New quantitative indices from 3D modeling by photogrammetry to monitor coral reef environments

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UMR 9220 ENTROPIE Ecologie mariNe TROpicale des océans Pacifique et IndiEn

THÈSE

Présentée pour l'obtention du grade de docteur de l'Université de La Réunion

Discipline : Écologie marine

Nouveaux indices quantitatifs pour le suivi des récifs coralliens issus de modélisation 3D par photogrammétrie

New quantitative indices from 3D modeling by photogrammetry to monitor coral reef environments

Par Isabel Urbina-Barreto

Soutenue le 12 novembre 2020 à l'Université de La Réunion devant le jury composé de :

Rodolphe **DEVILLERS**	UMR ESPACE-DEV- IRD, Montpellier - France	Rapporteur
Valeriano **PARRAVICINI**	USR CRIOBE, Perpignan - France	Rapporteur
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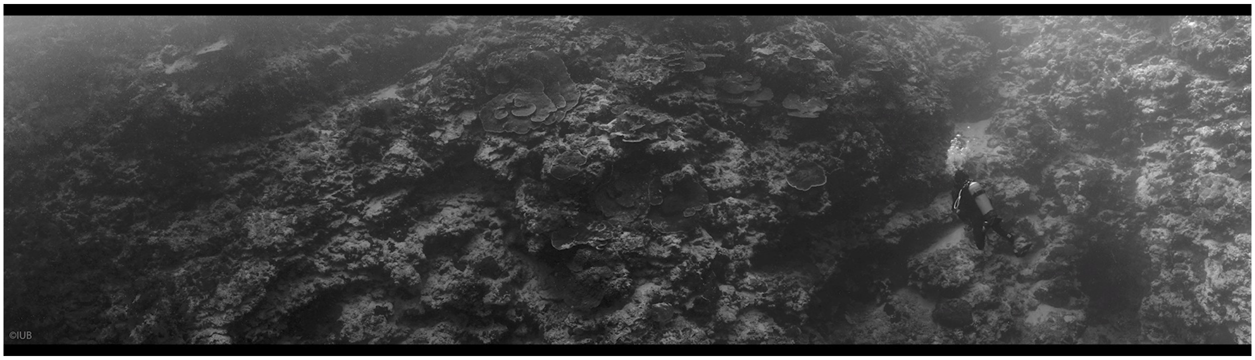
Mehdi **ADJEROUD**	Institut de Recherche pour le Développement	Directeur de thèse

« Pon tu ánimo en la acción, mas nunca en la recompensa. Actúa sin pensar en la retribución; mas no cejes en el cumplimiento de tu labor »
(Verso 2.47, Bhagavad-Gîtâ)

« Tu as le droit d'accomplir le devoir qui t'échoit, mais pas de disposer des fruits de l'acte.
Les fruits du travail ne peuvent pas être ton motif,
et à aucun moment ne cherche à fuir ton devoir»
(Verset 2.47, Bhagavad-Gîtâ)

« You have a right to perform your prescribed duties, but you are not entitled to the fruits of your actions. Never consider yourself to be the cause of the results of your activities,
nor be attached to inaction »
(Verse 2.47, Bhagavad-Gîtâ)



