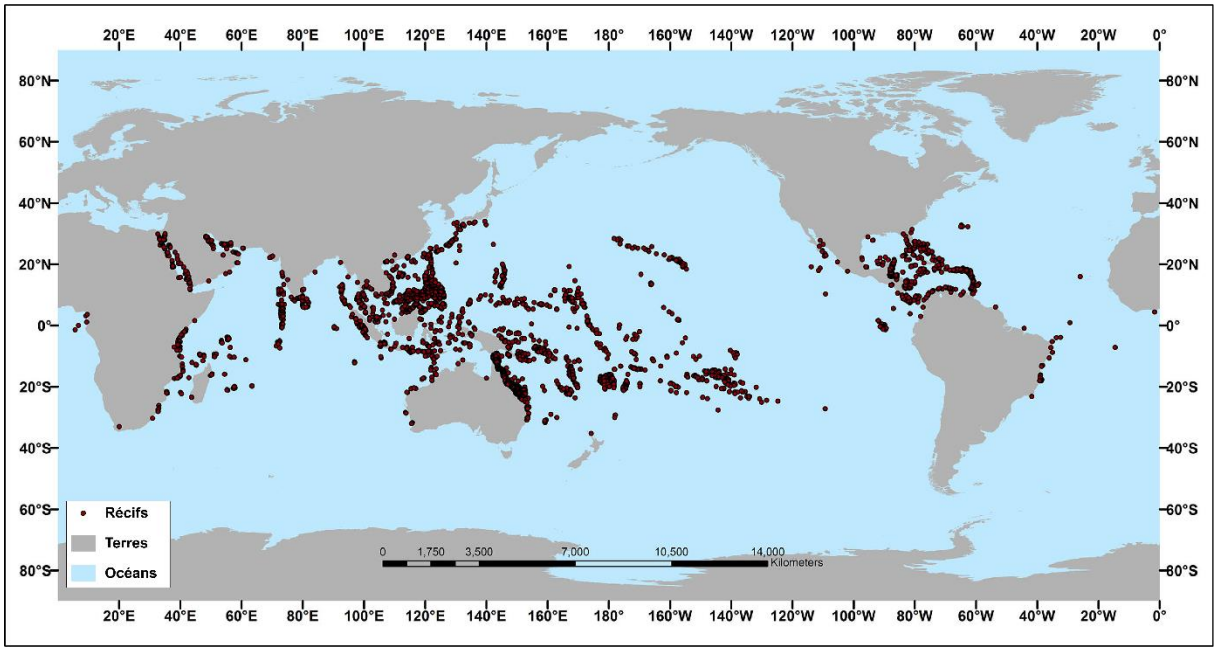


Figure 1. Carte de la répartition mondiale des récifs coralliens. La majorité des récifs se trouve entre les latitudes 30°N et 30°S (Modifié d'après NOAA 2018).

1.1.2. Les coraux scléractiniaires

Le terme « coraux » est généralement utilisé pour faire référence aux organismes benthiques de l'embranchement des Cnidaires qui sécrètent un squelette calcaire (Goldberg 2013). Cela inclut certains Hydrozoaires calcifiés, ainsi qu'un grand nombre d'Anthozoaires, en particulier les coraux durs dits « vrais » de l'ordre Scleractinia (autrement appelés scléractiniaires). Sur les 1605 espèces recensées appartenant à cet ordre, près de 50 % sont zooxanthellées, i.e. hébergent des algues unicellulaires symbiotiques du genre *Symbiodinium*, et érigent les récifs (= hermatypiques) dans les eaux chaudes peu profondes (Hoeksema & Cairns 2019). Les scléractiniaires vivent généralement en colonies coralliennes composées chacune d'un ensemble d'individus génétiquement identiques appelés polypes, capables d'utiliser du carbonate de calcium ($CaCO_3^{2-}$) dissous dans les océans pour synthétiser un squelette calcaire (Figure 2). Les polypes sont zoophages et capturent le plancton à l'aide de cnidocystes. Bénéficiant de déchets métaboliques et d'une protection par leur hôte corallien, les symbiotes algaux apportent en retour des sucres, du glycérol et des acides aminés essentiels pour survivre et croitre dans des eaux tropicales oligotrophes où la prédation sur le plancton n'est pas suffisante (Muscatine & Porter 1977, Hallock 2001, Yellowlees et al. 2008).

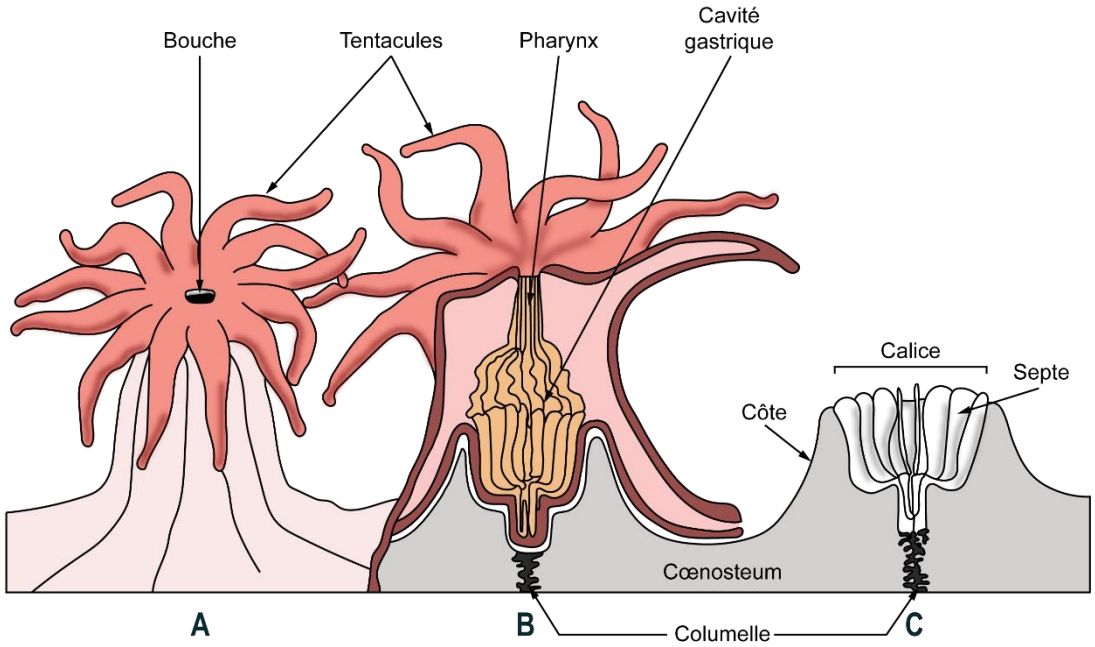


Figure 2. Représentation schématique d'un polype et du squelette corallien. A) polype entier ; B) coupe transversale du polype et de son squelette ; C) squelette seul (Modifié d'après Mather & Bennett 1993).

La formation des récifs coralliens et le maintien des communautés récifales sont étroitement liés au cycle de vie bentho-pélagique des scléractiniaires (Figure 3 ; Harrison & Wallace 1990). Par reproduction sexuée, les colonies adultes, gonochoriques ou hermaphrodites, émettent dans la colonne d'eau des gamètes pour une fécondation externe (espèces dites *spawners*) ou des larves pélagiques après fécondation interne (espèces dites *brooders*). Après dispersion, la larve se fixe sur le substrat pour se métamorphoser en polype. La phase benthique qui s'en suit comprend (i) le stade recrue, i.e. l'organisme récemment fixé non visible à l'œil nu, puis (ii) le stade juvénile lorsque la colonie devient clairement visible à l'œil nu et enfin (iii) le stade adulte capable de reproduction sexuée. Les critères de définition des jeunes stades étant subjectifs, ils peuvent sensiblement varier selon les auteurs mais l'on considère généralement comme recrues les coraux de moins de 1 cm de dimension maximale et comme juvéniles les colonies ne dépassant pas 5 cm de diamètre (Miller et al. 2000, Penin et al. 2010, Adjeroud et al. 2013, Fabricius et al. 2017).

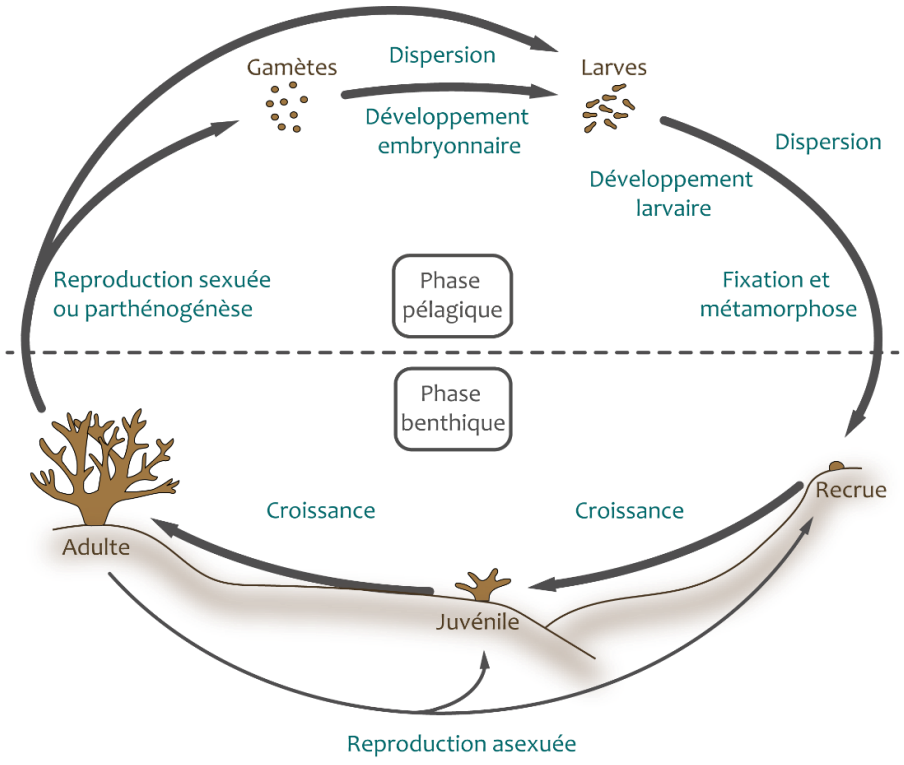


Figure 3. Cycle de vie des coraux scléractiniaires. Les adultes, généralement fixés au substrat, émettent des gamètes ou des larves par reproduction sexuée ou parthénogénèse. Les larves planulas se développent et se dispersent durant leur phase pélagique avant de se fixer au substrat et de se métamorphoser en polypes benthiques. Dans les premiers temps on parle alors de recrues puis de juvéniles lorsque les colonies atteignent une taille centimétrique et deviennent clairement visibles à l'œil nu. Après plusieurs années, les colonies capables de reproduction sexuée sont considérées comme des adultes. En parallèle, les coraux se reproduisent également par voie asexuée.

Parmi les processus influençant la phase benthique, le recrutement joue un rôle essentiel dans la structure et la dynamique des populations, ainsi que pour la colonisation des habitats.

1.1.3. Recrutement corallien

En écologie, le recrutement au sens large désigne l'ajout d'une nouvelle cohorte de jeunes individus à une population donnée (Sale 1990). Chez les scléractiniaires, le recrutement désigne principalement les processus post-fixation précoces liés aux recrues, juste après la fixation et la métamorphose des larves (Gleason 1996, Harrington et al. 2004, Nozawa et al. 2011, Martinez & Abelson 2013, Davies et al. 2013, Doropoulos et al. 2016), mais également ceux relatifs aux juvéniles (Edmunds 2000, Glassom & Chadwick 2006, Adjeroud et al. 2010, Penin & Adjeroud 2013, Doropoulos et al. 2015, Shlesinger & Loya 2016).

Les processus du recrutement corallien sont soumis à une grande variété de facteurs agissant à différentes échelles spatiales :

- L'émission des gamètes ou des larves peut être influencée par l'augmentation de la température de l'eau (Nozawa et al. 2006), la phase lunaire (Guest et al. 2008) ou encore le régime des vents (van Woesik 2010) ;
- la dispersion pélagique des larves dépend majoritairement de leur période de compétence et des conditions hydrologiques (Harii et al. 2002, Harii & Kayanne 2003, Vermeij et al. 2006) ;
- la fixation des larves est particulièrement conditionnée par la présence d'inducteurs biologiques (e.g. algues calcaires encroûtantes ; Vermeij 2005, Vermeij et al. 2011), la sédimentation (Salinas-de-León et al. 2013), l'intensité lumineuse (Babcock & Mundy 1996), la nature des peuplements installés (Gleason 1996) ou encore la prédation par broutage (Penin et al. 2011) ;
- la survie post-fixation des recrues et juvéniles est influencée par la compétition avec les autres organismes benthiques, par la prédation ainsi que par la sédimentation (Wittenberg & Hunte 1992, Box & Mumby 2007, Penin et al. 2010, Venera-Ponton et al. 2011, Gouezo et al. 2015).

Par conséquent, la notion d'échelle spatiale est cruciale dans l'étude du maintien des communautés car elle conditionne le degré d'influence de certains facteurs, notamment sur le recrutement (Adjeroud et al. 2007, O'Leary & Potts 2011, Penin & Adjeroud 2013).

La pérennité des récifs coralliens, et par extension leur résilience, viennent en partie de la capacité des coraux à maintenir des niveaux de recrutement suffisants afin de pallier la mortalité des adultes et permettre le renouvellement des populations (Harrison & Wallace 1990, Hughes & Tanner 2000, Hughes et al. 2000).

1.1.4. Résilience des récifs

1.1.4.1. Concept général

La résilience écologique a été définie par Holling (1973) comme la mesure de la persistance des systèmes et de leur capacité à absorber le changement et les perturbations tout en maintenant les mêmes relations entre les populations ou les variables d'état. Depuis, ce concept a évolué pour définir la capacité de l'écosystème à se maintenir ou revenir à son état initial après perturbation, via deux composantes : la résistance et la récupération. La première caractérise la faculté de l'écosystème à endurer les perturbations sans changer d'état fonctionnel, et la seconde la capacité de l'écosystème à revenir vers cet état initial après avoir été modifié (Figure 4 ; Nyström et al. 2008, McClanahan et al. 2012).

Dans le cas d'un récif corallien, la perte de résilience peut se caractériser par une diminution du recouvrement corallien, de la biodiversité, de la connectivité avec d'autres écosystèmes complexes ainsi que de l'hétérogénéité de l'habitat (Hughes et al. 2007, Nyström et al. 2008, Goldberg 2013). La perte de la fonction d'herbivorie et l'enrichissement du milieu sont les principaux facteurs qui favorisent le développement des communautés algales au détriment des coraux, entrainant de ce fait une perte de résilience des récifs (Burkepile & Hay 2006, Hughes et al. 2007).

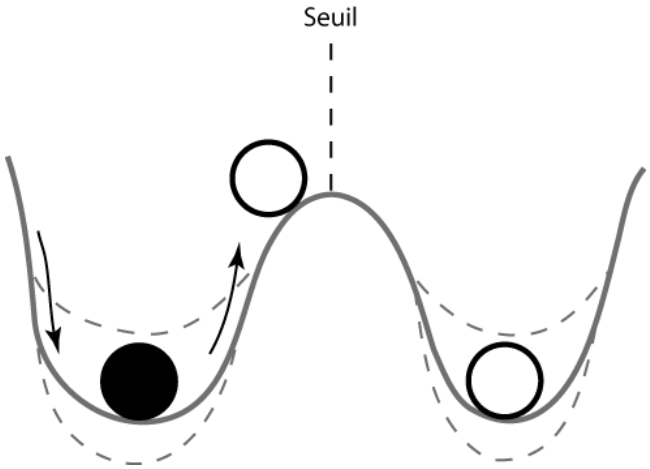


Figure 4. Concept de la résilience écologique. L'écosystème est représenté par la boule noire et son état par sa position sur le tracé comprenant des cuves, les domaines de stabilité. Les perturbations peuvent pousser l'écosystème à dépasser un certain seuil et atteindre un autre domaine. La résilience correspond à la capacité de l'écosystème à rester dans son domaine de stabilité ou à y revenir si possible. Les tracés en pointillés illustrent l'aspect dynamique des domaines de stabilité au cours du temps, en parallèle des changements subis par l'écosystème sous l'effet des perturbations. Illustré d'après les concepts traités par Desjardins et al. (2015).

Comme nombre d'écosystèmes terrestres, les récifs coralliens font face à une accentuation significative de la fréquence et de l'intensité des perturbations (IPCC 2013, Hughes, Anderson, et al. 2018). Ces dernières, associées aux effets des changements climatiques qui modifient les conditions de vie des organismes récifaux, mènent à une accélération du déclin des communautés coralliennes et à une dégradation des habitats, ainsi qu'à une diminution de la résilience des récifs (Hughes 2003, Bellwood et al. 2004, Bruno & Selig 2007, Hoegh-Guldberg et al. 2007, Bozec et al. 2015, Hughes, Kerry, et al. 2018).

Des perturbations naturelles affectent les communautés coralliennes à différentes échelles spatiales (de l'ordre de quelques mètres à plusieurs centaines de kilomètres) ; on distingue principalement les cyclones, les épisodes de blanchissement corallien de masse, les épidémies coralliennes ou les pullulations de prédateurs comme l'étoile de mer corallivore *Acanthaster* spp. (Hughes 1994, Hughes & Connell 1999, Lourey et al. 2000, Aronson & Precht 2001, Aronson et al. 2002, De'ath et al. 2012, Kayal et al. 2012). En parallèle, l'augmentation des températures de l'eau, l'acidification des océans, les pollutions terrigènes, les techniques de pêche destructrices ou encore la surpêche engendrent des effets délétères pour les populations coralliennes (Burke et al. 2011). Ces

perturbations d'origine anthropique sont également susceptibles d'interagir avec les perturbations naturelles, amplifiant leurs conséquences néfastes pour les récifs (Hughes 1994, Aronson & Precht 2001, Knutson et al. 2010, Fabricius et al. 2010).

Au cours du cycle de vie corallien, l'approvisionnement en nouveaux individus et leur survie sur les récifs (en d'autres termes le recrutement) sont également influencés par ces perturbations, qu'elles soient d'origine anthropique comme la pollution, l'eutrophisation, la sédimentation ou la surpêche (Harrison & Wallace 1990, Hughes & Connell 1999, Birrell et al. 2005, Abelson et al. 2005, Vermeij & Sandin 2008, Chui & Ang 2017) ou naturelle comme les cyclones, les explosions démographiques de prédateurs tels qu'*Acanthaster planci* et les épisodes de blanchissement corallien agissant à grande échelle spatiale (Edwards et al. 2001, De'ath et al. 2012, Kayal et al. 2012).

Lorsque l'écosystème n'est plus capable d'absorber les perturbations, on peut assister à un changement d'état, c'est à dire à des modifications radicales et pérennes de la structure de l'écosystème (*phase shift* en anglais). En milieu récifal, ce changement d'état se traduit souvent par un basculement d'un système dominé par les coraux scléractiniaires vers un système dominé par d'autres organismes, le plus souvent les macroalgues (Hughes 1994, McManus & Polsenberg 2004, Arias-González et al. 2017).

1.1.4.2. Mesurer la résilience : indicateurs et indices

Dans le contexte actuel des changements globaux, l'évaluation de l'état de santé des récifs (et de son évolution dans le temps) fait partie des enjeux cruciaux pour améliorer la conservation et la gestion des récifs coralliens. Déterminer la capacité de résilience des récifs par l'utilisation de variables traduisant la condition de l'écosystème permet d'améliorer la prise de décisions des gestionnaires et d'optimiser les mesures de conservation de ces écosystèmes (Anthony et al. 2015, Maynard et al. 2015).

À l'heure actuelle, on distingue deux types d'outils, souvent développés sous forme d'indices et basés sur différents types d'indicateurs : (i) des outils permettant d'évaluer l'état de santé des récifs et (ii) des outils permettant d'évaluer leur potentiel de résilience. Les premiers visent à évaluer l'état d'un récif à l'instant *t*, par rapport à d'autres récifs ou par rapport à un état de référence correspondant à un récif en bonne santé. Par exemple, Kaufman et al. (2011) ont développé un outil simplifié afin d'évaluer l'état de santé des

communautés coralliennes par le biais d'un indice appelé Coral Health Index (CHI). Ce dernier se base sur trois indicateurs ciblant chacun un compartiment de l'écosystème récifal (benthos, poissons et microbes) afin de renseigner la condition relative de différents récifs à travers le globe. Un tel indice est censé fournir un aperçu rapide de l'état de santé d'un récif en indiquant, par exemple, s'il est dégradé et nécessiterait des actions pour sortir d'un état indésirable, comme la mise en place d'une aire marine protégée (AMP).

À l'interface entre indices de santé et indice de résilience, Lasagna et al. (2014) ont développé un indice de condition corallienne basé sur la récupération des récifs après les épisodes de blanchissement. Il prend en compte l'abondance relative en colonies coralliennes classées selon différentes catégories traduisant le degré de sévérité des dommages reçus (e.g. les colonies cassées, blanchies, mortes récemment ou en bonne santé). Plus cet indice est grand (i.e. plus la proportion de colonies en bonne santé est grande), meilleur est l'état de santé du récif, à l'inverse de l'indice de détérioration (*Deterioration Index*) proposé par Ben-Tzvi et al. (2004) basé sur le ratio entre les taux de mortalité et les taux de recrutement de coraux branchus.

Les indices de santé sont intéressants pour dresser un état des lieux et/ou comparer l'état de différents récifs à un instant *t*, mais ils prennent en compte une quantité limitée de paramètres et n'ont pas vocation à dresser un bilan des capacités de résilience, i.e. de résistance et/ou de récupération des récifs face à l'intensification des perturbations de grande ampleur, même s'ils tiennent parfois compte de ces perturbations C'est l'objectif du second type d'outils, les indices de résilience.

Les indices de résilience se basent sur des indicateurs ou descripteurs (biologiques, physiques ou chimiques) issus de l'intégration de facteurs biotiques (e.g. les interactions trophiques) et abiotiques (substrat, lumière, température, nutriments, salinité, houle, sédimentation, pH) qui affectent les conditions de vie des organismes récifaux (Fujita et al. 2013). Ces indicateurs de résilience peuvent intégrer différentes échelles, de la communauté à la cellule en passant par la population et l'organisme (Hédouin & Berteaux-Lecellier 2014).

Bien que les conditions amenant à un changement d'état ou une récupération de l'écosystème soient diverses, la quantification de quelques facteurs clés avant

perturbation peut aider à anticiper la trajectoire que pourrait prendre l'écosystème récifal. À partir d'une liste de 61 facteurs énoncés par Obura & Grimsditch (2009), une dizaine de facteurs écologiques de résilience se démarque, avec dans l'ordre d'importance croissante : la pression de pêche, le recrutement corallien, l'abondance des macroalgues, les maladies coralliennes, les impacts humains physiques, la biomasse en herbivores, la diversité corallienne, la sédimentation, la pollution, la variabilité de la température et l'abondance d'espèces coralliennes résistantes (McClanahan et al. 2012). Particulièrement, la récupération des récifs coralliens semble favorisée pour les récifs présentant une structure complexe, une profondeur d'eau relativement importante ainsi que des densités en coraux juvéniles et en poissons herbivores relativement élevées (Graham et al. 2015). Pour qu'un indice de résilience soit efficace, il doit intégrer des indicateurs accessibles et suffisamment pertinents pour que leur association apporte des renseignements utiles à la mise en place de mesures de gestion.

Pour mieux cibler les actions de conservation favorisant la résilience, Maynard et al. (2010) ont développé un système basé sur un questionnaire uniformisé dans le but d'être utilisable pour tout site, permettant l'obtention d'un indice, ou « score de résilience ». Ce dernier est déterminé à partir de l'évaluation de 19 indicateurs de résilience pondérés en fonction de la force de la relation indicateur/résilience des récifs perçue dans la littérature (Tableau 1). Maynard et al. (2015) préconisent la mesure d'indicateurs de résilience à combiner avec les informations sur les stress anthropiques et la connectivité, afin d'identifier les cibles et les actions de gestion associées. Cette approche a été appliquée à différents sites de Keppel Bay (Grande Barrière de Corail) afin de promouvoir la gestion des récifs coralliens basée sur la résilience écologique (*resilience-based management* ou RBM).

La RBM est définie comme l'utilisation des connaissances relatives aux facteurs actuels et futurs qui ont et/ou auront une influence sur le fonctionnement des écosystèmes afin de prioriser, mettre en place ou adapter les actions de gestion (Mcleod et al. 2019). La RBM est un mode de gestion incluant des aspects écologiques et sociétaux qui mise sur l'adaptabilité des méthodes de gestion face aux risques et à l'incertitude des changements environnementaux (Mcleod et al. 2019). Ainsi, la RBM repose notamment sur l'analyse de la variation spatiale du potentiel de résilience des récifs afin d'adapter en permanence les actions de gestion et de conservation. Les indicateurs développés dans ce

but mettent davantage l'accent sur les processus écologiques et l'exposition aux facteurs environnementaux que les indicateurs utilisés dans les programmes de suivis conventionnels (Lam et al. 2017). Les indicateurs utilisés dans le cadre de la RBM ont donc pour objectif de mieux prédire les réactions futures des récifs face aux perturbations et aux changements environnementaux.

Tableau 1. Questionnaire proposé par Maynard et al. (2010) pour l'évaluation du potentiel de résilience des récifs coralliens. Entre parenthèses : note associée à chaque catégorie. Les couleurs traduisent l'importance de chaque facteur perçue dans la littérature et donc le poids qui leur est associé : rouge, importance critique ; jaune, importance élevée ; vert, importance moyenne. Traduction en français depuis l'anglais.

Indicateurs de résilience à large échelle	Inconnu **(0)**	Pas vraiment **(1)**	Un peu **(2)**	Certainement **(3)**
Le site est-il sous l'influence de phénomènes d'*upwelling* ?				
Des facteurs entrainent-ils l'augmentation des mouvements d'eau et donc le brassage ? (e.g. péninsules/chenaux, grandes marées, exposition aux vents et aux vagues)				
Des facteurs entrainent-ils la diminution de la lumière incidente ? (e.g. grandes îles, proximité d'écoulements fluviaux/panaches de sédiments)				
Le site est-il exempt de contamination/pollution ? (e.g. nutriments, déchets)				
Le site a-t-il déjà été exposé à des événements de réchauffement des eaux et y a survécu et/ou a récupéré rapidement ?				
Les récifs en amont sont-ils assez proches de ce site pour fournir des larves pour la recolonisation suite à une perturbation ?				
Le site est-il exempt de pression de pêche ?				
Le site est-il exempt d'impacts physiques ? (e.g. dégâts dus aux tempêtes, exploitation/mine, pêche destructive)				
Total				

Indicateurs de résilience à l'échelle locale				
Le site présente-t-il une topographie complexe ? (e.g. sillons, crêtes, large gamme de tailles et de morphologies coralliennes)				
Les coraux du site sont-ils toujours immergés à marée basse ?				
Le recouvrement corallien est-il plus important pour ce site que pour les autres sites que vous étudiez ?				
La communauté corallienne est-elle principalement composée d'espèces résistantes/tolérantes ?				
Les colonies coralliennes matures (grandes) sont-elles abondantes sur ce site ?				
Les herbivores (e.g. poissons, oursins, mollusques, tortues…) sont-ils abondants sur ce site ?				
Y a-t-il beaucoup de substrat dur disponible pour le recrutement corallien ?				
Le site est-il exempt de sédimentation ?				
Le site est-il exempt d'autres impacts physiques ? (e.g. dommages d'ancrage, dégâts dus aux plongeurs)				
Les bioérodeurs sont-ils très peu abondants ?				
Les maladies coralliennes sont-elles très peu abondantes ?				
Total				

Si la préservation des récifs actuels est un enjeu majeur, les changements globaux vont probablement entrainer la disparition de certains récifs (IPCC 2014) et entrainent déjà l'apparition de zones refuges et la colonisation par les coraux de nouveaux habitats (van Hooidonk et al. 2013, Yates et al. 2014, Cacciapaglia & van Woesik 2015, 2016, Kavousi & Keppel 2018). Ces zones sont d'une importance cruciale pour l'avenir des récifs coralliens et doivent faire l'objet d'une attention particulière.

1.1.5. Successions écologiques

1.1.5.1. Concept général

Développé pour des écosystèmes terrestres, le principe de succession écologique a été défini par Odum (1969) comme le processus raisonnablement prévisible de développement d'une communauté vers un stade climacique ou climax ; c'est-à-dire vers un état final, le plus stable dans les conditions abiotiques existantes. Lorsque les conditions environnementales ne subissent pas de changement majeur, ce processus est censé renforcer le contrôle biologique de l'environnement et conduire à un écosystème stabilisé (Copper 1988). Cependant, la succession écologique peut être interrompue dans des écosystèmes fréquemment perturbés par des événements à grande échelle ou des facteurs de stress locaux, empêchant ainsi d'atteindre une communauté climacique stable (Connell and Slatyer 1977). En conditions favorables, on parlera de série progressive, marquée par un accroissement général de la diversité des organismes dans le temps, et à l'inverse de série régressive, caractérisée par des peuplements successifs de plus en plus pauvres, quand l'impact des perturbations se fait significatif.

Sur un substrat vierge, les premières espèces capables de s'installer, appelées espèces pionnières, vont modifier leur environnement de telle sorte que d'autres espèces vont ensuite pouvoir s'y installer. Ces dernières vont parfois s'installer au détriment des espèces pionnières qui peuvent même finir par être totalement remplacées. On distingue de manière générale deux types de successions (Figure 5). La succession primaire a lieu lorsque des organismes colonisent un environnement nouvellement formé, dans une zone essentiellement sans vie, par exemple après le passage d'une coulée de lave (Kitayama et al. 1995) ou le retrait d'un glacier (Chapin et al. 1994). La succession secondaire désigne quant à elle le remplacement séquentiel du biote d'un écosystème à la suite d'une perturbation de moindre ampleur, c'est-à-dire n'entrainant ni une perte totale du biote ni la création d'un milieu « vierge », telle qu'un feu de forêt, qui n'endommage pas la banque de graines présente dans le sol (Walker & del Moral 2003, Prach & Walker 2011).

Ces notions développées à partir des végétaux en milieu terrestre peuvent également être transposées en milieu marin, notamment au travers des organismes sessiles. D'ailleurs, la menace croissante pesant sur les écosystèmes marins appelle des

investigations supplémentaires sur l'étendue des changements prévisibles et ordonnés des communautés marines à travers le principe de succession écologique (Sandin & Sala 2012).

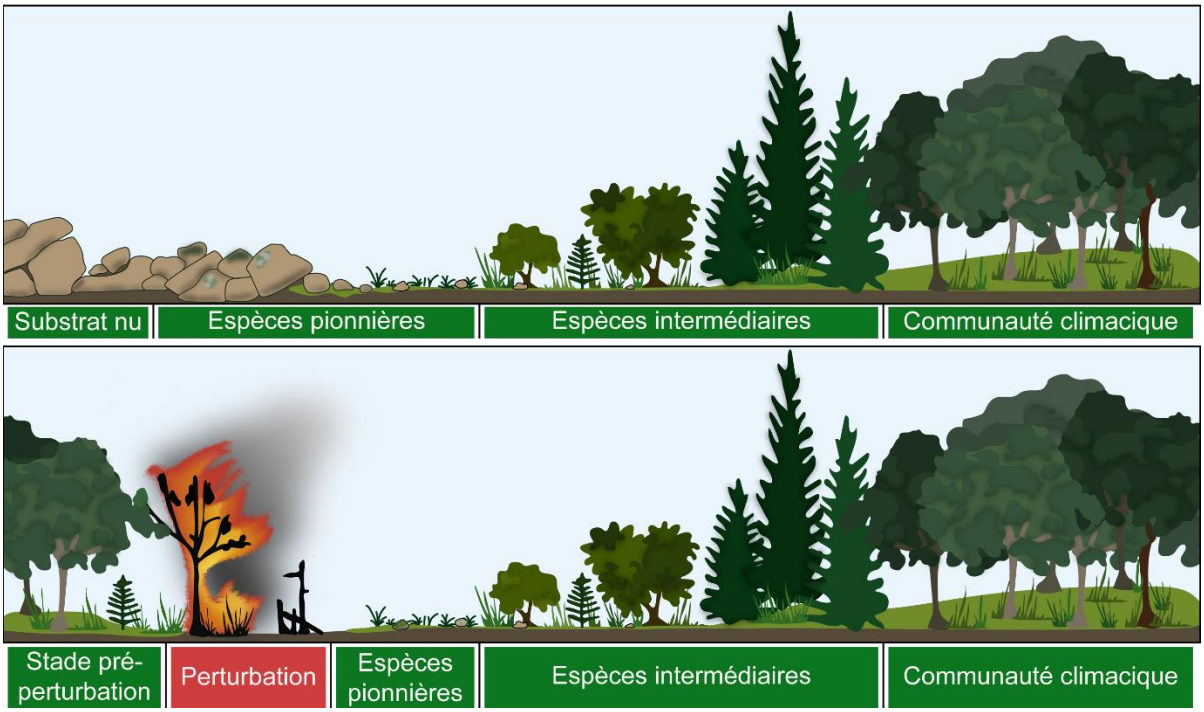


Figure 5. Schéma du principe de succession primaire (en haut) et secondaire (en bas) en milieu terrestre.

1.1.5.2. Communautés coralliennes et milieu récifal

À partir des définitions précédemment énoncées ciblant des végétaux terrestres, il est possible d'adapter le principe de succession écologique à d'autres organismes sessiles tels que les coraux. Dans une région propice à l'établissement de récifs, les coulées de lave sous-marines permettent d'observer *in situ* la colonisation d'un milieu vierge par les coraux, et donc une succession primaire. En parallèle, des récifs établis depuis des millénaires et faisant face à des perturbations diverses présentent le profil d'une succession secondaire, marquée par une alternance de séries progressives et régressives. Ces séries régressives tendent à être de plus en plus marquées compte tenu de l'accroissement de la fréquence et de l'intensité des perturbations naturelles et anthropiques affectant les récifs (Bellwood et al. 2004, Edmunds et al. 2014, Hughes, Barnes, et al. 2017).

Des successions secondaires ont été largement étudiées dans les écosystèmes récifaux via l'étude des changements intervenus dans les communautés à la suite de perturbations, telles que le blanchissement corallien, les cyclones et les changements soudains de l'abondance en espèces clés telles que les herbivores et les corallivores (Coles & Brown 2007, Trapon et al. 2011, Jouffray et al. 2015, Doropoulos et al. 2016). En revanche, outre le cas des communautés algales, caractérisées par leur capacité à coloniser rapidement le substrat vacant, leur court cycle de vie et leur croissance rapide, la succession primaire reste peu étudiée pour les écosystèmes coralliens (Hixon & Brostoff 1996, Burkepile & Hay 2010). Pour les coraux, ce manque d'information sur la succession primaire est principalement lié à la rareté des substrats nouvellement formés que les coraux peuvent coloniser, à leur long cycle de vie et à leur faible taux de croissance qui impliquent des efforts de surveillance à long terme associés un échantillonnage fréquent pour détecter les changements dans les communautés. De ce fait, seules quelques études ont été menées sur des coulées de lave sous-marines, se concentrant sur le rétablissement et les modifications ultérieures de la structure des communautés coralliennes (Grigg & Maragos 1974, Grigg 1983, Tomascik et al. 1996). Ainsi, l'examen des processus de succession est non seulement important pour comprendre les changements et les trajectoires de récupération des communautés coralliennes, mais également pour mieux évaluer la colonisation potentielle des zones refuges liées au changement climatique, tels que les environnements marginaux non récifaux ou des régions tempérées de haute latitude (van Hooidonk et al. 2013, Yates et al. 2014, Cacciapaglia & van Woesik 2015, 2016, Kavousi & Keppel 2018).

1.2. Objectifs, structure et enjeux

Dans le contexte écologique de « crise des récifs coralliens » précédemment établi, ce travail de thèse vise à analyser les processus démographiques (i.e. les descripteurs qui traduisent la dynamique des populations coralliennes du stade de recrue à celui de colonie adulte : installation, survie, croissance et mortalité) et la structure des assemblages coralliens à plusieurs échelles dans différents milieux insulaires. À l'aide de ces paramètres, le potentiel de récupération de différents récifs est également évalué. Ce projet se concentre sur des systèmes insulaires localisés dans la zone Sud-Ouest de l'Océan Indien (SOOI) à la fois dans le Canal du Mozambique et au sein de l'archipel des

Mascareignes. Les coulées de lave sous-marines issues de l'activité volcanique du Piton de La Fournaise à La Réunion offrent l'opportunité rare d'étudier *in situ* des cas de successions écologiques depuis le stade primaire. D'un autre côté, la zone SOOI abrite de nombreux récifs présentant des successions avancées, parfois à tendance régressive et donc caractérisées par un déclin des communautés coralliennes.

Ce manuscrit se découpe en trois axes de recherche associés chacun à un chapitre (chapitres 3, 4 et 5) et faisant l'objet d'un article scientifique publié (chap. 4), soumis (chap. 3) ou en préparation (chap. 5). Ces parties soulèvent différentes questions quant à l'écologie des communautés coralliennes.

Le chapitre 3 se concentre sur l'étude des successions en milieu récifal et sur les coulées de lave sous-marines. Ce chapitre aborde les questions suivantes :

- *La structure des assemblages coralliens et les processus démographiques sont-ils comparables entre des coulées de lave immergées et des récifs établis ? Entre coulées de lave d'âges différents ?*

- *Les communautés coralliennes des récifs et des coulées de laves de La Réunion reflètent-elles un schéma de succession écologique ?*

Pour répondre à ces questions, la structure des communautés coralliennes ainsi que les processus démographiques et le recrutement coralliens ont été étudiés sur quatre coulées de lave sous-marines d'âges différents (d'une dizaine à plusieurs centaines d'années) et sur des récifs établis à La Réunion. Différents descripteurs ont été évalués : la croissance corallienne, la mortalité corallienne, les taux de recrutement, la densité en coraux, la structure de taille des colonies, la diversité corallienne et le recouvrement corallien.

Le développement des écosystèmes récifaux est régulièrement contraint par des perturbations qui peuvent interrompre et/ou réguler les processus de succession dans le cas de zones nouvellement colonisées par les coraux et de récifs établis. Comme mentionné précédemment, le recrutement corallien est impliqué à la fois dans la colonisation de nouveaux espaces et dans le maintien et la résilience des communautés coralliennes. Si le recrutement corallien a été largement étudié sur la Grande Barrière de Corail (GBR) en Australie, ou encore en Polynésie française, peu de données sont à ce jour

disponibles dans les Mascareignes. Le chapitre 4 présente l'étude de la variabilité spatio-temporelle du recrutement pour les îles de La Réunion et de Rodrigues. Il se propose d'aborder les questions suivantes :

- *Quels sont les taux de recrutement corallien des récifs de La Réunion et de Rodrigues et quelle est la distribution des taxons des recrues récemment fixées ?*

- *Les taux de recrutement et la composition taxonomique varient-ils dans l'espace et dans le temps ?*

- *L'interdiction de pêcher dans certaines zones protégées améliore-t-elle les taux de recrutement des récifs et/ou modifie-t-elle la composition taxonomique des recrues ?*

Pour répondre à ces questions, une étude de terrain d'un an et demi basée sur l'utilisation de plaques de recrutement artificielles installées sur différents sites répartis entre deux îles des Mascareignes (La Réunion et Rodrigues) a été mise en place au cours de mes deux premières années de thèse. Les taux de recrutement et la composition taxonomique ont été examinés à l'échelle (i) régionale (entre les deux îles), (ii) de l'île (entre les sites de chaque île), (iii) locale (entre les plaques de chacun des sites) et (iv) micro-locale (sur chaque plaque). La variation des taux de recrutement et de la composition taxonomique a été examinée au sein et hors de zones interdites à la pêche dans les deux îles.

Comme précédemment mentionné le recrutement corallien est un facteur essentiel pour la résilience des récifs. Les données de recrutement obtenues dans le chapitre 4, combinées à des données relatives aux communautés coralliennes et ichtyologiques en place peuvent permettre d'évaluer le potentiel de résilience des récifs étudiés. Le chapitre 5 propose une approche méthodologique permettant d'aborder cette problématique, et vise à répondre à la question suivante :

- *Sur la base d'indicateurs reconnus comme ayant un fort impact sur la récupération des récifs, peut-on développer un indice permettant d'évaluer le potentiel de récupération des récifs coralliens de la zone SOOI ?*

Ce chapitre repose sur l'application d'une méthode de décision multicritères, TOPSIS (*Technique for Order of Preference by Similarity to Ideal Solution*) basée sur des

données de diversité corallienne, densité en coraux adultes et juvéniles, recouvrement corallien total et en espèces tolérantes au stress, recouvrement algal, biomasse en poissons herbivores et anomalies de températures des eaux de surface récoltées pour cinq îles de la zone SOOI : La Réunion, Rodrigues, Mayotte, Europa et Glorieuses. Ce type de méthode pourrait, à terme, aider les décisionnaires à mettre en place des solutions de gestion efficaces et cohérentes.

Les îles et sites d'études sont décrits dans le chapitre 2. Ce chapitre précise également les conditions d'acquisition des données de terrain afin de faire la distinction entre les informations recueillies au cours de la thèse et celles issues de partenariats.

Enfin, le chapitre 6 apporte la synthèse des résultats évoqués dans les chapitres précédents au regard du contexte écologique actuel de « crise des récifs coralliens ».

CHAPITRE 2.
SITES D'ÉTUDE ET ÉCHANTILLONNAGE

2.1. La zone sud-ouest de l'océan Indien

La région du SOOI comprend un ensemble de terres émergées au sud-est de l'Afrique. On y retrouve notamment la grande île de Madagascar, plusieurs archipels tels que les Comores et les Mascareignes, ainsi que les Îles Éparses : Les Glorieuses (ou plus simplement Glorieuses), Europa, Bassas da India, Juan de Nova et Tromelin (Figure 6).