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Résumé

La complexité structurelle de l'habitat joue un rôle clé dans la structure, la dynamique et la capacité de résilience des communautés récifales. La situation critique des récifs coralliens plaide pour l'amélioration des méthodes de suivi, afin d'assister la mise en œuvre de mesures de conservation efficaces. Aujourd'hui, les nouvelles technologies aident les chercheurs et gestionnaires à recueillir des informations spatio-temporelles de haute précision. Parmi elles, la photogrammétrie par *Structure-from-Motion* (SfM) permet de créer des modèles tridimensionnels et de cartographier les zones récifales à partir de photos, afin de réaliser des suivis quantitatifs des communautés benthiques. Quatre objectifs ont structuré cette thèse : 1) définir des protocoles de photogrammétrie sous-marine pour créer des modèles 3D des colonies coralliennes et des récifs permettant de mener des analyses physiques et écologiques, 2) développer de nouveaux descripteurs quantitatifs de l'habitat récifal, 3) déterminer les liens entre ces descripteurs et les fonctions clés assurées par les assemblages de poissons associés, 4) comparer les méthodes photogrammétriques avec une méthode de suivi traditionnellement employée, le *Line Intercept Transect* (LIT). Au total, 120 colonies coralliennes, 24 paysages récifaux de pentes externes et deux structures artificielles (digues) ont été modélisés dans deux régions biogéographiques : la Nouvelle-Calédonie (océan Pacifique), l'île d'Europa et La Réunion (océan Indien). Deux protocoles photogrammétriques ont été mis au point, correspondant aux deux échelles d'étude : la colonie de corail (≤ 2 m^3) et les paysages récifaux et digues (> 100 m^2). Les analyses des modèles 3D de colonies coralliennes ont fourni des mesures 2D et 3D permettant de quantifier le volume de refuge qu'elles offrent. Des modèles linéaires de prédiction ont ensuite été développés pour estimer la capacité de refuge à l'échelle des paysages récifaux. La cartographie des paysages récifaux a permis le calcul de 22 nouveaux descripteurs de l'habitat. Parmi eux, sept ont été retenus pour leur pertinence (la complexité de la surface, la capacité et la diversité des refuges, l'abondance des colonies branchues, tabulaires et massives, et le recouvrement corallienne totale), expliquant respectivement 63 % et 70 % de la distribution des biomasses et des abondances de poissons. L'importance de ces descripteurs pour le maintien de la diversité et la biomasse des groupes de poissons assurant des fonctions clés écosystémiques (herbivorie-bioérosion, production secondaire, assimilation du plancton, prédation, broutage des polypes coralliens) a été montrée. Des comparaisons entre les outils photogrammétriques et la méthode LIT ont révélé que la méthode d'analyse surfacique sur les orthomosaïques, couplée aux modèles numérique d'élévation, est la plus efficace en termes de temps et d'information écologique. Le LIT reste la méthode la moins chronophage et la plus efficace pour les identifications taxonomiques précises. En revanche, elle est la plus limitée en terme de représentativité de l'écosystème. Dans l'ensemble, les travaux de cette thèse ont démontré la pertinence des applications de la photogrammétrie sous-marine par SfM pour les études scientifiques, la gestion et les programmes de sensibilisation des environnements récifaux. En outre, les données collectées et les analyses réalisées contribuent à établir une base de référence pour améliorer les suivis et les mesures de gestion des récifs, et s'inscrivent dans les ambitieux objectifs de conservation du 21ème siècle.

Mots clés : récifs coralliens, SfM-photogrammétrie, modèles 3D, complexité structurelle, descripteurs de l'habitat, méthodes de suivi

Abstract

Habitat structural complexity plays a key role in the dynamics and resilience of coral reef communities. The critical situation of coral reef ecosystems beseeches a rapid improvement of monitoring tools to assist in the implementation of efficient conservation measures. Today, new reef assessment technologies support researchers and managers to collect information safer, faster, and with greater accuracy. Among them, photogrammetry by *Structure-from-Motion* (SfM) creates three-dimensional models and reef zone maps from overlapping images to conduct quantitative surveys of benthic communities. This thesis addressed four objectives: 1) define underwater photogrammetry protocols to create 3D models of coral colonies and reefscapes, in order to conduct physical and ecological assessments, 2) develop new quantitative reef habitat descriptors, 3) determine the links between these descriptors and the key functional processes ensured by associated fish assemblages, 4) compare photogrammetric methods with a traditional monitoring method, the *Line Intercept Transect* (LIT). Overall, 120 coral colonies, 24 reefscapes, and two artificial structures (breakwaters) were 3D modeled in two biogeographic provinces: New Caledonia (Pacific Ocean), Europa Island, and Reunion Island (Indian Ocean). Two photogrammetric protocols were defined corresponding to the study scales: the coral colony (≤ 2 m^3) and the reefscapes and breakwaters (> 100 m^2). Analyzing the 3D models of coral colonies provided 2D and 3D metrics to estimate their shelter volume. Predictive models were then built and fitted to estimate shelter capacity at the reefscape scale. Mapped reefscapes provided the necessary information to calculate 22 new quantitative descriptors. Among them, seven were the most complementary: surface complexity, shelter capacity, diversity of shelter - Shannon Shelter Index, the abundance of branching, massive and tabular, and total coral cover. They explained 63% and 70% of the distribution of reef fish biomass and abundance, respectively. Multifactorial analyses demonstrated the importance of these habitat descriptors in supporting five key functions of reef ecosystems that are ensured by groups of fishes (herbivory-bioerosion, secondary production, plankton assimilation, predation, and coral feeding). Comparisons between photogrammetric methods and the LIT method showed that the surface analysis on the orthomosaics is the most efficient method considering the quantity and quality of data that can be gathered and the time expenditure. The LIT method is less time-consuming and more efficient for specific taxonomic identifications, though it is the most limited method in terms of descriptors and the representativeness of the ecosystem. In addition to the four principle objectives, the 3D models and other photogrammetric outputs served as communication tools in different awareness actions.To sum up, this thesis demonstrated the relevance of underwater SfM photogrammetry applications for coral reef studies, management, and awareness actions. The collected data and their analyses also contribute to establishing a baseline for monitoring the state of reef ecosystems and their functions. In doing so, it provides new scientific information to enhance future management measures and confront the ambitious twenty-first-century conservation targets.

Keywords: coral reefs, SfM-photogrammetry, 3D-models**,** structural complexity, **h**abitat descriptors, survey methods.

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Réaliser un doctorat a été pour moi une extraordinaire aventure au niveau intellectuel, humain et même spirituel ! Je n'aurai clairement pas pu y arriver toute seule. J'essaie ci-dessous de remercier toutes les personnes qui y ont contribué de près ou de loin.

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Pour aller vers mes origines, je passe à l'espagnol pour remercier ma famille et mes amis au Venezuela. Gracias Mamá, Papá, ustedes nos dieron las bases sólidas para que fuéramos unos guerreros y lucháramos por nuestros sueños, éste era uno de mis grandes sueños y se los dedico con todo mi corazón. A mis hermanos, Ifi tu eres la persona con la que más conectada he estado desde que nací gracias por todos los consejos, el apoyo siempre y por ser una inspiración en esta etapa. Jota, tu fuerza y convicción por seguir adelante, no conformarte a medias tintas y escalar más hacia el éxito son ejemplo para mí. Vero, gracias por las ilustraciones hermosas que acompañan parte mis ideas. Keyla gracias por los ánimos en esta última etapa. A pesar de la diáspora que vivimos el apoyo y amor que nos damos es incondicional, la distancia es una prueba de todos los días pero la afrontamos con dignidad y entereza, los extraño enormemente. Je veux remercier aussi à ma belle famille, Claudine, Vic, Tristan, Tonton Jacques, mamie Hélène, Bertrand, Annie, les cousin.es... Merci de votre amour, je me sens très chanceuse de vous avoir.

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Pour finir, et c'est toujours pour la fin qu'on garde le plus difficile à exprimer en mots, merci Sim pour notre aventure sans limites. Qui aurait dit quand on s'est rencontré il y a plus de neuf ans dans un petit bout de terre dans la mer des Caraïbes qu'on allait tenir autant et qu'on allait s'aimer autant ! Celle-ci a été une épreuve de feu, mais on a réussi Doudi-du ! C'est fait, on arrive main dans la main à ce sommet auquel on rêvait. Le paysage qu'on a peint ces dernières années est magnifique et me procure un immense bonheur. Merci sans toi cette réussite n'aurait pas été si magique, on est prêts à regonfler les voiles et surfer la nouvelle aventure. Gracias flaco de mi vida, por estar ahí, por todo lo que hemos aprendido y todo lo que nos queda por aprender, teniéndonos siempre el uno al otro,

"Parecían que estaban a punto de caerse, pero no:
cuando ella tropezaba, la sostenía él,
cuando él se lamentaba, lo enderezaba ella.
A dúo andaban, bien agarraditos el uno del otro,
Pegados el uno al otro en los vaivenes del mundo"
Eduardo Galeano.

Seguiremos soñando grande...

Foreword

This Thesis was supported by a CIFRE fellowship (*Convention Industrielle de Formation par la Recherche*) from the French Association of Research and Technologies (ANRT) under the agreement number 2017/0322. This type of funding promotes developing skills in the applied sciences in the private domain while enhancing national competencies in technology and research. Thus, the fellowships require a host company and a research laboratory, in this case the environmental consultancy Creocean Océan Indien and the UMR Entropie at the University of Reunion Island, respectively. Geolab Company was also an essential technical partner in this Thesis, with participation logically corresponding to the interdisciplinary nature of the marine ecology and geomatic technologies in this study. From the beginning, Geolab provided technological and methodological guidance on essential aspects to achieve the objectives of this program and make efficient progress in the investigations. The project was also supported by Agence de l'Eau Rhône-Méditerranée-Corse. I found the diverse exchanges between actors in both applied and fundamental sciences greatly rewarding, reinforcing my conviction to continue in applied research and conservation science.