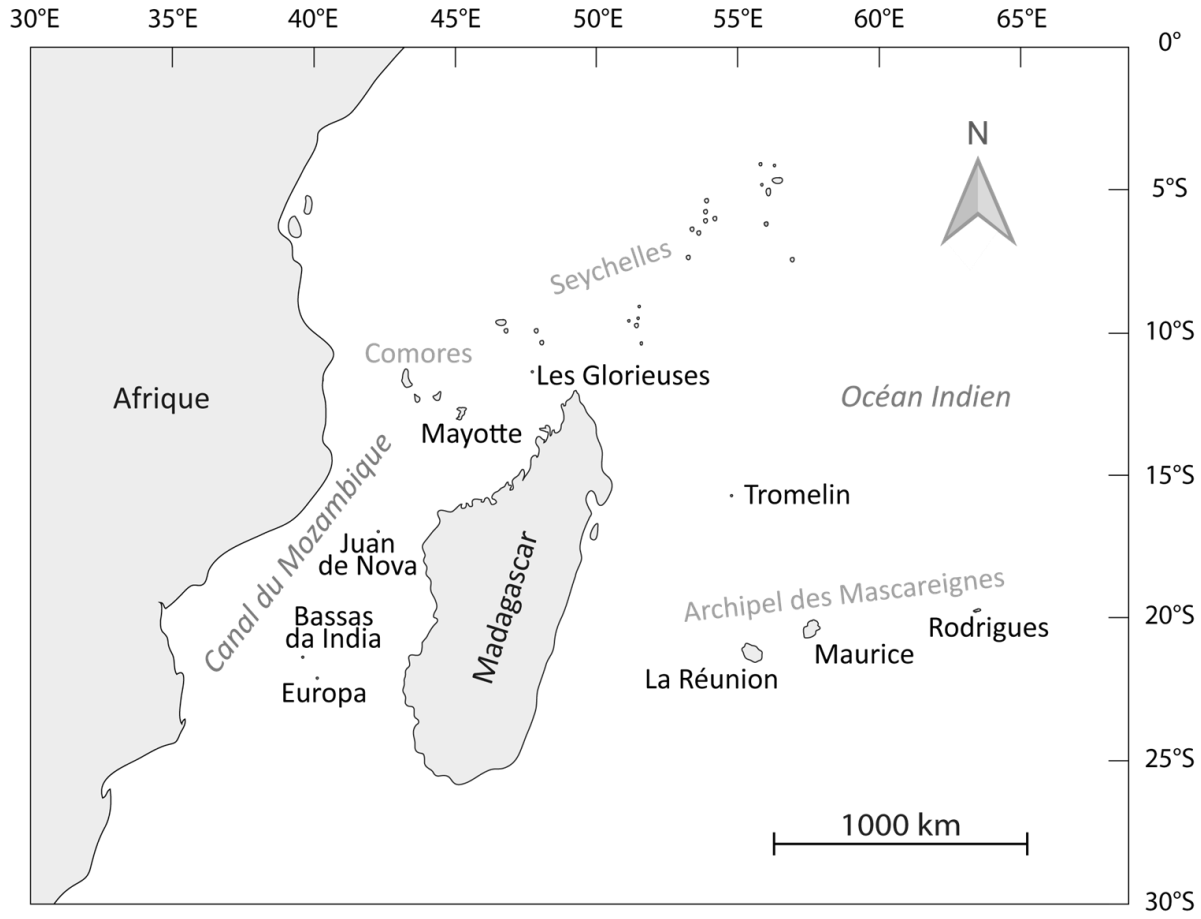


Figure 6. Carte des territoires de la zone sud-ouest de l'océan Indien.

Ces territoires forment l'un des 36 hotspots de biodiversité terrestre reconnus à l'heure actuelle (Figure 7 ; Mittermeier & Rylands 2018). Myers (1988) a défini les hotspots de biodiversité comme des aires géographiques présentant (i) un nombre d'espèces important avec des taux d'endémisme exceptionnels, et (ii) faisant face à des menaces exceptionnelles. Créé à la base pour des écosystèmes de forêts tropicales, ce concept a été décliné pour les récifs coralliens par Roberts et al. (2002). Parmi les centres d'endémisme fortement menacés identifiés par ces auteurs à partir des listes d'espèces

récifales figure la zone des Mascareignes, faisant de la région du SOOI une zone d'intérêt écologique majeur.

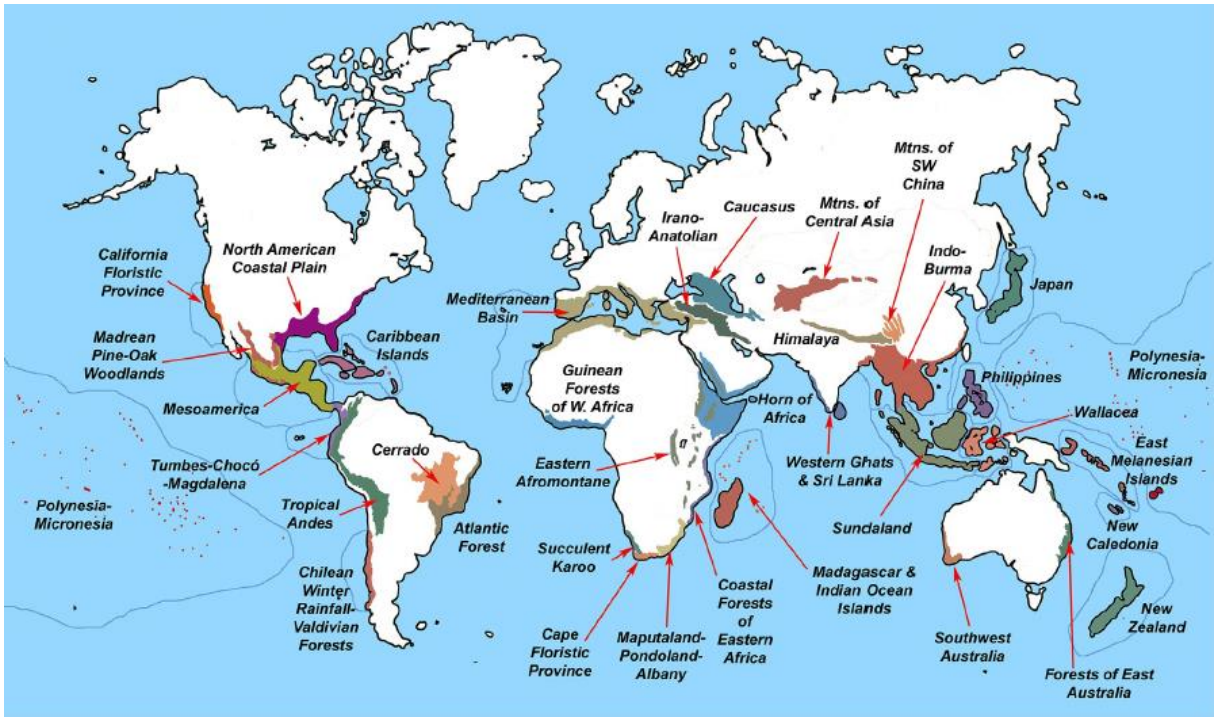


Figure 7. Les 36 hotspots actuels de biodiversité terrestre (Mittermeier & Rylands 2018).

Bien qu'associées au même hotspot de biodiversité, les récifs des îles de la zone SOOI diffèrent à plus d'un égard. Notamment, une classification des régions biogéographiques de la zone ouest de l'océan Indien a permis de mettre en évidence une diminution de la diversité en scléractiniaires de manière radiale depuis la zone du Canal du Mozambique Nord vers les zones avoisinantes (Figure 6 ; Obura 2012). Pour exemple, McClanahan et al. (2007) ont montré que la diversité en scléractiniaires observée sur les récifs de La Réunion est plus faible que celle des récifs du Canal du Mozambique (Figure 6). De même, l'île de Tromelin située en dehors du Canal du Mozambique, la plus à l'est des Îles Éparses, est également celle qui présente la plus faible diversité corallienne (Quod et al. 2007), phénomène également accentué par la petite taille de l'île et son isolement (Figure 6 ; Obura 2012). Ces patrons de diversité sont en adéquation avec les facteurs océaniques de la zone avec en tête le courant équatorial sud permettant le maintien d'une diversité importante dans la zone du Canal du Mozambique Nord, et l'export depuis cette région vers le nord, le sud puis les Seychelles et les Mascareignes (Figure 6 ; Obura 2012).

La réponse des différentes îles de la SOOI aux perturbations varie également, en fonction de la latitude notamment, mais pas uniquement (Obura 2005). Pour exemple, les

coraux de l'archipel des Mascareignes ont présenté bien moins de mortalité et de blanchissement que ceux d'autres récifs à même latitude lors de l'année 1998. Ceci est probablement dû au passage d'un cyclone aux abords de Maurice pendant la période d'augmentation des températures, résultant en une diminution de l'impact de l'ensoleillement (Obura 2005) et en une modification des mouvements d'eau permettant une meilleure circulation des flux au niveau de la zone récifale. En outre, les taux de recrutement corallien sur les récifs des Mascareignes semblent faibles en comparaison de récifs de même latitude (Hardman 2004, Massé 2014) ce qui peut être en partie expliqué par les facteurs océaniques rencontrés (Crochelet et al. 2013). Ainsi, au sein de la zone SOOI, une distinction apparait entre deux sous-régions biogéographiques qui sont (i) le Canal du Mozambique Nord qui présente des territoires avec une grande diversité corallienne et à forte connectivité et (ii) les îles des Mascareignes avec une diversité corallienne plus faible mais un endémisme des coraux élevé qui coïncident avec leur isolement géographique.

2.2. Îles et sites d'étude

Dans le cadre de ce travail doctoral, des échantillonnages ont été effectués sur les récifs coralliens de cinq îles tropicales de la zone SOOI : La Réunion, Rodrigues, Mayotte, Glorieuses et Europa ainsi que sur des coulées de lave sous-marines à La Réunion (Figure 8).

2.2.1. L'archipel des Mascareignes

Si les travaux de Faure (1976) montraient des similitudes morphologiques et bionomiques fortes entre les récifs de la pente externe des trois îles de l'archipel, La Réunion, Maurice et Rodrigues, les impacts anthropiques de ces dernières décennies entrainent des trajectoires temporelles différentes selon les sites (Myers et al. 2000, Tourrand et al. 2013).

2.2.1.1. La Réunion

L'île de La Réunion (21° 07' S, 55° 32' E) est un département français d'Outre-mer (70 km de long sur 50 km de large) situé à environ 700 km à l'est de Madagascar (Figure 8).

2.2.1.1.1. Les récifs réunionnais

Cette île volcanique, la plus jeune des Mascareignes, présente cinq récifs frangeants bordant les côtes ouest et sud de l'île (Bigot et al. 2019). Présents depuis environ 8000 ans, ces récifs s'étendent sur une longueur totale de 25 km, soit 16% du périmètre de l'île, et couvrent une superficie d'environ 15 km^2 (Camoin et al. 1997, Ahamada et al. 2008, Bigot et al. 2019). Ils sont également sous forte influence anthropique, avec une population humaine croissante (environ 516 000 habitants en 1982, contre 850 000 aujourd'hui), s'accompagnant d'une forte urbanisation des littoraux durant les dernières décennies. Cette anthropisation a eu pour conséquences notables une eutrophisation du milieu (Cuet 1989, Naim 1993, Riaux-Gobin et al. 2011) associée à une diminution des stocks de poissons récifaux sur certaines zones (Chabanet et al. 1995) entrainant une augmentation de la proportion de macroalgues vis-à-vis du gazon algal (*turf*) et des coraux (Naim 1993, Chazottes et al. 2002). D'autres études mettent en évidence une diminution du recouvrement corallien au profit du recouvrement algal faisant suite à l'épisode de blanchissement de 1998 (Bigot 2008, Tessier et al. 2008). Bien que l'on observe un bon niveau de résilience sur certaines portions des récifs réunionnais, notamment dans la zone de Saint-Leu (Ahamada et al. 2008, Bigot 2008, Scopélitis et al. 2009, Naim, Tourrand, Faure, et al. 2013), des zones restent dominées par un fort recouvrement algal (Naim, Tourrand, Ballesteros, et al. 2013, Tourrand et al. 2013).

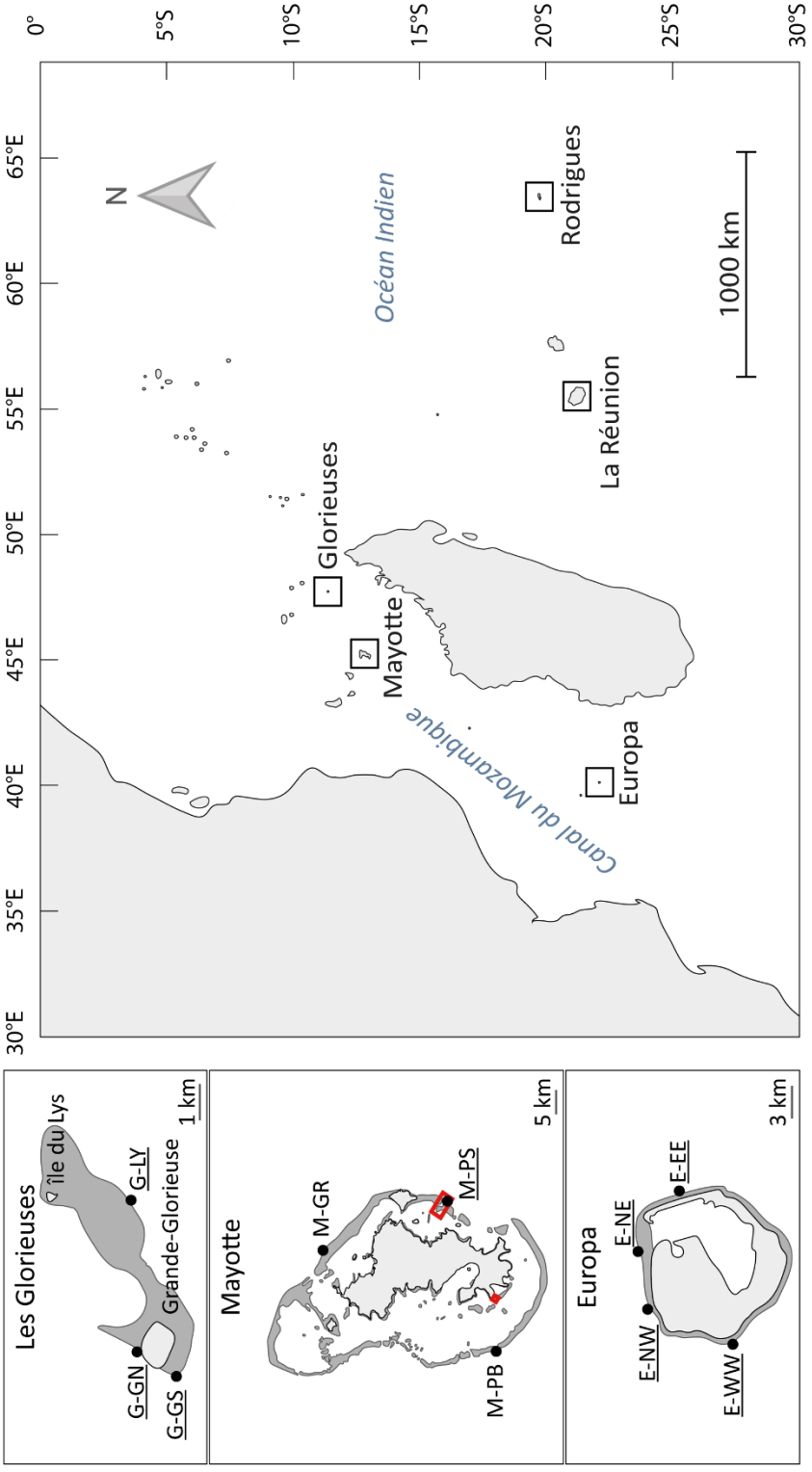


Figure 8. Localisation des sites d'étude dans la zone SOOI. ■ : terres ; ■ : récifs ; □ : AMP ; □ : NTZ ; ● : site d'étude. Les sites soulignés sont localisés dans une NTZ.

En réponse à une démographie humaine toujours croissante et une prise de conscience vis à vis de ces perturbations, une AMP, la Réserve Naturelle Marine de La Réunion a été créée en 2007 (RNMR ; Figure 9). S'étendant sur 35 km^2, elle présente un zonage qui établit des critères de protection sur trois niveaux, du moins au plus restrictif : (i) le périmètre général ouvert à la plupart des activités humaines, (ii) les zones de protection renforcée où les pêches traditionnelle et professionnelle sont partiellement autorisées et (iii) les zones de protection intégrale. Dans ces zones sanctuaires, toute activité humaine est interdite, pêche comprise, sans autorisation particulière de la RNMR.

2.2.1.1.2. Les coulées de lave sous-marines

En parallèle des récifs, La Réunion abrite le Piton de la Fournaise, l'un des volcans les plus actifs au monde, caractérisé par de fréquentes éruptions au cours des dernières décennies (27 éruptions de 1998 à 2007 ; Tanguy et al. 2011). Les coulées de lave terrestres ont facilité la propagation d'espèces végétales envahissantes sur l'île qui ont altéré la succession primaire et radicalement modifié les trajectoires de succession. La propagation continue de ces espèces invasives constitue une menace majeure pour les écosystèmes terrestres indigènes restants de La Réunion (Potgieter et al. 2014). Outre leur influence sur les écosystèmes terrestres, les coulées de lave du Piton de la Fournaise atteignent souvent l'océan le long d'une bande côtière de moins de 20 km de long au sud-est de l'île (Michon & Saint-Ange 2008).

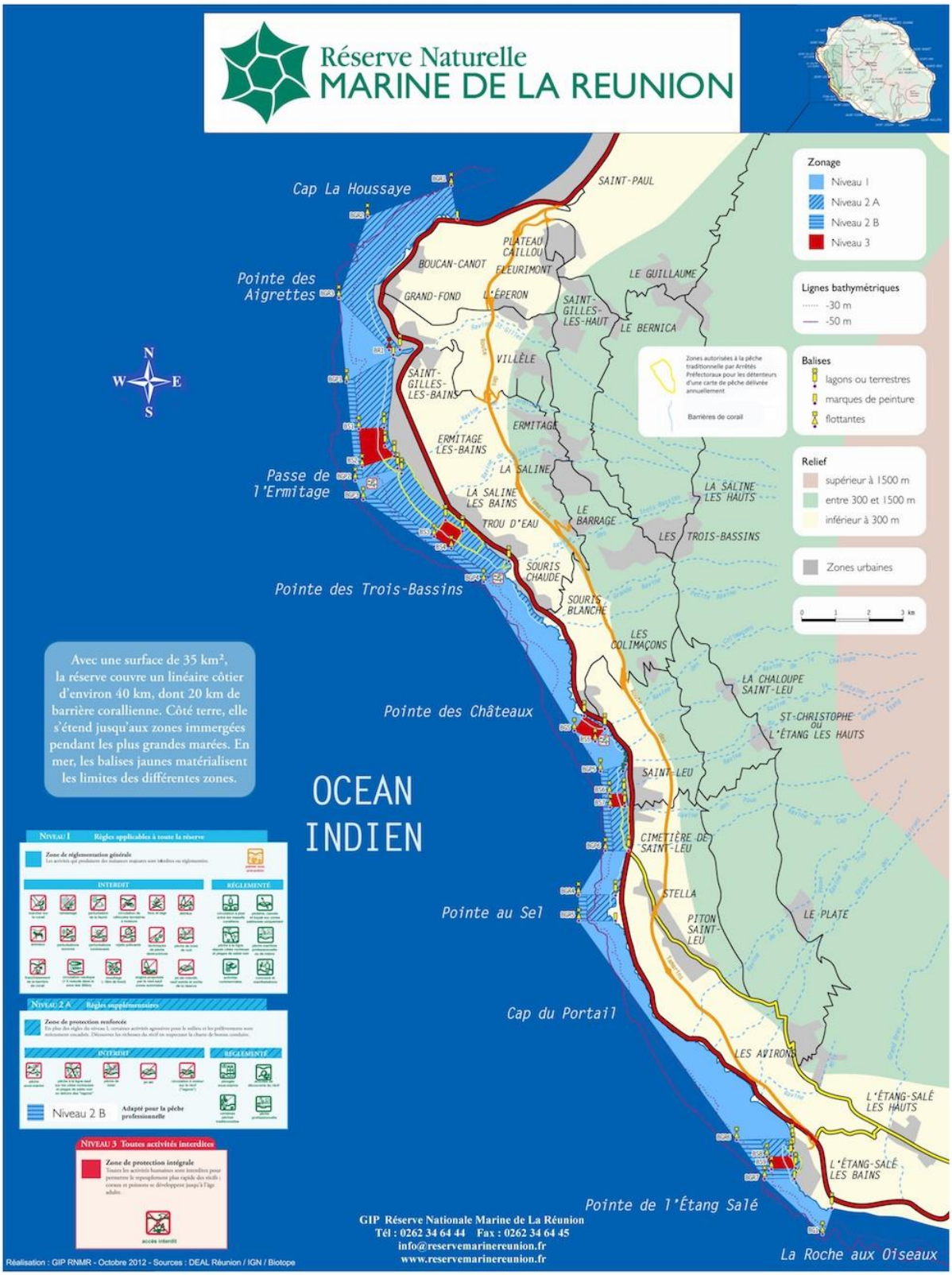


Figure 9. Carte de la Réserve Naturelle Marine de La Réunion présentant les niveaux de protection et la réglementation (Source : GIP Réserve Nationale Marine de La Réunion)

Au vu de l'intérêt majeur des habitats que constituent ces coulées de lave sous-marines pour la recherche en écologie, des études y ont été menées par l'ARVAM (Agence pour la Recherche et la Valorisation Marines) entre 2006 et 2013, notamment lors des expéditions BIOLAVE (2011-2012 ; Quod et al. 2013). La structure et la diversité des communautés de poissons (Pinault et al. 2013, 2014), d'échinodermes (Bollard et al. 2013), de la flore marine (Zubia et al. 2018) ainsi que des ascidies, éponges et octocoralliaires (Schleyer et al. 2016) ont ainsi été évaluées sur des coulées de lave d'âges différents. Ces expéditions ont également mené à la découverte d'espèces non décrites ou non répertoriées à La Réunion (par exemple le poisson *Cryptocentrus malindiensis*, Gobiidae ; Pinault et al. 2015). Les analyses faites sur les communautés coralliennes par Quod et al. (2013) à l'époque des expéditions BIOLAVE ont montré que les coulées sous-marines anciennes (>35 ans) présentent un recouvrement très important en coraux (>70 %) ainsi qu'une diversité (>100 espèces) similaire voire supérieure à celle des récifs de l'ouest de l'île de La Réunion et du reste des Mascareignes, à des profondeurs similaires (Faure 1982, Bigot 2008). Toujours selon Quod et al. (2013), la colonisation semble intervenir rapidement après le refroidissement des coulées. Les coulées les plus récentes, âgées de moins de dix ans, se caractérisaient par la dominance d'espèces considérées comme pionnières (genre *Pocillopora*), une diversité plus faible (quatre à six genres contre une vingtaine) et des abondances en juvéniles (≤ 5 cm de diamètre moyen) plus élevées que sur les coulées plus anciennes. Les coulées de moins de dix ans présentaient des taux de mortalité partielle et totale faibles (respectivement 10 % et 2,5 % sur une année) qui ont été associés à la faible compétition spatiale. Ainsi, l'étude de Quod et al. (2013) apporte des données préliminaires concernant l'état des communautés coralliennes sur des coulées sous-marines d'âges variés qui méritent d'être complétées.

2.2.1.2. Rodrigues

Rodrigues (19° 43' S, 63° 25' E) est une petite île isolée faisant partie de la République de Maurice, la plus à l'est de l'archipel des Mascareignes (Figure 8). D'environ 18 km de long pour 6,5 km de large et d'une superficie de 110 km^2, elle compte environ 38 000 habitants et est entourée d'un lagon d'environ deux fois sa taille. Les récifs forment une barrière presque continue de 90 km de long pour une superficie d'environ 200 km^2 (Montaggioni & Faure 1980, Rees et al. 2005). Il y a une dizaine d'années, Ahamada et al. (2008) considéraient les récifs de la pente externe de Rodrigues en relativement bonne

santé en comparaison d'autres récifs de la zone. Cependant, les effets de blanchissements de masse semblent s'y accentuer ces dernières décennies (Hardman et al. 2007), et certains sites ont été fortement dégradés par l'épisode de 2016 (obs. pers.). Les perturbations anthropiques majeures sont plutôt cantonnées au lagon, qui souffre notamment de techniques de pêches destructrices (pêche au poulpe sur les platiers peu profonds). Cependant, peu d'études documentent les effets des perturbations anthropiques sur les récifs de Rodrigues, d'autant plus pour la pente externe. Une AMP de près de 50 km^2, la South East Marine Protected Area (SEMPA) a été mise en place en 2009 dans le sud-est de l'île (Figure 8). Cette AMP comprend à la fois des portions de lagon interne et de pente externe, et se divise en zones de réglementation différente, incluant des *no-take zones* (NTZs), c'est-à-dire des zones notamment interdites à la pêche. En réponse à la surpêche, le gouvernement local a également décidé de mettre en place des réserves marines au nord de l'île il y a une dizaine d'années, mais sans mise en application véritable et la pêche a toujours lieu dans ces zones (Hardman et al. 2010, Pasnin et al. 2016).

2.2.2. Le Canal du Mozambique

2.2.2.1. Mayotte

Mayotte (12° 80' S, 45° 10' E) est un département français d'Outre-mer de 376 km^2 faisant partie de l'archipel des Comores situé au nord du canal du Mozambique (Figure 8). Mayotte comprend une île principale, Grande Terre (ou Maoré), une île plus petite, Petite Terre (ou Pamandzi), et plusieurs îlots. D'origine volcanique comme les îles de La Réunion et Rodrigues, Mayotte comprend également le plus grand lagon de l'océan Indien (environ 1100 km^2 soit près de quatre fois la surface des terres émergées, 15 km de large, 35-40 m de profondeur moyenne avec des canyons pouvant atteindre 80 m ; Chabanet 2002, Dinhut et al. 2008, Bigot et al. 2019). Des récifs frangeants bordent les différentes îles sur près de 250 km et le lagon est entouré par une barrière récifale interrompue par quelques chenaux (Guilcher 1971, PARETO 2013). Plus de 2300 espèces marines ont été identifiées et environ 250 espèces de coraux durs ont été répertoriées sur les récifs de Mayotte; mais ces écosystèmes font face à d'importantes menaces anthropiques du fait de la forte densité de la population humaine (Ahamada et al. 2008, Dinhut et al. 2008, Obura 2012).

Le Parc naturel marin de Mayotte, créé en 2010, est le premier d'Outre-mer en France. Il s'étend sur une zone très importante de près de 70 000 km² dont le périmètre correspond à celui de la zone économique exclusive (ZEE) de Mayotte. Le principal objectif de la création de ce parc marin est de concilier protection de l'environnement et développement durable des activités associées dans un contexte de pressions environnantes importantes. Au sein du Parc marin, quelques espaces protégés de taille bien plus modeste ont également été créés, présentant chacun une règlementation spécifique en termes d'accès et d'activités autorisés (Agence des aires marines protégées 2014). En parallèle, l'ensemble des îlots de Mayotte (à l'exception de la réserve de M'bouzi) et une partie du littoral a été acquise par le Conservatoire du littoral. Pour autant, la protection effective de ces espaces littoraux est difficile à mettre en œuvre et des moyens supplémentaires seraient nécessaires (Agence des aires marines protégées 2014).

Comme résumé par Bigot et al. (2019), les récifs de Mayotte, suivis régulièrement depuis une quinzaine d'années, présentent des recouvrements en coraux variés et des trajectoires différentes quant à leur résilience. Plusieurs évènements de blanchissement corallien (en 1983, 1998, 2010 et 2016 notamment) ont entrainé des mortalités importantes, particulièrement sur les récifs frangeants. En outre, les récifs barrière ont également été dégradés et un changement dans la communauté corallienne a été observé avec le remplacement des espèces d'origine par d'autres plus résistantes. Les niveaux de résilience des récifs de Mayotte semblent cependant élevés face aux épisodes de blanchissement rencontrés ces dernières décennies (Obura et al. 2018).

2.2.2.2. Les Îles Éparses : Les Glorieuses et Europa

Les Glorieuses et Europa appartiennent aux Îles Éparses tout comme Juan de Nova, Bassas da India et Tromelin. Ces petits territoires d'Outre-mer français, sous la tutelle des Terres Australes et Antarctiques Françaises (TAAF) depuis une dizaine d'années, sont tous situés dans le Canal du Mozambique à l'exception de Tromelin, à l'est de Madagascar (Figure 6).

Les Glorieuses sont un archipel situé au nord (11° 50' S, 47° 30' E) tandis qu'Europa est une île située au sud (22° 30' S, 40° 30' E) du Canal du Mozambique (Figure 8). Ces territoires possèdent tous deux des récifs et sont respectivement sujets à un climat plutôt

tropical humide et subaride (Quétel et al. 2016). L'île d'Europa, malgré sa présence dans la partie sud du Canal du Mozambique, se distingue notamment par son isolement (Obura 2012).

Contrairement aux îles précédemment évoquées dans ce chapitre, Les Glorieuses et Europa ne présentent pas d'habitants permanents. Classés réserves naturelles depuis 1975, seules une quinzaine de personnes au maximum se succèdent à l'année pour assurer la souveraineté française sur ces territoires isolés (Quod et al. 2007). Le Parc naturel marin des Glorieuses a été créé en 2012 afin de développer les activités humaines (e.g. pêche hauturière, écotourisme) tout en assurant la préservation du milieu marin. Il s'étend jusqu'à la limite de la ZEE des Glorieuses couvrant plus de 43 000 km^2 (Agence Française pour la Biodiversité 2018). Avec le Parc naturel marin de Mayotte, qui lui est contigu, la France est dotée d'une aire marine protégée de plus de 110 000 km^2.

Les environnements marins et donc les récifs des Glorieuses et d'Europa sont généralement considérés comme des environnements de référence au niveau mondial afin d'étudier la résilience des écosystèmes récifaux, ne faisant face qu'aux menaces à grande échelle spatiale telles que les cyclones, les explosions démographiques d'*Acanthaster* spp. ou les effets des changements climatiques (Quod & Bigot 2000, Quod et al. 2007, Chabanet et al. 2014, Bigot et al. 2019). L'interdiction généralisée de la pêche sur ces récifs a permis de préserver de grandes populations de poissons. Néanmoins, on distingue une diminution des stocks certainement liée à une augmentation de la pression de pêche illégale ces dernières années (Chabanet et al. 2016). Comme résumé par Bigot et al. (2019), des bateaux de pêche provenant de Madagascar et de l'archipel des Comores voisins parviennent dans les eaux des Glorieuses et pratiquent pêche et récolte illégales de poissons, holothuries et coquillages.

D'après Chabanet et al. (2016), les taux de recouvrement corallien des Glorieuses (au nord) avoisinent les 30 % tandis que ceux rencontrés à Europa (au sud) sont bien plus élevés (>80 %). Un profil latitudinal inversé a été observé par ces mêmes auteurs concernant le recouvrement en macroalgues dans le Canal du Mozambique. Ce gradient de recouvrement en coraux et algues pourrait faire écho aux impacts des épisodes de blanchissement qui ont eu lieu durant la dernière décennie dans la région, et à la capacité des différents récifs à récupérer (Bigot et al. 2019).

2.2.3. Choix et codification des sites d'étude

Au cours de cette thèse, les communautés récifales, et plus particulièrement coralliennes, de 22 sites répartis sur les cinq îles précédemment décrites ont été étudiées. La localisation des 22 sites est présentée Figure 8. Par soucis de clarté, les codes utilisés dans la suite du manuscrit pour désigner ces sites sont résumés dans le Tableau 2. Ainsi, ont été échantillonnés sur pentes externes :

- Quatre sites sur les récifs de l'ouest de l'île dans les secteurs de Saint-Leu et de La Saline : deux dans des zones de protection intégrale (= sanctuaires et donc NTZs) et deux autres dans les niveaux de protection inférieurs ;
- Quatre sites sur quatre coulées de lave délimitées, d'âge différent : une coulée centenaire (L-CA) ainsi que trois autres issues des évènements éruptifs de 1977 (L-1977), 2004 (L-2004) et 2007 (L-2007) ;
- Quatre sites sur les récifs de Rodrigues : deux au nord (hors NTZ) et deux au sud-est de l'île (en NTZ) ;
- Trois sites sur les récifs barrière de Mayotte : l'un aux abords d'une passe dans l'est (en NTZ), un aux abords d'une passe dans l'ouest (hors NTZ) et un au nord-est (hors NTZ) ;
- Trois sites sur les récifs des Glorieuses : deux à l'ouest de l'île principale, Grande-glorieuse, et un plus à l'est, au sud de l'île du Lys ;
- Quatre sites sur les récifs d'Europa répartis entre l'ouest, le nord et l'est.

Pour tous les sites, la première lettre du code utilisé correspond à l'initiale de l'île sauf pour (i) les sites localisés sur les coulées de lave de La Réunion (*L-* pour « Lava flow ») et (ii) les sites de Rodrigues (*O-* car le *R-* désigne déjà les récifs de La Réunion). Les deux lettres suivantes correspondent aux initiales ou aux deux premières lettres du nom intégral du site, sauf pour les sites des coulées de lave de 1977, 2004 et 2007 pour lesquels la date est conservée.

Tableau 2. Récapitulatif des sites échantillonnés.

Ile(s)	*Nom intégral du site*	*Code final*	*Code simplifié (chap. 4)*
Europa	West West	E-WW	-
Europa	East East	E-EE	-
Europa	North West	E-NW	-
Europa	North East	E-NE	-
Les Glorieuses	Grande glorieuse South	G-GS	-
Les Glorieuses	Lys	G-LY	-
Les Glorieuses	Grande glorieuse North	G-GN	-
Mayotte	Grand Récif	M-GR	-
Mayotte	Passe Bateau	M-PB	-
Mayotte	Passe en S	M-PS	-
La Réunion	Marine	R-MA	MA
La Réunion	Souris Blanche	R-SB	SB
La Réunion	Sanctuaire Sud	R-SS	SS
La Réunion	Varangue Sud	R-VS	VS
La Réunion	Caesari	L-CA	-
La Réunion	Coulée 1977	L-1977	-
La Réunion	Coulée 2004	L-2004	-
La Réunion	Coulée 2007	L-2007	-
Rodrigues	Ile aux Fous	O-IF	IF
Rodrigues	Mourouk	O-MO	MO
Rodrigues	Port sud-Est	O-PE	PE
Rodrigues	Rivière Banane	O-RB	RB

2.3. Échantillonnage et acquisition des données

L'ensemble des données utilisées au cours de cette thèse provient à la fois de différentes campagnes de terrain entreprises au cours et pour la thèse, et de partenariats. En revanche, le traitement et l'analyse des données ont été réalisés intégralement au cours de ce projet doctoral. Pour répondre aux différentes questions que nous nous sommes proposés d'étudier au cours de ce projet, différents types de données ont été acquises :

- Le recouvrement benthique, ici la proportion de substrat occupé par les coraux, d'une part, et les algues, d'autre part ;
- La diversité en coraux à travers la richesse spécifique et la composition taxonomique ;

- La densité en coraux, c'est à dire le nombre de colonies par m^2, et leur taille (mesurée via le diamètre maximal des colonies) ;
- Les communautés ichtyologiques à travers la mesure de la biomasse en poissons herbivores ;
- L'abondance et la composition taxonomique des recrues coralliennes évaluées sur substrat artificiel ;
- Les processus démographiques des coraux par le suivi de l'intégrité et de la taille de colonies à intervalles réguliers et l'établissement des taux de croissance et de mortalité.

Toutes ces données n'ont pas été récoltées sur l'ensemble des sites d'étude, et certaines ont été acquises au cours de programmes scientifiques antérieurs à la thèse. Par soucis de clarté, l'ensemble des échantillonnages et leur origine sont présentés Figure 10.

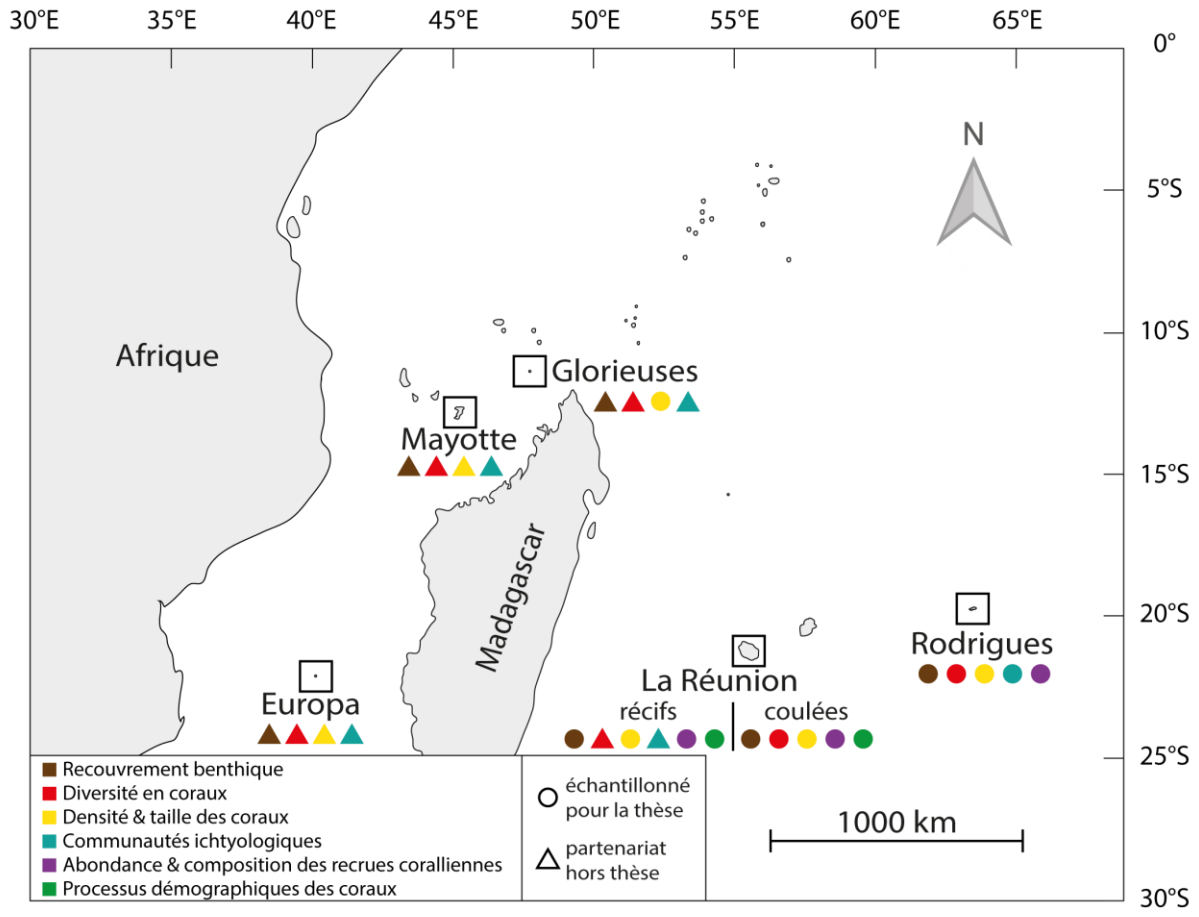
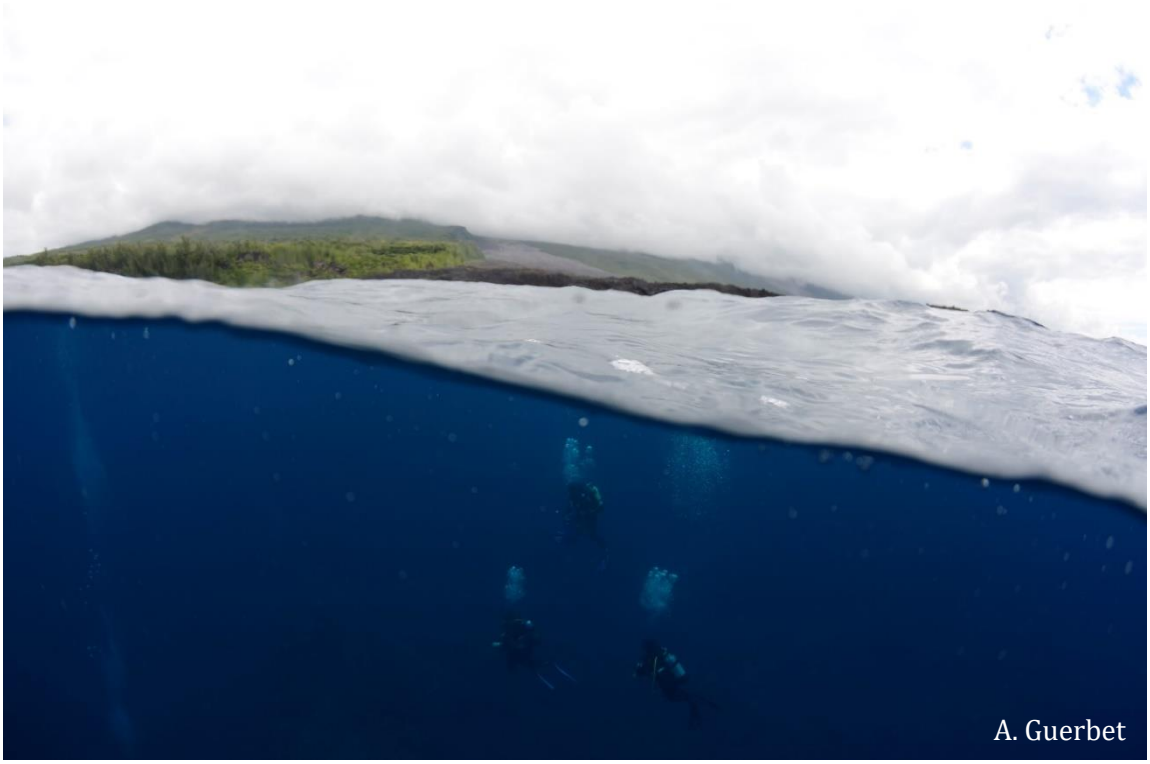


Figure 10. Résumé graphique de l'échantillonnage des données pratiqué dans le cadre de cette thèse ainsi que leur origine.

CHAPITRE 3.

STRUCTURE DES COMMUNAUTÉS CORALLIENNES ET SUCCESSIONS ÉCOLOGIQUES : CAS DES RÉCIFS ET DES COULÉES DE LAVE À LA RÉUNION



3.1. Synthèse

Dans le contexte actuel de "crise des récifs coralliens", comprendre comment les communautés coralliennes récupèrent suite aux perturbations et colonisent de nouveaux habitats est essentiel pour la conservation des récifs. Cependant, les études relatives aux successions écologiques et à la colonisation d'habitats par les communautés coralliennes sont peu nombreuses. En effet, les substrats nouvellement formés que les coraux sont capables de coloniser sont rares, le cycle de vie des coraux est long et leurs taux de croissance sont faibles ce qui implique des efforts de surveillance à long terme.

Au cours de cette étude, nous avons analysé un ensemble de données original portant sur la diversité, la structure et la démographie des assemblages coralliens sur des récifs établis et des coulées de lave sous-marines d'âges différents (allant de dix ans à quelques centaines d'années) à La Réunion.