This Ph.D. began in October 2017, and I spent most of my time at the UMR Entropie lab (80%) and at Creocean OI (20%) at Reunion Island. Complementing my study in Reunion, I participated in the CORCOPA program, which studied ecoacoustics and the 3D modeling of reefs around Europa Island (BEST 2.0 grant). I also carried out a scientific mission studying reefs in New Caledonia, hosted by the Institut de Recherche pour le Dévelopment in Nouméa (IRD - UMR Entropie). Overall, these experiences fostered constructive collaborations and allowed for a wide representation of study sites, which was crucial to address the different axes of this Ph.D.

On a personal note, this Thesis allowed me to contribute my humble grain of sand to the worldwide efforts for coral reef ecosystem preservation. There is more to do, enhancing and applying tools and knowledge, and I will for sure keep going on this passionate adventure!

Scientific Contributions

Publications

Urbina-Barreto I., Chiroleu F., Pinel R., Fréchon L., Mahamadaly V., Elise S., Kulbicki M., Quod J.P., Dutrieux E., Garnier R., Bruggemann J. H., Penin L., Adjeroud M. (2020) Quantifying the shelter capacity of coral reefs using photogrammetric 3D modelling, from colonies to reefscapes. *Ecological Indicators.* https://doi.org/10.1016/j.ecolind.2020.107151

Urbina-Barreto I., Elise S., Bruggemann J. H., Pinel R., Kulbicki M., Vigliola L., Mou-Tham G., Guilhaumon F., Mahamadaly V., Facon M., Bureau S., Peignon C., Dutrieux E., Garnier R., Penin L., Adjeroud M. (in review). Underwater photogrammetry reveals new links between the habitat and fish community structures that ensure key functions of coral reefs. *Ecological Applications.*

Urbina-Barreto I., Garnier R., Elise S., Pinel R., Dumas P., Peignon C., Mahamadaly V., Facon M., Bureau S., Quod J.P., Dutrieux E., Penin L., Adjeroud M. (submitted) Which method for which purpose? A comparison of Line Intercept Transect and underwater photogrammetry for coral reef survey. *Coral Reefs.*

Elise S., Bailly A., **Urbina-Barreto I.,** Mou-Tham G., Chiroleu F., Vigliola L., William D. R., Bruggemann J. H. (2019a). An optimised passive acoustic sampling scheme to discriminate among coral reefs' ecological states. *Ecological Indicators, 107(August),* 105627. doi:10.1016/j.ecolind.2019.105627.

Elise S., **Urbina-Barreto I.,** Pinel R., Mahamadaly V., Bureau S., Penin L., Adjeroud M., Kulbucki M., Bruggemann J. H. (2019b). Assessing key ecosystem functions through soundscapes: A new perspective from coral reefs. *Ecological Indicators, 107(April).* doi:10.1016/j.ecolind.2019.105623.

International conferences

Urbina-Barreto I., Pinel R., Mahamadaly V., Elise S., Facon M., Bureau S., Garnier R., Penin L., Adjeroud M. (2019). Photogrammetric three-dimensional modeling as a promising tool for characterization and management of coral reef ecosystems. 11th WIOMSA Scientific Symposium, Mauritius, 1-6, **July 2019**. **Oral presentation**.

Urbina-Barreto I., Chiroleu F., Pinel R., Fréchon L., Mahamadaly V., Elise S., Kulbicki M., Quod J.P., Dutrieux E., Garnier R., Penin L., Adjeroud M. (2021). Predicting shelter capacity of reef building corals using 3D modeling by photogrammetry, from colonies to reefscapes. International Coral Reef Symposium, Bremen, **1-7 July 2020**, postponed to 18-23 July 2021**. Oral presentation.**

Mahamadaly V., **Urbina-Barreto I.,** Pinel R., Fréchon L., Garnier R, Reveret C, Dutrieux E, Penin L, Adjeroud M (2021). Underwater photogrammetry as a tool to quantify coral colonies and reef seascapes characteristics. XXIV Congress of the International Society for Photogrammetry and Remote Sensing, Nice, **14-20 June 2020,** postponed to 4-10 July 2021**. Oral presentation**

Mahamadaly V., Garnier R., **Urbina-Barreto I.,** Pinel R., Delaunay T. Underwater photogrammetric 3D models as environmental assessment tools for artificial structures and coral reefs management. Offshore Technology Conference (2021).

Internship supervision

Fréchon, Louis. (January to June 2019). Analyses de modèles de colonies coralliennes obtenues pas photogrammétrie sous-marine. Co-supervision with Romain Pinel (Geolab). Master 2 BEST-ALI - University of Reunion.

Scientific outreach and awareness actions

September 2018 – Presentation "*Tecniques innovantes pour l'étude des récifs coralliens : la photogrammétrie sous-marine et ses possibles applications"* - La Semaine des Récifs Coralliens à L'Université de La Réunion, Saint Denis, Reunion Island.

September 2018 – Participation in the first edition of "*La Nuit de Chercheurs.euse*" workshop "*Speed Searching"* (https://www.youtube.com/watch?v=UWi-CXZgxT4), Saint Denis, Reunion Island.

December 2018 – Media Ph.D. Thesis video (https://www.youtube.com/watch?v=73kOjif8pHE).

February 2019 – Oral presentation "*Parcours de recherche en écologie de récifs coralliens: des methods traditionelles aux méthodes innovantes, les applications de la photogrammétrie sous-marine* " BioEcoTrop seminary – University of Reunion Island.

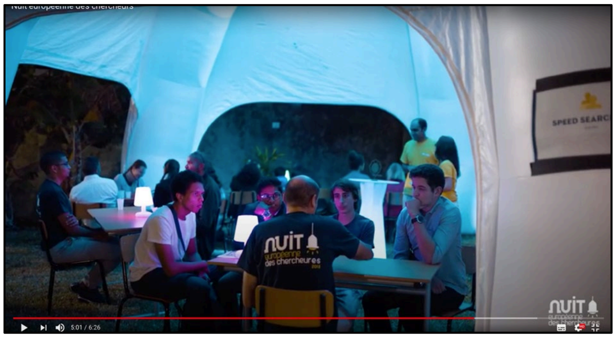
April 2019 – oral presentation of Ph.D. program and first results – IRD Nouméa, New Caledonia.

September 2019 – Participation in the second edition "*La Nuit de Chercheurs.euse*", workshop "*Bureau des Histoires"* (https://www.youtube.com/watch?v=1YVLJRjCqw4) and documentary projection of Corpcopa project: https://www.youtube.com/watch?v=WKosR7e4FoY (English version); https://www.youtube.com/watch?v=2c-S13h-AtE&t=5s (French version), and exchanges with the audience after the screening, Saint Denis, Reunion Island.

November 2019 – Participation in *"La Fête de la Science"*, workshop immersive experience in Virtual Reality of the Antonio Lorenzo shipwreck (https://vimeo.com/247301736) and printed 3D models of corals colonies versus real colonies skeletons - University of Reunion Island.

Photos of awareness actions





Nuit des chercheur.euses - 2018/2019



Fête de la Science 2019

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Glossary of abbreviations

AUV	Autonomous Underwater Vehicles
CCA	Canonical Correspondence Analyses
CIFRE	Conventions Industrielles de Formation par la REcherche
CORCOPA	Conservation Optimisée des Récifs COralliens d'EuroPA
DEM	Digital Elevation Model
DRR	Digital Reef Rugosity
GIS	Geographic Information System
GPS	Global Positioning System
GSD	Ground Sampling Distance
FE	Functional Entity
FD	Fractal Dimension
ISPRS	International Society for Photogrammetry and Remote Sensing
LIT	Line Intercept Transect
LHT	Life History Trait
MPA	Marine Protected Area
MSA	Medium Scale Approach
NGO	Non-Governmental Organization
NOAA	National Oceanic and Atmospheric Administration
PIT	Point Intercept transect
RHI	Reef Health Index
SfM	Structure from Motion
SSI	Shannon Shelter Index
ROV	Remote Operate Vehicles
SCUBA	Self-Contained Underwater Breathing Apparatus
UVC	Underwater Visual Census
VIF	Variance Inflation Factor

Synthèse des travaux en français

1. Contexte et objectifs

Les écosystèmes coralliens sont parmi les plus diversifiés de la planète. A travers les pêcheries, la protection du trait de côte, les matériaux de construction ou le tourisme, ils fournissent des biens et des services à plusieurs millions de personnes au niveau mondial (Moberg and Folke 1999 ; NOAA Office for Coastal Management; Costanza et al. 2014). Bien qu'ils ne représentent qu'environ 0,1% de la surface des océans, les récifs coralliens abritent 25% des espèces marines. Les coraux, qui sont les principaux bio-constructeurs de récifs, ont un rôle clef dans le maintien de cette biodiversité, car ils représentent une source d'habitat et de nourriture pour de nombreuses espèces récifales. Dans ce contexte, l'objectif majeur des gestionnaires des écosystèmes coralliens est de mettre en œuvre des mesures efficaces pour maintenir leur structure et leur biodiversité, ainsi que leur capacité à fournir des biens et des services (Bellwood et al., 2004). La détection des liens qui existent entre la biodiversité, le fonctionnement des écosystèmes et les services écosystémiques qui leur sont associés fait figure de priorité (Costanza et al., 1997, 2014 ; Naeem et al., 2012 ; Belwood et al., 2019).