Alors que la richesse spécifique et la composition taxonomique distinguaient clairement les récifs coralliens des coulées de lave, les deux habitats étaient similaires en termes de densité, de recouvrement, de taille moyenne des colonies, ainsi que de taux de recrutement et de mortalité des coraux. En outre, les assemblages coralliens à La Réunion se caractérisaient par une hétérogénéité spatiale marquée entre les sites au sein de chaque habitat, les coulées de lave d'une part et les récifs d'autre part. Nos résultats ont permis d'identifier des espèces présentes exclusivement sur les coulées de lave, mais n'ont pas permis d'établir une relation claire entre l'âge des coulées et la composition spécifique observée sur ces coulées. Nous avons cependant mis en évidence un patron de succession au cours duquel la taille des coraux et la richesse spécifique augmentaient avec le temps en raison de l'établissement de nouvelles espèces, jusqu'à ce que les interactions interspécifiques, comme la compétition pour l'espace, conduisent à leur diminution. De plus, nous avons observé une forte dominance du genre *Pocillopora* sur tous les sites de coulées de lave. Nos résultats ont donc permis de confirmer la nature pionnière des espèces du genre *Pocillopora* et d'avancer que leurs traits d'histoire de vie présentent un avantage pour coloniser et dominer les stades secondaires des successions. Ces résultats ont finalement permis de souligner la difficulté d'observer, en milieu marin, des patrons de successions écologiques telles que théorisés pour les écosystèmes terrestres.

Les résultats de ce chapitre ont été soumis pour publication sous forme d'article dans *Ecology*.

3.2. Article – Diversité, structure et démographie des communautés coralliennes à travers les successions écologiques à La Réunion

Title: Diversity, structure and demography of coral communities through ecological succession: coral reefs vs. underwater lava flows at Reunion Island

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Keywords: Ecological successions; Lava flows; Coral reefs; Scleractinian corals; Indian Ocean; Population dynamics

3.2.1. Introduction

Ecological succession was defined by Odum (1969) as the reasonably predictable process of community development to a stabilized climax stage. When environmental conditions are not undergoing major changes, this process is expected to increase the biological control of the environment and lead to a stabilized ecosystem (Copper 1988). However, ecological succession may be interrupted for ecosystems frequently impacted by large-scale disturbances or local stressors, thus preventing to attain such stable climax community (Connell & Slatyer 1977, Sandin & Sala 2012, Vercelloni et al. 2019). In fact, on highly diverse ecosystems such as coral reefs and tropical rain forests, community structure, diversity and successional trajectories are largely controlled by disturbances (Connell 1978, Grigg 1983). Two major types of ecological succession have been distinguished. Primary succession characterizes the colonization of a newly formed environment, such as lava flows, mainly by opportunistic species characterized by small bodies, dietary flexibility and high reproductive rates (Kitayama et al. 1995). Secondary succession refers to the sequential replacement of biota of an ecosystem following a disturbance, such as forest fires or cyclones (Walker & del Moral 2003, Prach & Walker 2011). Although successional theory has been mainly developed with terrestrial ecosystems, the increasing threats to marine ecosystems calls for additional

investigations on the extent of predictable and orderly changes of marine communities (Connell and Slatyer 1977, Sandin and Sala 2012).

Coral reefs are characterized by high biodiversity and ecosystem complexity, and provide critical ecological and economic resources for hundreds of millions of people (Moberg & Folke 1999, Wilkinson 2008, Kittinger et al. 2012). Like many other ecosystems, coral reefs are facing increasing frequency and intensity of natural and anthropogenic perturbations of various origin (Bellwood et al. 2004, Edmunds et al. 2014, Hughes, Barnes, et al. 2017). These perturbations have caused widespread mortality of scleractinian corals, the primary framework builders and key components of reef health and biodiversity, and have transformed the structure and dynamics of coral assemblages worldwide (Bruno & Selig 2007, Adjeroud et al. 2018, Hughes, Kerry, et al. 2018). Although the term 'succession' was not necessarily employed by the authors, secondary succession has been widely studied in coral reef ecosystems, through changes in community organization following large-scale disturbances, such as thermally induced coral bleaching events, cyclones and the sudden changes in abundance of keystones species such as herbivores and corallivores (Coles & Brown 2007, Trapon et al. 2011, Jouffray et al. 2015, Doropoulos et al. 2016). In contrast, and despite some progress on algal communities which are characterized by their ability for rapid colonization of vacant substrate, their shorter life cycle and faster growth, primary succession remains poorly investigated in coral reef ecosystems (Hixon & Brostoff 1996, Burkepile & Hay 2010). For corals, this lack of information on primary succession is mainly related to the rarity of newly formed substrate that corals can colonize, and to their long life cycle and slow growth rate that imply long-term monitoring efforts and frequent sampling to detect community changes. Indeed, the few studies on primary succession of coral communities have been conducted on submerged lava flows, and have focused on recovery and subsequent changes in community structure (Grigg & Maragos 1974, Grigg 1983, Tomascik et al. 1996). In Hawaii, Grigg and Maragos (1974) observed that succession appeared to be frequently interrupted, resulting in early successional stages with clearly identified pioneer species. They estimated a recovery period of 20 years for areas exposed to strong hydrodynamic forces, and over 50 years on sheltered ones. Tomascik et al. (1996) investigated early successional dynamics of coral communities following the 1988 volcanic eruption of Gunung Api, in Indonesia. They provided evidence for rapid coral

colonization (5 years) and growth on sheltered lava flows, with higher diversity, abundance and cover of coral assemblages than on adjacent carbonate reefs not covered by lava. However, the underlying ecological processes associated to recovery and temporal dynamics of coral assemblages, such as recruitment, early mortality and growth, and therefore, mechanisms of ecological succession remain elusive (Pearson 1981, Doropoulos et al. 2016, Kayal et al. 2018). In the context of 'coral reef crisis', examining succession processes is not only important for understanding changes and recovery trajectories of coral communities, but is also critical to better evaluate the potential colonization of climate change refugia, such as non-reef marginal tropical environments or high-latitude temperate regions, that is predicted under climate change scenario (van Hooidonk et al. 2013, Yates et al. 2014, Cacciapaglia & van Woesik 2015, 2016, Kavousi & Keppel 2018).

Reunion Island (Western Indian Ocean) hosts the Piton de la Fournaise, one of the most active volcanos characterized by frequent eruptions in recent decades (27 from 1998 to 2007; Tanguy et al. 2011). Terrestrial lava flows have facilitated the spread of invasive vegetal species on the island, which have altered primary succession and radically changed successional trajectories, thus increasing the rate of succession. The continued spread of these species poses a major threat for the remaining native terrestrial ecosystems at Reunion Island (Potgieter et al. 2014). Also, Piton de la Fournaise lava flows often reach the ocean along less than 20 km of the south-east coast (Michon & Saint-Ange 2008). These spatially closed and delimited submerged lava flows of different ages offer a unique opportunity to study the succession of reef communities. Surveys on submerged lava flows of the Piton de la Fournaise have been conducted between 2006 and 2013 by ARVAM (Agence pour la Recherche et la Valorisation Marines), notably during the BIOLAVE expeditions (2011-2012; Schleyer et al. 2016, Zubia et al. 2018). The structure and diversity of fish (Pinault et al. 2013, 2014), echinoderm (Bollard et al. 2013), marine flora (Zubia et al. 2018), and ascidian, sponge and octocoral (Schleyer et al. 2016) communities were assessed on lava flows of different ages.

Here, we analyzed an original data set on coral assemblages on submerged lava flows of different ages and on established coral reefs around Reunion Island. Our main objective was to explore the strength and mechanisms of ecological succession in coral assemblages, by comparing the diversity, structure (density, cover, size-structure) and

demography (recruitment, growth, mortality) of coral assemblages among coral reef and lava flow habitats.

3.2.2. Material and methods

3.2.2.1. Study sites

Reunion (21° 07' S, 55° 32' E) is a volcanic island (ca. 70 km long and 50 km wide) of the Mascarene Archipelago in the western Indian Ocean, located 700 km east of Madagascar. Fringing reefs line the island in 12 km^2 area along 25 km of the west-southwest coast (Montaggioni & Faure 1980, Camoin et al. 1997). Sampling strategy consisted of eight study sites, all located at ~12 m depth (Figure 11). Four sites were disposed on outer reef slopes of coral reef habitats (coded R-), including two sites (R-SS and R-VS) inside the no-take zone (NTZ) of the marine protected area (Réserve Naturelle Marine de La Réunion; RNMR), and two sites (R-SB and R-MA) outside the NTZ. Additionally, four sites were disposed on underwater lava flows of different ages (coded L-): one is a centennial lava flow (L-CA) and the others correspond to eruptive events of 1977 (L-1977), 2004 (L-2004) and 2007 (L-2007).

3.2.2.2. Sampling strategy

Coral composition (scleractinians and the calcareous hydrocoral *Millepora*), density, cover, and size-structure were recorded in September 2016 at coral reef sites (R-SS, R-SB, R-VS and R-MA) and in March 2017 at the lava flow sites (L-CA, L-1977, L-2004 and L-2007). Densities of adult and juvenile corals were evaluated on photographs taken along three belt-transects (1 × 10 m) deployed at each site (ca. 18 photographs per belt-transect). Each coral colony encountered was identified to the genus and its maximal diameter (cm) measured using a tape present in each photograph. At each site, coral cover was evaluated using the Line Intercept Transect method (LIT; Loya 1972) using three linear 20 m transects laid parallel to depth contours and separated by 5 m. As some species may be omitted using belt-transects and LIT (Beenaerts & Vanden Berghe 2005), coral species diversity was assessed during a 45 min prospection at each site.

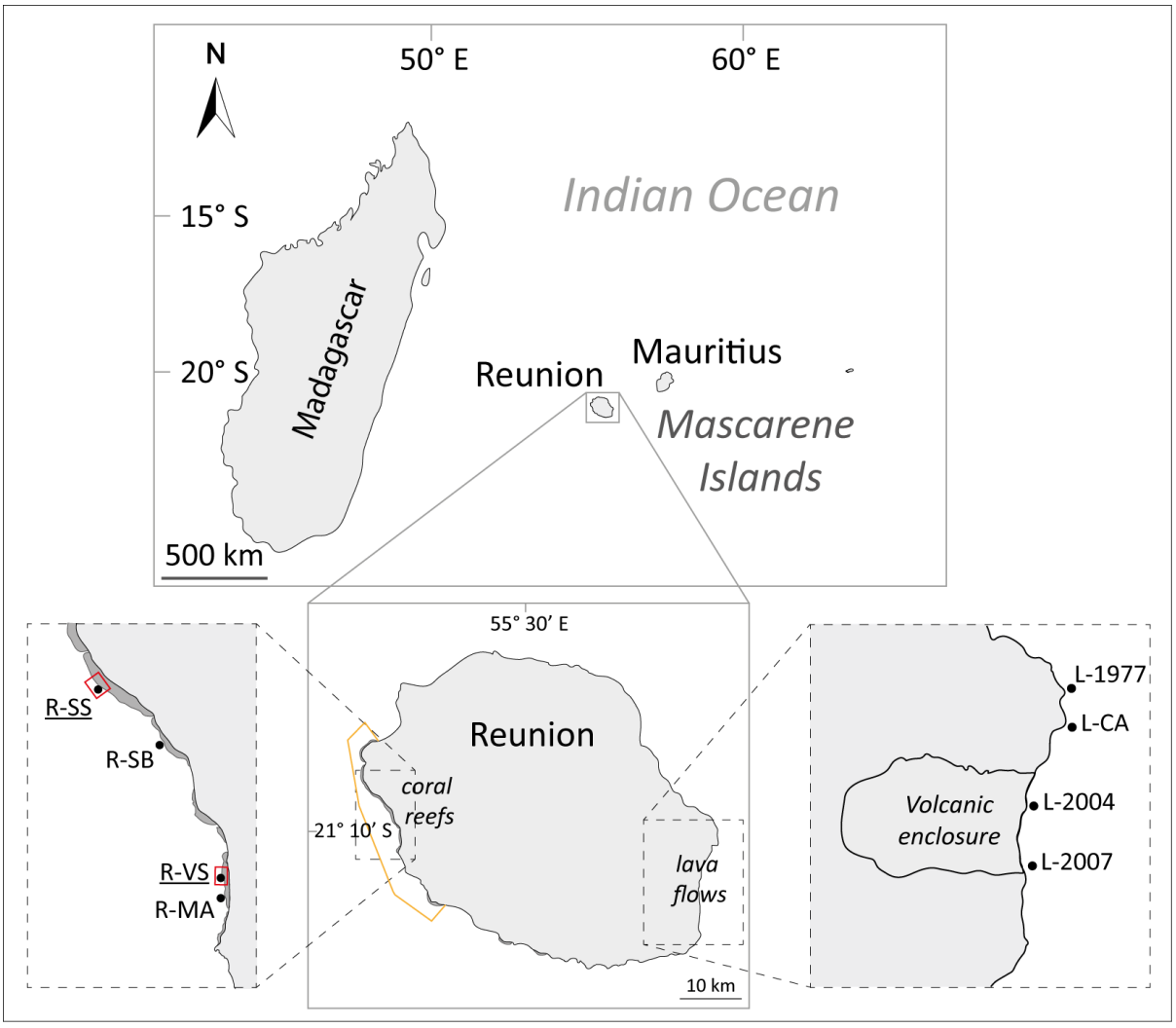

Figure 11. Location of the sampling sites at Reunion Island. ☐, land; ▒, reef flat; ☐, marine reserve; ☐, no take zones; ●, sampling sites. Four sites were disposed on outer reef slopes of coral reef habitats (coded R-), and four sites on underwater lava flows of different ages (coded L-). Underlined sampling sites belong to no-take zones. R-SS: Sanctuaire Sud; R-SB: Souris Blanche; R-VS: Varangue Sud; R-MA: Marine; L-1977: 1977 lava flow; L-CA: Caesari: secular lava flow; L-2004: 2004 lava flow; L-2007: 2007 lava flow.

Coral recruitment was characterized through the spatio-temporal variability of the abundance and taxonomic composition of early recruits over artificial settlement tiles. Individual unglazed terracotta tiles attached to a stainless steel support anchored to the substrate were used (Appendix A1; Mundy 2000, Adjeroud et al. 2007). For each site, 20 individual tiles (ca. 10 × 10 × 2 cm) were immersed for six months over two summer periods (October 2016–March 2017, October 2017–March 2018). At the end of the immersion periods, tiles were retrieved, bleached and sun dried. The skeletons of coral

recruits (coral spats) were then counted and identified. Recruits of Acroporidae, Pocilloporidae and Poritidae families were discriminated according to morphological traits (Appendix A2; Babcock et al. 2003). Other coral recruits were assigned to the category 'others', or to the category 'broken' when the skeleton was too damaged for identification (Adjeroud et al. 2007). Coral recruits found on the different sides of tiles (upper and lower surfaces, and sides) were pooled to estimate mean recruitment rates at each site (recruits / m^2).

Demographic processes were evaluated through the monitoring of juvenile (immature colonies ≤ 5 cm in diameter) and adult (mature colonies > 5 cm in diameter) stages of the three dominant coral genera, *Acropora*, *Pocillopora* and *Porites* (which represent ~96 % and ~70 % of the total coral cover on lava flows and reefs, respectively) for one year. At each site, colonies were spatially referenced and measured every six months (two periods: October 2016–March 2017 and April 2017–September 2017) within three replicate belt-transects of 10 m^2 (1 × 10), laid parallel to depth contours and separated by ~1 m. Colony dimension $D = \frac{d1+d2}{2}$ (in mm) was calculated with $d1$ the maximal diameter and $d2$ the length of its perpendicular. Growth rates (%) and mortality rates (%) were assessed for each colony over the two periods. Mean positive growth rates (ΔD_+) and mean negative growth rates (ΔD_-) were evaluated for each genus-stage combination. To define demographic transitions, each coral growth rate ΔDi was compared to ΔD_+ and ΔD_- associated to the genus-stage combination of the coral i. If $\Delta Di > \Delta D_+$ coral was assigned to *positive growth* transition, if $\Delta Di < \Delta D_-$ coral was assigned to *negative growth* transition, otherwise coral was assigned to *retention*. *Mortality* (total loss of a colony living tissues), *fusion* (merging of the living tissues from two colonies of the same species) and *fragmentation* (physical separation from one colony to several ones) were also recorded on the field and taken into account as demographic transitions.

3.2.2.3. Data analyses

Species composition was compared among sites using a correspondence analysis (*CA* function from *FactoMineR* package for R software; Lê et al. 2008). Densities, cover, size structure, recruitment and growth of corals were compared between habitats (coral reefs *vs.* lava flows) and sites using an ANOVA model (eq. 1).

$$X_{ij} = Habitat_i + Site_j/Habitat_i + \varepsilon_{ij} \qquad \text{(eq. 1)}$$

Where *i* and *j* respectively stand for the habitat and the site, and ε is the residual variance (within sites variance). These spatial factors correspond to a two-level nested design with sites within the habitat. Coral density and size structure were log-transformed and recruitment rates were log(x+1) transformed to meet the assumptions of normality. To identify differences between levels of significant factors, pairwise *t*-test with Bonferroni correction was used. Coral mortality rates and demographic transitions (positive and negative growth, retention and mortality) were compared among habitats and sites using Fisher's exact tests. Data analyses were conducted using R software (R Core Team 2018).

3.2.3. Results

3.2.3.1. Coral diversity

A total of 86 species belonging to 33 genera were identified on coral reefs and lava flows (Appendix A3). Species richness was higher at coral reef sites (44-57 species per site) compared to lava flows (23-38 species per site; Figure 12). We identified 23 species on the youngest lava flow (L-2007) and 35 ± 3 species on the older ones. The first axis of the correspondence analysis of coral species composition clearly discriminated lava flow sites from those located on coral reefs (Figure 12). Among the 86 species identified, 11 were recorded exclusively on lava flow sites (*Astreopora listeri*, *Dipsastraea matthaii*, *Gardineroseris planulata*, *Pavona explanulata*, *Cyphastrea* sp., *Favites* sp. 1, and *F.* sp. 2, *Montipora* sp. 1, *M.* sp. 2, *M.* sp. 3, and *Pocillopora* sp.) and 36 species were found only on coral reef sites. The second axis showed that among coral reef sites, R-SS had a distinct species composition, with *Goniopora cellulosa*, *Acropora humilis*, *Astreopora ocellata*, *Cyphastrea serailia*, *Echinopora hirsutissima*, *Favites abdita*, *Goniastrea edwardsi*, *Montipora efflorescens*, *Platygyra lamellina*, *Pavona maldivensis* and one species of *Dipsastraea* recorded at this site exclusively. A large number of species were recorded at both habitats, with 12 ubiquitous, and 39 species found in at least one reef site and one lava flow site.

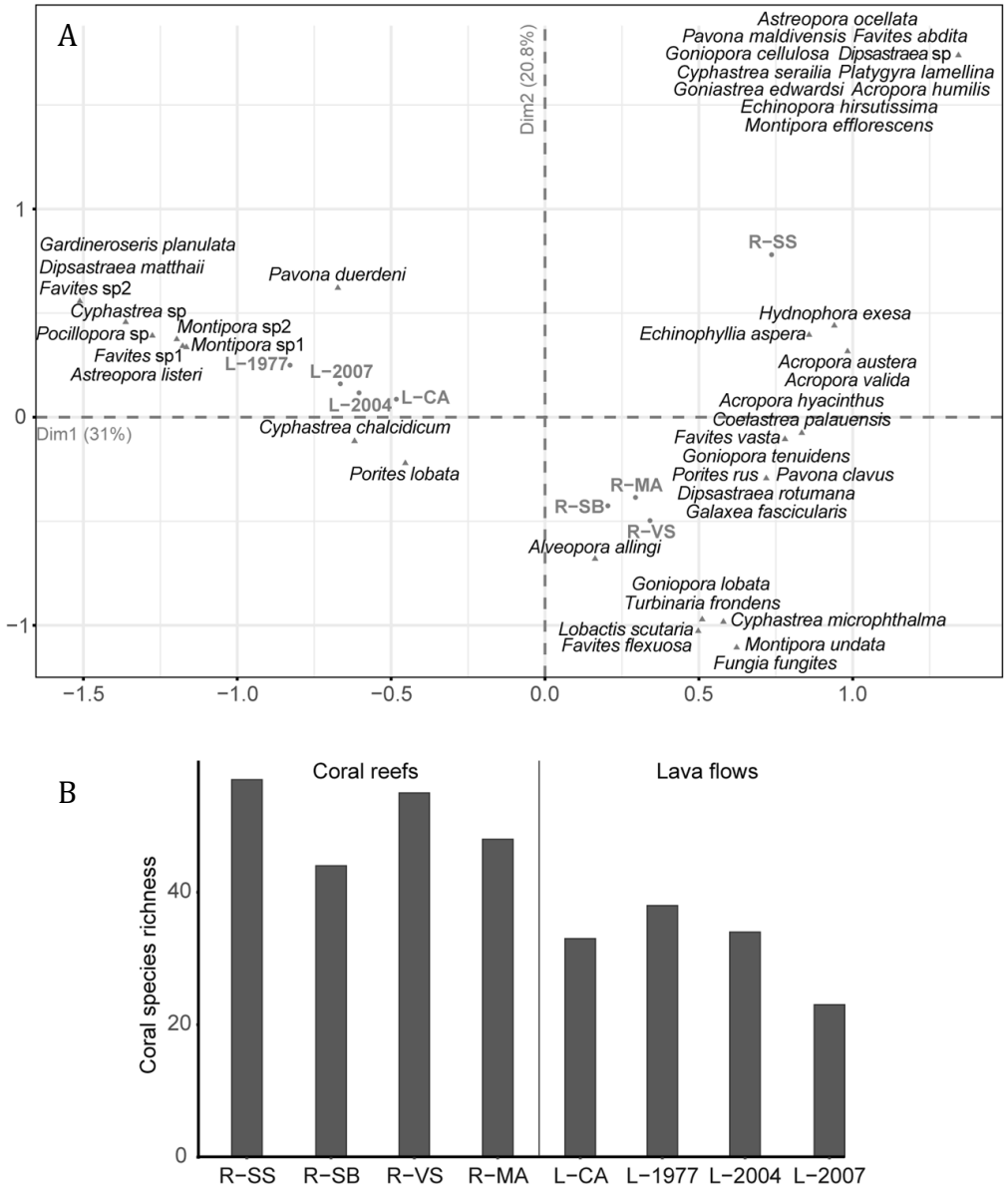

Figure 12. Correspondence analysis showing the spatial variation in the species composition of coral assemblages (A), and variation in species richness (B) among coral reef and lava flow sites. See legend of Figure 11 for site's codes.

3.2.3.2. Coral density

Adult coral densities ranged from 865 (at R-VS) to 5835 colonies / 100 m^2 (at L-2004), while juvenile coral densities ranged from 273 (at R-VS) to 1168 colonies / 100 m^2 (at L-2004; Figure 13). Coral densities for both adults and juveniles were not significantly different between habitats (coral reefs *vs.* lava flows; ANOVA, $p = 0.32$ for adults and $p = 0.30$ for juveniles; Appendix A4). However, significant differences were found among sites for both adults and juveniles (ANOVA, all $p < 0.0001$; Appendix A4). Adult density was higher on 2004 lava flow site than at any other site of this habitat (1458 colonies / 100 m^2 in average; pairwise *t*-test with Bonferroni correction, $p < 0.001$). For coral reef sites, adult density was significantly lower at R-VS compared to the three other sites of this habitat (1233 colonies / 100 m^2 in average; post-hoc tests, $p < 0.04$). Juvenile density was also significantly higher at L-2004 compared to other lava flow sites (414 colonies / 100 m^2 in average; post-hoc tests, $p < 0.01$), and at R-MA (601 colonies / 100 m^2) compared to R-SS and R-VS (285 colonies / 100 m^2 in average; post-hoc tests, $p < 0.02$). Coral assemblages were generally dominated by *Pocillopora* (43 ±17 %) and *Porites* (15 ±11 %) and, in a lesser extent, by *Acropora* species (6 ± 4 %; mean ± standard deviation).

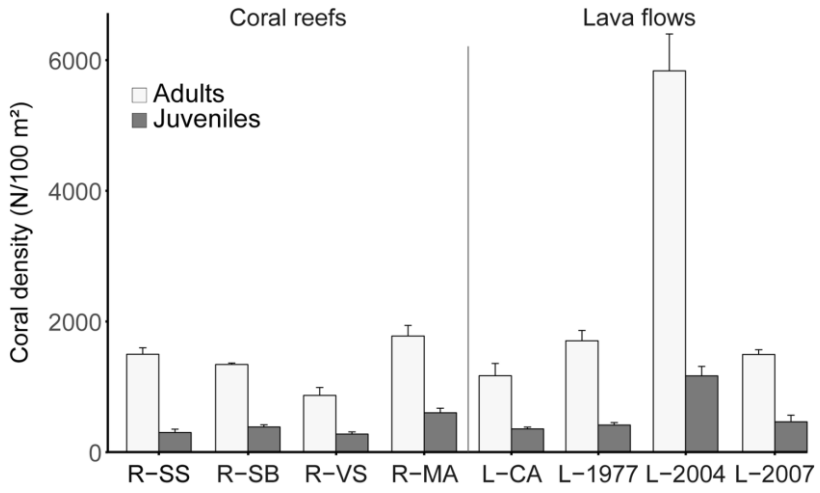

Figure 13. Coral densities of juvenile and adult coral colonies among reef and lava flow sites at Reunion Island (n / 100 m^2 ± SE). See legend of Figure 11 for site's codes.

3.2.3.3. Coral cover

Mean coral cover ranged between 20.2 ± 2.7 % (mean ± standard deviation) and 27.9 ± 2.4 % on coral reef sites, and between 17.8 ± 4.4 % and 55.4 ± 4.1 % on lava flows (Figure 14), but no significant difference was recorded between habitats (ANOVA, $p = 0.23$; Appendix A4), nor among reef sites (pairwise *t*-test with Bonferroni correction, all $p = 1$). In contrast, we found a significant difference among lava flow sites, with higher values at L-2004 and L-1977 compared to L-2007 and L-CA (pairwise *t*-test with Bonferroni correction, $p < 0.02$). The four genera presenting the highest densities (*Pocillopora, Porites*, *Acropora* and *Astreopora*) were also the most important in terms of coral cover. *Pocillopora* dominated coral assemblages for two of the four coral reef sites (ca. 48.7 ± 12.6 % at R-SB and R-SS vs. 27.5 ± 15.7 % at R-VS and R-MA) and for all lava flow sites (from 64.7 ± 7.5 % at L-2004 to 93.9 ± 6.3 % at L-2007; Figure 14). While cover of *Porites* could reach high values at coral reef sites (48.4 ± 19.6 % at R-VS), this genus was poorly represented at lava flow sites (3.30 ± 0.03 %; Figure 14). Similarly, cover of *Astreopora* ranged from 10.9 ± 9.5 % to 20.5 ± 4.1 % at coral reef sites, but was less than 0.1 ± 0.3 % at lava flow sites (Figure 14). For *Acropora*, 14.2 ± 8.0 % were recorded at both lava flow (L-2004, L-1977 and L-CA) and coral reef (R-SS and R-VS) sites, whereas coral cover of this genera was null at R-MA and R-SB coral reef sites and at the youngest lava flow (L-2007; Figure 14).

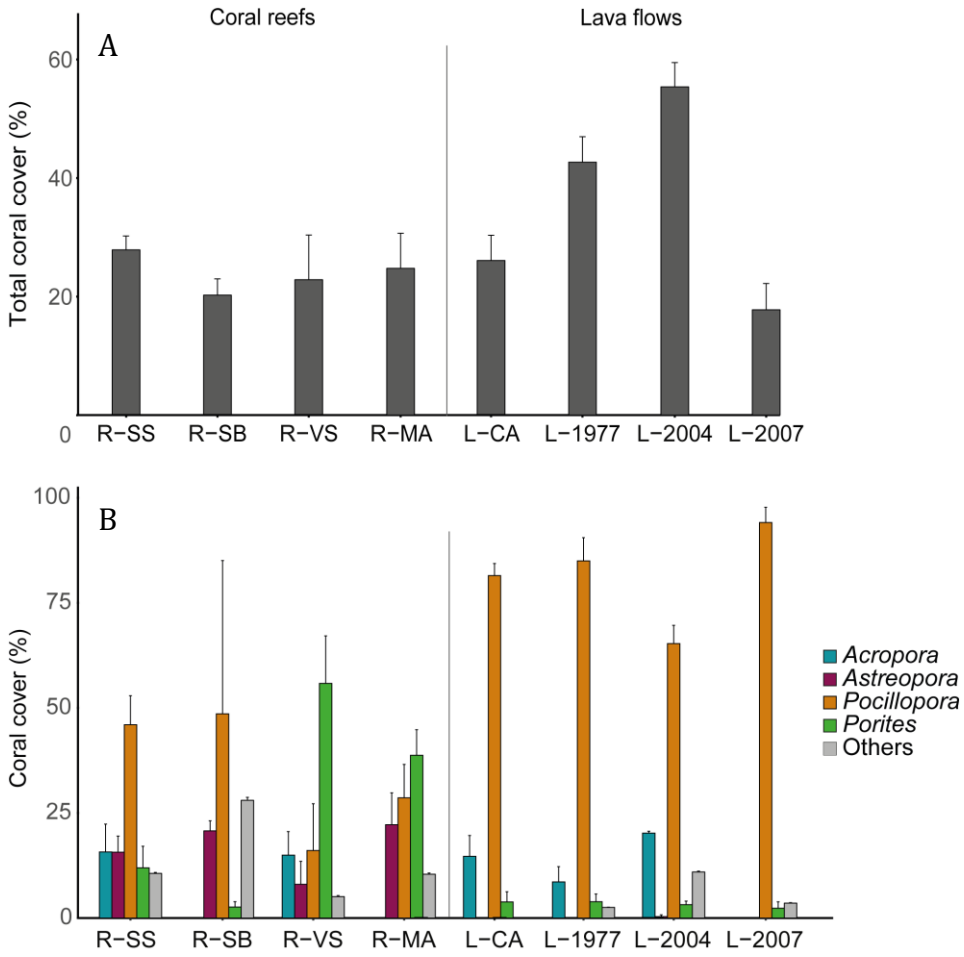

Figure 14. Total coral cover (A) and coral cover of dominant genera (B) among reef and lava flow sites at Reunion Island (% ± SE). See legend of Figure 11 for site's codes.

3.2.3.4. Size structure

Mean colony size of the dominant genera (*Pocillopora, Porites, Acropora* and *Astreopora*) was not significantly different between habitats (ANOVA, all $p > 0.1$; Appendix A4), but significantly varied among sites within habitats for *Acropora*, *Astreopora* and *Pocillopora* colonies (ANOVA, all $p < 0.02$; Appendix A4; Figure 15). At coral reef sites, the mean size of *Acropora* colonies was higher at R-SS (22.3 ± 2.3 cm) than on the other sites (8.47 ± 2.9 cm; pairwise *t*-test with Bonferroni correction, $p < 0.02$). Mean size of *Astreopora* colonies was significantly higher at R-SS (12.8 ± 1.1 cm) than at R-VS (9.3 ± 0.7 cm; pairwise *t*-test with Bonferroni correction, $p = 0.02$), while the mean size of *Pocillopora* colonies was significantly higher at R-SB and R-SS (12.6 ± 0.5 cm) than at R-MA and R-VS (8.9 ± 1.3 cm; pairwise *t*-test with Bonferroni correction, $p < 0.01$). At

lava flow sites, the mean size of *Acropora* and *Pocillopora* colonies were lower on the youngest (2007) lava flow (6.1 ± 0.6 cm and 11.2 ± 0.3 cm, respectively; Figure 15) than at the other lava flow sites (14.8 ± 0.5 cm and 14.9 ± 1.0 cm respectively; pairwise *t*-test with Bonferroni correction, $p < 0.03$). The number of recorded *Astreopora* colonies was too low on the lava flows to allow pairwise comparisons.

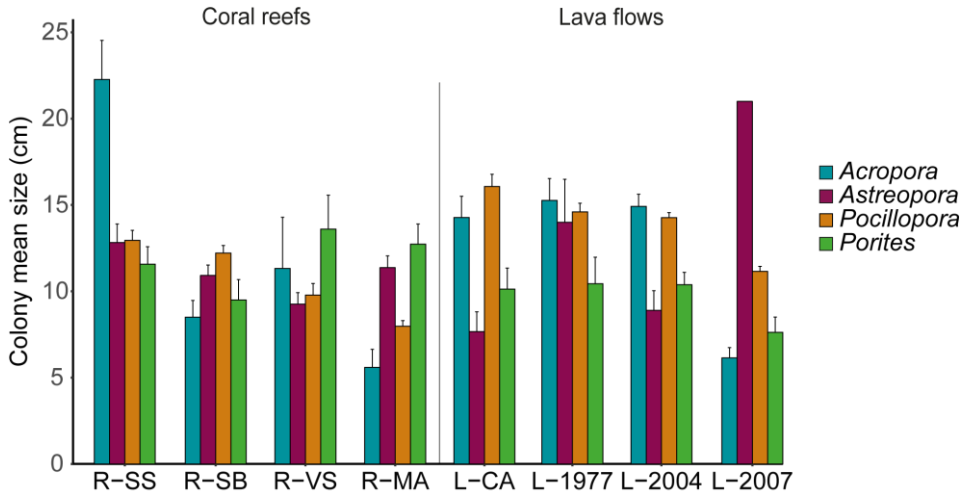

Figure 15. Colony mean size of the dominant coral genera among reef and lava flow sites at Reunion Island (cm ± SE). See legend of Figure 11 for site's codes.

3.2.3.5. Recruitment patterns

Over the two studied summer periods (October 2016–March 2017 and October 2017–March 2018), recruit assemblages were largely dominated by Pocilloporidae on both coral reef (77 %) and lava flow (83 %) habitats (Figure 16). Acroporidae represented respectively 4 % of recruit assemblages in both habitats, Poritidae 4 % on coral reefs and 2 % on lava flows, whereas the other taxa represented 8 % and 5 %, and the broken recruits 7 % and 5 %, respectively. Mean recruitment rates were not significantly different between reef and lava flow habitats for Acroporidae, Pocilloporidae and Poritidae (ANOVA; all $p > 0.05$; Appendix A4). Abundance of Pocilloporidae recruits was higher at R-SB and R-VS (36.5 ± 3.5 recruits / m^2) and greatly reduced at R-SS (5.4 ± 1.2 recruits / m^2) for coral reef sites (pairwise *t*-test with Bonferroni correction, $p < 0.01$), whereas no differences were found among lava flow sites .

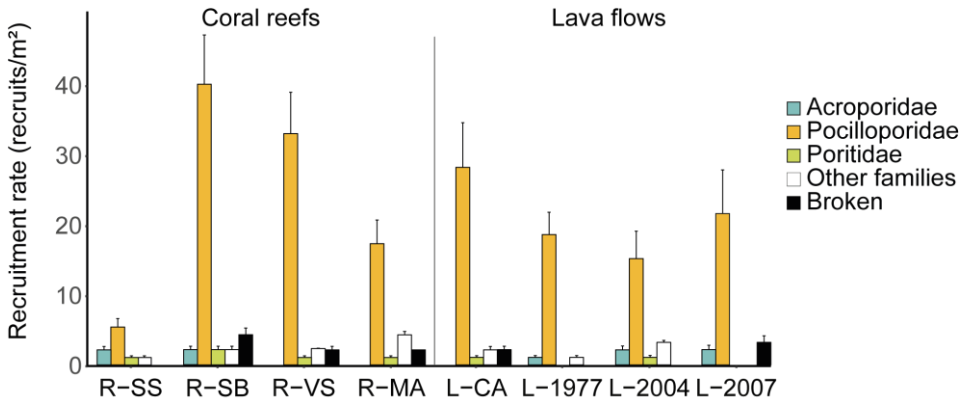

Figure 16. Mean coral recruitment rates observed during two summer periods (October 2016–March 2017 and October 2017–March 2018) on artificial settlement tiles among reef and lava flow sites at Reunion Island (recruits / m^2 ± SE). See legend of Figure 11 for site's codes.

3.2.3.6. Demographic process

Annual growth rates of the three major coral genera did not significantly differ between habitats (reef sites vs. lava flow sites) for both adult and juvenile colonies, except for juveniles of *Pocillopora* that showed higher growth rates on coral reef sites (ANOVA, $p = 0.01$; Appendix A4; Figure 17). Moreover, growth rates were not significantly different among sites within habitats for any of the three genera considered (ANOVA, all $p > 0.05$; Appendix A4). Mean growth rate of *Acropora* was higher for juvenile (+56 %, which consider the initial size of the colony, or +17 mm of linear growth which does not) than for adult (+8 % or +9 mm of linear growth) colonies. For *Pocillopora*, mean growth rate reached +10 % (+11 mm) for adults and +37 % (+13 mm) for juveniles. Gain and loss of living tissue were equivalent for adult colonies of *Porites*, resulting in a mean growth rate of +0.5 % (but -2 mm of mean linear growth), whereas growth rate averaged +16 % for juveniles (+4 mm). Except for *Pocillopora* at R-SB, mortality rates were higher for juvenile compared to adult colonies on all sites. No significant differences in mortality rates of *Acropora*, *Pocillopora* and *Porites* colonies were detected between habitats, for both adults and juveniles (Fisher's exact tests, all $p > 0.05$; Figure 17). Mortality of adult *Pocillopora* significantly varied between the four sites of both reefs (from 0 to 39 ± 17 %) and lava flows (from 0 to 33 ± 18 %; Fisher's exact tests, both $p < 0.03$). Mortality rates of adult *Acropora* and *Porites* and juvenile of the three genera were not significantly different among sites at both habitats (Fisher's exact tests, all $p > 0.14$).

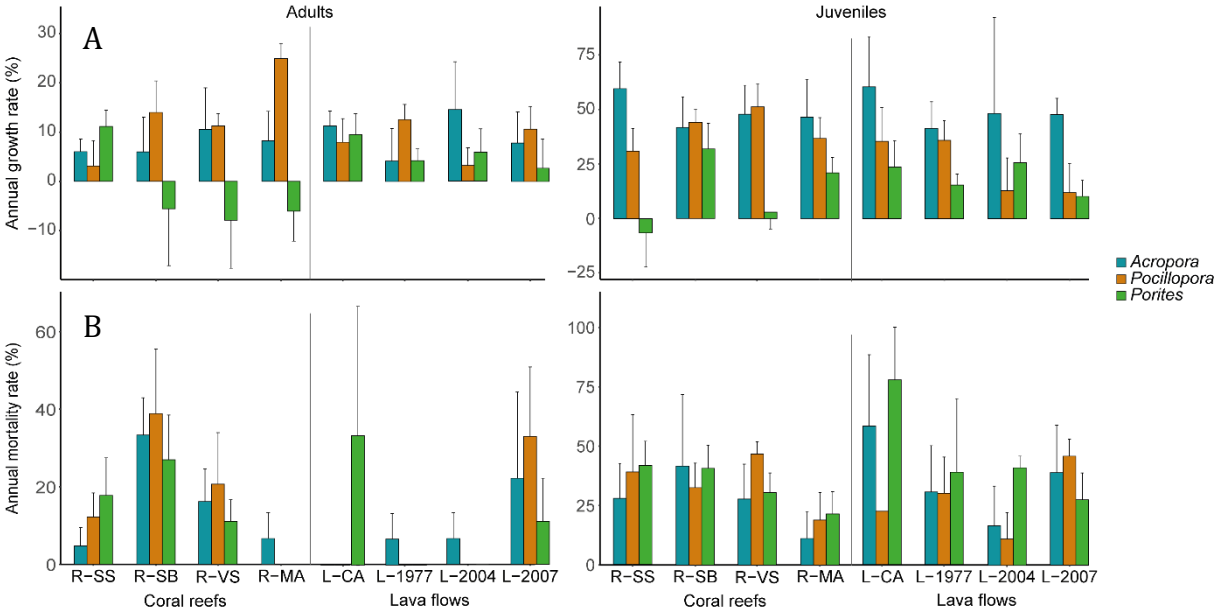

Figure 17. Annual coral growth (A) and mortality rates (B) of adult (left) and juvenile (right) colonies of *Acropora*, *Pocillopora* and *Porites* in reef and lava flow sites at Reunion Island (% ± SE). See legend of Figure 11 for site's codes.

Demographic transitions were significantly different between coral reef and lava flow sites for adult *Pocillopora* and *Porites* (Fisher's exact tests, all $p < 0.02$; Figure 18). On coral reef sites, 44 % of adult *Pocillopora* colonies showed *positive growth*, and 27 % on lava flow sites. In contrast, adult colonies of *Porites* with *positive growth* represented 31 % on lava flow sites, and 17 % on coral reef sites, where *mortality* were three times higher. Adult colonies of *Pocillopora* also showed significant differences in demographic transitions within habitats, for both lava flow and coral reef sites (Fisher's exact tests, $p = 0.006$ and $p = 0.003$ respectively). For adult *Acropora*, such within-habitat differences were found between reef sites (Fisher's exact tests, $p = 0.003$).

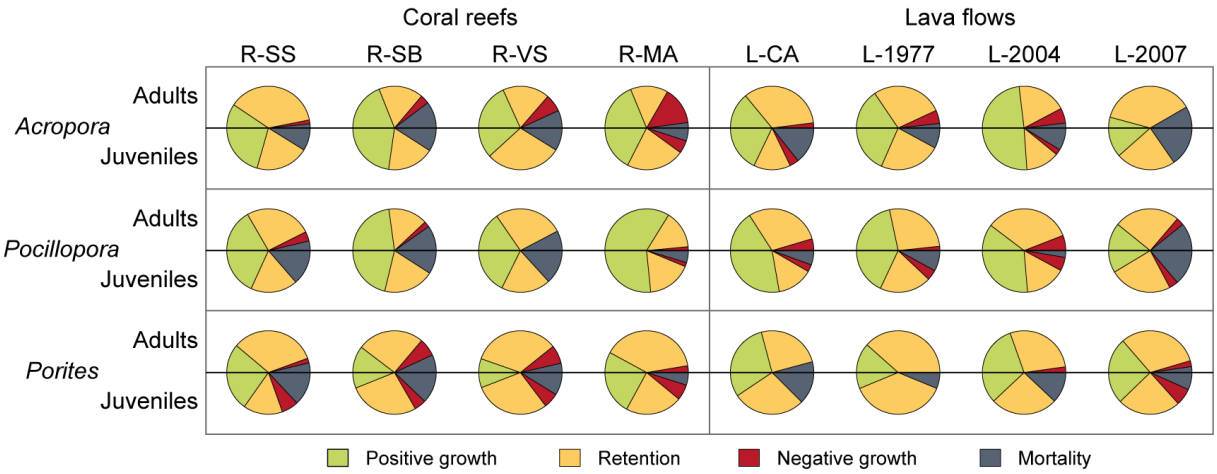

Figure 18. Demographic transitions of juvenile and adult colonies of *Acropora*, *Pocillopora* and *Porites* for two 6-months consecutive periods (October 2016–March 2017 and April 2017–September 2017) in reef and lava flow sites at Reunion Island. See legend of Figure 11 for site's codes.