Depuis les premières études quantitatives sur la structure des communautés benthiques récifales dans les années 60, différentes méthodologies ont été développées. Les techniques *in situ* les plus utilisées ont été les transects (lignes matérialisées par un ruban ou un décamètre en dessous desquels sont recensées les espèces cibles) et les quadrats (carrés ou rectangles à l'intérieur desquels sont recensées les espèces cibles ; Hill and Wilkinson 2004 ; Leujak and Ormond 2007 ; Facon et al., 2015). Les avancées technologiques et la popularisation de la photo et de la vidéo sous-marines ont permis l'avènement d'autres méthodes d'échantillonnage comme les photoquadrats et les suivis par vidéo. Toutes ces techniques (transect, quadrats, photo et vidéo) permettent notamment de calculer des pourcentages de recouvrement en projection plane (2D), un des descripteurs les plus couramment utilisé pour évaluer l'état de santé des récifs, mais ne sont pas ou peu adaptées à la caractérisation tridimensionnelle (3D) d'un récif (ex. volume des colonies, complexité structurelle et rugosité de l'habitat). Cette limitation est particulièrement problématique pour l'étude des écosystèmes coralliens dont la complexité structurelle, définie comme étant la structure physique tridimensionnelle, est une caractéristique fondamentale (Friedman et al., 2012 ; Graham and Nash, 2013 ; Figueira et al., 2015 ; Gutierrez-Heredia et al., 2016).

Dans les récifs coralliens, la complexité structurelle résulte de l'interaction entre les structures tridimensionnelles créées par les organismes bio-constructeurs et les caractéristiques géomorphologiques du substrat (Kovalenko et al., 2012 ; Graham and Nash 2013). La structure et la dynamique des communautés récifales sont étroitement liées à la complexité structurelle (Mouillot et al., 2014 ; Pratchett et al., 2014 ; Ferrari et al., 2016; González-Rivero et al., 2017), qui conditionne de nombreux processus écologiques (Friedman et al., 2012 ; Figueira et al. 2015 ; Gutierrez-Heredia et al. 2016). Ainsi, une structure tridimensionnelle élevée offre davantage de micro-habitats propices à l'installation de nombreux invertébrés benthiques et poissons (Chabanet et al., 1997 ; Ferrari et al., 2017a). Ces organismes y trouvent refuge, notamment au cours des premiers stades de vie. De plus, les processus écologiques majeurs, comme la fixation et le recrutement des larves de coraux semblent liés aux caractéristiques 3D de l'écosystème (dimensions fractales), mais peu d'études précises ont pu tester précisément cette hypothèse et les mécanismes sous-jacents demeurent mal connus. Par ailleurs, la complexité structurelle semble conditionner la stabilité des écosystèmes et leur résistance aux perturbations. Par exemple, de nombreuses études indiquent que l'abondance et la diversité d'habitats conditionnent la résilience et les processus écologiques clés du maintien des récifs (Luckhurst and Luckhurst 1978 ; Sano et al., 1984 ; Wilson et al., 2007 ; Nyström et al., 2008 ; Graham et al., 2011b). La compréhension du rôle de la complexité structurelle dans les récifs coralliens est devenue fondamentale pour préserver leur biodiversité et les services écosystémiques dans le contexte de dégradation croissante de ces écosystèmes (Beukers and Jones 1997 ; Hu et al., 2012 ; Kovalenko et al., 2012 ; Graham and Nash 2013 ; Bozec et al., 2015). Malgré l'importance d'estimer ces caractéristiques tridimensionnelles dans les récifs coralliens (Beukers and Jones 1997 ; Johansen et al., 2008 ; Rogers et al., 2014), leur quantification reste difficile à l'heure actuelle (Bellwood et al., 2004 ; Alvarez-Filip et al., 2009 ; Kovalenko et al., 2012). De nouvelles approches, qui cherchent à étudier les liens entre la structure 3D et les traits de vies des espèces de coraux, ouvrent de nouvelles perspectives d'études (Denis et al., 2017).

En parallèle, les avancées récentes dans les domaines de l'informatique, dont l'amélioration de la puissance des traitements numériques, permettent aujourd'hui de générer des modèles 3D et des orthomosaïques (imagerie 2D) de façon efficace en termes de coût et de temps (McCarthy and Benjamin 2014 ; Burns et al., 2015a,b ; Gutierrez-Heredia et al., 2016). La photogrammétrie par « Structure from Motion » (SfM) est une technique qui permet de générer un modèle 3D d'une structure à partir de photos 2D prises selon différents angles. Cette technique, déjà éprouvée en milieu aérien et terrestre, se révèle être une approche efficace, accessible et à bas coûts (en comparaison à d'autres techniques 3D, comme par exemple le LIDAR aéroporté) pour représenter des topographies complexes (Westoby et al., 2012 ; Fonstad et al., 2013 ; D'Urban et al., 2020). En milieu sous-marin, la photogrammétrie, bien que moins développée qu'en milieu aérien et terrestre, permet de créer des modèles tridimensionnels de récifs et a montré son intérêt à différentes échelles spatiales, allant de la colonie corallienne ou de l'organisme benthique (e.g. Bythell et al., 2001 ; Cocito et al., 2003 ; Abdo et al., 2006 ; Figueira et al., 2015 ; Gutierrez-Heredia et al., 2016 ; Denis et al., 2017) à la communauté et au paysage (e.g. Hu et al., 2012 ; Burns et al. 2015a; Rende et al. 2015 ; Ferrari et al. 2016 ; Storlazzi et al. 2016, Fukunaga et al. 2019). La reconstitution 3D par photogrammétrie sous-marine permet également le suivi temporel des communautés récifales (Burns et al., 2016a ; Storlazzi et al., 2016 ; Ferrari et al., 2017b). Outre le calcul précis des descripteurs classiques utilisés pour caractériser les communautés et les habitats benthiques (pourcentages de recouvrement, diversité, etc.), les analyses photogrammétriques permettent de définir de nouveaux descripteurs des caractéristiques physiques du récif, tels que la complexité du substrat, les volumes des colonies coralliennes, ainsi que la rugosité, la pente et des composantes benthiques et du paysage.

Dans ce contexte, l'objectif principal de cette thèse est de mieux comprendre le rôle de la complexité structurelle du récif corallien dans la structure de ses communautés benthiques et de la biodiversité ichtyologique associée, à partir de l'analyse quantitative des modèles 3D. L'objectif est également de tester l'application de ces nouveaux outils pour les suivis écologiques des environnements récifaux et structures artificielles immergées. Cette thèse comprend une introduction générale (Chapitre 1), une présentation des matériels et méthodes utilisés pour l'étude (Chapitre 2), les études publiés ou en révision dans des journaux scientifiques internationaux (Chapitres 3, 4, 5) et une discussion générale (chapitre 6). Dans l'ensemble l'étude se structure en trois axes de recherche (à l'origine des trois publications), qui abordent des questions complémentaires :

Axe 1 – Développement de descripteurs quantitatifs des caractéristiques physiques de l'habitat à partir des modèles 3D

- Quels descripteurs issus des modèles 3D permettent de quantifier précisément la capacité et la diversité de refuge à l'échelle des colonies coralliennes ?
- Quels sont les descripteurs les plus pertinents pour caractériser la structure tridimensionnelle des habitats à l'échelle des paysages récifaux et quantifier leur variabilité spatiale et temporelle ?

Axe 2 – Analyse des liens entre la complexité structurelle des habitats récifaux, la dynamique des communautés benthiques et la biodiversité associée (peuplements de poissons)

- Les différences de capacité de refuge et des caractéristiques de l'habitat des paysages récifaux expliquent-t-elles la variabilité des assemblages de poissons associés à ces paysages ?
- Dans quelle mesure les processus écologiques sont-ils déterminés par ces caractéristiques de l'habitat ?

Axe 3 – Comparaison de l'approche 3D par photogrammétrie avec les méthodes traditionnelles

- Quels sont les avantages et inconvénients de la méthode photogrammétrique pour la caractérisation et le suivi des communautés benthiques par rapport à la méthode traditionnelle LIT ?

A partir de ces trois objectifs principaux, un objectif technique majeur de la thèse est proposé :

- Développer des protocoles photogrammétriques faciles à déployer et reproductibles pour générer des modèles tridimensionnels adaptés aux deux échelles d'étude : (i) colonie de corail (deux mètres cubes ou moins), (ii) paysage récifal et structure artificielle (centaines de mètres carrés).