3.2.4. Discussion

As in many other coral reefs throughout the world (Huston 1985, Connell et al. 1997, Karlson and Cornell 2002, Adjeroud et al. 2019, among others), our results demonstrate that coral assemblages at Reunion Island are characterized by a marked spatial heterogeneity. Density, cover, size-structure, recruitment patterns and mortality of corals show significant differences among sites both within coral reefs and lava flows, the two major habitats studied during this survey. However, except for demographic transitions of adult *Pocillopora* and *Porites* and for growth rate of juvenile *Pocillopora*, no marked differences between habitats were found for these descriptors. In fact, the distinction between coral reef and lava flow sites was mostly reflected in the species diversity and composition of coral assemblages, with 11 (out of 86) species exclusively recorded at lava flow sites, and 36 species observed only at coral reef sites. Species richness was always higher at coral reef sites (44-57 species per site) compared to lava flow (23-38 species per site). As proposed for ascidians, sponges and octocorals for which similar patterns were observed (Schleyer et al. 2016), the lower diversity at lava flow habitats may results from different history of perturbations and contrasted environmental conditions between the west and southeast coasts, such as exposure to dominant swell and regional currents, but also in terms of light availability and sedimentation. In fact, darkness of the black

volcanic substrata on lava flows may absorb rather than reflect incident light, thus limiting light availability. Furthermore, the resuspension of volcanic sand, which is responsible for smothering and abrading sessile invertebrates, together reduce the growth of endosymbiotic organisms such as scleractinian corals (Schleyer et al. 2016). But the structure of coral assemblages at lava flow sites can also be considered through the angle of ecological succession.

During primary succession, different sets of species are expected to replace each other through time. These species range from pioneer species, characterized by high rates of reproduction and growth and able to rapidly colonize bare substrates, to late successional species that require more time and/or complex environment to establish (Odum 1969). Our results identified a set of species typical of lava flow habitat, but did not detect a clear relationship between the age of the lava flow and the species composition. Even if some 'lava flow' species were recorded at contemporary sites (L-2007, L-2004, and L-1977) and not at the older centennial site (L-CA), no strictly pioneer species (e.g. present exclusively on the youngest lava flow) was recorded. These outcomes contrast with those obtained at the same location for echinoderms, for which several pioneer species were exclusively recorded at the youngest lava flow (Bollard et al. 2013), and for algae, for which species composition was correlated to the age of the lava flows with a high occurrence of opportunistic species on recent sites (Zubia et al. 2018).

However, our results show that species richness, density and cover of coral assemblages were lower at the youngest lava flow site (L-2007, 10 yo) compared to older ones, where maximal values were recorded at the 1977 and 2004 lava flow sites. Despite the limited number of sites on lava flow habitats, and the limited duration of our survey, these results coincide with the theoretical pattern of succession (Odum 1969, Connell 1978). Ecological succession predicts an increase in species abundance and diversity during early colonization stages, associated with reduced dominance of one or few species through time. This increase in species richness is generally faster at the beginning of the succession, leading to convex rate-of-change curves (Odum 1969). After these early successional stage, the relationship between species diversity and the ecosystem development becomes more controversial (Odum 1969). Our results are also consistent with patterns of community succession recorded in Hawaii, where species richness on lava flows of 2 to 100 yo increased for 45 years and then decreased (Grigg & Maragos

1974). This reveals a succession pattern in which colony size and species richness of corals increase over time due to the settlement of new species, until species interactions such as competition for space lead to their decrease (Grigg & Maragos 1974, Grigg 1983). This general pattern have already been observed for echinoderms (Bollard et al. 2013) and sessile soft bodied organisms (Schleyer et al. 2016) on lava flows at Reunion Island, but contrasts with those obtained for fish communities for which species richness tended to be higher closer to the most recent lava flow (Pinault et al. 2013, 2014). The lower species richness, the higher mortality rates, and the lowest proportion of colonies demonstrating *positive growth* recorded at the youngest 2007 lava flow compared to the three-years older 2004 site may be due to specific types of physical stressors, such as freshwater resurgences, sediment resuspension and rubble displacement (F. Jouval; pers. obs.) that likely occur at the youngest lava flow site.

Our results highlight the strong dominance of the genus *Pocillopora*, notably *P. verrucosa* and *P. meandrina*, at all lava flow sites, and at two coral reef sites. This dominance of *Pocillopora* spp. was also recorded during the 2011-2012 BIOLAVE expeditions, notably on the 2007 lava flow (80% of counted colonies). These results indicate that the dominance of *Pocillopora* spp. was established soon (at least four years) after the eruption and was maintained up to ten years thereafter. The pioneer nature of *Pocillopora* has already been highlighted on natural and artificial reefs (Connell 1973, Clark & Edwards 1994, Adjeroud et al. 2018, Kayal et al. 2018) but also over a 1.6 yo basaltic lava flow in Hawaii (Grigg and Maragos 1974). However, Tomascik et al. (1996) suggested that the pioneer nature of species depends on local environmental conditions such as the type of substrate and/or exposure to strong hydrodynamic forces. These authors found that *Acropora* species were the most efficient colonizers on a five years old sheltered (in terms of winds and waves) andesitic lava flow, whereas on unstable aggregate of pyroclastic deposits of the same age, *Pocillopora*, *Montipora* and *Porites* were the best colonizers (Tomascik et al. 1996). *Pocillopora* spp. were also found in high abundance on coral reef habitats of the west coast of Reunion Island, being the dominant taxa at some sites. This suggests that *Pocillopora* is not only a successful pioneer taxa during primary succession, but also has life-history traits advantageous to colonization and dominance of secondary successional stages, making it an opportunistic taxa. At Reunion Island, *Pocillopora* showed higher growth and recruitment rates compared to

other coral taxa (Jouval et al. 2019). Such observations were also reported in Hawaii, where *Pocillopora*, the dominant taxa on lava flows and surrounding habitats, had the highest recruitment rates (Grigg & Maragos 1974). As in many other coral reefs, *Pocillopora* at Reunion Island exhibits an opportunistic life strategy, with a high population turnover resulting from comparatively higher growth and recruitment rates, and with a high potential for larval dispersal and colonization (Penin et al. 2010, Darling et al. 2012, Kayal et al. 2015).

3.2.5. Conclusions

This study highlights the strong spatial heterogeneity of coral community structure at local scales (within habitat) at Reunion Island, that likely distort the overall differences between habitats at the island scale. In fact, very few differences in terms of colony density, cover, size-structure, growth and mortality were recorded between sites of primary (lava flows) and secondary succession (coral reefs). The most obvious distinction was in terms of species richness and composition, with lower diversity and a set of typical species at lava flow sites. These outcomes underline that the sequences of ecological successions as theorized by Odum (1969) and Connell (1978) are difficult to observe in the marine environment and especially coral reefs, compared to some terrestrial ecosystems (Walker & del Moral 2003). This can be linked to the high complexity of reef ecosystems, where several interacting biological and physical processes that vary in frequency, intensity, and spatial scales, can influence the structure of coral assemblages, thus masking the expected succession patterns, such as the primary succession at Reunion lava flows. The relatively high occurrence of large-scale disturbances, such as cyclones, bleaching events and outbreaks of the coral predator *Acanthaster* spp. (Scopélitis et al. 2009), is most probably the major cause of the maintenance of coral reefs of Reunion Island at early successional stages, with few chances to reach maturity/climax state, as suggested for other coral reefs worldwide (Connell 1978, Grigg 1983, Vercelloni et al. 2019).

Due to the highly dynamic nature of reef ecosystems in general, and of Reunion Island in particular (Scopélitis et al. 2009), the outcomes of the present survey should be reinforced by a long-term monitoring of coral assemblages at lava flow sites, in conjunction with the ongoing one on coral reef habitats of the west coast. It will be also

necessary to examine the role of abiotic and biotic factors during the early stages of benthic community succession, as well as density-dependence mechanisms, in facilitating or inhibiting the succession, as subtle changes in the young stages may have profound effects on coral recruitment and dynamics (Connell & Slatyer 1977, Karlson & Hurd 1993, Doropoulos et al. 2016, Bramanti & Edmunds 2016, Edmunds et al. 2018).

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3.2.6. Appendix

3.2.6.1. Appendix A1- Tiles anchoring system

The terracotta tiles are anchored to the reef substrate using perennial systems directly screwed into the substrate. Particularly difficult swell conditions and the nature of the substrate on the lava flows led to the development of a new anchoring system.

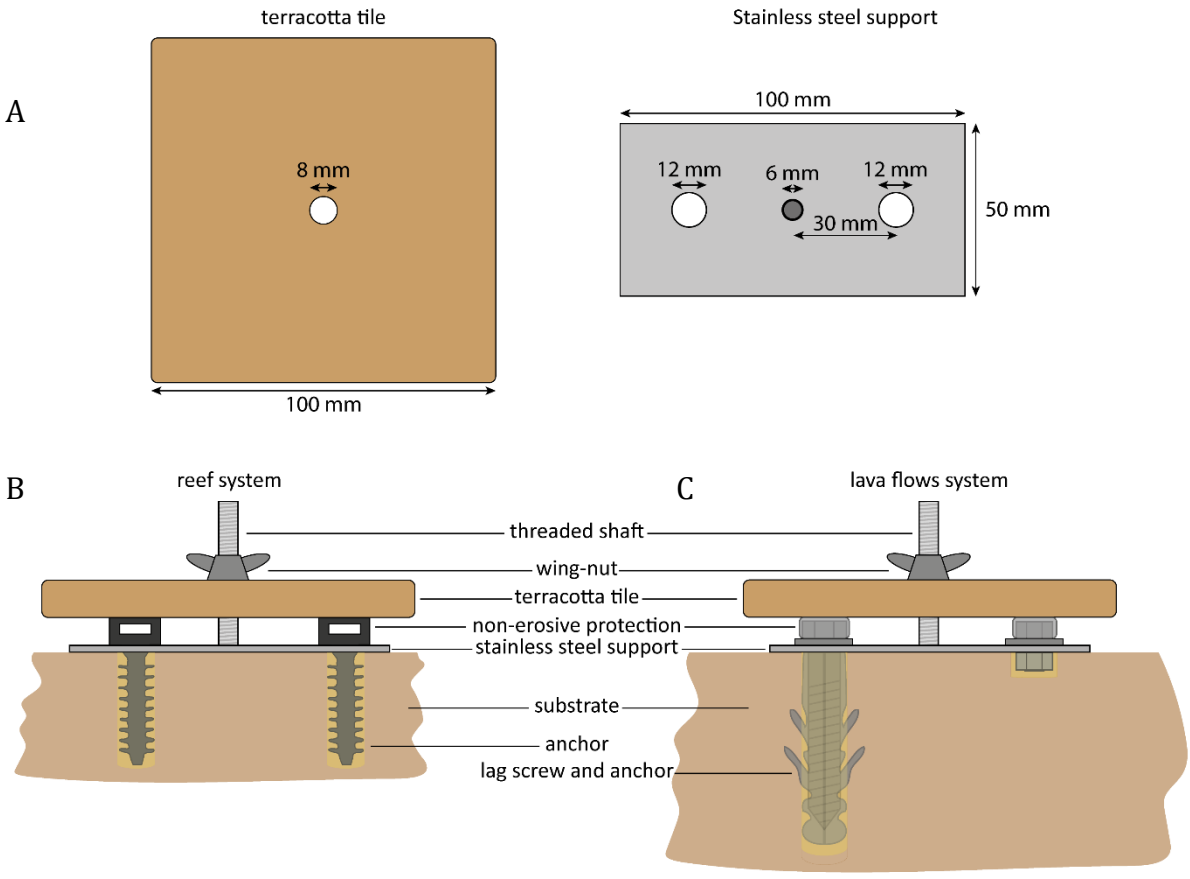

Figure A1. Scheme of the anchoring system used to assess recruitment rates and composition on unglazed terracotta tiles (A) on Reunion reef (B) and lava flow sites (C).

3.2.6.2. Appendix A2 - Identification of recruits

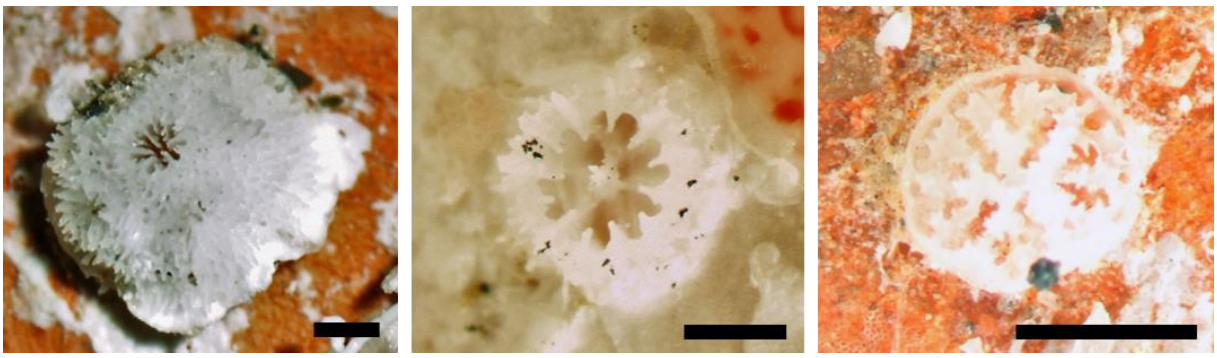

Figure A2. Photographs of the skeleton of coral recruits (coral spats) of Acroporidae (left), Pocilloporidae (middle) and Poritidae (right) families. Black bar = 0.5 mm

3.2.6.3. Appendix A3 – Coral species

Table A1. List of coral species (scleractinians and the calcareous hydrocoral *Millepora*) recorded at each of the coral reef and lava flow sites at Reunion Island.

	Coral reef sites				***Lava flow sites***			
Species	R-SS	R-SB	R-VS	R-MA	L-CA	L-1977	L-2004	L-2007
Acanthastrea echinata	√	√	√	√		√	√	√
Acropora abrotanoides	√	√	√	√	√	√	√	
Acropora austera	√		√					
Acropora digitifera	√	√	√	√	√	√	√	√
Acropora gemmifera	√		√	√	√	√	√	
Acropora granulosa	√		√	√	√		√	
Acropora humilis	√							
Acropora hyacinthus	√		√	√				
Acropora valida	√		√					
Alveopora allingi		√	√	√	√			
Astrea annuligera	√	√	√	√	√	√	√	√
Astrea curta				√				
Astreopora listeri					√	√	√	
Astreopora myriophtalma		√	√	√	√	√	√	
Astreopora ocellata	√							
Coelastrea palauensis	√		√	√				
Coscinaraea monile	√	√	√	√	√	√	√	√
Cyphastrea chalcidicum		√	√		√	√	√	√
Cyphastrea microphthalma			√	√				
Cyphastrea serailia	√							
Cyphastrea sp.						√		√
Dipsastraea favus	√	√	√	√	√	√	√	√
Dipsastraea matthaii						√		
Dipsastraea pallida	√	√	√		√			√
Dipsastraea rotumana	√	√	√	√				
Dipsastraea sp.	√							
Dipsastraea speciosa	√	√	√	√	√	√	√	√
Echinophyllia aspera	√	√						
Echinopora gemmacea	√	√	√	√	√	√	√	√
Echinopora hirsutissima	√							
Favites abdita	√							
Favites flexuosa		√	√					
Favites pentagona	√	√	√	√	√	√	√	√
Favites sp. 1					√	√	√	√
Favites sp. 2						√		
Favites vasta	√	√	√					
Fungia fungites			√					
Galaxea fascicularis	√	√	√	√				
Gardineroseris planulata						√		
Goniastrea edwardsi	√							
Goniastrea pectinata	√	√	√	√	√			
Goniastrea stelligera	√		√	√	√			
Goniopora cellulosa	√							
Goniopora lobata		√	√	√				

Table A1. Suite

	Coral reef sites				*Lava flow sites*			
Species	R-SS	R-SB	R-VS	R-MA	L-CA	L-1977	L-2004	L-2007
Goniopora tenuidens	√	√	√	√				
Hydnophora exesa	√			√				
Hydnophora microconos	√	√		√		√		
Leptastrea bottae				√				
Leptastrea pruinosa	√	√	√		√	√		
Leptastrea transversa	√	√	√	√			√	
Leptoria phrygia	√	√	√	√		√		
Leptoseris mycetoseroides	√			√			√	
Lobactis scutaria		√	√					
Millepora exaesa	√	√	√	√	√			
Millepora platyphylla	√	√	√	√	√	√	√	√
Montipora efflorescens	√							
Montipora sp. 1					√	√	√	
Montipora sp. 2					√	√		
Montipora sp. 3							√	
Montipora tuberculosa				√				
Montipora undata			√					
Montipora venosa	√	√	√	√			√	√
Paramontastraea peresi		√	√	√		√	√	
Pavona clavus	√	√	√	√				
Pavona duerdeni	√				√	√	√	√
Pavona explanulata							√	
Pavona maldivensis	√							
Pavona varians	√	√	√	√		√	√	
Pavona venosa	√	√	√	√	√	√		√
Platygyra daedalea	√	√	√	√	√	√	√	
Platygyra lamellina	√							
Platygyra pini	√	√	√	√		√		√
Plesiastrea versipora		√						
Pocillopora damicornis			√					
Pocillopora grandis	√	√	√	√	√	√	√	√
Pocillopora meandrina	√	√	√	√			√	
Pocillopora sp.						√	√	√
Pocillopora verrucosa	√	√	√	√	√	√	√	√
Pocillopora woodjonesi			√					
Porites lobata		√	√	√	√	√	√	√
Porites lutea	√	√	√	√	√	√	√	√
Porites rus	√	√	√	√				
Porites solida	√		√	√	√	√	√	
Psammocora profundacella	√	√	√	√	√	√	√	√
Turbinaria frondens		√	√	√				
Turbinaria mesenterina	√		√		√	√		
Total	57	44	55	48	33	38	34	23

3.2.6.4. Appendix A4 - ANOVA tests

Table A2. Summary of the ANOVA tests to analyze spatial variation of density, percent cover, size-structure, recruitment and annual growth rates of coral assemblages among sites and habitats at Reunion Island. Df: degrees of freedom. In bold: significant p values (at 5 % threshold).

Variable	*Detail*	*Factor*	*Df*	*Mean Square*	*F*	p *value*
Density	Adults	Habitat	1	1.11	1.20	0.32
		Site (in habitat)	6	0.92	30.57	**<0.0001**
	Juveniles	Habitat	1	0.79	1.27	0.30
		Site (in habitat)	6	0.62	10.98	**<0.0001**
Percent cover	Total	Habitat	1	800.42	1.82	0.23
		Site (in habitat)	6	440.11	6.60	**<0.01**
Size structure	*Pocillopora*	Habitat	1	35.59	3.53	0.11
		Site (in habitat)	6	10.08	26.59	**<0.0001**
	Porites	Habitat	1	0.01	0.01	0.95
		Site (in habitat)	6	1.02	1.23	0.29
	Acropora	Habitat	1	2.87	0.62	0.46
		Site (in habitat)	6	4.65	9.48	**<0.0001**
	Astreopora	Habitat	1	0.01	0.01	0.94
		Site (in habitat)	6	0.91	2.61	**0.02**
Recruitment rate	Pocilloporidae	Habitat	1	2.07	0.16	0.70
		Site (in habitat)	6	12.66	3.37	**<0.01**
	Poritidae	Habitat	1	0.14	1.97	0.21
		Site (in habitat)	6	0.07	0.22	0.97
	Acroporidae	Habitat	1	$1.84E^{-03}$	0.01	0.09
		Site (in habitat)	6	0.34	0.92	0.48
Annual growth rate	*Pocillopora* adults	Habitat	1	1021.20	1.74	0.24
		Site (in habitat)	6	586.27	2.18	0.05
	Pocillopora juveniles	Habitat	1	2700.60	13.56	**0.01**
		Site (in habitat)	6	199.10	0.18	0.98
	Porites adults	Habitat	1	1717.40	5.22	0.06
		Site (in habitat)	6	328.79	0.60	0.73
	Porites juveniles	Habitat	1	292.80	0.27	0.62
		Site (in habitat)	6	1095.22	1.23	0.30
	Acropora adults	Habitat	1	7.49	0.17	0.69
		Site (in habitat)	6	43.69	0.13	0.99
	Acropora juveniles	Habitat	1	508.50	0.29	0.61
		Site (in habitat)	6	1774.20	0.54	0.78

CHAPITRE 4.
ÉVALUATION MULTI-ÉCHELLES DU RECRUTEMENT CORALLIEN ET EFFET « RÉSERVE » DANS L'ARCHIPEL DES MASCAREIGNES

4.1. Synthèse

Le recrutement corallien désigne les processus permettant le maintien et le renouvellement des communautés coralliennes. Le succès du recrutement est donc indispensable pour la récupération des récifs coralliens ayant subi des perturbations.

Les processus de recrutement sont régis par de nombreux facteurs intervenant à toutes les échelles spatiales et temporelles, du centimètre à plusieurs centaines de kilomètres. Dans le contexte actuel d'augmentation en fréquence et en intensité des perturbations, il est capital de mieux comprendre l'importance relative des différentes échelles dans la variation du recrutement et, si possible, les facteurs associés à ces échelles.

La variabilité spatio-temporelle multi-échelles du recrutement des coraux scléractiniaires a été évaluée sur les récifs de deux îles de l'archipel des Mascareignes : La Réunion et Rodrigues. Les taux de recrutement et la composition taxonomique ont été examinés pendant trois périodes consécutives de six mois, de l'échelle régionale à l'échelle micro-locale (i.e. de plusieurs centaines de kilomètres à quelques centimètres) et entre deux niveaux de protection (zones interdites à la pêche et zones de protection générale).

De faibles taux de recrutement ont été observés. Rodrigues affichait des taux de recrutement inférieurs à ceux de La Réunion. L'assemblage des recrues était dominé par les Pocilloporidae (77,9 %), suivis des Acroporidae (9,9 %) et des Poritidae (5,2 %).

Aucun effet de la protection sur le recrutement corallien n'a été mis en évidence, malgré des différences de taux de recrutement entre sites au sein des îles. Les recrues étaient réparties en patchs à l'intérieur des sites, mais aucun effet agrégatif n'a été détecté, c'est-à-dire que les plaques préférentiellement colonisées n'étaient pas groupées spatialement. Les recrues se sont installées principalement sur les côtés des plaques, en particulier à Rodrigues, ce qui pourrait être dû aux concentrations importantes de matières en suspension. La variabilité des patrons de recrutement à différentes échelles spatiales souligne l'importance des variations de l'environnement, de l'échelle micro à l'échelle macro-locale, dans la dynamique et le maintien des populations coralliennes.

Une forte variabilité temporelle a également été détectée, entre les saisons et les années, pouvant être liée à l'événement de blanchissement corallien du début de 2016 à Rodrigues. Les faibles taux de recrutement et l'absence d'effet de protection soulèvent des questions quant au potentiel de récupération des récifs coralliens dans les îles des Mascareignes après perturbation.

Les résultats de ce chapitre ont fait l'objet d'une publication dans PLoS ONE en Mars 2019 : Jouval F, Latreille AC, Bureau S, Adjeroud M, Penin L (2019) Multiscale variability in coral recruitment in the Mascarene Islands: From centimetric to geographical scale. PLoS One 14:e0214163 (Annexe 1).

4.2. Article – Variabilité multi-échelles du recrutement corallien dans les Mascareignes

Title: Multiscale variability in coral recruitment in the Mascarene Islands: from centimetric to geographical scale.

Authors: Jouval, F.; Latreille, A. C.; Bureau, S.; Adjeroud, M. and Penin, L.

Keywords: Coral reefs; Scleractinian corals; Recruitment; Spatio-temporal variability; No-take zones; Mascarene Islands; Indian Ocean

4.2.1. Introduction

Coral recruitment processes, i.e. settlement of larvae and early post-settlement events occurring in the first weeks and months of benthic life largely shape coral reef community structure (Hughes et al. 1999), allowing maintenance and renewal of coral communities through replacement of dead adults (Harrison & Wallace 1990, Hughes et al. 2000). An essential component of reef resilience, recruitment largely influences reef recovery following mass mortalities induced by large-scale disturbances (Hughes et al. 1999, Golbuu et al. 2007, Graham et al. 2013). Coral recruitment success is thus necessary for coral reef recovery after disturbances, and recruitment failure is a known factor of phase shift (Hughes & Tanner 2000, Hughes et al. 2000).

Recruitment processes are governed by a variety of factors occurring at all spatial and temporal scales, from centimetres to hundreds of kilometres, and from seasons to decades. This creates spatio-temporal variability in measures of recruitment descriptors at all scales that have been investigated so far (Dunstan & Johnson 1998, Glassom et al. 2004, Green & Edmunds 2011, Sola et al. 2015, Chui & Ang 2017). Among factors that can be cited, recruitment depends upon spawning of adults, that is generally initiated by increasing sea temperature (Nozawa et al. 2006), moon phase (Guest et al. 2008) and wind fields (van Woesik 2010). Fertilization success and embryo survival are influenced by local environmental factors (Oliver & Babcock 1992, Heyward & Negri 2012). Larval dispersal is mainly driven by larval survival and pelagic larval duration, associated with oceanographic conditions experienced by larvae, like tidal or wind-driven currents (Harii

& Kayanne 2003). Larval settlement and survival depend on local (metric scale) and micro-local (centimetric scale) parameters such as the presence of biological inducers or competitors (Maida et al. 1995, Heyward & Negri 1999, Vermeij 2005, Vermeij et al. 2011), light (Babcock & Mundy 1996), sedimentation (Salinas-de-León et al. 2013) or herbivorous grazing (Penin et al. 2011). At large geographic scales, the biological and ecological processes that sustain coral communities may be affected by disturbances such as cyclones, bleaching events or outbreaks of the coral predator *Acanthaster planci* (De'ath et al. 2012, Kayal et al. 2012). Moreover, anthropogenic impacts interfere with recruitment processes at the local scale. For example, stressors such as pollution, eutrophication, sedimentation or overfishing have been linked to deleterious effects on coral recruitment (Hughes & Connell 1999, Birrell et al. 2005, Abelson et al. 2005, Chui & Ang 2017). In the present context of rising disturbance frequency and intensity, coral reefs will have to recover more often than in previous decades (Bellwood et al. 2004, Bruno & Selig 2007, Edmunds et al. 2014). It is thus of capital importance to better understand the relative importance of different scales in the spatial and temporal variation of recruitment, and where possible, the factors associated with these variations.

A growing body of literature describes spatio-temporal variability of coral recruitment. Even if long-term studies are scarce (but see Adjeroud et al. 2018), important year to year variation has been documented (Hughes et al. 1999, Adjeroud et al. 2007, 2018). Seasonal variation is also well established, with summer periods typically more favourable for coral settlement (Wallace 1985, Glassom et al. 2004, Adjeroud et al. 2007). Regarding spatial variability, regional variation appears to be important; six-fold differences were observed among reef regions on the Great Barrier Reef (GBR; Hughes et al. 1999), and five-fold differences reported among islands of the Society Archipelago (French Polynesia; Penin & Adjeroud 2013). Within a region or an island, at the scale of a few kilometres, some reefs or sites also typically receive more recruits than others, and these large-scale patterns seem to be consistent in time, among seasons and years (Fisk & Harriott 1990, Hughes et al. 1999, Adjeroud et al. 2007, Penin & Adjeroud 2013). At a much smaller scale, settlement and recruitment vary among micro-habitats as described by differences in recruitment rates among tile orientations (Fisk & Harriott 1990, Maida et al. 1994, Adjeroud et al. 2007). Between these two scales, local variation patterns, i.e. within-site variation, at the scale of the metre, and its consistency in time has rarely been

investigated (but see Luter et al. 2016). This overlooked scale of variation deserves better investigation since many biotic and abiotic factors like competition, predation, light or hydrodynamic conditions vary greatly at this scale (e.g. Maida et al. 1994, Baird & Hughes 2000, Birrell et al. 2005, Penin et al. 2011).

In recent decades, management tools, such as marine protected areas (MPAs), have been developed around the world to limit the anthropogenic impacts on the marine environment. In general, these MPAs delimit different areas in which certain activities, and fishing in particular, are allowed or prohibited (Edgar et al. 2007). While fishing bans generally improve fish biomass and diversity when enforced (Halpern 2003, Lester et al. 2009), their effects on coral abundance, while generally positive, are more tenuous (Selig & Bruno 2010, Graham et al. 2011). Mechanisms involved in positive effects on corals include lower damage from fishing gear (Baird et al. 2005) and higher rates of herbivory, tipping the coral-algal competition balance towards coral success (Lester et al. 2009). Increases in coral recruitment rates can be expected in this context of lower competition with turf and macroalgae, which are known to limit settlement and survivorship (Kuffner & Paul 2004, Birrell et al. 2005, Kuffner et al. 2006, Arnold et al. 2010). In contrast, higher herbivorous fish biomass in MPAs can be linked with higher incidental predation of early stage corals by herbivores (Penin et al. 2010), but see Mumby (2009). While some studies have compared recruitment rates inside and outside MPAs (e.g. Mangubhai et al. 2007, Sola et al. 2015, Machendiranathan et al. 2017, Chui & Ang 2017), few have concluded a positive effect of MPAs on coral recruitment (but see Mumby et al. 2007).

The present study aims to evaluate (i) the temporal variability of coral recruitment at interannual and seasonal scales, as well as the spatial variation of coral recruitment between two islands of the Mascarene Archipelago (hundreds of kms), among sites of each island (km), among tiles within sites (m), and within settlement tiles (cm); as well as (ii) the effects of MPA status (fishing ban) on coral recruitment. Recruitment rates and taxonomic composition were thus examined during three consecutive six-month periods at regional (between two islands, Reunion and Rodrigues), island (between four sites at each island), local (between 20 artificial settlement tiles at each site) and micro-local levels through the orientation of recruits on artificial settlement tiles. The variation of recruitment rates and composition were also examined within and outside no-take zones (NTZs) at both Reunion and Rodrigues reefs.

4.2.2. Material and methods

4.2.2.1. Ethics statements

Fieldwork was conducted within the Réserve Naturelle Marine de La Réunion (MPA) at Reunion, under research authorization N°2014-27 DEAL/SEB/UBIO, and within South East Marine Protected Area at Rodrigues, under Rodrigues Regional Assembly research authorization N°RA 402/17 Vol II.

4.2.2.2. Study sites

Reunion and Rodrigues islands are part of the Mascarene Islands, along with Mauritius, in the South-Western Indian Ocean (SWIO). Reunion (21° 07' S, 55° 32' E), one of the overseas French territories, is a volcanic island (ca. 70 km long and 50 km wide) located 700 km east of Madagascar. Fringing reefs line the island in a 12 km^2 area along 25 km of coastline on its west and south coasts (Camoin et al. 1997). Rodrigues (19° 43' S, 63° 25' E) is a small isolated island that is part of the Republic of Mauritius (18.3 km long and 6.5 km wide), and is the easternmost of the Mascarene Islands. It is surrounded by an almost continuous 90 km long reef rim and constitutes a reef area of ca. 200 km^2 (Rees et al. 2005). Deleterious effects of coral bleaching are growing stronger over the decades in the Mascarene Islands (see Hardman et al. 2007 at Rodrigues). Reunion and Rodrigues reefs are not immune to other anthropogenic stress either. Increased urbanisation of the Reunion coastline during the last decades drove noticeable eutrophication in the reef environment (Naim 1993) and a decrease in reef fish stocks in some areas (Chabanet et al. 1995). These phenomena have led to an increase in the relative cover of algae compared to corals (Naim 1993, Chazottes et al. 2002, Naim, Tourrand, Ballesteros, et al. 2013). Consequently, a multiple-use MPA (Réserve Naturelle Marine de La Réunion) was set up in 2007 to address the deterioration of reefs. This MPA, covering an area of over 35 km^2, is divided into three levels of protection: open areas for human activities (general protection zones or GPZs), restricted areas where only some traditional and commercial fishing activities are allowed, and sanctuaries where no activity is allowed, thus corresponding to NTZs (Figure 19).

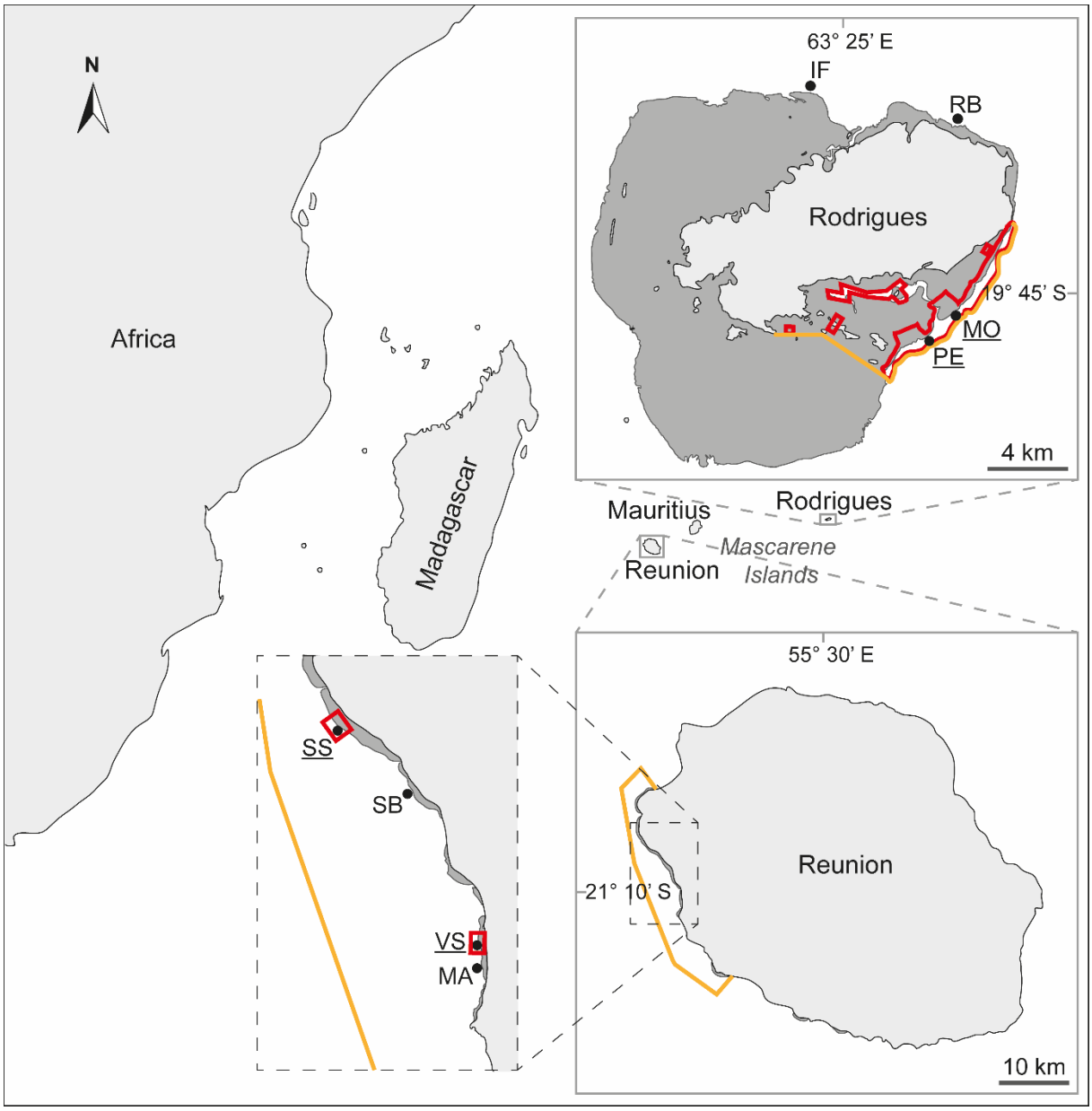

Figure 19. Location of the sampling sites (black dots) on Reunion and Rodrigues reefs. Light grey: land; dark grey: reef flat; orange: MPAs boundaries; red: NTZs boundaries. Underlined sampling sites belong to NTZs. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine; IF: Ile aux Fous; RB: Rivière Banane; MO: Mourouk; PE: Port Sud-Est.

Human pressure is less documented for the Rodrigues reef. In response to overfishing 10 years ago, the local government of Rodrigues implemented four MPAs to the north of the island, but only partial management has been set up and fishing still occurs in these areas (Hardman et al. 2010, Pasnin et al. 2016). In addition, the South East Marine Protected Area (SEMPA) is an area in the south-eastern of Rodrigues designated as an MPA in 2009. It includes both inner and outer lagoon covering a total 43.7 km^2 divided into different multiple-use zones, including NTZs where fishing is prohibited (Figure 19).

4.2.2.3. Sampling strategy

The sampling strategy used four sites on the outer reef slopes at both Reunion and Rodrigues islands, including two sites within a NTZ and two sites outside NTZ for each island (Figure 19). Eight sites were thus sampled and coded as follows: Reunion (SS: Sanctuaire Sud and VS: Varangue Sud in the NTZ; SB: Souris Blanche and MA: Marine in GPZs); Rodrigues (MO: Mourouk and PE: Port Sud-Est in the NTZ; IF: Ile aux Fous and RB: Rivière Banane in GPZs). At all sites, the abundance and taxonomic composition of coral recruits was characterised at 12 m depth on unglazed terracotta settlement tiles (Harriott & Fisk 1987, Mundy 2000, Edmunds et al. 2010, Lukoschek et al. 2013, Hsu et al. 2014). For each site, 20 individual tiles (ca. 10 × 10 × 2 cm) were immersed for six months over two austral summer periods (October 2015–March 2016, October 2016–March 2017) and one winter period (April–September 2016). Tiles were deployed and spatially referenced within each site at Reunion by measuring distances and azimuth between each tile and a reference point. Typical distance between two consecutive tiles was 1-2 m, while most distant tiles were around 15 to 20 m apart from each other. At the end of the immersion periods, the tiles were retrieved, bleached and sun dried to expose the skeleton of coral recruits (coral spats) for identification and counting under a dissecting microscope. Recruits of the families Acroporidae, Pocilloporidae and Poritidae were discriminated according to morphological traits (Babcock et al. 2003). Other recruits were assigned to the category 'others' if not associated with one of the previously cited families, or to the category 'broken' when the skeleton was too damaged for identification (Adjeroud et al. 2007).

4.2.2.4. Data analyses

In all the analyses described hereafter, abundance of recruits counted per tile was expressed as recruitment rate per m^2 (recruits m^{-2}). Spatio-temporal variation of overall recruitment rates (all taxa combined) was evaluated at three different spatial scales: between islands, between protection levels (i.e. within NTZ or outside MPA), and between sites, for three periods (two summers and one winter) using an ANOVA model (eq. 2).

$$T_{ijkl} = m + I_i + Pr_j + S_k + \mathrm{Pe}_l + (IPe)_{il} + (PrPe)_{jl} + \varepsilon_{ijkl} \quad (eq\ 2)$$

where *i*, *j*, *k* and *l* stand for the island, the protection levels, the sites and the periods, respectively, and ε is the residual variance (within sites). The spatial factors correspond to a three-level nested design with protection levels within islands and sites within protection levels. Sites were considered as a random factor. Prior to analyses, normality and homogeneity of the variance of the data set were tested using Shapiro-Wilk and Bartlett tests, respectively. Recruitment rate variable was log(x+1) transformed to meet the assumptions of normality. To analyse differences between levels of the significant factors, Student Pairwise t-tests (SPT) were used.

Spatio-temporal variation of the taxonomic composition was also evaluated at the three different spatial scales (between islands, between protection levels and between sites) for three periods using Chi-squared tests or Fisher's exact test when assumptions for Chi-squared test were not met.

The spatial variation of coral recruitment between tiles was determined by evaluating the effect of geographical distance between pairs of tiles using a Mantel test. These tests will be referred to as Mantel 1 for overall recruitment rates and Mantel 2 for taxonomic composition. Temporal variations of overall recruitment rates were then tested using a Spearman rank correlation test to compare the overall recruitment rates between all period pairs, for each site.

Spatio-temporal variation of recruitment within tiles was assessed by comparing the orientation of recruits over the different surfaces of the tiles (upper, sides and lower) between islands, protection levels and periods independently for four taxonomic categories (Acroporidae, Pocilloporidae, Poritidae and other families) using Chi-squared tests or Fisher's exact test when assumptions for Chi-squared test were not met.

4.2.3. Results

4.2.3.1. Spatio-temporal variations of recruitment rates

Recruitment rates ranged from 48 to 150 recruits m^{-2} during the first summer (October 2015–March 2016) at Reunion while fewer than 7 recruits m^{-2} were recorded over the same period at Rodrigues (Figure 20). Over the following summer (October 2016–March 2017), recruitment rates were slightly lower at Reunion (20–

98 recruits m^{-2}) compared to the previous summer, while they were higher than observed the year before at Rodrigues, reaching 11–40 recruits m^{-2}. During the winter (April–September 2016), recruitment rates were extremely low, with fewer than 11 recruits m^{-2} recorded at Reunion and no recruits at all at Rodrigues.

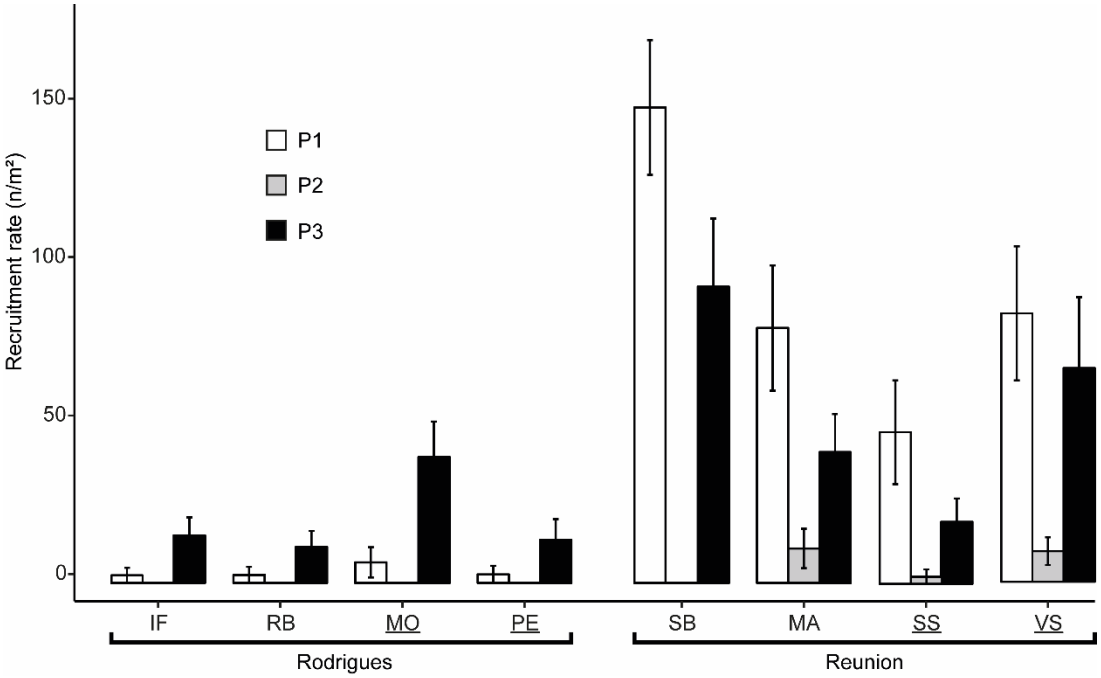

Figure 20. Recruitment rates observed during three consecutive 6-month periods on artificial settlement tiles at 12 m depth among reef slope sites on Rodrigues and Reunion reefs (recruits m^{-2} ± SE). P1: period 1, i.e. summer 2015–2016 (October 2015–March 2016); P2: winter 2016 (April–September 2016); P3: summer 2016–2017 (October 2016–March 2017). NTZs are underlined. No recruits were observed at Rodrigues (at any site) or at SB site during winter 2016. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine; IF: Ile aux Fous; RB: Rivière Banane; MO: Mourouk; PE: Port Sud-Est.

Recruitment rates (all taxa pooled) varied significantly between islands (ANOVA, $P < 0.0001$; Table 3) and among periods (ANOVA, $P < 0.0001$; Table 3). Moreover, the island × period interaction was significant (ANOVA, $P < 0.0001$; Table 3). These differences between periods were mainly due to recruitment variation between both summers and the winter (SPT, $P < 0.0001$; Figure 20), while there were no significant differences between the two summers (SPT, $P > 0.05$; Figure 20). Also, recruitment rates were slightly higher in the NTZ in Rodrigues compared to the GPZ, while it was the contrary at Reunion (Figure 20). Nevertheless, effects of protection level or

protection × period interaction on recruitment rates were not significant (ANOVA, $P > 0.05$; Table 3).

Table 3. ANOVA table of the analyses of spatio-temporal variations of coral recruitment rates. Df: degrees of freedom; F: F-statistic.

Factor	***Df***	***Mean Square***	***F***	***P-value***
Island	1	90.378	75.9253	2.20E-16
Protection (within Island)	2	5.153	4.3292	0.67
Site (within Protection)	4	5.864	4.926	5.92E-04
Period	2	48.318	40.5911	2.20E-16
Island x Period	2	26.175	21.9896	3.50E-10
Protection (within Island) x Period	4	2.046	1.719	0.14
Residuals	2204	1.19		

A significant inter-site variability of recruitment rates was recorded (ANOVA, $P < 0.001$; Table 3). While no differences were found between Rodrigues sites, post-hoc tests revealed significant differences between each pair of Reunion sites except between MA and VS, and MA and SS (SPT, $0.0001 < P < 0.05$; Figure 20).

Moreover, an important variability of recruitment rates among individual tiles was observed within each site at Reunion, whatever the protection level (Figure 21). However, no aggregative effects were highlighted among groups of tiles; the geographical distances between tiles were not related to recruitment rates observed on tiles (Mantel 1, $P > 0.05$; Figure 21). From a temporal point of view, there was no relationship in recruitment rates on individual tiles within each site between the two summers (2015–2016 and 2016–2017; Spearman rank tests, $P > 0.05$; Figure 21). This means highest recruitment rates were not observed on the same tile spots over the two consecutive summers.

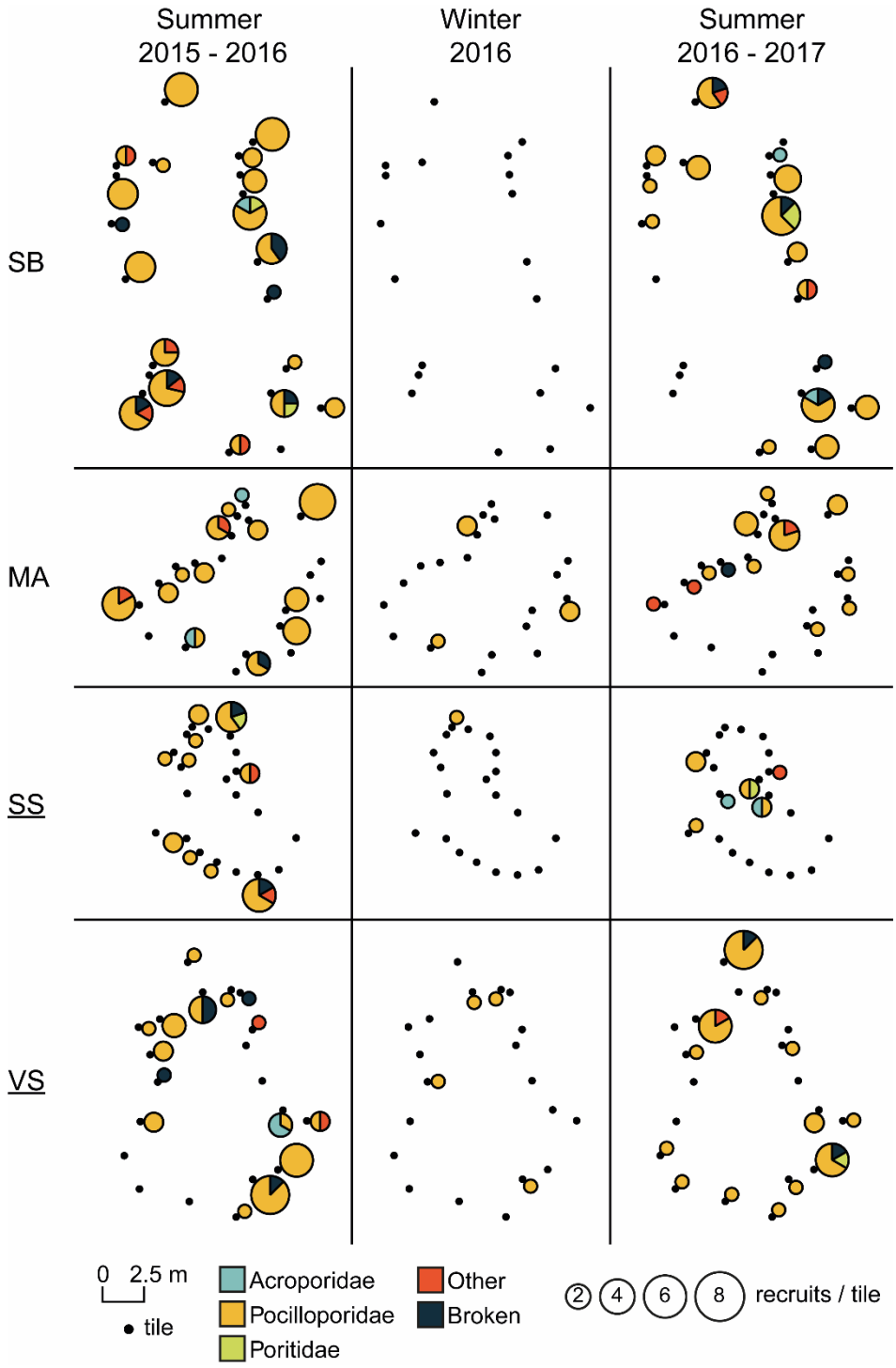

Figure 21. Spatio-temporal variations of number and composition of recruits observed on settlement tiles as they were arranged on the field. Data presented for the four sites at 12 m depth at Reunion, for the three studied periods. Size of pie chart is proportional to numbers of recruits. NTZs sites are underlined. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine.

4.2.3.2. Spatio-temporal variations of taxonomic composition

The relative contribution of the different families varied significantly between islands (Chi-squared test, $P < 0.0001$; Figure 22). During the two summers, a large

dominance of Pocilloporidae (86% on average) was observed at Reunion (Figure 22). At Rodrigues, a shift of the dominant family between summers was noted. Poritidae recruits dominated the first summer (October 2015–March 2016, 80%) while Acroporidae recruits dominated the second summer (October 2016–March 2017; 69%). Consistently, taxonomic composition only varied significantly between the two summers at Rodrigues (Fisher's exact test, $P < 0.04$; Figure 22) and not at Reunion (Fisher's exact test, $P > 0.05$). During the winter, all recruits recorded at Reunion (n = 10) belonged to the Pocilloporidae family.

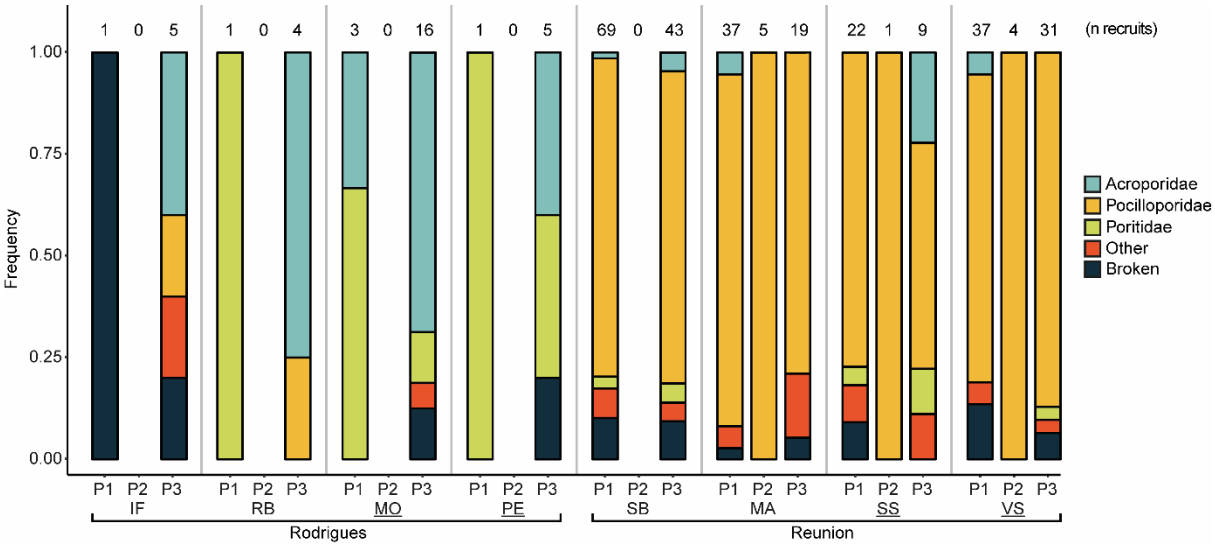

Figure 22. Taxonomic composition of coral recruits observed on artificial settlement tiles at 12 m depth among reef slope sites on Rodrigues and Reunion reefs. P1: period 1, i.e. summer 2015–2016 (October 2015–March 2016); P2: winter 2016 (April–September 2016); P3: summer 2016–2017 (October 2016–March 2017). NTZs sites are underlined. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine; IF: Ile aux Fous; RB: Rivière Banane; MO: Mourouk; PE: Port Sud-Est.

At both islands, taxonomic composition did not differ significantly between NTZs and GPZs (Fisher's exact tests, $P > 0.05$; Figure 22). Moreover, no difference of taxonomic composition was observed for each pair of sites within both islands (Fisher's exact tests, $P > 0.05$; Figure 22).

As with recruitment rates, taxonomic composition was not related to the relative position of tiles within sites (Mantel 2, $P > 0.05$; Figure 21), implying that tiles close to each other did not display more similar relative proportions of taxa than distant ones.

4.2.3.3. Spatio-temporal variations of the orientation of recruits

Orientation of recruits on tiles varied significantly between islands (Fisher's exact test, $P < 0.01$). At Rodrigues, recruits settled mainly on the sides of the tiles, to a lesser extent on the upper side and never on the lower surfaces where light availability was the lowest. At Reunion, recruitment was more evenly distributed, although recruitment rates were higher on the sides of the tiles than on other orientations. The orientation of recruits on tiles was not influenced by the protection level nor by the time period for both islands (Fisher's exact tests, $P > 0.05$).

4.2.4. Discussion

4.2.4.1. Abundance of recruits

The present study is the first published on coral recruitment within the Mascarene Islands. Results reveal that overall recruitment rates measured on outer reef slopes at Reunion and Rodrigues islands from 2015 to 2017 were low, not exceeding 150 recruits m^{-2} at Reunion and 40 recruits m^{-2} at Rodrigues, during the summer. When compared to other reefs in the SWIO, recruitment rates from the present study were much lower than those on the Nyali reef in Kenya (908 recruits m^{-2} y^{-1}; Mangubhai et al. 2007), along the coast of South Africa (1000 recruits m^{-2} during peak settlement; Glassom et al. 2006), or on the reefs of Vamizi island in Mozambique (1130 recruits m^{-2} y^{-1}; Sola et al. 2015). However, the recruitment rates at Reunion and Rodrigues islands were similar to those recorded at Coral Gardens in Kenya (101 recruits m^{-2} y^{-1}; Mangubhai et al. 2007). Recruitment rates observed in this study were also comparable to levels observed in Moorea, French Polynesia (Gleason 1996, Adjeroud et al. 2007, Edmunds et al. 2010) and in some locations of the Red Sea (Glassom et al. 2004). Even if artificial settlement tiles have been commonly used as a standardised assay of coral recruitment, the comparison

of coral recruitment on artificial materials is challenging, due to varying methodology, as noted by Edmunds (2017).

4.2.4.2. Variations of recruitment through protection level

Contrary to what was expected, no significant differences in recruitment rates were found between the NTZs and GPZs. Preservation of fish stocks by NTZ implementation is known to foster herbivore communities and consequently to promote recovery potential and thus resilience of coral reefs (West & Salm 2003, Hughes 2003, Mumby & Harborne 2010). Indeed, herbivory is one of the major factors controlling algal development, which inhibits coral recruitment through competition for space and smothering of recruits by trapped sediments (Birrell, McCook, Willis, & Harrington 2008). However, herbivorous grazers, like fish and urchins, can also exert incidental predation on young coral stages (Hughes et al. 2007, Birrell, McCook, Willis, & Diaz-Pulido 2008, Christiansen et al. 2009, Penin et al. 2011). Overall, most authors consider increasing herbivory as beneficial for coral recruitment (see reviews by Graham et al. 2011, Adjeroud et al. 2017).

Lack of protection effect on coral recruitment rates in the studied locations may have several causes. The NTZs of both Reunion and Rodrigues islands were set up less than 10 years ago and the direct role of fishing pressure reduction on coral recruitment might not be effective yet. Absence of positive effects on the coral communities in recently protected areas has been previously highlighted (McClanahan et al. 2008, Huntington et al. 2011). In addition, Graham et al. (Graham et al. 2011) noted that spatial differences in recruitment rates may not necessarily align with NTZs placement and therefore, even if NTZs are effective at enhancing coral cover, this would not necessarily translate into higher local recruitment. These results support the idea that coral recruitment is sensitive mainly to large-scale disturbances whose deleterious effects cannot be directly mitigated by the establishment of a NTZ. In this context, it may be worthwhile to investigate the benefits of placing NTZs in areas of high recruitment, as they are more likely to recover from disturbances than areas with low recruitment rates.

4.2.4.3. Spatial variability of recruitment

We found significant differences in recruitment rates among Reunion sites while both recruitment rates and taxonomic composition were similar in all sites at Rodrigues.

This was surprising as sites at Reunion were all facing west, but sites at Rodrigues faced south-east and north. Thus, differences in recruitment rates could not be attributed to site configuration alone. At Rodrigues, the similarity in taxonomic composition may be mainly due to the low number of recruits.

Rodrigues is a very small and isolated island (about 600 km eastward from Mauritius and several thousand kilometres away from the land towards the other cardinal points). Reefs of the Mascarene Islands are under the influence of the South Equatorial Current (SEC) flowing east to west. Larval dispersal simulations highlighted connections within the Mascarene Islands from Rodrigues to Reunion (Crochelet et al. 2013, 2016). This is consistent with some recent genetic studies conducted on *Pocillopora damicornis* type beta (Pocilloporidae) in the SWIO highlighting that unidirectional gene flows occur, even if limited, from east to west (Gélin et al. 2018). Moreover, Gélin et al. (2017) showed that populations of *P. damicornis* type beta from the south of Reunion were genetically differentiated from those located in the north and the west of the island. The authors attributed this genetic isolation to a particular connection between the southern reefs of Reunion and Mauritius or Rodrigues reefs through the SEC. However, it was also suggested that the complex currents occurring along the west coast of Reunion might prevent non-local larvae from reaching the western reef, and instead only retain local larvae (Gélin et al. 2017). Thus, it could be interesting to (i) add sites on the south coast of Reunion to determine whether recruitment rates and taxonomic composition are closer to those observed at Rodrigues and (ii) to combine recruitment and genetic analyses to determine the origin of the recruits and to better understand gene flow occurring among the Mascarene Islands.

Among the different settlement tiles of each site, recruitment rates and taxonomic composition varied greatly, reflecting a patchy distribution, as previously observed in French Polynesia (Adjeroud et al. 2007) and on the GBR (Trapon et al. 2013). This variability has also been observed in the structure of adult and juvenile corals in many reefs (e.g. Ruiz-Zárate & Arias-González 2004, Penin et al. 2007), and is likely to be related to the strong environmental heterogeneity encountered at small scales in reef ecosystems (Adjeroud et al. 2010) and induced by different factors, such as local-scale hydrodynamic regimes (Bode et al. 2006), disturbance history (Connell et al. 1997) or predation (Penin et al. 2010). However, no aggregative effect was revealed among spatial groups of tiles

when tested within sites at Reunion. This means that tiles with high numbers of recruits were not located in the same area of the site, or particularly close to each other. In parallel, tiles close to each other did not display more similar relative proportions of taxa than distant ones. In terms of methodology, this shows that spatial variability at the scale of the site is correctly sampled. At the same spatial scale, highest recruitment rates were not observed on the same tile spots over the two consecutive summers, suggesting that processes responsible for spatial variation at this scale are not spatially consistent among years.

Within tiles, higher recruitment rates were found on the sides of the tiles deployed both at Reunion and Rodrigues islands, compared to the upper and lower surfaces. These observations were especially true at Rodrigues, where recruits rarely settled on the upper and lower faces of tiles. This may be linked to the higher concentration of suspended matter at Rodrigues than at Reunion (Jouval, pers. obs.). Indeed, this could (i) increase sedimentation on the upper surface of tiles, preventing the recruits from settling on this face and (ii) limit light penetration through the water column, which can prevent recruits from settling on the shady (lower) surface of the tiles. The effects of sedimentation and light availability on coral larvae settlement are often invoked as factors influencing the position of recruits over tiles (Maida et al. 1994, Nozawa et al. 2011, Chui & Ang 2017). The very weak presence of Pocilloporidae recruits on the upper faces of tiles, while being the most represented recruits in our study, illustrates their sensitivity to sedimentation, as previously observed (Price 2010). The low proportion of recruits found on the upper surfaces of the tiles at both islands may also be a consequence of grazing by herbivorous fish and/or urchins (Gleason 1996, Adjeroud et al. 2007). Larval sensitivity to high-intensity light highlighted by other studies (e.g. Wellington & Fitt 2003, Suzuki et al. 2008) is unlikely to have inhibited settlement of recruits on upper surfaces of the tiles in our study because of the depth of immersion of the tiles.

4.2.4.4. Temporal variability of recruitment

At each spatial scale, from regional (between islands) to micro-local (within tiles), a strong period effect was highlighted both on recruitment rates and taxonomic composition, linked to the very low recruitment rates during the winter (April–September 2016), with only Pocilloporidae recruits at Reunion and the complete absence of recruits

at Rodrigues. These results were consistent with observations made in the Indo-Pacific, where larval settlement is highly seasonal (e.g. reviewed in Guest et al. 2005, Adjeroud et al. 2007 in French Polynesia, Baird et al. 2009 on the Great Barrier Reef). The dominance of Pocilloporidae recruits on Reunion reefs was consistent with many observations across tropical and sub-tropical reefs of the Indo-Pacific (Glassom et al. 2006, Adjeroud et al. 2007, Mangubhai et al. 2007, Penin et al. 2010, Bauman et al. 2015). The presence of some Pocilloporidae recruits during the winter at Reunion may have resulted from local asexual reproduction of adult colonies, already documented for this family, by polyp bail-out (*Seriatopora hystrix*, Sammarco 1982) or by the production of parthenogenetic larvae (*Pocillopora damicornis*, Combosch & Vollmer 2013). In particular, at Reunion, Gélin et al. (2017) suggested that the lagoonal species *P. damicornis* produces parthenogenetic larvae, but information is lacking for other Pocilloporidae species present on reef slopes. During the two summers (October to March), recruitment rates were higher and the taxonomic composition more diversified compared to the winter (April to September). On Rodrigues reef, recruits of Poritidae were dominant in the first summer, but Acroporidae recruits were highest in the second, while recruitment rates were slightly higher. The first summer studied corresponded to the massive bleaching event of 2016 that affected coral communities of Reunion and Rodrigues islands, thus potentially modifying coral recruitment rates and taxonomic composition. Indeed, numerous studies have revealed that adults of the Acroporidae family are among the most susceptible to bleaching events (Brown & Suharsono 1990, Gleason & Wellington 1993, Edwards et al. 2001). The 2016 coral bleaching greatly affected adults of Acroporidae species, especially *Acropora abrotanoides*, which was dominant in some sites at Rodrigues, leading to the death of the majority of them (Jouval, pers. obs.). Since recruitment at Rodrigues is likely to rely mainly on local coral populations, based on the observations about connectivity and currents, this could explain the greater representation of Poritidae recruits in the year of bleaching in Rodrigues. Nevertheless, these observations are related to an overall very low number of recruits at Rodrigues, and thus need to be considered with caution. On the tiles, the highest or lowest recruitment rates were not detected on the same tile from one period to the next. Spatial patterns of variation of recruitment rates within sites were not consistent over the three consecutive periods studied.

4.2.5. Conclusions

Our results demonstrate that recruitment rates were low in the Mascarene Islands, especially at Rodrigues. Recruitment patterns varied greatly at several spatial scales: between islands, and between and within tiles. To a lesser extent, recruitment rates also varied between sites only at Reunion. Both recruitment rates and taxonomic composition displayed great seasonal variation, with very low recruitment rates during the winter. These observations suggested the importance of studying a minimum number of sites, each represented by several replicates (i.e. tiles), to correctly assess the spatio-temporal variability of recruitment patterns between or within reefs. The spatio-temporal variations of recruitment patterns described here have direct implications in terms of conservation, showing that some sites present higher overall recruitment rates, potentially giving these sites a higher capacity for recovery following disturbances. Our study did not highlight any effect of protection on coral recruitment. With low recruitment rates, versatile taxonomic composition over time, and high concentration of suspended matter, Rodrigues appears to be particularly vulnerable to large-scale disturbances.

ACKNOWLEDGMENTS

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CHAPITRE 5.
ÉVALUATION DU POTENTIEL DE RÉCUPERATION DES RÉCIFS CORALLIENS DANS LE SUD-OUEST DE L'OCÉAN INDIEN

5.1. Synthèse

Les récifs coralliens font vivre des centaines de millions de personnes, mais depuis plusieurs décennies, ces écosystèmes connaissent une augmentation significative de la fréquence et de l'intensité des perturbations qui les frappent, qu'elles soient d'origine naturelle (e.g. cyclones, blanchissement corallien) ou anthropique (e.g. pollution, surpêche). Ces perturbations, associées aux effets du changement climatique qui modifie les conditions de vie des organismes récifaux, entraînent une accélération de la dégradation de l'habitat et une diminution de la résilience des récifs.

Dans ce contexte, la gestion des récifs coralliens peut être améliorée en se concentrant sur leurs capacités de résilience. La mesure d'indicateurs de résilience, combinée à des informations relatives aux stress anthropiques subis et à la connectivité permettent d'identifier des cibles de management et des actions de conservation adaptées. Le développement d'indices de résilience basés sur des indicateurs clés constitue une approche utile pour synthétiser l'information collectée sur les récifs et, par conséquent, simplifier la prise de décision des gestionnaires. Ce type d'indice synthétique a été développé par le passé pour traiter de l'état de santé des récifs mais rarement pour évaluer leur potentiel de récupération.

L'objectif de ce chapitre était de développer un indice de récupération multi-facteurs (*RI*) basé sur des indicateurs clés : diversité corallienne, recouvrement corallien, proportion de recouvrement corallien par des espèces tolérantes aux stress, recouvrement algal, biomasse en poissons herbivores, anomalies de températures de surfaces des eaux et recrutement corallien (uniquement à La Réunion et Rodrigues où des données étaient disponibles, cf. chapitres 3 et 4). Le but de cet indice était de classer les récifs de cinq îles du sud-ouest de l'océan Indien (SOOI) en fonction de leur potentiel de récupération : Europa et Glorieuses (Canal du Mozambique), Mayotte (archipel des Comores), La Réunion et Rodrigues (archipel des Mascareignes). Pour cela, la méthode TOPSIS (Technique for Order Preferences by Similarity to an Ideal Solution), utilisée dans de nombreux domaines de recherches tels que la logistique, l'ingénierie, le marketing ou encore l'énergie ou la chimie a été adaptée aux problématiques d'écologie et de conservation des écosystèmes récifaux. Cette méthode consiste à comparer des

alternatives (dans notre cas, des sites) à la meilleure et à la pire des alternatives possibles (*IS* pour *Ideal Solutions*).

Les résultats de cette approche ont révélé que l'île d'Europa avait le meilleur potentiel de récupération quel que soit le site considéré. Les potentiels de récupération les plus faibles ont été estimés dans les Mascareignes, bien que les *RI* soient très variables d'un site à l'autre. Ces données sont cohérentes avec les observations passées de la récupération des récifs étudiés suite à des perturbations de type blanchissement corallien ou cyclone. Elles sont également cohérentes avec les niveaux d'anthropisation des îles étudiées : de manière générale, plus la pression humaine est importante et plus les indices de récupération sont faibles. L'ajout des taux de recrutement dans le calcul des *RI* pour La Réunion et Rodrigues modifie nettement le classement : les sites ayant les plus forts taux de recrutement sont également les mieux classés en termes de potentiel de récupération. Les résultats de cette étude suggèrent également qu'il est nécessaire de faire varier légèrement les *IS* pour optimiser les estimations du potentiel de récupération. En effet, les conditions optimales n'étant pas les mêmes pour tous les récifs, limiter la comparaison des sites à la meilleure et la pire des situations peut entrainer un biais dans l'estimation du potentiel de récupération.

Cette étude a permis de développer un indice de récupération des récifs à la fois simple à mettre en place et adaptable. Bien qu'il ne soit pas complétement optimisé, il donne des résultats prometteurs et pourrait s'avérer un outil utile à la gestion basée sur la résilience (RBM). L'un des principaux risques était de proposer un indice qui ne traduise pas le potentiel de récupération des récifs mais plutôt leur état de santé, ce qui n'est pas le cas dans la mesure où le potentiel de récupération de récifs considérés en mauvaise santé a été estimé élevé. Pour optimiser cet indice et évaluer pleinement son potentiel, il serait bien sûr nécessaire de continuer à suivre les récifs des cinq îles et de comparer les *RI*s estimés avec les réponses observées sur le terrain, à la lumière des perturbations subies.

Le chapitre présenté sous cette forme est le résultat de mes travaux personnels mais sera soumis à terme pour publication dans un journal pour le moment non déterminé après relecture et validation par les futurs co-auteurs.

5.2. Reef recovery potential assessment using the TOPSIS method in the South-Western Indian Ocean

5.2.1. Introduction

Coral reefs are supporting the livelihoods of hundreds of millions of people (Cinner 2014) but for several decades, these ecosystems have experienced a significant increase in the frequency and intensity of disturbances (IPCC 2013, Hughes, Anderson, et al. 2018). From local to global-scale, anthropogenic impacts such as ocean warming, pollution, destructive fishing techniques or overfishing threaten the survival of coral reefs (Burke et al. 2011, Bozec & Mumby 2014), and are also likely to interact with natural disturbances, amplifying their negative consequences for reefs (Hughes 1994, Aronson & Precht 2001, Knutson et al. 2010, Fabricius et al. 2010). These disturbances, associated to the effects of climate change that alter the living conditions of reef organisms, lead to an acceleration of habitat degradation and a decrease of reef resilience (Hughes 2003, Bellwood et al. 2004, Bruno & Selig 2007, Hoegh-Guldberg et al. 2007, Bozec et al. 2015, Hughes, Kerry, et al. 2018).

Holling (1973) defined the resilience as “a measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables”. Since then, this concept has evolved to define the ability of an ecosystem to maintain or return to its original state after facing disturbances via two components: resistance, which is the capacity of an ecosystem to absorb stressors without changing its functional state, and recovery, which is the ability of an ecosystem to return to its initial state after being modified (Nyström et al. 2008, McClanahan et al. 2012).

In this era of growing pressures, the management of coral reefs can be enhanced by focusing on their resilience capacities (Anthony et al. 2015). Indeed, Mcleod et al. (2019) defined the resilience-based management (RBM) as “using knowledge of current and future drivers influencing ecosystem function (e.g., coral disease outbreak, changes in land-use, trade, or fishing practices) to prioritize, implement, and adapt management actions that sustain ecosystems and human well-being”. Thus, RBM is partly based on the

analysis of the spatial variation of the resilience potential of reefs in order to continuously adapt management and conservation actions.

The measurement of resilience indicators, combined with information on anthropogenic stress and connectivity, allows the identification of specific management targets and associated conservation actions (Maynard et al. 2015). These resilience indicators are biological, physical or chemical metrics from biotic and/or abiotic factors, acting from the community to the cell scales (Hédouin & Berteaux-Lecellier 2014) and that affect the living conditions of reef organisms (Fujita et al. 2013). Among those indicators, coral recruitment, coral diversity, abundance of resistant coral species, macroalgae abundance, herbivore biomass, coral diseases, human physical impacts, fishing pressure, sedimentation, pollution and temperature variability were identified as being of major importance (McClanahan et al. 2012).

The development of a resilience index (or indices) based on key indicators is a useful approach to synthesize the information collected on reefs and thus facilitate decision-making by reef managers. Synthetic indices have been developed for several years to address the health or condition status of reef organisms (Ben-Tzvi et al. 2004, Kaufman et al. 2011, Lasagna et al. 2014) but few were designed to assess the resilience potential of reefs (but see Maynard et al. 2010) using a sufficient number of ecological indicators.

In this context, our objective is to develop a multi-factor reef resilience index based on indicators related to reef recovery: coral diversity, coral density, coral cover, stress tolerant coral species cover, algal cover, herbivorous fish biomass, water temperature anomalies. The purpose of this index is to classify reefs according to their recovery potential. Thus, we consider reef recovery potential as a multi-criteria decision-making problem using resilience indicators as criteria. To solve this problem, we use the TOPSIS method (Technique for Order Preference by Similarity to an Ideal Solution; Hwang & Yoon 1981). TOPSIS has the advantage of being based on simple calculations, and therefore usable by a large number of people and has been extensively used since the beginning of the 21st century in various fields of research such as logistics, engineering, marketing, human resources, human health, or even energy, chemistry or water resources (reviewed by Behzadian et al. 2012). This method has also been experimented in the field of ecology and conservation of reef environments by Parravicini et al. (2014) who used the TOPSIS

method to assess the taxonomic and functional vulnerability of fish assemblages in tropical reefs.

We therefore apply the TOPSIS method to assess the recovery potential of reefs experiencing various degrees of pressure in the South-Western Indian Ocean (SWIO) region: Europa, Glorieuses and Mayotte in the Mozambique Channel, Reunion and Rodrigues islands in the Mascarene archipelago. The following questions were addressed: (i) are the different steps of the TOPSIS method adaptable to assess reef recovery potential? (ii) are the results of TOPSIS analyses consistent with the background knowledge about SWIO reef recovery?

The results of this study will also contribute to improving knowledge of the recovery potential of SWIO reefs and consequently to improving reef management programs.

5.2.2. Material and Methods

5.2.2.1. Study sites

The present study concerns several sites in the SWIO: Rodrigues and Reunion islands in the Mascarene Archipelago, Mayotte in the Comoro Archipelago and the Scattered Islands Glorieuses and Europa in the Mozambique Channel (Figure 23).

Reunion and Rodrigues islands are part of the Mascarene Islands, along with Mauritius. Reunion Island (21° 07’ S, 55° 32’ E), one of the overseas French territories, is a volcanic island (ca. 70 km long and 50 km wide) located 700 km east of Madagascar. Fringing reefs line the island in a 12 km^2 area along 25 km of coastline on its west and south coasts (Montaggioni & Faure 1980, Camoin et al. 1997). Rodrigues (19° 43’ S, 63° 25’ E) is a small isolated island that is part of the Republic of Mauritius (18.3 km long and 6.5 km wide), and is the easternmost of the Mascarene Islands. It is surrounded by an almost continuous reef rim of 90 km long and constitutes a reef area of ca. 200 km^2 (Montaggioni & Faure 1980, Rees et al. 2005). Deleterious effects of coral bleaching are growing stronger over the decades in the Mascarene Islands (see Hardman et al. 2007 at Rodrigues). Reunion and Rodrigues reefs are not immune to other anthropogenic stress either. Increased urbanisation of the Reunion coastline during the last decades drove noticeable eutrophication in the reef environment (Naim 1993) and a decrease in reef fish

stocks in some areas (Chabanet et al. 1995). These changes have led to an increase in the relative cover of algae compared to corals (Naim 1993, Chazottes et al. 2002, Naim, Tourrand, Ballesteros, et al. 2013). Consequently, a multiple-use marine reserve (Réserve Naturelle Marine de La Réunion) was set up in 2007 to address the deterioration of reefs. This Marine Protected Area (MPA), covering an area of over 35 km^2, is divided into three levels of protection: open areas for human activities, restricted areas where only some traditional and commercial fishing activities are allowed, and sanctuaries where no activity is allowed, thus corresponding to no-take zones (Figure 23). Human pressure is less documented for the Rodrigues reef. In response to overfishing 10 years ago, the local government of Rodrigues implemented four marine reserves to the north of the island, but only partial management has been set up and fishing still occurs in these areas (Hardman et al. 2010, Pasnin et al. 2016). In addition, the South East Marine Protected Area (SEMPA), an area in the south-eastern of Rodrigues, was designated as an MPA in 2009. It includes both inner and outer lagoon covering a total 43.7 km^2 divided into different multiple-use zones including no-take zones (NTZ) where fishing is prohibited (Figure 23).

Mayotte is the oldest island of the Comoro Archipelago, located in the northern Mozambique Channel (12° 80' S, 45° 10' E). This volcanic island has a jagged coastline surrounded by one of the largest lagoon of the Indian Ocean (ca. 1500 km^2, 15 km width and reaching 80 m depth; Chabanet 2002, Dinhut et al. 2008). The lagoon is surrounded by a continuous barrier reef interrupted by a few channels (Guilcher 1971). More than 2300 marine species have been identified including about 600 species of fish and 250 species of hard corals recorded in Mayotte reefs; but these ecosystems are facing important anthropogenic threats through increasing human population densities (Ahamada et al. 2008, Dinhut et al. 2008, Obura 2012). In 2010, Mayotte's marine park has been created (Parc Naturel Marin de Mayotte) with the objective of reconciling protection of the marine environment and sustainable development of associated activities.

Glorieuses and Europa are two of the French overseas island territories in the Western Indian Ocean called Scattered Islands (Îles Éparses in French) and respectively located in the north (11° 50' S, 47° 30' E) and the south (22° 30' S, 40° 30' E) of Mozambique Channel. Unlike the islands mentioned above, these territories do not have

permanent inhabitants. They are under the authority of the French Southern and Antarctic Lands (Terres Australes et Antarctiques Françaises) since 2007. They were both classified as nature reserves in 1975 and have since been occupied by small rotating military detachments (ca. 15 people) to ensure French sovereignty (Quétel et al. 2016). Although being considered as pristine ecosystems, the reefs of these islands are also affected by cyclones, pollution or the effects of climate change, as the other reefs in the SWIO region. Monitoring of the effects of these disturbances on reef communities started a few years ago and had already shown a decrease in fish stocks probably linked to an increase in illegal fishing pressure in recent years (Chabanet et al. 2016). A natural marine park has been created in 2012 at Glorieuses (Parc naturel marin des Glorieuses) to develop sustainable human activities while preserving marine environment (Quétel et al. 2016).

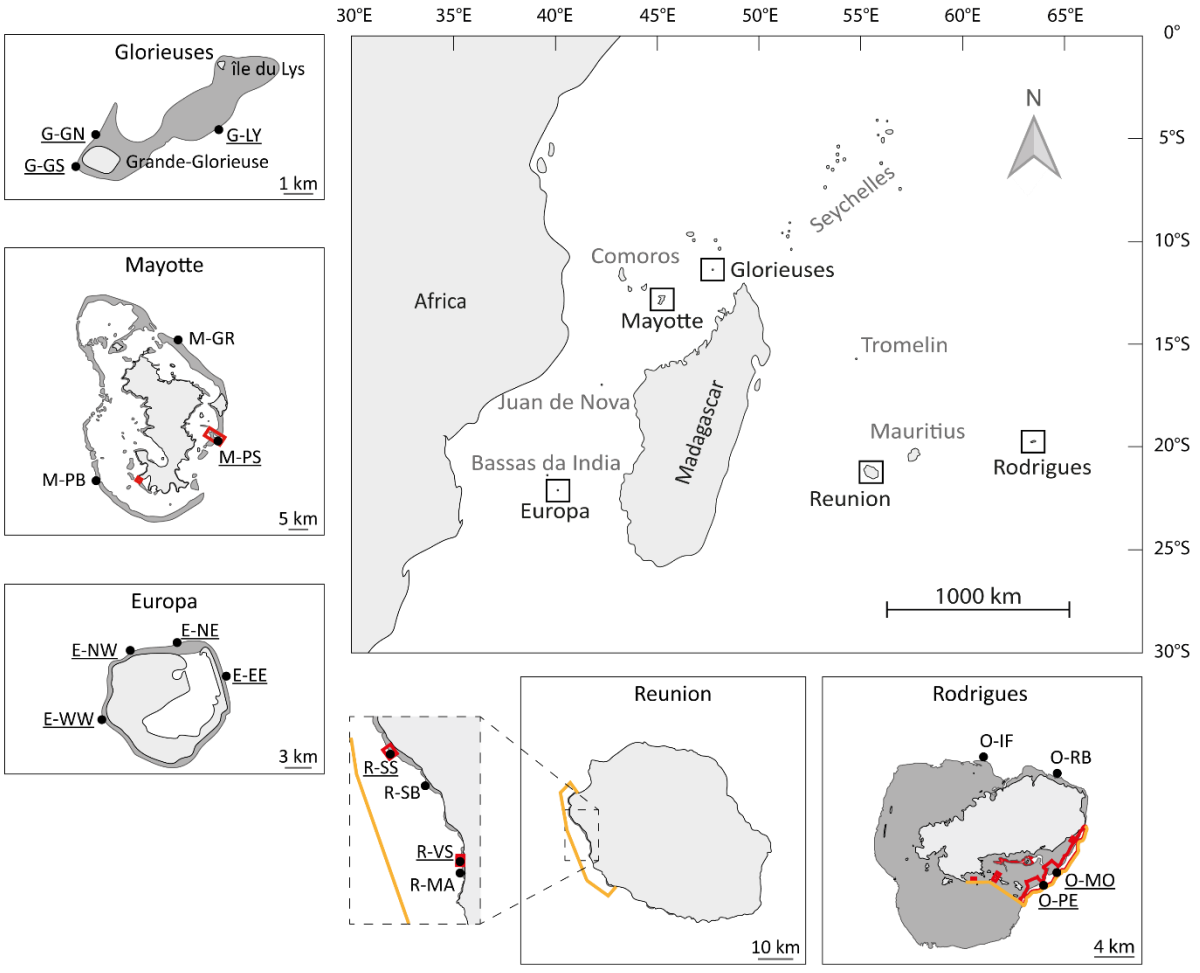

Figure 23. Location of the sampling sites in the South-Western Indian Ocean region. ☐, land; ■, reef flat; ☐, MPA; ☐, NTZ; ●, sampling site.

5.2.2.2. Sampling strategy

A set of eight variables have been selected according to (i) the data availability from all the sampled sites and feasibility of measures and (ii) their interest in characterizing the resilience potential of the reefs, and more specifically the recovery. This selection is mainly based on the findings of McClanahan et al. (2012) about scaled importance of resilience factors, associated with recent advances on coral reef resilience including recovery (Graham et al. 2015). Thus, the selected variables were: coral diversity, coral density (total and juvenile only), hard coral cover, proportion of stress-tolerant coral species cover, algal cover, herbivorous fish biomass and sea-surface temperature anomalies. Given the importance of coral recruitment in resilience processes, especially for recovery, recruitment rates recently evaluated on artificial substrate at Reunion and Rodrigues islands were also integrated (Jouval et al. 2019).

Coral density

Densities were evaluated along three belt-transect of 1 × 10 m (i) on photographs (ca. 20 photographs per transect) at Reunion (2016), Rodrigues (2017) and Glorieuses (2015) and (ii) with underwater visual census at Mayotte (2016) and Europa (2016). In both case, each coral colony encountered was identified to the genus level and its maximal diameter measured on the field or using a tape present on each photographs. The maximal diameter measures were used to distinguish adult (i.e. mature colonies of > 5 cm in diameter) from juvenile (i.e. immature colonies of ≤ 5 cm in diameter) coral colonies (Penin et al. 2010).

Coral diversity

Coral diversity was evaluated in 2012 at Glorieuses, 2013 at Reunion, 2014 and 2016 at Mayotte, 2016 at Europa and 2017/2018 at Rodrigues. Coral species diversity was assessed during a 45 min prospection by a taxonomic expert at each site.

Coral and algal cover and proportion of resistant coral species

Benthic cover data was assessed in 2015 at Glorieuses, 2016 at Europa and Mayotte and 2016/2017 at Reunion and Rodrigues. At each site, coral and algal (macro-algae and turf) cover was evaluated using the Line Intercept Transect method (LIT; Loya 1972),

with three linear 20 m transects laid parallel to depth contours and separated by 5 m. Coral colonies were identified to the species level when possible. Each species was associated with one of the following statuses: stress-tolerant, competitive, generalist, weedy or undetermined according to Darling et al. (2012) or, for the taxa not referenced in this study, according to expert opinion (L. Penin and L. Bigot, pers. com). The proportion of stress-tolerant coral species among total coral cover was then calculated.

Herbivorous fish biomass

Fish biomass was evaluated in 2015 at Glorieuses, 2016 at Europa and Mayotte, 2017 at Reunion and 2018 at Rodrigues. At each site, number and total length of observed herbivorous fish species were collected using belt-transects through underwater visual censuses. These parameters were then used to evaluate mean fish biomass from the length-weight relationships on *Fishbase* (Froese & Pauly 2018).

Sea surface temperature anomalies

Monthly sea surface temperatures anomalies (SSTa) were downloaded from the IRI/LDEO Climate Data Library (http://iridl.ldeo.columbia.edu) from November 1981 to December 2018 and for each island location. SSTa were calculated by subtracting, by month of year, the 1971-2000 mean SST from the monthly SST values of the considered period (1981-2018) according to Reynolds et al. (2002). Then, the proportion of months for which the SSTa were equal or greater than 1°C (i.e. when the monthly SST was warmer by 1°C compared to the temperatures recorded for the same month between 1971 and 2000) was evaluated over the considered period. This variable will be referred to as $SSTa^{+1}$.

Coral recruitment on artificial tiles

The abundance of coral recruits was characterised at 12 m depth at Reunion and Rodrigues islands on artificial settlement tiles (Jouval et al. 2019). For each site, 20 individual unglazed terracotta tiles (ca. 10 × 10 × 2 cm) attached to a stainless steel support anchored to the substrate were deployed about 2 cm from the substrate (Mundy 2000, Adjeroud et al. 2007). Tiles were immersed for six months during two austral summer periods (October 2015–March 2016, October 2016–March 2017). At the end of

the immersion periods, the tiles were retrieved, bleached and sun dried to expose the skeleton of coral recruits (coral spats) for identification and counting under a dissecting microscope.

5.2.2.3. Data analyses

Principal component analysis (PCA) was conducted in order to discriminate the 18 sites according to their recovery characteristics. The *FactoMineR* package (v.1.41; Lê et al. 2008) of the R software (R Core Team 2018; https://www.R-project.org/) was used for this analysis.

TOPSIS method

The TOPSIS method, developed by Hwang and Yoon (1981) and modified by Yoon (1987) and Hwang et al. (1993) is a multi-criteria method for identifying solutions from a panel of alternatives. The objective is to classify these alternatives according to their relative distance to two "ideal", positive and negative solutions. The basic principle of the TOPSIS method is that the chosen alternative must have the shortest distance to the ideal positive solution, and thus the largest distance to the ideal negative solution. The method can be described as a series of six steps:

STEP 1: Multi-criteria decision matrix

$$M = \begin{array}{c} \\ S_1 \\ S_2 \\ S_i \end{array} \begin{array}{c} \begin{array}{ccc} V_1 & V_2 & V_j \end{array} \\ \begin{pmatrix} x_{11} & x_{12} & x_{1j} \\ x_{21} & x_{22} & x_{2j} \\ x_{i1} & x_{i2} & x_{ij} \end{pmatrix} \end{array} \qquad \text{(eq. 3)}$$

where x_{ij} correspond to the value measured for the variable V_j at site S_i.

STEP 2: Normalization of the multi-criteria decision matrix

This step ensure that each variable has the same range: between 0 and 1.

$$n_{ij} = x_{ij} \Big/ \sqrt{\sum_{j=1}^{i} (x_{ij})^2} \qquad \text{(eq. 4)}$$

STEP 3: Weighting of the normalized multi-criteria decision matrix

To weight the variables according to their perceived importance for coral reef recovery, we asked 23 experts to rank each variable from 1 (low importance) to 5 (high importance; Appendix A5), except $SSTa^{+1}$ and recruitment rates which were added later in the analyses. Each variable is weighted such as:

$$v_{ij} = w_j \times n_{ij} \qquad \text{(eq. 5)}$$

where w_j is the mean rank given to the variable V_j.

Recruitment rate (on artificial tiles) is weighted using the mean rank given to the juvenile coral density since both variables are related to coral recruitment. $SSTa^{+1}$ is weighted using the average weight of all the other variables.

STEP 4: Ideal positive and negative solutions

Ideal positive (*IPS*) and negative (*INS*) solutions were respectively defined as:

$$IPS = \left\{v_1^+, v_2^+, \dots, v_j^+\right\} = \left\{\left(\max v_{ij} \,|j \in P\right) or \left(\min v_{ij} \,|j \in N\right)\right\} \qquad \text{(eq. 6)}$$

$$INS = \left\{v_1^-, v_2^-, \dots, v_j^-\right\} = \left\{\left(\min v_{ij} \,|j \in P\right) or \left(\max v_{ij} \,|j \in N\right)\right\} \qquad \text{(eq. 7)}$$

where v_{ij} corresponds to the normalized and weighted elements of the multi-criteria decision matrix, *P* is for the variables expected to enhance reef recovery and *N* is for the variables expected to reduce reef recovery. Thus, the *IPS* corresponds to the conditions where coral diversity, density (total and juvenile), cover (total and stress-tolerant species), herbivorous fish biomass and coral recruitment rates are maximized while algal cover and $SSTa^{+1}$ are minimized. On the contrary, the *INS* corresponds to the conditions where algal cover and $SSTa^{+1}$ are maximized while coral diversity, density (total and juvenile), cover (total and stress-tolerant species), herbivorous fish biomass and coral recruitment rates are minimized. Two analyses are conducted: one using all the 18 sites and the other using only the eight sites of Reunion and Rodrigues islands for which recruitment rates data are available. Thus, two sets of ideal solutions (*IS*) are defined, hereafter referred to as IS_{Tot} and IS_{RR} respectively.

STEP 5: Measures of separation

The measures of separation of each alternative (i.e. site) from the ideal positive and negative solutions are measured as the distance (*D*) of the alternative to *IPS* and *INS* respectively in the Euclidean space of the variables:

$$D_i^+ = \sqrt{\sum_{i=1}^{j}\left(v_{ij} - v_j^+\right)^2} \text{ and } D_i^- = \sqrt{\sum_{i=1}^{j}\left(v_{ij} - v_j^-\right)^2} \qquad \text{(eq. 8)}$$

STEP 6: Relative proximity to the ideal solutions

$$RI_i = D_i^- / (D_i^+ + D_i^-) \qquad \text{(eq. 9)}$$

The relative proximity to the ideal solution index (*RI*) ranges from 0 when the variable measure (v_{ij}) corresponds to *INS* (v_j^-; eq. 7) to 1 when the variable measure (v_{ij}) corresponds to *IPS* (v_j^+; eq. 6).

Robustness of the RI index

As previously described, the ideal positive and negative solutions are calculated on the basis of the maximum and minimum values of each variable at the 18 studied sites. However, these sites may be exposed to different disturbances (of both anthropogenic and natural origin), currents, or meteorological conditions. The conditions considered optimal for a site were therefore not necessarily optimal for all the studied sites. In an attempt to validate the TOPSIS analysis with respect to the ideal solutions, we randomly generate 1000 *IPS* and *INS* for both analyses (using all the 18 sites and using only the eight sites of Reunion and Rodrigues islands for which recruitment data were available) as follows:

- 1000 values from the 25 % extreme values of the distribution of the variable *j*:

$$IPS^{25} = \left\{v_1^{25+}, v_2^{25+}, \dots, v_j^{25+}\right\} = \left\{\left(q_{75} < v_{ij} < q_{100} \,|j \in P\right) or \left(q_0 < v_{ij} < q_{25} \,|j \in N\right)\right\} \text{ (eq. 10)}$$

$$INS^{25} = \left\{v_1^{25-}, v_2^{25-}, \dots, v_j^{25-}\right\} = \left\{\left(q_0 < v_{ij} < q_{25} \,|j \in P\right) or \left(q_{75} < v_{ij} < q_{100} \,|j \in N\right)\right\} \text{ (eq. 11)}$$

- 1000 values from the 50 % extreme values of the distribution of the variable *j*:

$$IPS^{50} = \{v_1^{50+}, v_2^{50+}, \dots, v_j^{50+}\} = \{(q_{50} \leq v_{ij} < q_{100} | j \in P) \; or \; (q_0 < v_{ij} < q_{50} | j \in N)\} \quad \text{(eq. 12)}$$

$$INS^{50} = \{v_1^{50-}, v_2^{50-}, \dots, v_j^{50-}\} = \{(q_0 < v_{ij} < q_{50} | j \in P) \; or \; (q_{50} \leq v_{ij} < q_{100} | j \in N)\} \quad \text{(eq. 13)}$$

Steps 5 and 6 are repeated for each of the 1000 iterations. For the measures of separation, we use the equation 14, derived from the equation 8:

$$D_i^+ = \begin{cases} 0, & if \; v_{ij} > v_j^{25/50+} \\ \sqrt{\sum_{i=1}^{j} \left(v_{ij} - v_j^{25/50+}\right)^2}, & elsewhere \end{cases} \quad \text{and}$$

$$D_i^- = \begin{cases} 0, & if \; v_{ij} < v_j^{25/50-} \\ \sqrt{\sum_{i=1}^{j} \left(v_{ij} - v_j^{25/50-}\right)^2}, & elsewhere \end{cases} \quad \text{(eq. 14)}$$

For greater clarity, the abbreviations used in the rest of the manuscript are summarized in Table 4.

Table 4. Abbreviations used to describe the Ideal Solutions (*IS*) according to the performed analyses.

Ideal solutions		***Based on all the 18 sites***	***Based on 8 sites (Reunion and Rodrigues islands)***
Based on minimal/maximal values	Positive	IPS_{Tot}	IPS_{RR}
	Negative	INS_{Tot}	INS_{RR}
	Both	IS_{Tot}	IS_{RR}
Based on random sampling within the 25 % of extreme values of each variable distribution	Positive	IPS_{Tot}^{25}	IPS_{RR}^{25}
	Negative	INS_{Tot}^{25}	INS_{RR}^{25}
	Both	IS_{Tot}^{25}	IS_{RR}^{25}
Based on random sampling within the 50 % of extreme values of each variable distribution	Positive	IPS_{Tot}^{50}	IPS_{RR}^{50}
	Negative	INS_{Tot}^{50}	INS_{RR}^{50}
	Both	IS_{Tot}^{50}	IS_{RR}^{50}

5.2.3. Results

The PCA explains 72.5 % of the recovery potential variability measured among sites (Figure 24). Coral density (total and juveniles), coral cover (total and stress-tolerant species) and algal cover mainly contribute to the first axis of the PCA (16 to 21 %) while $SSTa^{+1}$ contributes the most to the second axis (39 %). Indeed, Europa sites, M-GR and M-PS at Mayotte and G-GN and G-GS at Glorieuses are characterized by higher total coral cover and density and lower algal cover compared to Rodrigues sites, Reunion sites, M-PB and G-LY (Figure 24 and Figure 25; Appendix A6). Moreover, Rodrigues and Europa sites exhibit higher percentage of stress-tolerant coral species cover and higher $SSTa^{+1}$ compared to Mayotte, Glorieuses and Reunion sites (Figure 24 and Figure 25; Appendix A6). Overall, the first axis of the PCA discriminates the sites of the Mascarene Archipelago (Reunion and Rodrigues islands) from the sites of the Mozambique Channel (Europa, Glorieuses and Mayotte). Within this latter sub-group, the second axis discriminates the sites of Europa from the sites of Glorieuses and Mayotte.

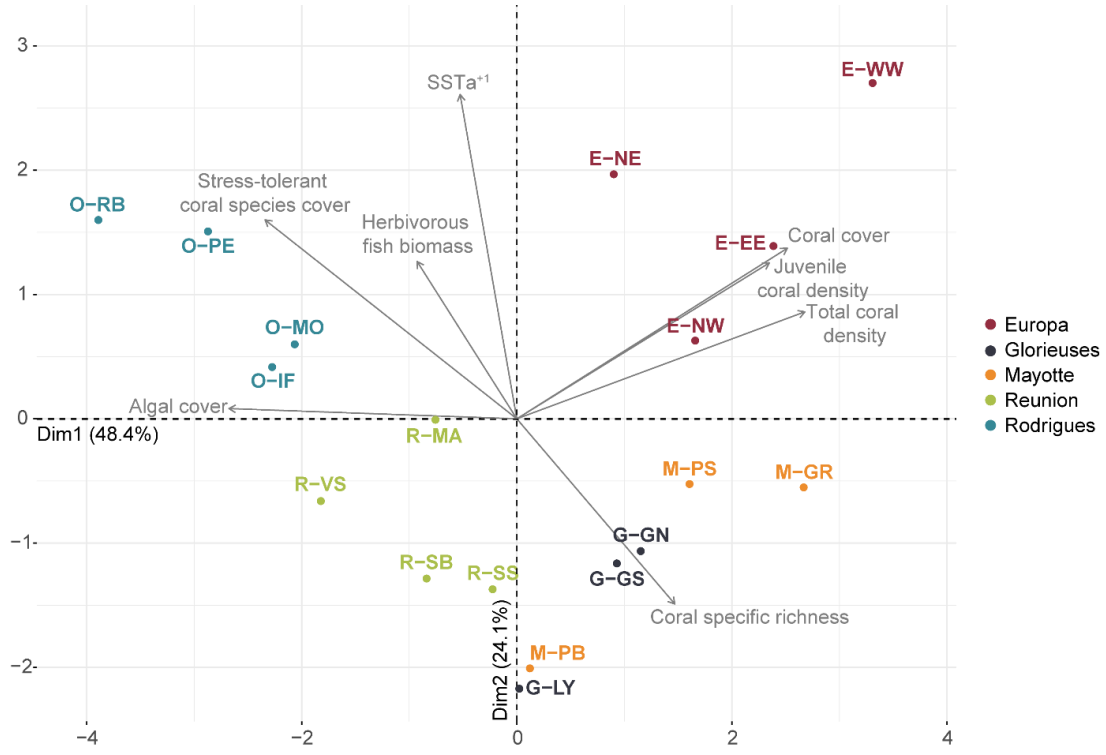

Figure 24. Principal components analysis (PCA) in the space of summary variables used to characterize the recovery potential of 18 reef sites in the SWIO.

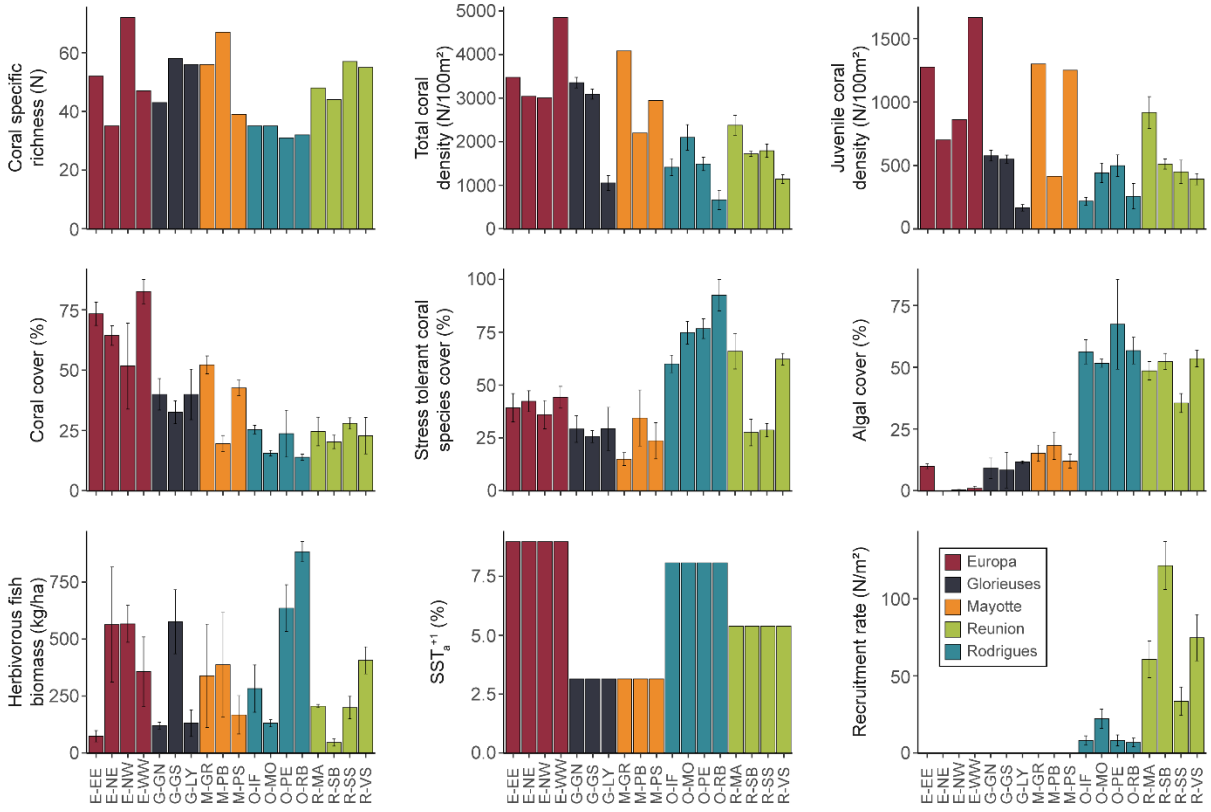

Figure 25. Summary of the data measured for each variable in the 18 study sites (Mean ± SE). SE were not available for densities in Europa and Mayotte.

Coral cover and density (total and juvenile) are highly positively correlated, while algal cover is significantly and negatively correlated to coral density (total and juvenile), coral cover and coral specific richness (Figure 26). Stress-tolerant coral species cover is significantly and negatively correlated with coral specific richness and total coral density while it is significantly and positively correlated to algal cover and $SSTa^{+1}$ (Figure 26). At both Rodrigues and Reunion, recruitment rates are not significantly correlated to the other variables.

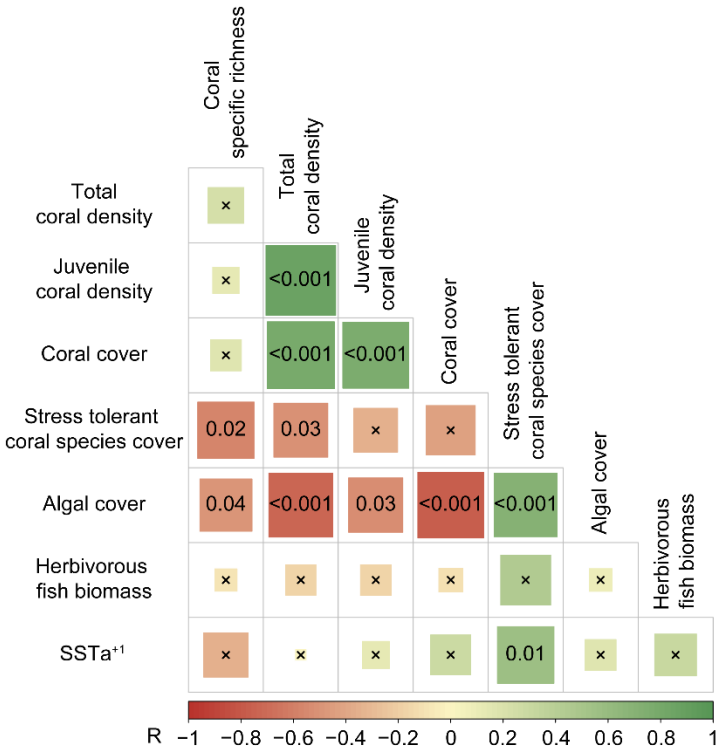

Figure 26. Correlation matrix between the variables used to characterize the recovery potential of the 18 studied sites. Square size and color shade are proportional to the absolute value of R. The color of the square depends on the sign of R: red, negative R; green, positive R. The correlation p-values are indicated inside each square (x corresponds to $p > 0.05$).

According to the TOPSIS analyses carried out on the 18 study sites, the Europa sites, M-GR and G-GS have the highest *RIs* (all *RIs* ≥ 0.5) and therefore the closest to the *IPS* (Figure 27-A). These six sites are among those with the highest density of juvenile corals (on average twice as many individuals as on the other sites, ca. 1000/100m^2 vs. 500/100m^2 respectively; Figure 25). These sites also have a high coral cover (ca. 59 % compared to 26 % for other sites). Proportionally, the percentage of stress-tolerant coral species cover is relatively low at these sites (ca. 34 % versus 50 % at other sites). While the sites of Europa (south of the Mozambique Channel) are the most exposed to strong SST anomalies (SSTa^{+1} of 9 %), the sites of Glorieuses and Mayotte (north of the Mozambique Channel) are the least exposed (SSTa^{+1} of 3 %; Figure 25).

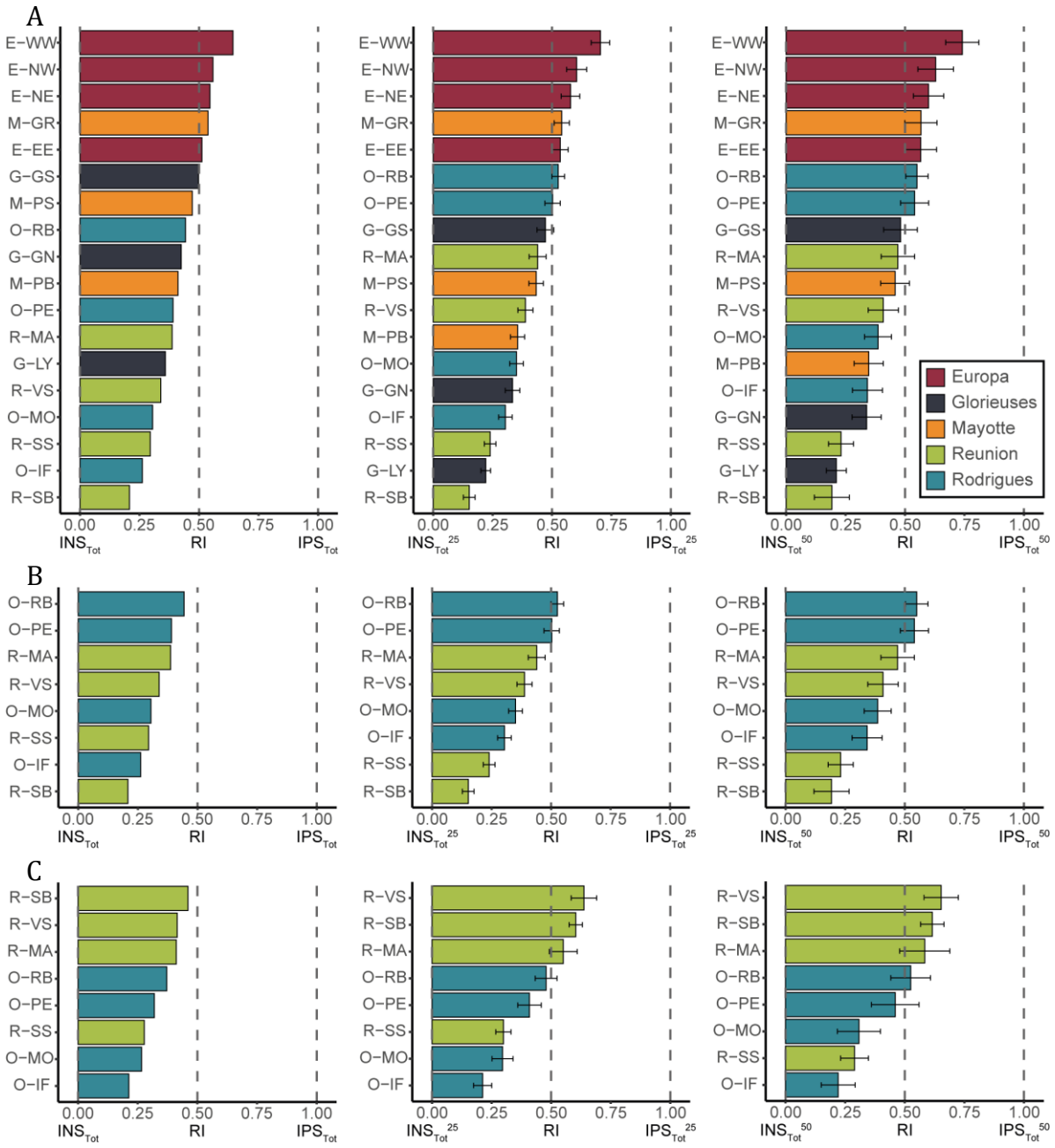

Figure 27. Ranking of the reef sites according to their recovery potential evaluated through the TOPSIS relative index (*RI*). A, all sites without *recruitment rate* variable; B, Rodrigues and Reunion sites, without *recruitment rate* variable; C, Rodrigues and Reunion sites, including *recruitment rate* variable. In each case, *INS*/*IPS* are based on the values measured from the 18 sampling sites (IS_{Tot}).

Reunion sites have low recovery potential (average *RI* = 0.31; Figure 27-A and B), which is explained in particular by a high algal cover (ca. 47%; Figure 25) and a low coral density (ca. 1750/100m^2). However, the south-western sites (Saint Leu reefs: R-MA and R-VS) have a higher *RI* (0.36 in average) than the north-western sites (La Saline reefs: R-SS and R-SB; average *RI* = 0.25). The Rodrigues sites have more contrasting recovery potentials ranging from *RI* = 0.26 (O-IF) to 0.44 (O-RB; Figure 27-A and B). The main

difference between the highest ranked (O-RB and O-PE) and lowest ranked (O-IF and O-MO) sites of Rodrigues come from the values of herbivorous fish biomass which are the most important of all the data set in O-RB and O-PE (about 759 kg/ha; Figure 25) and are much lower in the two other sites (about 206 kg/ha). Both Reunion and Rodrigues islands are exposed to strong SST anomalies ($SSTa^{+1}$ of 5 and 8 % respectively).

The modification of the *IS* by randomly sampling within the 25 % of extreme values of each variable distribution significantly modify sites ranking (Figure 27-A). Indeed, only 5 sites are found at the same position in more than 75 % of the cases in IS_{Tot} and IS_{Tot}^{25} analyses (E-WW, E-NW, E-NE, R-SS and R-SB, respectively ranked in 1st, 2nd, 3rd, 16th and 18th positions in both IS_{Tot} and IS_{Tot}^{25} analyses; Table 5). On the contrary, the ranking of sites at intermediate positions (from 6th to 15th and 17th) are not or little consistent between the two analyses. However, of all the 1000 iterations of the IS_{Tot}^{25} analyses, the 11 sites concerned stay at the same position in more than 40 % of the cases. Thus, while positions are poorly maintained between IS_{Tot} and IS_{Tot}^{25} analyses, it is highly consistent over the 1000 IS_{Tot}^{25} iterations.

There is less variation in ranking between analyses based on IS_{Tot}^{50} and on IS_{Tot}^{25} than between analyses based on IS_{Tot}^{25} and IS_{Tot} (Figure 27; Table 5). Indeed, 14 sites maintain the same position in the two analyses based on IS_{Tot}^{50} and on IS_{Tot}^{25} (Figure 27-A). However, over the 1000 iterations performed with the IS_{Tot}^{50}, the sites positions change more frequently from one iteration to another (Table 5).

Applied to the sites of Rodrigues and Reunion islands, the addition of recruitment rate (on artificial tiles) variable has a strong influence on the *RI* and thus on the ranking of the sites of these two islands (Figure 27-C). The measured recruitment rates, higher on Reunion (73 recruits/m^2 on average) than in Rodrigues reefs (11 recruits/m^2; Figure 25), move 3 of the 4 sites of Reunion at the top of the ranking. In addition, the R-SB site has the lowest *RI* without taking recruitment rates into account (*RI* = 0.21; Figure 27-B) but has the highest *RI* when considering it (122 recruits/m^2 for this site; *RI* = 0.46; Figure 27-C).

Table 5. Percentage of occurrence of each of the 18 site at each TOPSIS ranking position (1 to 18) for the 1000 iterations of IS_{Tot}^{25} (top) and IS_{Tot}^{50} (bottom). White, 0 %; yellow, 0 < % ≤ 25; orange, 25 < % ≤ 50; light red, 50 < % ≤ 75; dark red, 75 < % ≤100. The diagonal corresponds to the positions observed for each site with the IS_{Tot}.

Position	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
E-WW	99.9	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E-NW	0.1	94.1	5.7	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E-NE	0	3.5	78.5	10.5	7.4	0.1	0	0	0	0	0	0	0	0	0	0	0	0
M-GR	0	0	5.5	41.4	31.2	16.1	5.8	0	0	0	0	0	0	0	0	0	0	0
E-EE	0	2.1	7.4	18.6	33.4	20.1	14.0	4.4	0	0	0	0	0	0	0	0	0	0
G-GS	0	0	0	0.1	0.2	1.6	10.7	69.3	13.2	4.9	0	0	0	0	0	0	0	0
M-PS	0	0	0	0	0	0	1.3	5.1	37.2	49.7	6.6	0.1	0	0	0	0	0	0
O-RB	0	0.2	2.9	29.1	14.8	52.2	0.8	0	0	0	0	0	0	0	0	0	0	0
G-GN	0	0	0	0	0	0	0	0	0	0	1.4	5.2	21.2	61.2	11.0	0	0	0
M-PB	0	0	0	0	0	0	0	0	0	0	0.1	52.4	38.1	9.4	0	0	0	0
O-PE	0	0	0	0.2	13.0	9.9	67.4	8.9	0.6	0	0	0	0	0	0	0	0	0
R-MA	0	0	0	0	0	0	0	12.3	48.6	39.1	0	0	0	0	0	0	0	0
G-LY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.4	92.6	0
R-VS	0	0	0	0	0	0	0	0	0.4	6.3	91.7	1.6	0	0	0	0	0	0
O-MO	0	0	0	0	0	0	0	0	0	0	0.2	40.7	40.7	18.4	0	0	0	0
R-SS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	92.6	7.4	0
O-IF	0	0	0	0	0	0	0	0	0	0	0	0	0	11.0	89.0	0	0	0
R-SB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100.0

Position	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
E-WW	95.0	4.3	0.6	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E-NW	4.1	54.2	23.3	14.6	2.9	0.7	0.2	0	0	0	0	0	0	0	0	0	0	0
E-NE	0	11.8	38.8	18.8	23.8	3.7	2.5	0.5	0.1	0	0	0	0	0	0	0	0	0
M-GR	0	5.0	14.0	23.5	15.3	14.7	21.0	5.3	0.8	0.3	0.1	0	0	0	0	0	0	0
E-EE	0	14.2	10.3	15.0	18.1	17.4	13.1	11.1	0.6	0.2	0	0	0	0	0	0	0	0
G-GS	0	0	0.2	0.9	3.4	9.1	8.0	27.7	18.3	24.1	4.9	2.4	1.0	0	0	0	0	0
M-PS	0	0	0	0	1.3	6.4	3.8	10.5	35.2	19.3	15.1	5.3	2.8	0.3	0	0	0	0
O-RB	0.7	5.3	7.3	16.3	16.0	28.2	16.8	6.3	2.8	0.3	0	0	0	0	0	0	0	0
G-GN	0	0	0	0	0	0	0	0	0	0.3	8.9	7.1	18.9	25.4	37.9	0.9	0.6	0
M-PB	0	0	0	0	0	0	0	0	0.1	0.5	3.0	16.6	21.7	33.5	23.1	1.5	0	0
O-PE	0.2	5.0	4.8	9.6	17.4	15.4	27.5	12.5	5.9	1.6	0.1	0	0	0	0	0	0	0
R-MA	0	0.2	0.7	1.2	1.8	4.1	6.7	24.4	24.8	33.5	2.4	0.2	0	0	0	0	0	0
G-LY	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	23.0	40.7	35.8
R-VS	0	0	0	0	0	0.3	0.4	1.3	10.0	15.1	43.8	18.0	9.1	2.0	0	0	0	0
O-MO	0	0	0	0	0	0	0	0.4	1.4	4.7	20.7	45.9	17.8	8.7	0.4	0	0	0
R-SS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.0	48.1	46.5	4.4
O-IF	0	0	0	0	0	0	0	0	0	0.1	1.0	4.5	28.7	29.9	34.3	1.2	0.3	0
R-SB	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	2.8	25.3	11.9	59.8

When considering recruitment rate, the ranking of Reunion and Rodrigues sites are highly maintained between analyses based on IS_{Tot}^{25} and IS_{Tot}, on one hand, and IS_{Tot}^{50} and IS_{Tot}, on the other hand (Table 6). Indeed, six of the eight sites keep their position in more than 56 % of cases between the analyses based on IS_{Tot}^{25} and IS_{Tot}. Moreover, three sites hold their position in more than 71 % of the cases between the analyses based on IS_{Tot} and IS_{Tot}^{50} while the three first sites in one hand, and the sites ranked at 6th and 7th positions in the other hand switch their positions.

Table 6. Percentage of occurrence of each Reunion and Rodrigues site at each TOPSIS ranking position (1 to 8) for the 1000 iterations of IS_{Tot}^{25} (left) and IS_{Tot}^{50} (right). The analyses included the recruitment rate on artificial tiles. White, 0 %; yellow, 0 < % ≤ 25 %; orange, 25 < % ≤ 50 %; light red, 50 < % ≤ 75 %; dark red, 75 < % ≤100 %. The diagonal corresponds to the positions observed for each site with the IS_{Tot}.

Position	1	2	3	4	5	6	7	8
R-SB	24.2	61.1	14.7	0	0	0	0	0
R-VS	75.8	24.2	0	0	0	0	0	0
R-MA	0	14.3	81.0	4.7	0	0	0	0
O-RB	0	0.4	4.3	95.3	0	0	0	0
O-PE	0	0	0	0	100.0	0	0	0
R-SS	0	0	0	0	0	56.0	44.0	0
O-MO	0	0	0	0	0	44.0	56.0	0
O-IF	0	0	0	0	0	0	0	100.0

Position	1	2	3	4	5	6	7	8
R-SB	20.5	35.3	32.5	9.2	2.5	0	0	0
R-VS	60.6	36.5	2.8	0.1	0	0	0	0
R-MA	11.7	16.9	46.5	13.9	11.0	0	0	0
O-RB	7.2	8.7	12.5	71.4	0.2	0	0	0
O-PE	0	2.6	5.7	5.4	86.3	0	0	0
R-SS	0	0	0	0	0	43.4	45.8	10.8
O-MO	0	0	0	0	0	56.5	41.3	2.2
O-IF	0	0	0	0	0	0.1	12.9	87.0

The modification of the *IS* by taking the minimal and maximal values of only the sub-sample corresponding to the sites of Reunion and Rodrigues Islands (i.e. IS_{RR}) lead to significant changes in the ranking: only two sites maintain the same position with the IS_{Tot} and the IS_{RR} (Figure 27-B and Figure 28-A). As observed with IS_{Tot}, when adding recruitment rate, the ranking of Reunion and Rodrigues sites are highly maintained between both analyses based on IS_{RR}^{25} and IS_{RR} and IS_{RR}^{50} and IS_{RR} (Figure 28-B; Appendix A7).

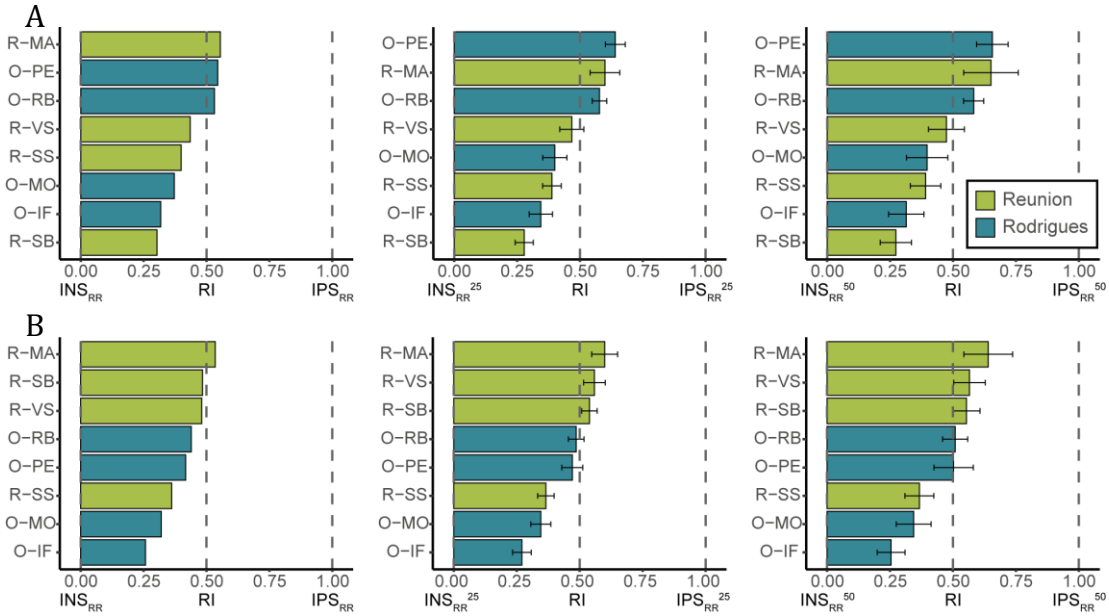

Figure 28. Ranking of the Reunion and Rodrigues reef sites according to their recovery potential evaluated through the TOPSIS relative index (*RI*). A, without *recruitment rate* variable; B, including *recruitment rate* variable. In each case, *INS*/*IPS* are based on values measured from the 8 sampling sites of Reunion and Rodrigues islands (IS_{RR}).

5.2.4. Discussion

The objective of this study was to propose a tool to assess the recovery potential of different reefs, and to apply it in the SWIO area. We have developed a tool based on the TOPSIS method, rarely used in the ecology of natural environments (Behzadian et al. 2012). As it stands, the *RI* index developed shows to assess that the island of Europa (south of the Mozambique Channel) has a high recovery potential, regardless of the site considered. The estimated recovery potential for the islands in the northern part of the Mozambique Channel, Glorieuses and Mayotte, are highly variable among sites, whereas the Mascarene Islands (Reunion and Rodrigues) display the overall lowest recovery potentials, although the measured *RI* vary greatly from site to site, especially for Rodrigues.

5.2.4.1. Recovery potential of reefs of the SWIO

In addition to the fact that Europa present the reefs that can be considered both among the most pristine (as part of the French Scattered Islands; Quod et al. 2007, Chabanet et al. 2016) and the healthiest (according to the measured coral and algal cover and coral densities) of the studied environments, Europa sites are also found to have a high recovery potential. Indeed, these sites are always found at the top of the *RI* ranking, regardless of the TOPSIS analyses considered (based on IS_{Tot}, IS_{Tot}^{25} or IS_{Tot}^{50}). Our results confirm the results of previous monitoring programs conducted in the Mozambique Channel showing that the southern islands (including Europa) showed better recovery than the northern islands (including Glorieuses and Mayotte; Chabanet et al. 2016). Chabanet et al. (2016) suggested that this difference may be due to warmer conditions in the north of the Mozambique Channel leading to more frequent minor bleaching episodes and mortality events and/or to chronic stresses that may delay the recovery of coral communities. Indeed, based on Reynolds et al. (2002), mean annual SSTs between 1981 and 2018 were ~1°C higher in Mayotte and Glorieuses than in Europa. Previous monitoring programs conducted in Europa also showed that coral communities of this island were highly resistant to bleaching events. In particular, compared to the other studied territories of the SWIO region, Europa reefs were the least affected by mass bleaching of 2016. This was especially patent on reef slopes (Nicet et al. 2016, Bigot et al. 2019). However, over the 1981-2018 period, Europa had the highest proportion of

months for which the mean SSTs exceeded the monthly SSTs values (calculated over the 1971-2000 period) by at least 1°C ($SSTa^{+1}$). As previously mentioned, while $SSTa^{+1}$ are higher in Europa, the mean annual SSTs are also the lowest in Europa compared to the other sites in the Mozambique Channel. This island thus displays high variability in temperature, but with overall lower values than in nearby sites, which may explain why this factor ultimately have little influence on the resilience potential (resistance and recovery) of Europa sites to bleaching events.

The sites of the two other islands of the Mozambique Channel, Glorieuses and Mayotte, are more heterogeneous in terms of recovery potential (e.g. in Mayotte, *RI*s ranged from 0.35 to 0.54). Previous studies suggested that unlike what has been observed for Europa, bleaching events that occurred over the last 30 years in Mayotte (1983: Faure et al. 1984; 1998: Quod et al. 2002; 2010 and 2016: Nicet et al. 2016, Obura et al. 2018) have strongly impacted reef slopes assemblages. The sensitivity of Mayotte reefs to mass bleaching events could be explained by the composition of coral communities, dominated by *Acropora* (Obura et al. 2018), known to be very sensitive to disturbances and particularly to bleaching. However, despite fluctuating responses, Mayotte reefs showed high levels of recovery after bleaching events, maintaining the dominance of *Acropora* until then, this genera representing more than 50 % of the coral cover for the three studied sites of Mayotte. These recovery levels can be partly explained by the high levels of connectivity (Obura 2012, Obura et al. 2019) due to the complex currents occurring in the north of the Mozambique channel (Crochelet et al. 2016). Nevertheless, given the greater impact of these bleaching on the outer slopes, the reduction of the period of time between each event and the influence of other anthropogenic disturbances in Mayotte (e.g. degraded water quality, overfishing), the recovery capacity of these reefs may tend to decrease in the future (Obura et al. 2018). Moreover, we also observe that M-GR site which have the best *RI* is also the most remote site from densely populated areas of Mayotte, thus further analyses focusing on human population impacts would be interesting, given that RBM must take into account social aspects and not only purely ecological issues (Bruggemann et al. 2012, Mcleod et al. 2019).

At the extreme north of the Mozambique Channel, Glorieuses present the lower mean *RI* of the Mozambique Channel sites (0.34 compared to 0.60 for Europa and 0.44 for Mayotte) and, as for Mayotte, a highly variable *RI* from one site to another (ranging from

0.22 to 0.47). Although considered as pristine, Glorieuses reefs have lower coral cover and coral densities (especially in juveniles), and higher algal cover than Europa. In addition, previous studies have shown that in Glorieuses, following 2016 bleaching event, mortality was relatively high on the outer slopes resulting in a loss of coral cover ranging from 10 to 50 % (Nicet et al. 2016, Bigot et al. 2019). From 2002 to 2015, a 25 % decline in fish biomass was observed, probably linked to the increase of illegal fishing pressure (Chabanet et al. 2016). Glorieuses reefs seem therefore more subject to anthropogenic pressures than the others Scattered Islands and has a lower potential for recovery, which raises concerns for their future.

It would be interesting to compare the temporal trajectories of the reefs of Glorieuses and Mayotte (with higher *RI*s) over the next decades. Indeed, despite the geographical proximity of these two territories, the anthropogenic pressures are different; the reefs of Mayotte are more strongly and directly affected by the impacts of local human populations. The establishment of the Glorieuses marine park, adjacent to the Mayotte marine park, could be an encouraging sign but may only help to address part of the anthropogenic disturbances affecting these reefs. In addition, the effects of marine protected areas can only be patent if these areas are large enough, if regulations are properly enforced and if water quality is maintained. Moreover, local management cannot protect reefs indefinitely from ever-increasing temperature linked to global change (Knowlton & Jackson 2008).

Lowest *RI*s of the SWIO are obtained in the Mascarene Islands (on average, 0.36 compared to 0.48 in the Mozambique Channel). As in the north of the Mozambique Channel, the *RI* is highly variable among Reunion and Rodrigues sites. At Rodrigues, two sites have medium/high recovery potential (O-RB and O-PE, mean *RI* of 0.51) while the two others have low recovery potential (O-IF and O-MO, mean *RI* of 0.33). These differences could be explained by the very high biomass in herbivorous fish observed in O-RB and O-PE and by the high recovery of stress-tolerant coral species (up to 92% of coral cover in O-RB). These differences in *RI* cannot be explained by the geographical position of the sites nor by their protection level.

In 2002 and 2005, bleaching events have impacted Rodrigues reefs, with spatial differences among sites, highest mortality rates being observed in the North and West

sites (Hardman et al. 2004, 2007). While outer reef slopes were often impacted by bleaching events in the past (1998, 2001, 2002, 2005, 2012, 2016; Obura et al. 2017), they also demonstrated substantial recovery, especially in terms of coral cover (Hardman et al. 2004, 2007, Obura et al. 2017). For example, after the bleaching event of 1998, the coral cover measured at 13 Rodrigues sites increased steadily, reaching 50% in 2014 (Obura et al. 2017). In the present study, the data collected in Rodrigues were directly influenced by the 2016 bleaching event, which had a strong impact, especially at O-RB (pers. obs.). Like Hardman et al. (2008), we observed a decrease in coral cover, particularly in favour of the macroalgae *Asparagopsis taxiformis*. Despite the strong impact of bleaching in Rodrigues in 2016, the *RI*s measured are high for O-RB and O-PE, which suggests a good potential for recovery at these sites, as previously observed by Hardman et al. (2008). However, data were collected between 4 months (coral cover) and 2 years (herbivorous fish biomass) after this event, i.e. at different steps in the recovery process, which probably had an impact on the *RI* values. As in Mayotte, the increase in the frequency of bleaching events, combined with anthropogenic stresses is likely to have a significant impact on the recovery potential of Rodrigues sites in the coming years and decades.

On average, Reunion reefs have the lowest measured *RI*s (0.30 compared to 0.42 on average in Rodrigues). The Reunion reefs are more vulnerable than the other studied reefs. Indeed, they are young and therefore weakly developed, and are close to the coast (reef slope included). This proximity leads to many anthropogenic pressures: eutrophication through nutrient inputs, pollution, freshwater inputs or overfishing are particularly important, especially compared to the Scattered Islands (Riaux-Gobin et al. 2011, Naim, Tourrand, Ballesteros, et al. 2013, Bigot et al. 2019). Indeed, the high fishing pressure at Reunion is illustrated by low total fish biomass (not only herbivores) on reef slopes compared with other studied islands. Recovery potential can be greatly reduced by the presence of anthropogenic stresses, such as fishing pressure, coastal development or pollution (West & Salm 2003, Fabricius 2005, Anthony et al. 2015), which could explain the low *RI*s recorded at Reunion sites. In addition, strong cyclones and swells regularly impact the coral communities of Reunion. For example, the strong swells in 2007 have modified the coral community structure on reef slopes, significantly reducing the cover in *Acropora* colonies which have not yet recovered (Bigot et al. 2019). Therefore, we expected to find an important proportion of stress tolerant coral species on these sites.

This is what we observe, especially on the reef sites of Saint Leu (R-MA and R-VS) and this can partly explain the lower impact of the 2016 bleaching event on Reunion reefs compared to Rodrigues (Nicet et al. 2016, Obura et al. 2017) where some sites were greatly dominated by *Acropora* species (like O-RB, largely dominated by *A. abrotanoides* prior to bleaching event, pers. obs.).

Furthermore, since 2007, a decline in diversity and coral cover has been observed on the outer slope of Reunion, accompanied by an increase in algal turf (Bigot et al. 2014), despite the establishment of the Réserve Naturelle Marine de La Réunion MPA, and regardless of the protection status. Conversely, an increase in fish biomass has been observed over the same period. Unlike Rodrigues, the variations in *RI* are consistent with the geographical position of the sites: the reefs of Saint-Leu in the south (R-MA and R-VS) have a better recovery potential than the reefs of La Saline in the north (R-SS and R-SB). However, as for Rodrigues reefs, these variations are not related to the protection status of the sites.

Overall, although only one point in time is available yet, previous studies corroborated that ranking obtained using TOPSIS method is consistent with the responses of the 8 studied sites of Rodrigues and Reunion islands to past disturbances. In addition, our results reveal the overall absence of a relationship between reef recovery potential and the level of protection (outside or within a no-take zone or no-entry zone). Indeed, for Reunion, Rodrigues and Mayotte (where sites exhibit different protection levels), the sites where fishing or human presence are banned do not systematically exhibit the highest *RI*.

This study do not allow us to explain the high variability of *RI* among sites within each island (except Europa). It may be necessary to include more abiotic data through chemical water analyses or turbidity assessment which can influence recovery to improve our understanding of this *RI* variability (McClanahan et al. 2012).

5.2.4.2. The TOPSIS method: strengths and limits in the context of the reef recovery assessment

One of the main principle when choosing a multi-criteria decision method (MCDM) is the simplicity of execution (Saaty & Ergu 2015). In our case, this is particularly

important because the index we developed have to be calculable by any people involved in reef environment conservation, regardless of their mathematical skills. From this point of view, the TOPSIS tool seems interesting as its implementation do not require any particular software (the entire method can be implemented using an excel data sheet or an R environment) nor particular modelling skills. The calculation steps are simple and thus, the TOPSIS analysis does not require a long calculation time (Parkan & Wu 1997) nor high computing power.

Moreover, decisions from MCDM analyses can be relevant only if the decision matrix contain sufficient information, i.e. a sufficient number of variables to identify the problem to be solved as a whole (Saaty & Ergu 2015). In our case, the variables must not only be in sufficient number, but also easy to collect in the field. We use eight variables that can easily be obtained from many reefs by following protocols usually used in reef monitoring programs (see for example Heenan & Williams 2013, Chabanet et al. 2016, Obura et al. 2017). While the number of variables used in the present study may seem small, all were very relevant to assess the potential for reef recovery, as suggested by the literature (McClanahan et al. 2012) and the weight given by the experts to each of these variables (from 3.7/5 for algal cover to 4.3/5 for the proportion of stress-tolerant coral species). However, while the variables must be relatively numerous, they must also be independent (Saaty & Ergu 2015). Indeed, adding highly correlated variables to the decision matrix can increase the complexity of the analysis without providing additional information in order to meet the objectives. In our case, some variables used to characterize reef recovery potential are highly correlated, including coral cover, coral density and algal cover. We also observe that the addition of coral recruitment on artificial tiles (for the sites of Rodrigues and Reunion islands only) in the analyses, a completely independent variable, changes the *RI* ranking of the studied sites but also stabilizes it when the ideal solutions are randomly sampled within the 25 to 50 % of extreme values of the variables distribution ($IS_{Tot/RR}^{25}$ and $IS_{Tot/RR}^{50}$). It would therefore be interesting to complete this analysis by including variables uncorrelated to those already included in the decision matrix, and which would allow a better understanding of the reef's recovery potential. These variables could be related to nutrient load (pollution), sedimentation, connectivity, substrate suitability or coral growth rate (McClanahan et al. 2012). However, these variables are more challenging to collect compared to those used in our study.

The various TOPSIS analyses conducted during this study show that when switching from *IS* based on minimum and maximum values ($IS_{Tot/RR}$) to randomly sampled $IS_{Tot/RR}^{25}$ and $IS_{Tot/RR}^{50}$, the *RI* values and thus the resulting ranking are highly modified. These observations raise the question of the basis on which it is most appropriate to compare the alternatives, here the sites. Classically, one of the challenges of TOPSIS analysis is to avoid the problem of "rank reversal", i.e. the fact that the addition of an alternative (in our case, another sampled site) results in a significant change in the ranking (which can happen if this new alternative has extreme values that will therefore modify the *IS*). This "rank reversal" problem may lead to wrong decision-making (Wang & Luo 2009, García-Cascales & Lamata 2012). Indeed, one of the main criticisms that can be made of the TOPSIS analysis is that it compares the alternatives to ideal solutions one at a time, as if they were independent. However, the ideal solutions themselves are derived from the existing alternatives (Saaty & Ergu 2015). Thus, the ranking of each alternative indirectly depends on the ranking of all the alternatives used to form the ideal solutions. As a result, the addition of an alternative, if it exhibits extreme values, can lead to a change of the overall ranking and, in extreme cases, to the low ranking of initially optimal alternatives and vice versa (García-Cascales & Lamata 2012). In the context of reef recovery, the rank reversal problem arises differently. Indeed, as a solution may be ideal for one island or site but digress from the optimal for another, it is expected that a variation in *IS*, regardless of its origin, will result in a change in ranking. However, this variation reflects an ecological reality and is an interesting and important element to be taken into account in the decision-making process. From our point of view, it is therefore important not to rely only on the ranking obtained with *IS* based on the minimum and maximum values of each variable, but to vary the *IS* within the limits of the observable conditions for each variable, in order to take into account the variability of the optimums that exist between the studied localities.

Besides, assessing recovery potential suggests the use of a baseline state, corresponding to the initial state to which the reef ecosystem may return after facing disturbance(s). The establishment of a reference state requires long-term monitoring of reefs, which remains challenging. Moreover, the reference state of a reef is constantly evolving and the question of the state to be considered as "reference" is complicated, if not impossible to resolve. Indeed, in the absence of long-term surveys, including pre-

global warming data and historical anthropogenic disturbances, it remains difficult to determine the optimal value that each of the variables could reach at any site. The use of a variable *IS* could thus also be an alternative to this baseline problem.

In the present case, we found that using $IS_{Tot/RR}^{25}$ gave a quite stable ranking that was generally consistent with what has been previously observed about reef recovery in the studied sites. We therefore suggest that it could be a simple and effective solution to improve the TOPSIS method in the context in which we used it, even if it would benefit from further experimentations. It should be noted that the rankings obtained with the $IS_{Tot/RR}^{50}$ are very similar, when not identical to those obtained with the $IS_{Tot/RR}^{25}$. However, this $IS_{Tot/RR}^{50}$ option digress from the initial objective of comparing sites to an "optimal" reference. Indeed, in using the $IS_{Tot/RR}^{50}$, the ideal positive and negative solutions may have haphazardly took similar values that were far from the optimums. Moreover, the ranking of each site varied considerably from one iteration to another.

Our results also show ranking changes for the Reunion and Rodrigues islands when the *IS* are based on minimum and maximum values observed for these 8 sites (i.e. when using IS_{RR} rather than IS_{Tot}). These observations raise the question of the spatial scale at which the *IS* should be assessed. In our case, considering the IS_{Tot}, we conclude that the RB and PE sites of Rodrigues have the best potential for recovery in the Mascarene, while considering IS_{RR}, we conclude that the MA site of Reunion have better potential for recovery than both RB and PE sites. In terms of decision-making, the variation in ranking observed between the two types of analyses can have important consequences. Our analysis does not allow us to conclude about the best solution to use (IS_{Tot} or IS_{RR}) but further investigations are to be considered. By computing TOPSIS analyses on the basis of pre-disturbance data with IS_{Tot} and IS_{RR}, and comparing them with recovery data observed in the field, we may determine with which *IS* the closest ranking to reality is obtained.

It would also be interesting to test the effect of adding new variables to the decision matrix on the variation in rankings with IS_{Tot} and IS_{RR}. Indeed, we note that the rankings obtained with both IS_{Tot} and IS_{RR} are very similar when including coral recruitment on artificial tiles variable. We can therefore assume that the number of variables also has an influence on the stability of the TOPSIS ranking.

5.2.5. Conclusion

Our study led to the development of a reef recovery index applied to the SWIO area that is easy to compute and adaptable. Although this index is not yet optimized, particularly in terms of choosing the ideal solutions, it gives promising results and could prove to be a good tool to support RBM. One of the main risks was to propose an index that ultimately reflects health status rather than reef resilience. We avoided this pitfall, since strong recovery potentials are attributed to some "unhealthy" reefs (e.g. characterized by low coral cover or coral density), notably in Rodrigues, which highly suffered from the severe 2016 bleaching event. To optimize this index and fully assess its potential, it would be necessary to monitor the same reefs and compare the previously calculated *RI*s with the responses observed in the field afterwards, in the light of the disturbances experienced.

5.2.6. Appendix

5.2.6.1. Appendix A5 - Expert judgment results

Table A3. Ranking of variables used in TOPSIS analyses performed by 23 experts according to their perceived importance (1: low importance to 5: high importance). The mean ranking was used to weight the variables (STEP3 of the TOPSIS analysis).

Expert answer n°	*Coral specific richness*	*Total coral density*	*Juvenile coral density*	*Coral cover*	*Stress tolerant coral species cover*	*Algal cover*	*Herbivorous fish biomass*
1	1	3	5	3	5	4	5
2	4	3	4	4	5	3	4
3	5	4	4	5	5	3	4
4	5	4	5	4	2	4	3
5	3	3	2	3	5	5	5
6	4	4	5	4	5	4	4
7	5	5	5	5	5	5	5
8	5	3	4	3	5	4	5
9	3	5	4	5	3	5	4
10	5	4	4	3	4	3	2
11	5	4	3	5	4	5	5
12	2	4	5	4	5	3	5
13	4	4	4	3	5	5	4
14	4	3	5	4	5	4	5
15	4	3	4	4	5	3	3
16	5	5	5	5	3	1	3
17	5	4	5	4	4	4	3
18	4	4	3	3	5	4	4
19	5	5	5	5	5	5	5
20	3	4	3	4	3	3	4
21	3	2	2	1	5	2	2
22	4	3	3	3	4	2	3
23	5	5	2	5	2	5	3
Mean	**4.0**	**3.8**	**4.0**	**3.9**	**4.3**	**3.7**	**3.9**

5.2.6.2. Appendix A6 - Multi-criteria decision matrix

Table A4. Summary of the data measured for each variable in the 18 study sites (Mean ± SE). SE were not available for densities in Europa and Mayotte.

Island	*Site*	*Coral specific richness (N)*	*Total coral density (N/100m²)*	*Juvenile coral density (N/100m²)*	*Coral cover (%)*	*Stress tolerant coral species cover (%)*	*Algal cover (%)*	*Herbivorous fish biomass (kg/ha)*	*$SSTa^{+1}$ (%)*
Europa	E-WW	47	4851.52	1666.67	82.58 ± 5.04	44.21 ± 5.18	0.92 ± 0.92	356.84 ± 151.85	8.97
Europa	E-EE	52	3475.00	1275.00	73.32 ± 4.79	39.30 ± 6.67	9.87 ± 0.95	73.28 ± 24.82	8.97
Europa	E-NW	72	3002.86	860.00	51.67 ± 17.81	35.97 ± 6.70	0.25 ± 0.25	566.41 ± 81.04	8.97
Europa	E-NE	35	3040.00	700.00	64.33 ± 4.05	42.32 ± 4.95	0.00 ± 0.00	563.34 ± 252.38	8.97
Glorieuses	G-GS	58	3090.19 ± 112.86	549.51 ± 31.97	32.50 ± 4.73	25.63 ± 2.82	8.33 ± 7.24	575.68 ± 140.49	3.14
Glorieuses	G-LY	56	1051.49 ± 168.85	165.66 ± 25.85	39.93 ± 10.47	29.23 ± 10.17	11.55 ± 0.53	130.37 ± 57.93	3.14
Glorieuses	G-GN	43	3356.16 ± 121.40	576.41 ± 42.45	39.97 ± 6.53	29.20 ± 6.30	9.03 ± 4.18	119.69 ± 14.99	3.14
Mayotte	M-GR	56	4082.40	1300.00	52.17 ± 3.73	14.95 ± 3.04	15.25 ± 3.22	338.70 ± 226.55	3.14
Mayotte	M-PB	67	2199.60	414.29	19.50 ± 3.36	34.42 ± 13.25	18.25 ± 5.53	386.51 ± 229.81	3.14
Mayotte	M-PS	39	2945.20	1250.00	42.58 ± 3.27	23.67 ± 8.57	11.92 ± 2.85	167.45 ± 84.25	3.14
Reunion	R-MA	48	2376.08 ± 227.79	917.18 ± 124.83	24.58 ± 5.93	66.00 ± 8.44	48.54 ± 3.71	205.62 ± 7.08	5.38
Reunion	R-SB	44	1719.90 ± 56.92	510.16 ± 39.87	20.23 ± 2.75	27.56 ± 6.28	52.29 ± 3.29	45.63 ± 15.61	5.38
Reunion	R-SS	57	1792.97 ± 150.22	449.17 ± 91.60	27.87 ± 2.35	28.65 ± 3.13	35.46 ± 3.84	198.90 ± 49.08	5.38
Reunion	R-VS	55	1137.98 ± 101.22	391.43 ± 44.08	22.83 ± 7.54	62.20 ± 2.74	53.50 ± 3.33	406.34 ± 59.25	5.38
Rodrigues	O-IF	35	1413.35 ± 197.50	217.76 ± 31.11	25.32 ± 1.76	60.00 ± 4.11	56.20 ± 4.88	282.35 ± 103.77	8.07
Rodrigues	O-MO	35	2097.49 ± 294.57	440.65 ± 76.51	15.58 ± 1.12	74.77 ± 5.33	51.60 ± 1.65	130.50 ± 15.62	8.07
Rodrigues	O-PE	31	1487.30 ± 154.28	497.57 ± 84.12	23.63 ± 9.72	76.69 ± 4.67	67.38 ± 18.17	635.46 ± 102.77	8.07
Rodrigues	O-RB	32	662.53 ± 223.74	256.66 ± 99.88	13.82 ± 1.29	92.51 ± 7.49	56.72 ± 5.37	883.05 ± 44.46	8.07

5.2.6.3. Appendix A7 - TOPSIS analyses on Rodrigues and Reunion sites

Table A5. Percentage of occurrence of each Reunion and Rodrigues site at each TOPSIS ranking position (1 to 8) for the 1000 iterations of IS_{RR}^{25} (left) and IS_{RR}^{50} (right), without (top) or with (bottom) recruitment rate variable. White: 0 %; Yellow: 0 < % ≤ 25 %; Orange: 25 < % ≤ 50 %; Light red: 50 < % ≤ 75 %; Dark red: 75 < % ≤100 %. The diagonal corresponds to the positions observed for each site with the IS_{RR}.

Position	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
R-MA	24.2	35.9	39.9	0	0	0	0	0
O-PE	75.8	24.2	0	0	0	0	0	0
O-RB	0	39.9	60.1	0	0	0	0	0
R-VS	0	0	0	97.9	2.1	0	0	0
R-SS	0	0	0	0	31.4	62.2	6.4	0
O-MO	0	0	0	2.1	66.3	31.0	0.6	0
O-IF	0	0	0	0	0	6.8	88.1	4.9
R-SB	0	0	0	0	0	0	4.9	95.1

Position	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
R-MA	43.2	25.0	31.8	0	0	0	0	0
O-PE	56.6	43.4	0	0	0	0	0	0
O-RB	0.2	31.6	66.1	2.1	0	0	0	0
R-VS	0	0	2.1	86.8	9.5	1.6	0	0
R-SS	0	0	0	1.8	43.1	51.5	3.6	0
O-MO	0	0	0	9.3	46.8	38.1	5.7	0.1
O-IF	0	0	0	0	0.6	8.8	65.5	25.1
R-SB	0	0	0	0	0	0	25.2	74.8

Position	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
R-MA	89.3	9.9	0.7	0.1	0	0	0	0
R-SB	0.8	23.3	64.3	5.4	6.2	0	0	0
R-VS	9.7	65.0	24.8	0.4	0.1	0	0	0
O-RB	0.2	1.1	7.1	76.8	14.8	0	0	0
O-PE	0	1	3.1	17.3	78.9	0	0	0
R-SS	0	0	0	0	0	81.6	18.4	0
O-MO	0	0	0	0	0	18.4	81.6	0
O-IF	0	0	0	0	0	0	0	100.0

Position	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
R-MA	78.9	12.7	6.2	2.2	0	0	0	0
R-SB	3.6	30.2	36.1	9.7	20.4	0	0	0
R-VS	8.5	38.8	36.5	13.4	2.8	0	0	0
O-RB	2.4	6.4	11.1	57.5	22.2	0.4	0	0
O-PE	6.6	11.9	10.1	17.2	54.2	0	0	0
R-SS	0	0	0	0	0.1	71.2	28.6	0.1
O-MO	0	0	0	0	0.3	28.4	69.2	2.1
O-IF	0	0	0	0	0	0	2.2	97.8

CHAPITRE 6.
DISCUSSION GÉNÉRALE

L'objectif de cette thèse était d'analyser les processus démographiques et la structure des assemblages coralliens à plusieurs échelles dans différents milieux insulaires de la zone du SOOI : des récifs soumis à différents niveaux de pressions anthropiques et des coulées de lave sous-marines. Cette analyse a été menée par le biais de différentes approches : (i) étude des successions écologiques, (ii) caractérisation de la variabilité spatio-temporelle du recrutement, (iii) évaluation du potentiel de récupération des récifs. Au cours de cette discussion générale, je m'attacherai à synthétiser les résultats au regard du contexte écologique actuel de « crise des récifs coralliens ».

6.1. Hétérogénéité spatiale des assemblages coralliens

Les résultats de mes analyses conduites sur la pente externe des récifs de La Réunion (chapitres 3 & 4) et de Rodrigues (chapitre 4) ainsi que sur les coulées de lave de La Réunion (chapitre 3), à profondeur équivalente, ont mis en évidence une hétérogénéité spatiale des assemblages coralliens marquée entre les îles mais également entre les sites d'étude d'une même île voire d'un même récif, en termes de densité, de recouvrement, de structure de taille, de taux de mortalité ou encore de recrutement.

Cette hétérogénéité de la structure des communautés au sein d'un même complexe récifal (quelques centaines de mètres à quelques kilomètres) et d'un même habitat (pente externe, platier récifal ou lagon) a souvent été mise en évidence chez les recrues (e.g. Adjeroud et al. 2007, Sola et al. 2015) ainsi que chez les juvéniles et les adultes coralliens (e.g. Ruiz-Zárate & Arias-González 2004, Penin et al. 2007, Adjeroud et al. 2010, 2013). Si mes travaux de thèses se sont peu concentrés sur les facteurs extrinsèques (biotiques ou abiotiques) qui pourraient expliquer cette hétérogénéité, de précédentes études l'ont associée à la forte variabilité environnementale observée à petite échelle dans les écosystèmes coralliens et induite par de nombreux facteurs tels que les régimes hydrodynamiques locaux (Bode et al. 2006), l'historique des perturbations (Connell et al. 1997), ou encore les interactions benthiques (Adjeroud et al. 2010), parmi lesquels la prédation (Penin et al. 2010).

Comme évoqué dans la discussion du chapitre 3, mes résultats ont montré l'absence de relation claire entre l'hétérogénéité spatiale des assemblages coralliens et les patrons

théoriques de succession (primaire et secondaire) étudiés sur les coulées de lave sous-marines et les récifs de La Réunion.

L'hétérogénéité des assemblages coralliens aux échelles régionale (inter-îles) et locale (inter-sites) s'est également illustrée au travers de l'indice de récupération (RI) évalué pour cinq îles de la zone SOOI (chapitre 5). En effet, toutes les îles excepté Europa ont présenté une grande variabilité de *RI* entre les sites, reflétant la variabilité des différents indicateurs sélectionnés pour leur action sur la capacité de récupération : la diversité et la densité corallienne, le recouvrement en coraux et en algues, la proportion en espèces coralliennes résistantes, la biomasse en poissons herbivores et les anomalies de température des eaux de surface. La variabilité de la capacité de récupération et plus largement de la résilience des récifs a déjà été montrée aux échelles régionale et locale à travers l'étude des taux de recouvrement, de la composition, de la densité, de la structure de taille des coraux ou encore de la densité en poissons sur des récifs de Polynésie française (Done et al. 1991, Adjeroud et al. 2018) et de la Grande Barrière de Corail (Done et al. 1991, Bierwagen et al. 2018). Les résultats de cette thèse sont donc cohérents avec ces références et rappellent l'importance de la notion d'échelle dans l'étude des processus et de la capacité de récupération des récifs face aux perturbations. Si l'on considère la méthode employée (TOPSIS) pour l'évaluation du potentiel de récupération comme robuste et fiable, les résultats obtenus soulignent l'importance de ne pas synthétiser la capacité de récupération à l'échelle d'un récif, au risque de masquer une variabilité importante de cette capacité et d'entrainer des prises de décision erronées ou pour le moins biaisées, en termes de stratégie de conservation.

Bien que l'on ait observé une forte hétérogénéité spatiale des assemblages coralliens, les données de recrutement évalué sur substrats artificiels à La Réunion et Rodrigues (chapitre 4) et les *RI* calculés pour les cinq îles (chapitre 5) suggèrent l'absence d'effet des mesures de protection sur les communautés récifales. En effet, deux sites d'une même île soumis à une réglementation identique en termes de protection peuvent s'avérer plus différents entre eux sur le plan des capacités de recrutement et/ou du potentiel de récupération, que deux sites soumis à des niveaux de protection différents. Les sites étudiés au cours de cette thèse sont pour la plupart intégrés à des AMPs, au sein de zones répondant à des réglementations variées. Tandis que les récifs des Glorieuses et d'Europa (Iles Éparses) sont isolés et interdits d'accès dans leur globalité (ce qui inclus

l'ensemble des sites d'études sélectionnés pour ces îles), certains sites d'études de Mayotte, de Rodrigues et de La Réunion sont situés dans des zones de réglementation générale où l'accès et la pêche sont autorisés tandis que d'autres font partie de zones à minima interdites à la pêche (NTZs). Au cours de ce travail, nous n'avons pas révélé d'effet statistiquement significatif de la protection (à travers l'effet de l'interdiction de la pêche) sur le recrutement corallien dans les récifs de La Réunion et de Rodrigues. Nous avons également observé cette absence d'effet protection sur le potentiel de récupération des récifs de la zone SOOI. Ces observations posent la question de l'efficacité des AMPs notamment dans le contexte actuel du changement climatique et de l'augmentation de la température des eaux.

6.2. Les AMPs face aux enjeux de conservation actuels et futurs

La mise en place d'AMPs reste préconisée afin de soutenir la gestion des récifs coralliens (Roberts et al. 2017), notamment au travers de la RBM, approche particulièrement plébiscitée depuis plusieurs années pour la préservation des récifs coralliens dans le contexte des changements climatiques (Mcleod et al. 2019). Il a été démontré par le passé que les AMPs avaient le potentiel de réduire les explosions démographiques de prédateurs (Sweatman 2008), de restaurer les chaînes alimentaires (Bellwood et al. 2004), de réduire les stress locaux (Bellwood et al. 2004, Wooldridge 2009), de réduire les pertes en coraux (Mellin et al. 2016, Wolff et al. 2018), d'augmenter l'herbivorie qui à son tour facilite le recrutement corallien (Mumby et al. 2007, Selig & Bruno 2010) ou encore d'encourager la récupération des récifs (Mumby & Harborne 2010, Micheli et al. 2012, Perry et al. 2015).

Pour autant, les AMPs ne peuvent pas limiter la fréquence ni l'intensité des événements liés aux changements climatiques, tels que l'augmentation des températures de surface entrainant les blanchissements de masse, qui représentent la principale problématique à laquelle les récifs devront faire face dans les prochaines décennies (Hughes, Barnes, et al. 2017, Hughes, Kerry, et al. 2017, Hughes, Anderson, et al. 2018, Wolff et al. 2018). De plus, l'effet des AMPs sur l'impact de ces épisodes de blanchissement sur les communautés coralliennes n'est pas toujours clairement établi. Si certains auteurs

soulignent l'absence d'effet des AMPs sur l'intensité du blanchissement (Hughes 2003, Mumby & Steneck 2008) et la mortalité qu'il induit (Graham et al. 2007, 2008, McClanahan, Ateweberhan, Muhando, et al. 2007), d'autres montrent que l'atténuation des facteurs de stress locaux via les AMPs (comme la lutte contre des prédateurs corallivores) peut atténuer l'impact des phénomènes de blanchissement corallien à la fois sur la résistance et sur la récupération des assemblages (Mellin et al. 2016, Shaver et al. 2018). Toutefois, Côté and Darling (2010) suggèrent que l'hypothèse d'un effet bénéfique des AMPs pourrait être erronée en ce qui concerne la capacité des communautés coralliennes à résister aux stress d'origine climatique. Les auteurs estiment qu'en protégeant des communautés récifales dominées par des espèces de coraux sensibles aux stress locaux, les AMPs diminuent les capacités de résistance de ces communautés. Au contraire, les récifs protégés, ou peu dégradés, ont tendance à retourner plus rapidement à leur état d'origine suite à une perturbation que les récifs non protégés ou dégradés (Carilli et al. 2009, Mumby & Harborne 2010), bien que plusieurs études suggèrent le contraire (Pratchett et al. 2009, Darling et al. 2010). Mes résultats ne permettent pas de trancher quant à cette question, puisque les indices de récupération calculés au cours de ma thèse ne mettent pas en évidence de relation nette entre le niveau de protection des récifs et leur potentiel de récupération. En effet, si le *RI* moyen le plus élevé est estimé pour l'île supposée la plus préservée et la moins soumise aux pressions anthropiques (Europa), les sites soumis aux plus hauts niveaux de protection (NTZs) à Mayotte, La Réunion et Rodrigues ont des *RI*s équivalents à d'autres sites de ces mêmes îles pour lesquels la protection est minimale.

Quel que soit le niveau de protection légalement décrété, l'efficacité des aires marines protégées dépend, entre autres, de la capacité des populations locales à appliquer les règles associées (Jameson et al. 2002, Arias et al. 2015) et de la capacité des institutions à faire respecter ces règles (Jameson et al. 2002). Dans le cas présent, il est très difficile de savoir si les réglementations associées aux aires marines protégées que j'ai étudiées sont respectées et, le cas échéant, dans quelle mesure elles sont contournées et quel est l'impact sur les populations marines concernées. Des études ont cependant fait état de braconnage dans les parcs marins des îles Éparses (Chabanet et al. 2016) et des braconniers sont régulièrement arrêtés dans la réserve marine de La Réunion (com. RNMR).

Des études de modélisation ont mis en évidence l'effet négatif du braconnage sur l'efficacité des AMPs (Byers & Noonburg 2007, Sethi & Hilborn 2008, Bergseth et al. 2015). Ces études ont montré qu'en plus de l'effet direct sur les populations de poissons au sein des réserves marines et sur les communautés coralliennes associées, le braconnage entrainait également des diminutions du rendement des pêches en dehors des zones protégées en diminuant l'apport larvaire issu des réserves dans les zones avoisinantes (Byers & Noonburg 2007, Sethi & Hilborn 2008). Cependant, si les densités plus importantes de poissons incitent généralement les pêcheurs à braconner au sein des réserves, un investissement initial dans les moyens nécessaires à l'application de la loi permet le maintien des avantages de la mise en réserve pour les pêcheries hors de la zone protégée (Byers & Noonburg 2007).

6.3. RBM et mesures complémentaires pour l'amélioration de la gestion des récifs

Dans le contexte de la RBM, Mcleod et al. (2019) proposent un certain nombre de mesures complémentaires à la mise en place d'AMPs telles que :

- Le maintien des patrons de connectivité : il parait essentiel d'identifier les récifs sources et puits et les récifs fortement connectés de manière à prioriser la conservation des récifs sources les plus susceptibles de favoriser la récupération au sein d'une zone récifale (Schill et al. 2015). Peu de données de connectivité sont disponibles pour les organismes benthiques récifaux à l'échelle de la zone SOOI [mais voir Boissin et al. (2018) sur 17 espèces d'hydraires, et Gélin et al. (2018) sur *Pocillopora damicornis*]. Toutefois, les quelques études qui ont analysé la connectivité d'organismes benthiques à cette échelle ont mis en évidence des niveaux de connectivité faibles, quels que soient les traits d'histoire de vie des organismes étudiés, et la présence de quelques haplotypes (i.e. génotype haploïde) partagés entre bassins océaniques différents, suggérant de rares événements de dispersion dus aux courants (Gélin et al. 2018) ou aux mouvements humains (Boissin et al. 2018). Des analyses complémentaires, notamment sur les trois taxons de scléractiniaires majoritairement observés au cours de cette thèse (*Pocillopora*, *Porites* et *Acropora*) permettraient d'améliorer considérablement les plans de gestions des récifs du SOOI.

- L'adaptation de la gestion en fonction des incertitudes et du changement : à l'avenir, les méthodes de gestion devront être adaptatives, et répondre notamment aux défis liés à l'incertitude, au manque de données sur les processus (e.g. le recrutement) ou encore aux menaces identifiées (Walters 2007).

- L'intégration d'indicateurs sociaux (e.g. changements démographiques ou de politique de gestion) et écologiques afin de mieux évaluer les signaux d'alerte, les patrons de récupération et les changements de régime dans les plans de conservation et de gestion (Bruggemann et al. 2012, Hicks et al. 2016).

Mes travaux de thèse s'inscrivent complétement dans ces deux derniers points puisqu'ils ont permis d'apporter des informations liées aux processus de recrutement corallien et de successions écologiques dans les Mascareignes qui pourront être utilisées pour améliorer les plans de gestion des récifs de la zone. Ils ont de plus permis l'élaboration d'un indice de récupération des récifs du SOOI, intégrant des indicateurs écologiques et notamment le recrutement corallien.

Dans les Mascareignes, les taux de recrutement corallien sont faibles, bien que des taux équivalents aient été observés sur d'autres récifs de la zone SOOI (e.g. Mangubhai et al. 2007). Ces taux, associés à la faible connectivité (Boissin et al. 2018, Gélin et al. 2018) présumée dans cette zone soulèvent la question du potentiel de résilience de ces récifs. Dans le chapitre 5 de ce manuscrit, j'ai mis en évidence le fort impact du recrutement sur les capacités de récupération des récifs des Mascareignes ce qui confirme les recommandations de Obura and Grimsditch (2009) et de McClanahan et al. (2012). En effet, la prise en compte du recrutement au stade le plus précoce (recrutement sur substrats artificiels) augmente nettement le *RI* moyen des sites de La Réunion (0.30 sans recrutement contre 0.52 avec) et le diminue nettement pour les sites de Rodrigues (0.42 sans recrutement contre 0.35 avec).

Cette diminution des *RI*s pour les sites de Rodrigues, lorsqu'on considère le recrutement, est relativement alarmante. En effet, bien qu'aucune différence significative des taux de recrutement n'ait été mise en évidence entre les différents étés testés (périodes durant lesquelles le recrutement est le plus important), une tendance à la diminution sur les sites de La Réunion a été observée et semble se confirmer sur les sites de Rodrigues au regard des derniers relevés effectués (été 2017-2018 ; Sacco J., stage de

M1 en cours). Cette diminution peut en partie être associée à l'événement de blanchissement corallien de masse survenu en 2016 et qui a fortement impacté les récifs de Rodrigues (Hoareau & Lutrand 2017). Ce type d'observation a également été faite sur la GBR où les taux de recrutement ont diminués de 89 % en 2018 par rapport aux niveaux historiques mesurés sur 20 ans (1996-2016) après des stress thermiques survenus en 2016 et 2017 et qui ont entrainé la mortalité massive des communautés coralliennes adultes (Hughes et al. 2019). En parallèle, Hughes et al. (2019) ont montré que, pour la première fois en 2018, les Pocilloporidae « brooders » ont remplacé les Acroporidae « spawners » en tant que taxon dominant du pool de recrutement sur la GBR. À La Réunion comme à Rodrigues, une dominance des Pocilloporidae dans le pool de recrues, quels que soient le site, la saison ou l'année étudiés, a également été observée.

Ces résultats suggèrent que les changements climatiques en cours et à venir pourraient entrainer une augmentation de la dominance des assemblages coralliens par les espèces du genre *Pocillopora* à l'échelle de l'Indo-Pacifique.

6.4. Le cas du genre *Pocillopora* au travers de l'étude des successions écologiques

Le genre *Pocillopora* a déjà été décrit tantôt comme un genre de type opportuniste (Loya 1976, Adjeroud et al. 2005, Perkol-Finkel & Benayahu 2007), tantôt comme un genre pionnier (Connell 1973, Grigg & Maragos 1974, Grigg 1983). Les coraux du genre *Pocillopora* dominent les assemblages coralliens à la fois des adultes, des juvéniles et des recrues sur les récifs de La Réunion (chapitres 3 et 4) comme sur les coulées de laves immergées étudiés au cours de cette thèse (chapitre 3). Mes analyses ont montré que le statut de pionnier, au sens de « premier à s'installer », pouvait en effet être accordé aux espèces du genre *Pocillopora*, notamment *P. grandis* et *P. verrucosa*, présentes sur les coulées de lave les plus jeunes (moins de 10 ans). Toutefois, contrairement aux espèces pionnières décrites dans la théorie de la succession écologique en milieu terrestre (voir Odum 1969, Walker and del Moral 2003), ces travaux de thèse mettent en évidence que les colonies du genre *Pocillopora* ne disparaissent pas au profit d'autres espèces au cours de la succession à La Réunion. Au contraire, elles restent majoritaires en termes de recouvrement corallien et de densité sur l'ensemble des sites de coulées et sur la moitié

des sites de récifs. Ce taxon ne peut donc pas être considéré uniquement comme un taxon pionnier mais également comme un taxon opportuniste caractérisé par une longévité limitée, un turn-over des populations élevé et une aptitude à coloniser des habitats (primaires ou secondaires) à grande échelle spatiale (Kayal et al. 2015).

Les résultats de cette thèse montrent également que les représentants du genre *Pocillopora* semblent être les mieux adaptés aux conditions difficiles (fortes houles notamment cycloniques en saison chaude ou pendant l'hiver austral, fortes houles liées aux dépressions polaires, alizées constants ; Bigot et al. 2019) rencontrées sur les récifs et sur les coulées de lave à La Réunion. Ces observations sont cohérentes avec le classement proposé par Darling et al. (2012) qui considère les espèces de *Pocillopora* (à l'exception de *Pocillopora damicornis*, peu présent sur les pentes externes) comme des compétitrices, c'est à dire des espèces particulièrement efficaces dans leur utilisation des ressources et capables de dominer les communautés coralliennes dans des environnements productifs (Grime 1977, Grime & Pierce 2012). Les résultats de cette thèse suggèrent cependant que les *Pocillopora* sont bien meilleurs compétiteurs que ce qui est simplement considéré par Darling et al. (2012). En effet, les auteurs estiment que les coraux de formes branchues (tels que les *Pocillopora*) ou en plateaux, auraient un avantage compétitif dans des environnements d'eaux calmes, peu profonds, où la luminosité est importante (Baird & Hughes 2000) ; leur croissance rapide permettant la création de canopées faisant ombre et limitant l'accès aux ressources phytoplanctoniques aux compétiteurs (Darling et al. 2012). Au contraire, les espèces caractérisées par ces formes branchues ou en plateaux sont également supposées plus sensibles aux cassures et aux délogements pendant les tempêtes suggérant qu'elles sont moins compétitives en milieu ouvert et agité. La dominance de recouvrement et de densité des espèces du genre *Pocillopora* sur les coulées de lave de La Réunion suggèrent au contraire qu'elles supportent bien ces conditions difficiles.

6.5. Conclusion générale

Les objectifs de ce projet de thèse étaient (i) d'analyser les processus démographiques (installation, survie, croissance et mortalité corallienne) et la structure des assemblages coralliens à plusieurs échelles et dans différents milieux insulaires de la zone SOOI, (ii) d'utiliser ces paramètres pour évaluer le potentiel de récupération des

récifs de cinq îles de cette même zone. Les principaux résultats de mes travaux de thèse peuvent être résumés comme suit :

- Les taux de recrutement corallien sont particulièrement faibles dans les Mascareignes et tendent à diminuer ces dernières années ;

- S'il existe des tendances de succession des communautés coralliennes sur les coulées de lave à La Réunion, elles ne sont pas complétement conformes aux patrons théoriques des successions écologiques. Les résultats de cette thèse associés à ceux basés sur d'autres communautés, notamment en milieu marin, posent des questions quant à l'application des principes de successions écologiques, d'autant plus au regard de l'accroissement des perturbations ;

- Le potentiel de récupération des récifs du SOOI est le plus fort pour les récifs d'Europa et de manière générale plus faible pour les récifs des Mascareignes, soumis à davantage de pressions anthropiques. Le potentiel de récupération des sites de La Réunion augmente toutefois lorsqu'on ajoute le recrutement corallien sur substrats artificiels au calcul de l'indice à l'inverse de celui des sites de Rodrigues ;

- Il existe une forte variabilité des assemblages coralliens, des processus démographiques et du potentiel de récupération des récifs entre les sites au sein des îles ; cette variabilité n'est toutefois liée ni au stade de succession ni au niveau de protection des sites. Aucun effet de la protection (mise en réserve, zones interdites à la pêche) n'a été mis en évidence, ni pour les processus démographiques, ni pour les assemblages coralliens, ni pour le potentiel de récupération des récifs étudiés.

Les résultats acquis au cours de cette thèse apportent un certain nombre d'informations originales, notamment dans le contexte de la gestion basée sur la résilience des récifs coralliens (ou RBM) dont l'objectif est d'assurer la pérennité des écosystèmes dans le contexte actuel des changements globaux. Ils apportent également un outil prometteur pour l'évaluation du potentiel de récupération des récifs coralliens.

Toutefois mes travaux de thèse ont également soulevé un certain nombre de questions d'intérêt majeur dans le contexte actuel de « crise des récifs ». Parmi elles, la question de la connectivité des récifs de la zone SOOI me parait particulièrement

importante. En effet, peu d'études se sont attachées à décrire la connectivité des organismes benthiques dans la zone SOOI (voir Boissin et al. 2018, Gélin et al. 2018) et ces dernières mettent en évidence de faibles taux de connectivité, quels que soient les traits d'histoire de vie des organismes étudiés, ce qui est particulièrement préoccupant. Ces données mériteraient d'être complétées par des études à grande échelle menées sur d'autres espèces de scléractiniaires.

D'autre part, la question de l'évaluation des méthodes de calcul des capacités de récupération des récifs me parait être un élément clé dans le cadre de la RBM. En effet, comme déjà évoqué dans ce manuscrit, pour pouvoir valider les outils d'évaluation du potentiel de récupération des récifs, il est nécessaire de suivre l'ensemble de ces récifs, idéalement avant, pendant et après perturbation, ce qui nécessite toutefois un investissement conséquent en termes de temps et de moyens.

Ainsi, ce travail de recherche doctorale, qui a répondu aux objectifs initiaux, a permis d'établir un socle de connaissances solides sur la structure, la dynamique et les processus de maintien des communautés coralliennes dans la région SOOI. Au vu des changements rapides que les récifs coralliens subissent en réponse aux changements environnementaux, ces travaux devront néanmoins être étoffés et complétés par des travaux de recherche supplémentaires. Cet effort reste indispensable pour améliorer les actions de conservation et de gestion de ces écosystèmes si vulnérables.

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Annexe 1. Article : Variabilité multi-échelles du recrutement corallien dans les Mascareignes (chapitre 4)

PLOS ONE

RESEARCH ARTICLE

Multiscale variability in coral recruitment in the Mascarene Islands: From centimetric to geographical scale

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Abstract

Coral recruitment refers to the processes allowing maintenance and renewal of coral communities. Recruitment success is therefore indispensable for coral reef recovery after disturbances. Recruitment processes are governed by a variety of factors occurring at all spatial and temporal scales, from centimetres to hundreds of kilometres. In the present context of rising disturbances, it is thus of major importance to better understand the relative importance of different scales in this variation, and when possible, the factors associated with these scales. Multiscale spatio-temporal variability of scleractinian coral recruitment was investigated at two of the Mascarene Islands: Reunion and Rodrigues. Recruitment rates and taxonomic composition were examined during three consecutive six-month periods from regional to micro-local scales (i.e. from hundreds of kilometres to few centimetres) and between two protection levels (no-take zones and general protection zones). Very low recruitment rates were observed. Rodrigues displayed lower recruitment rates than Reunion. Recruit assemblage was dominated by Pocilloporidae (77.9%), followed by Acroporidae (9.9%) and Poritidae (5.2%). No protection effect was identified on coral recruitment, despite differences in recruitment rates among sites within islands. Recruits were patchily distributed within sites but no aggregative effect was detected, i.e. the preferentially colonised tiles were not spatially grouped. Recruits settled mainly on the sides of the tiles, especially at Rodrigues, which could be attributed to the high concentration of suspended matter. The variability of recruitment patterns at various spatial scales emphasises the importance of micro- to macro-local variations of the environment in the dynamics and maintenance of coral populations. High temporal variability was also detected, between seasons and years, which may be related to the early 2016 bleaching event at Rodrigues. The low recruitment rates and the absence of protection effect raise questions about the potential for recovery from disturbances of coral reefs in the Mascarene Islands.

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Introduction

Coral recruitment processes, i.e. settlement of larvae and early post-settlement events occurring in the first weeks and months of benthic life largely shape coral reef community structure [1], allowing maintenance and renewal of coral communities through replacement of dead adults [2,3]. An essential component of reef resilience, recruitment largely influences reef recovery following mass mortalities induced by large-scale disturbances [1,4,5]. Coral recruitment success is thus necessary for coral reef recovery after disturbances, and recruitment failure is a known factor of phase shift [2,6].

Recruitment processes are governed by a variety of factors occurring at all spatial and temporal scales, from centimetres to hundreds of kilometres, and from seasons to decades. This creates spatio-temporal variability in measures of recruitment descriptors at all scales that have been investigated so far [7–11]. Among factors that can be cited, recruitment depends upon spawning of adults, that is generally initiated by increasing sea temperature [12], moon phase [13] and wind fields [14]. Fertilization success and embryo survival are influenced by local environmental factors [15,16]. Larval dispersal is mainly driven by larval survival and pelagic larval duration, associated with oceanographic conditions experienced by larvae, like tidal or wind-driven currents [17]. Larval settlement and survival depend on local (metric scale) and micro-local (centimetric scale) parameters such as the presence of biological inducers or competitors [18–21], light [22], sedimentation [23] or herbivorous grazing [24]. At large geographic scales, the biological and ecological processes that sustain coral communities may be affected by disturbances such as cyclones, bleaching events or outbreaks of the coral predator *Acanthaster planci* [25,26]. Moreover, anthropogenic impacts interfere with recruitment processes at the local scale. For example, stressors such as pollution, eutrophication, sedimentation or overfishing have been linked to deleterious effects on coral recruitment [11,27–29]. In the present context of rising disturbance frequency and intensity, coral reefs will have to recover more often than in previous decades [30–32]. It is thus of capital importance to better understand the relative importance of different scales in the spatial and temporal variation of recruitment, and where possible, the factors associated with these variations.

A growing body of literature describes spatio-temporal variability of coral recruitment. Even if long-term studies are scarce (but see [33]), important year to year variation has been documented [1,33,34]. Seasonal variation is also well established, with summer periods typically more favourable for coral settlement [e.g. 8,34,35]. Regarding spatial variability, regional variation appears to be important; six-fold differences were observed among reef regions on the Great Barrier Reef (GBR) [1], and five-fold differences reported among islands of the Society Archipelago (French Polynesia [36]). Within a region or an island, at the scale of a few kilometres, some reefs or sites also typically receive more recruits than others, and these large-scale patterns seem to be consistent in time, among seasons and years [1,34,36,37]. At a much smaller scale, settlement and recruitment vary among micro-habitats as described by differences in recruitment rates among tile orientations [34,37,38]. Between these two scales, local variation patterns, i.e. within-site variation, at the scale of the metre, and its consistency in time has rarely been investigated (but see [39]). This overlooked scale of variation deserves better investigation since many biotic and abiotic factors like competition, predation, light or hydrodynamic conditions vary greatly at this scale (e.g. [24,29,38,40]).

In recent decades, management tools, such as marine protected areas (MPAs), have been developed around the world to limit the anthropogenic impacts on the marine environment. In general, these MPAs delimit different areas in which certain activities, and fishing in particular, are allowed or prohibited [41]. While fishing bans generally improve fish biomass and diversity when enforced [42,43], their effects on coral abundance, while generally positive, are

more tenuous [44,45]. Mechanisms involved in positive effects on corals include lower damage from fishing gear [46] and higher rates of herbivory, tipping the coral-algal competition balance towards coral success [43]. Increases in coral recruitment rates can be expected in this context of lower competition with turf and macroalgae, which are known to limit settlement and survivorship [29,47–49]. In contrast, higher herbivorous fish biomass in MPAs can be linked with higher incidental predation of early stage corals by herbivores [50], but see Mumby [51]. While some studies have compared recruitment rates inside and outside MPAs (e.g. [10,11,52,53]), few have concluded a positive effect of MPAs on coral recruitment (but see [54]).

The present study aims to evaluate (i) the temporal variability of coral recruitment at inter-annual and seasonal scales, as well as the spatial variation of coral recruitment between two islands of the Mascarene Archipelago (hundreds of kms), among sites of each island (km), among tiles within sites (m), and within settlement tiles (cm); as well as (ii) the effects of MPA status (fishing ban) on coral recruitment. Recruitment rates and taxonomic composition were thus examined during three consecutive six-month periods at regional (between two islands, Reunion and Rodrigues), island (between four sites at each island), local (between 20 artificial settlement tiles at each site) and micro-local levels through the orientation of recruits on artificial settlement tiles. The variation of recruitment rates and composition were also examined within and outside no-take zones (NTZs) at both Reunion and Rodrigues reefs.

Material and methods

Ethics statements

Fieldwork was conducted within the Réserve Naturelle Marine de La Réunion (MPA) at Reunion, under research authorization N°2014–27 DEAL/SEB/UBIO, and within South East Marine Protected Area at Rodrigues, under Rodrigues Regional Assembly research authorization N°RA 402/17 Vol II.

Study sites

Reunion and Rodrigues islands are part of the Mascarene Islands, along with Mauritius, in the South-Western Indian Ocean (SWIO). Reunion (21° 07' S, 55° 32' E), one of the overseas French territories, is a volcanic island (*ca*. 70 km long and 50 km wide) located 700 km east of Madagascar. Fringing reefs line the island in a 12 km^2 area along 25 km of coastline on its west and south coasts [55]. Rodrigues (19° 43' S, 63° 25' E) is a small isolated island that is part of the Republic of Mauritius (18.3 km long and 6.5 km wide), and is the easternmost of the Mascarene Islands. It is surrounded by an almost continuous 90 km long reef rim and constitutes a reef area of *ca*. 200 km^2 [56]. Deleterious effects of coral bleaching are growing stronger over the decades in the Mascarene Islands (see [57] at Rodrigues). Reunion and Rodrigues reefs are not immune to other anthropogenic stress either. Increased urbanisation of the Reunion coastline during the last decades drove noticeable eutrophication in the reef environment [58] and a decrease in reef fish stocks in some areas [59]. These phenomena have led to an increase in the relative cover of algae compared to corals [58,60,61]. Consequently, a multiple-use MPA (Réserve Naturelle Marine de La Réunion) was set up in 2007 to address the deterioration of reefs. This MPA, covering an area of over 35 km^2, is divided into three levels of protection: open areas for human activities (general protection zones or GPZs), restricted areas where only some traditional and commercial fishing activities are allowed, and sanctuaries where no activity is allowed, thus corresponding to NTZs (Fig 1). Human pressure is less documented for the Rodrigues reef. In response to overfishing 10 years ago, the local government of Rodrigues implemented four MPAs to the north of the island, but only partial management has

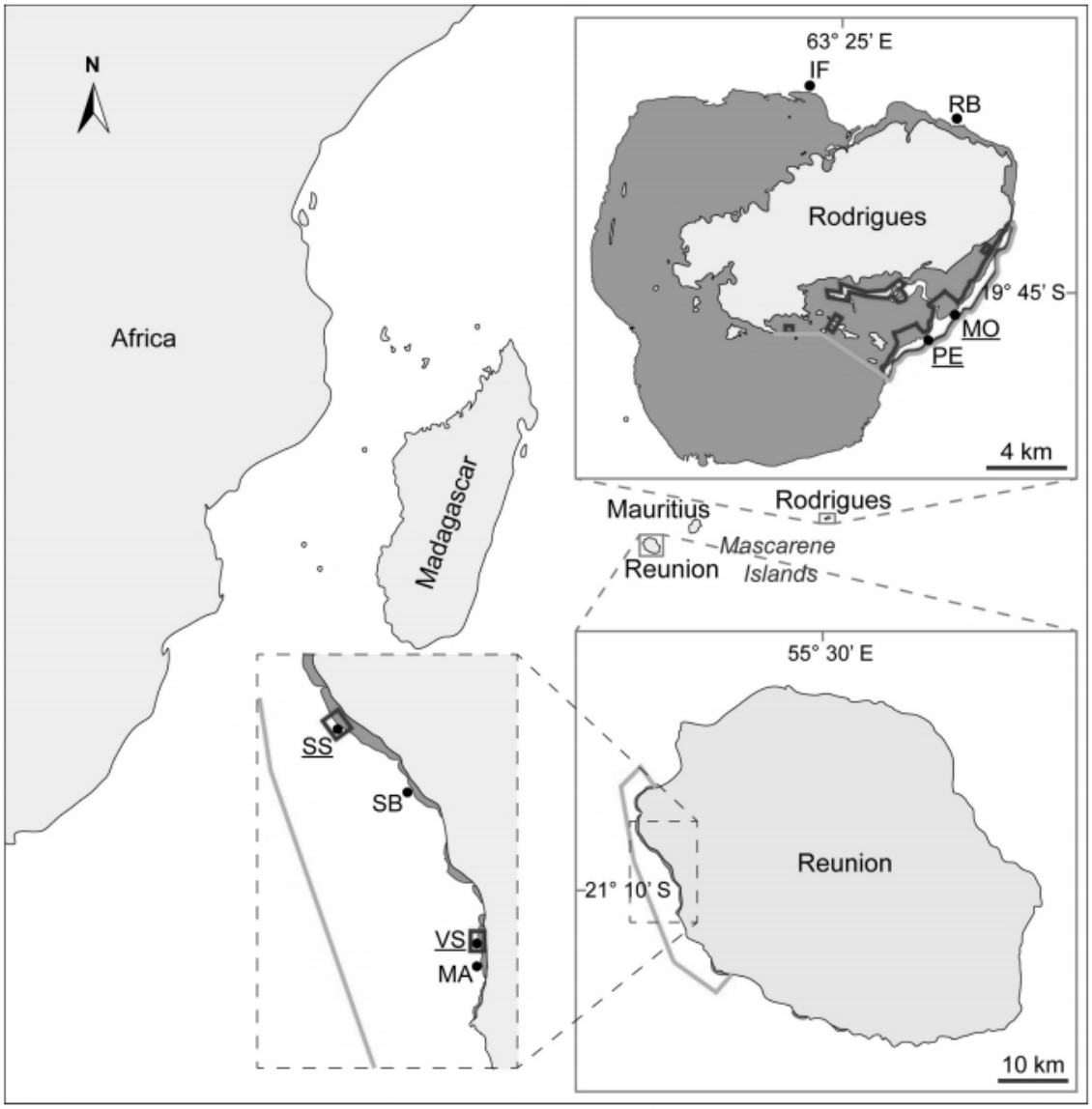

Fig 1. Location of the sampling sites (black dots) on Reunion and Rodrigues reefs. Light grey: land; dark grey: reef flat; orange: MPAs boundaries; red: NTZs boundaries. Underlined sampling sites belong to NTZs. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine; IF: Ile aux Fous; RB: Rivière Banane; MO: Mourouk; PE: Port Sud-Est.

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been set up and fishing still occurs in these areas [62,63]. In addition, the South East Marine Protected Area (SEMPA) is an area in the south-eastern of Rodrigues designated as an MPA in 2009. It includes both inner and outer lagoon covering a total 43.7 km^2 divided into different multiple-use zones, including NTZs where fishing is prohibited (Fig 1).

Sampling strategy

The sampling strategy used four sites on the outer reef slopes at both Reunion and Rodrigues islands, including two sites within a NTZ and two sites outside NTZ for each island (Fig 1). Eight sites were thus sampled and coded as follows: Reunion (SS: Sanctuaire Sud and VS: Varangue Sud in the NTZ; SB: Souris Blanche and MA: Marine in GPZs); Rodrigues (MO: Mourouk and PE: Port Sud-Est in the NTZ; IF: Ile aux Fous and RB: Rivière Banane in GPZs). At all sites, the abundance and taxonomic composition of coral recruits was characterised at 12 m depth on unglazed terracotta settlement tiles [64–68]. For each site, 20 individual tiles (*ca.* 10 × 10 × 2 cm) were immersed for six months over two austral summer periods (October 2015–March 2016, October 2016–March 2017) and one winter period (April–September 2016). Tiles were deployed and spatially referenced within each site at Reunion by measuring distances and azimuth between each tile and a reference point. Typical distance between two consecutive tiles was 1–2 m, while most distant tiles were around 15 to 20 m apart from each other. At the end of the immersion periods, the tiles were retrieved, bleached and sun dried to expose the skeleton of coral recruits (coral spats) for identification and counting under a dissecting microscope. Recruits of the families Acroporidae, Pocilloporidae and Poritidae were discriminated according to morphological traits [69]. Other recruits were assigned to the category 'others' if not associated with one of the previously cited families, or to the category 'broken' when the skeleton was too damaged for identification [34].

Data analyses

In all the analyses described hereafter, abundance of recruits counted per tile was expressed as recruitment rate per m^2 ($recruits m^{-2}$). Spatio-temporal variation of overall recruitment rates (all taxa combined) was evaluated at three different spatial scales: between islands, between protection levels (i.e. within NTZ or outside MPA), and between sites, for three periods (two summers and one winter) using an ANOVA model (Eq 1).

$$T_{ijkl} = m + I_i + Pr_j + S_k + \mathrm{Pe}_l + (IPe)_{il} + (PrPe)_{jl} + \varepsilon_{ijkl} \quad \text{(Eq1)}$$

where i, j, k and l stand for the island, the protection levels, the sites and the periods, respectively, and ε is the residual variance (within sites). The spatial factors correspond to a three-level nested design with protection levels within islands and sites within protection levels. Sites were considered as a random factor. Prior to analyses, normality and homogeneity of the variance of the data set were tested using Shapiro-Wilk and Bartlett tests, respectively. Recruitment rate variable was log(x+1) transformed to meet the assumptions of normality. To analyse differences between levels of the significant factors, Student Pairwise t-tests (SPT) were used.

Spatio-temporal variation of the taxonomic composition was also evaluated at the three different spatial scales (between islands, between protection levels and between sites) for three periods using Chi-squared tests or Fisher's exact test when assumptions for Chi-squared test were not met.

The spatial variation of coral recruitment between tiles was determined by evaluating the effect of geographical distance between pairs of tiles using a Mantel test. These tests will be referred to as Mantel 1 for overall recruitment rates and Mantel 2 for taxonomic composition. Temporal variations of overall recruitment rates were then tested using a Spearman rank correlation test to compare the overall recruitment rates between all period pairs, for each site.

Spatio-temporal variation of recruitment within tiles was assessed by comparing the orientation of recruits over the different surfaces of the tiles (upper, sides and lower) between islands, protection levels and periods independently for four taxonomic categories

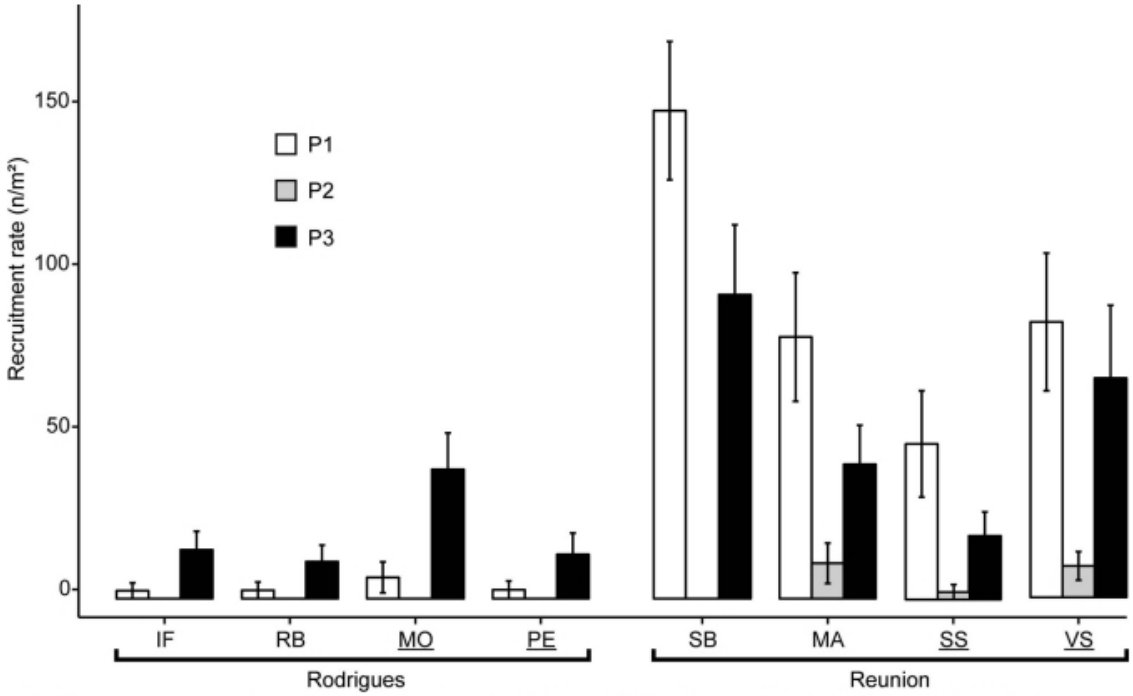

Fig 2. Recruitment rates observed during three consecutive 6-month periods on artificial settlement tiles at 12 m depth among reef slope sites on Rodrigues and Reunion reefs (recruitsm^{-2} ± SE). P1: period 1, i.e. summer 2015–2016 (October 2015–March 2016); P2: winter 2016 (April–September 2016); P3: summer 2016–2017 (October 2016–March 2017). NTZs are underlined. No recruits were observed at Rodrigues (at any site) or at SB site during winter 2016. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine; IF: Ile aux Fous; RB: Rivière Banane; MO: Mourouk; PE: Port Sud-Est.

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(Acroporidae, Pocilloporidae, Poritidae and other families) using Chi-squared tests or Fisher's exact test when assumptions for Chi-squared test were not met.

Results

Spatio-temporal variations of recruitment rates

Recruitment rates ranged from 48 to 150 recruitsm^{-2} during the first summer (October 2015–March 2016) at Reunion while fewer than 7 recruitsm^{-2} were recorded over the same period at Rodrigues (Fig 2). Over the following summer (October 2016–March 2017), recruitment rates were slightly lower at Reunion (20–98 recruitsm^{-2}) compared to the previous summer, while they were higher than observed the year before at Rodrigues, reaching 11–40 recruitsm^{-2}. During the winter (April–September 2016), recruitment rates were extremely low, with fewer than 11 recruitsm^{-2} recorded at Reunion and no recruits at all at Rodrigues. Recruitment rates (all taxa pooled) varied significantly between islands (ANOVA, $P < 0.0001$; Table 1) and among periods (ANOVA, $P < 0.0001$; Table 1). Moreover, the island × period interaction was significant (ANOVA, $P < 0.0001$; Table 1). These differences between periods were mainly due to recruitment variation between both summers and the winter (SPT, $P < 0.0001$; Fig 2), while there were no significant differences between the two summers (SPT, $P > 0.05$; Fig 2). Also, recruitment rates were slightly higher in the NTZ in Rodrigues compared to the GPZ, while it was the contrary at Reunion (Fig 2). Nevertheless, effects of protection level or

protection × period interaction on recruitment rates were not significant (ANOVA, $P > 0.05$; Table 1).

A significant inter-site variability of recruitment rates was recorded (ANOVA, $P < 0.001$; Table 1). While no differences were found between Rodrigues sites, post-hoc tests revealed significant differences between each pair of Reunion sites except between MA and VS, and MA and SS (SPT, $0.0001 < P < 0.05$; Fig 2).

Moreover, an important variability of recruitment rates among individual tiles was observed within each site at Reunion, whatever the protection level (Fig 3). However, no aggregative effects were highlighted among groups of tiles; the geographical distances between tiles were not related to recruitment rates observed on tiles (Mantel 1, $P > 0.05$; Fig 3). From a temporal point of view, there was no relationship in recruitment rates on individual tiles within each site between the two summers (2015–2016 and 2016–2017; Spearman rank tests, $P > 0.05$; Fig 3). This means highest recruitment rates were not observed on the same tile spots over the two consecutive summers.

Spatio-temporal variations of taxonomic composition

The relative contribution of the different families varied significantly between islands (Chi-squared test, $P < 0.0001$; Fig 4). During the two summers, a large dominance of Pocilloporidae (86% on average) was observed at Reunion (Fig 4). At Rodrigues, a shift of the dominant family between summers was noted. Poritidae recruits dominated the first summer (October 2015–March 2016, 80%) while Acroporidae recruits dominated the second summer (October 2016–March 2017; 69%). Consistently, taxonomic composition only varied significantly between the two summers at Rodrigues (Fisher's exact test, $P < 0.04$; Fig 4) and not at Reunion (Fisher's exact test, $P > 0.05$). During the winter, all recruits recorded at Reunion (n = 10) belonged to the Pocilloporidae family.

At both islands, taxonomic composition did not differ significantly between NTZs and GPZs (Fisher's exact tests, $P > 0.05$; Fig 4). Moreover, no difference of taxonomic composition was observed for each pair of sites within both islands (Fisher's exact tests, $P > 0.05$; Fig 4).

As with recruitment rates, taxonomic composition was not related to the relative position of tiles within sites (Mantel 2, $P > 0.05$; Fig 3), implying that tiles close to each other did not display more similar relative proportions of taxa than distant ones.

Spatio-temporal variations of the orientation of recruits

Orientation of recruits on tiles varied significantly between islands (Fisher's exact test, $P < 0.01$). At Rodrigues, recruits settled mainly on the sides of the tiles, to a lesser extent on

Table 1. ANOVA table of the analyses of spatio-temporal variations of coral recruitment rates.

Factor	Df	Mean Square	F	P-value
Island	1	90.378	75.9253	2.20E-16
Protection (within Island)	2	5.153	4.3292	0.67
Site (within Protection)	4	5.864	4.926	5.92E-04
Period	2	48.318	40.5911	2.20E-16
Island x Period	2	26.175	21.9896	3.50E-10
Protection (within Island) x Period	4	2.046	1.719	0.14
Residuals	2204	1.19		

Df: degrees of freedom; F: F-statistic.

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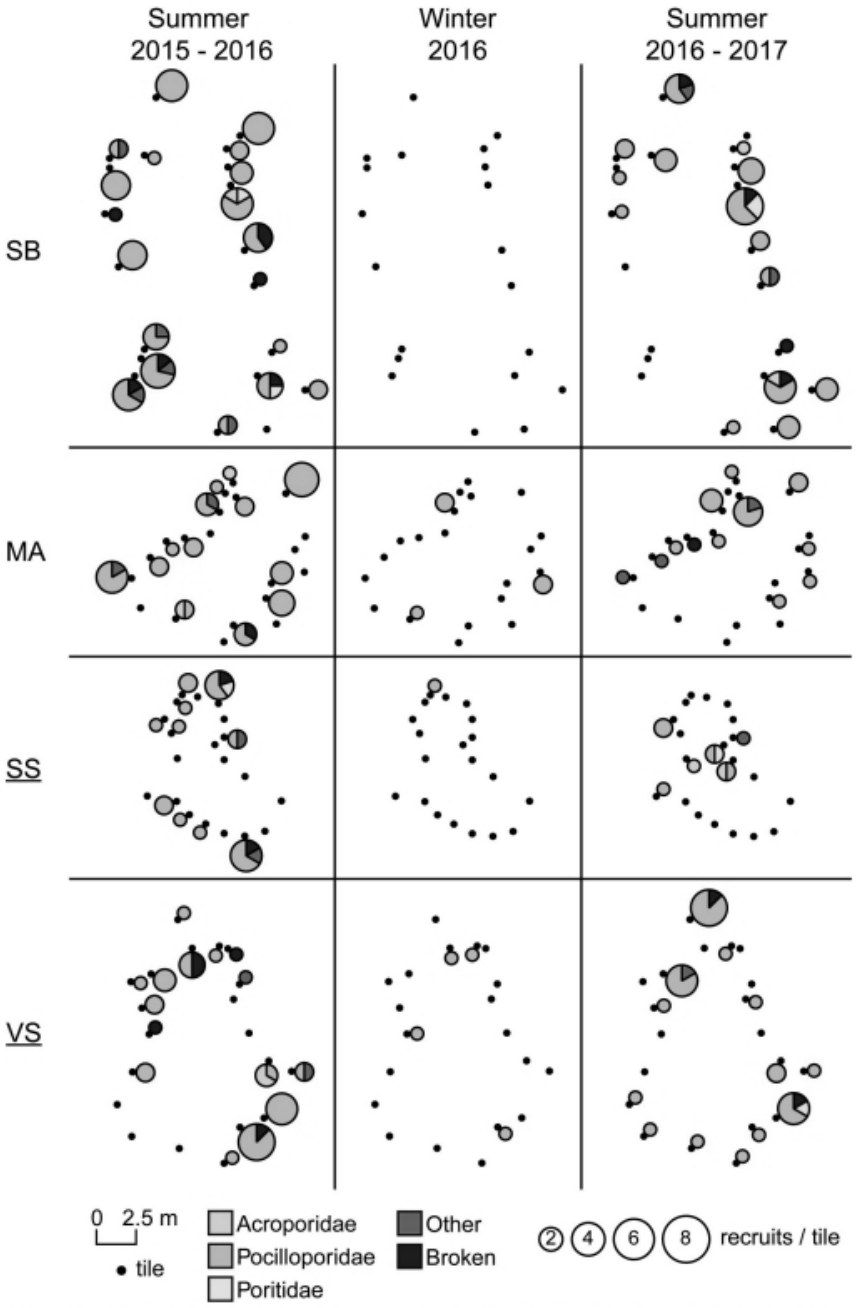

Fig 3. Spatio-temporal variations of number and composition of recruits observed on settlement tiles as they were arranged on the field. Data presented for the four sites at 12 m depth at Reunion, for the three studied periods. Size of pie chart is proportional to numbers of recruits. NTZs sites are underlined. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine.

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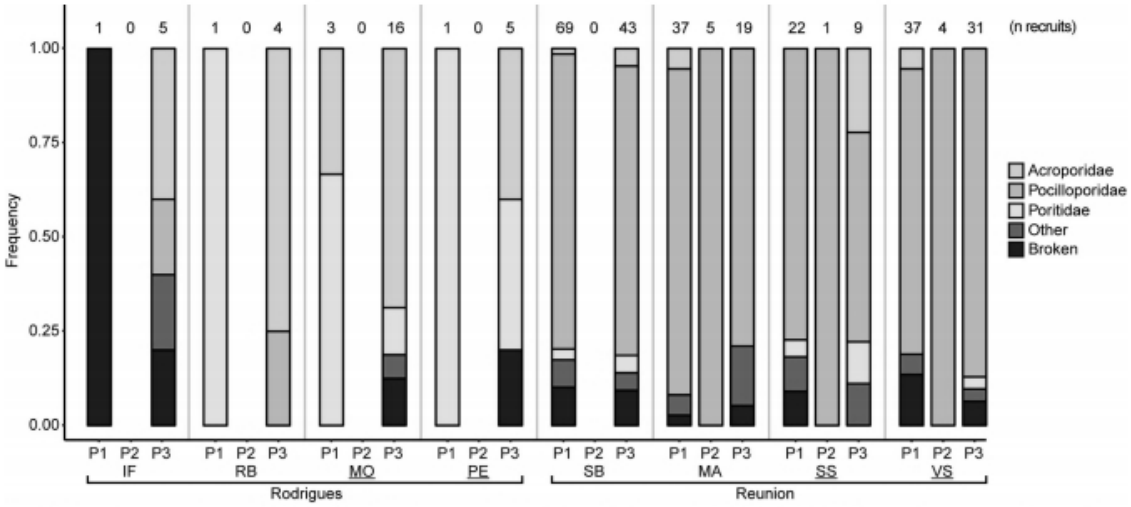

Fig 4. Taxonomic composition of coral recruits observed on artificial settlement tiles at 12 m depth among reef slope sites on Rodrigues and Reunion reefs. P1: period 1, i.e. summer 2015–2016 (October 2015–March 2016); P2: winter 2016 (April–September 2016); P3: summer 2016–2017 (October 2016–March 2017). NTZs sites are underlined. SS: Sanctuaire Sud; SB: Souris Blanche; VS: Varangue Sud; MA: Marine; IF: Ile aux Fous; RB: Rivière Banane; MO: Mourouk; PE: Port Sud-Est.

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the upper side and never on the lower surfaces where light availability was the lowest. At Reunion, recruitment was more evenly distributed, although recruitment rates were higher on the sides of the tiles than on other orientations. The orientation of recruits on tiles was not influenced by the protection level nor by the time period for both islands (Fisher's exact tests, $P > 0.05$).

Discussion

Abundance of recruits

The present study is the first published on coral recruitment within the Mascarene Islands. Results reveal that overall recruitment rates measured on outer reef slopes at Reunion and Rodrigues islands from 2015 to 2017 were low, not exceeding 150 recruitsm^{-2} at Reunion and 40 recruitsm^{-2} at Rodrigues, during the summer. When compared to other reefs in the SWIO, recruitment rates from the present study were much lower than those on the Nyali reef in Kenya (908 recruitsm^{-2} y^{-1}; [53]), along the coast of South Africa (1000 recruitsm^{-2} during peak settlement; [70]), or on the reefs of Vamizi island in Mozambique (1130 recruitsm^{-2} y^{-1}; [10]). However, the recruitment rates at Reunion and Rodrigues islands were similar to those recorded at Coral Gardens in Kenya (101 recruitsm^{-2} y^{-1}; [53]). Recruitment rates observed in this study were also comparable to levels observed in Moorea, French Polynesia [34,66,71] and in some locations of the Red Sea [8]. Even if artificial settlement tiles have been commonly used as a standardised assay of coral recruitment, the comparison of coral recruitment on artificial materials is challenging, due to varying methodology, as noted by Edmunds [72].

Variations of recruitment through protection level

Contrary to what was expected, no significant differences in recruitment rates were found between the NTZs and GPZs. Preservation of fish stocks by NTZ implementation is known to

foster herbivore communities and consequently to promote recovery potential and thus resilience of coral reefs [73–75]. Indeed, herbivory is one of the major factors controlling algal development, which inhibits coral recruitment through competition for space and smothering of recruits by trapped sediments [76]. However, herbivorous grazers, like fish and urchins, can also exert incidental predation on young coral stages [24,77–79]. Overall, most authors consider increasing herbivory as beneficial for coral recruitment (see reviews by [44,80]).

Lack of protection effect on coral recruitment rates in the studied locations may have several causes. The NTZs of both Reunion and Rodrigues islands were set up less than 10 years ago and the direct role of fishing pressure reduction on coral recruitment might not be effective yet. Absence of positive effects on the coral communities in recently protected areas has been previously highlighted [81,82]. In addition, Graham et al. [44] noted that spatial differences in recruitment rates may not necessarily align with NTZs placement and therefore, even if NTZs are effective at enhancing coral cover, this would not necessarily translate into higher local recruitment. These results support the idea that coral recruitment is sensitive mainly to large-scale disturbances whose deleterious effects cannot be directly mitigated by the establishment of a NTZ. In this context, it may be worthwhile to investigate the benefits of placing NTZs in areas of high recruitment, as they are more likely to recover from disturbances than areas with low recruitment rates.

Spatial variability of recruitment

We found significant differences in recruitment rates among Reunion sites while both recruitment rates and taxonomic composition were similar in all sites at Rodrigues. This was surprising as sites at Reunion were all facing west, but sites at Rodrigues faced south-east and north. Thus, differences in recruitment rates could not be attributed to site configuration alone. At Rodrigues, the similarity in taxonomic composition may be mainly due to the low number of recruits.

Rodrigues is a very small and isolated island (about 600 km eastward from Mauritius and several thousand kilometres away from the land towards the other cardinal points). Reefs of the Mascarene Islands are under the influence of the South Equatorial Current (SEC) flowing east to west. Larval dispersal simulations highlighted connections within the Mascarene Islands from Rodrigues to Reunion [83,84]. This is consistent with some recent genetic studies conducted on *Pocillopora damicornis* type beta (Pocilloporidae) in the SWIO highlighting that unidirectional gene flows occur, even if limited, from east to west [85]. Moreover, Gélin et al. [86] showed that populations of *P. damicornis* type beta from the south of Reunion were genetically differentiated from those located in the north and the west of the island. The authors attributed this genetic isolation to a particular connection between the southern reefs of Reunion and Mauritius or Rodrigues reefs through the SEC. However, it was also suggested that the complex currents occurring along the west coast of Reunion might prevent non-local larvae from reaching the western reef, and instead only retain local larvae [86]. Thus, it could be interesting to (i) add sites on the south coast of Reunion to determine whether recruitment rates and taxonomic composition are closer to those observed at Rodrigues and (ii) to combine recruitment and genetic analyses to determine the origin of the recruits and to better understand gene flow occurring among the Mascarene Islands.

Among the different settlement tiles of each site, recruitment rates and taxonomic composition varied greatly, reflecting a patchy distribution, as previously observed in French Polynesia [34] and on the GBR [87]. This variability has also been observed in the structure of adult and juvenile corals in many reefs (e.g. [88,89]), and is likely to be related to the strong environmental heterogeneity encountered at small scales in reef ecosystems [90] and induced by different

factors, such as local-scale hydrodynamic regimes [91], disturbance history [92] or predation [50]. However, no aggregative effect was revealed among spatial groups of tiles when tested within sites at Reunion. This means that tiles with high numbers of recruits were not located in the same area of the site, or particularly close to each other. In parallel, tiles close to each other did not display more similar relative proportions of taxa than distant ones. In terms of methodology, this shows that spatial variability at the scale of the site is correctly sampled. At the same spatial scale, highest recruitment rates were not observed on the same tile spots over the two consecutive summers, suggesting that processes responsible for spatial variation at this scale are not spatially consistent among years.

Within tiles, higher recruitment rates were found on the sides of the tiles deployed both at Reunion and Rodrigues islands, compared to the upper and lower surfaces. These observations were especially true at Rodrigues, where recruits rarely settled on the upper and lower faces of tiles. This may be linked to the higher concentration of suspended matter at Rodrigues than at Reunion (Jouval, pers. obs.). Indeed, this could (i) increase sedimentation on the upper surface of tiles, preventing the recruits from settling on this face and (ii) limit light penetration through the water column, which can prevent recruits from settling on the shady (lower) surface of the tiles. The effects of sedimentation and light availability on coral larvae settlement are often invoked as factors influencing the position of recruits over tiles [11,38,93]. The very weak presence of Pocilloporidae recruits on the upper faces of tiles, while being the most represented recruits in our study, illustrates their sensitivity to sedimentation, as previously observed [94]. The low proportion of recruits found on the upper surfaces of the tiles at both islands may also be a consequence of grazing by herbivorous fish and/or urchins [34,71]. Larval sensitivity to high-intensity light highlighted by other studies (e.g. [95,96]) is unlikely to have inhibited settlement of recruits on upper surfaces of the tiles in our study because of the depth of immersion of the tiles.

Temporal variability of recruitment

At each spatial scale, from regional (between islands) to micro-local (within tiles), a strong period effect was highlighted both on recruitment rates and taxonomic composition, linked to the very low recruitment rates during the winter (April–September 2016), with only Pocilloporidae recruits at Reunion and the complete absence of recruits at Rodrigues. These results were consistent with observations made in the Indo-Pacific, where larval settlement is highly seasonal (e.g. reviewed in [97], [34] in French Polynesia, [98] on the Great Barrier Reef). The dominance of Pocilloporidae recruits on Reunion reefs was consistent with many observations across tropical and sub-tropical reefs of the Indo-Pacific [34,50,53,70,99]. The presence of some Pocilloporidae recruits during the winter at Reunion may have resulted from local asexual reproduction of adult colonies, already documented for this family, by polyp bail-out (*Seriatopora hystrix*, [100]) or by the production of parthenogenetic larvae (*Pocillopora damicornis*, [101]). In particular, at Reunion, Gélin et al. [86] suggested that the lagoonal species *P. damicornis* produces parthenogenetic larvae, but information is lacking for other Pocilloporidae species present on reef slopes. During the two summers (October to March), recruitment rates were higher and the taxonomic composition more diversified compared to the winter (April to September). On Rodrigues reef, recruits of Poritidae were dominant in the first summer, but Acroporidae recruits were highest in the second, while recruitment rates were slightly higher. The first summer studied corresponded to the massive bleaching event of 2016 that affected coral communities of Reunion and Rodrigues islands, thus potentially modifying coral recruitment rates and taxonomic composition. Indeed, numerous studies have revealed that adults of the Acroporidae family are among the most susceptible to bleaching

events [102–104]. The 2016 coral bleaching greatly affected adults of Acroporidae species, especially *Acropora abrotanoides*, which was dominant in some sites at Rodrigues, leading to the death of the majority of them (Jouval, pers. obs.). Since recruitment at Rodrigues is likely to rely mainly on local coral populations, based on the observations about connectivity and currents, this could explain the greater representation of Poritidae recruits in the year of bleaching in Rodrigues. Nevertheless, these observations are related to an overall very low number of recruits at Rodrigues, and thus need to be considered with caution. On the tiles, the highest or lowest recruitment rates were not detected on the same tile from one period to the next. Spatial patterns of variation of recruitment rates within sites were not consistent over the three consecutive periods studied.

Conclusions

Our results demonstrate that recruitment rates were low in the Mascarene Islands, especially at Rodrigues. Recruitment patterns varied greatly at several spatial scales: between islands, and between and within tiles. To a lesser extent, recruitment rates also varied between sites only at Reunion. Both recruitment rates and taxonomic composition displayed great seasonal variation, with very low recruitment rates during the winter. These observations suggested the importance of studying a minimum number of sites, each represented by several replicates (i.e. tiles), to correctly assess the spatio-temporal variability of recruitment patterns between or within reefs. The spatio-temporal variations of recruitment patterns described here have direct implications in terms of conservation, showing that some sites present higher overall recruitment rates, potentially giving these sites a higher capacity for recovery following disturbances. Our study did not highlight any effect of protection on coral recruitment. With low recruitment rates, versatile taxonomic composition over time, and high concentration of suspended matter, Rodrigues appears to be particularly vulnerable to large-scale disturbances.

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RÉSUMÉ

Les récifs coralliens subviennent aux besoins de millions de personnes à travers le monde. Toutefois, les effets du changement climatique et l'accentuation de la fréquence et de l'intensité des perturbations mènent à une accélération de leur dégradation et au déclin des communautés de coraux scléractiniaires. Les préoccupations actuelles portent sur les capacités de résilience de ces écosystèmes vulnérables. Dans ce contexte, il apparait essentiel d'améliorer la compréhension des mécanismes de maintien des communautés coralliennes dans l'optique d'aider à la conservation et à la gestion des récifs.

Ce travail de thèse vise à analyser les processus démographiques, y compris le recrutement, et la structure des assemblages coralliens à plusieurs échelles dans différents milieux insulaires de la zone sud-ouest de l'océan Indien. Ces descripteurs ont été abordés au travers de la succession écologique sur les récifs et coulées de lave sous-marines de La Réunion et par l'évaluation du potentiel de récupération des récifs de cinq systèmes insulaires de la zone.

Les résultats montrent que le recrutement corallien est faible dans les Mascareignes (La Réunion et Rodrigues) et très variable à toutes les échelles spatiales étudiées, de quelques centimètres à plusieurs centaines de kilomètres. Cette variabilité spatiale est également observée entre sites en termes de recouvrement benthique, de densité, de structure de taille, de mortalité ou encore de potentiel de récupération des communautés coralliennes. Cette variabilité spatiale n'est cependant pas clairement liée aux niveaux de protection des sites ni aux patrons théoriques de la succession écologique (étudiés à La Réunion). Un patron de succession est toutefois mis en évidence, au cours duquel la taille des coraux et la richesse spécifique augmentent avec le temps jusqu'à ce que les interactions interspécifiques (e.g. la compétition pour l'espace) conduisent à leur diminution. De plus, une forte dominance du genre *Pocillopora* est observée sur tous les sites de coulées de lave, confirmant sa nature pionnière et compétitive. L'indice de récupération (*RI*) développé suggère que le potentiel de récupération des récifs du canal du Mozambique est supérieur (notamment pour Europa) à celui des récifs des Mascareignes, soumis de manière plus générale aux pressions anthropiques directes. Ces résultats sont cohérents avec les observations passées de la récupération des récifs étudiés suite à des perturbations diverses. L'ajout des taux de recrutement au calcul des *RI* pour La Réunion et Rodrigues modifie nettement le potentiel de récupération des sites de ces îles : les sites ayant les taux de recrutement les plus forts sont également ceux dont le *RI* est le plus élevé.

Ce projet apporte ainsi des informations essentielles sur les communautés récifales de l'océan Indien qui permettront d'améliorer les plans de gestion pour la conservation des récifs coralliens.

Mots clés : Récifs coralliens ; Coulées de lave ; Coraux scléractiniaires ; Succession écologique ; Recrutement ; Potentiel de récupération ; Structure des communautés ; Démographie ; Océan Indien.

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