Objectif transversal : les modèles 3D comme supports de communication efficaces

Utiliser des modèles 3D comme supports visuels pour la présentation des résultats des communautés benthiques et plus largement participer à des activités de vulgarisation scientifique. En effet, la qualité du rendu visuel des modèles 3D améliore la communication et compréhension des résultats aux gestionnaires, décideurs et mandataires de services et peut se révéler un outil majeur d'éducation et de sensibilisation grand public.

2. Matériels et méthodes

Les travaux de thèse ont été conduits dans la région l'Indo-Pacifique, dans deux localités à l'ouest de l'Océan Indien, à l'île Europa et l'île de La Réunion, et dans une localité à l'ouest de l'Océan Pacifique, en

Nouvelle-Calédonie. Au total, 26 sites d'études ont été échantillonnés dans trois catégories de substrats :

- Substrats coralliens (bioconstruits) : récifs de pente externe de La Réunion (5 sites), d'Europa (9 sites) et de la Nouvelle Calédonie (8 sites).
- Substrats rocheux (basaltiques) : communautés coralliennes développées sur des coulées de lave à l'est de La Réunion, sur une coulée de 1977 (1 site) et une coulée centenaire, la roche de Çaesari (1 site).
- Substrats artificiels (béton) : digues construites par des aménagements littoraux, dont une digue portuaire (1 site) et une digue d'autoroute (1 site).

Echelles de l'étude et méthodes de suivi écologique

<u>La colonie corallienne</u> : les colonies coralliennes ont été pour la plupart échantillonnées dans le lagon récifal de La Réunion. Des campagnes sur les pentes externes et l'arrière-récif des deux autres localités ont permis de compléter les morphologies coralliennes non-présentes à La Réunion. Les colonies ont été catégorisées dans les morphologies suivantes : branchue, columnaire, encroûtante, foliacée, massive et tabulaire (Veron 2000). Les modèles 3D ont été générés et étudiés pour quantifier les mesures d'intérêt (surface, volume, capacité de refuge).

<u>Les paysages récifaux</u> : représentés par les sites de pente externes de trois localités (24 sites au total). Les paysages ont été modélisés et les descripteurs physiques et écologiques ont été calculés à partie des modèles numériques d'élévation (MNE) et des orthomosaïques. Des suivis biologiques ont été couplés aux relevés photogrammétriques pour évaluer :

Les peuplements de poissons : à La Réunion des comptages visuels (Underwater Visual Census) ont été réalisés avec le protocole décrit par Labrosse et al. (2002). À Europa et en Nouvelle-Calédonie, des comptages vidéo ont été réalisés avec la méthodologie décrite par Elise et al. (2019b).

Les communautés benthiques : à La Réunion des suivis avec la méthode LIT (Line Intercept Transect) suivant le protocole du Global Coral Reef Monitoring Network (GCRMN - Obura, 2014) ont été réalisés dans les sites de pente externe et coulées de lave. Ces suivis ont été nécessaires pour répondre à l'étude proposée dans l'axe 3 de la thèse.

<u>Les structures artificielles – digues</u> : deux sites ont été modélises : la digue ouest du Port Est (D-PE) et une partie de la digue de la Nouvelle Route Littorale (D4-NRL). Ces sites ont été d'un intérêt particulier pour l'entreprise d'accueil de la thèse CIFRE, Creocean OI et le partenaire technique, Geolab. Les mêmes suivis biologiques (communautés benthiques et ichtyologiques) que ceux effectués dans les paysages récifaux, ont été réalisés sur ces deux sites de digues.

Equipement et protocoles photogrammétriques, analyses écologiques

L'équipement photographique a été choisi en considérant les caractéristiques recommandées pour la photogrammétrie, à savoir une haute résolution et une qualité d'images pour la finesse des résultats, le faible niveau de bruit numérique pour la précision des résultats et le large champ de vision afin de limiter le nombre de photos nécessaires pour couvrir une surface donnée (dans le cas des paysages récifaux). Le matériel suivant a donc été validé, après confirmation du choix par des essais en mer et des traitements photogrammétriques préliminaires :

- **Appareil photo :** Sony Alpha 7II, 24Mp (capteur 24x36mm)

- **Objectif :** Sony FE16-35 mm F4

- **Caisson :** Nauticam A7II

- **Dôme :** N120 – 180mm en verre

Les protocoles de photogrammétrie sous-marine développés ont été est basés sur les fondements théoriques de cette technique. Des patrons précis de parcours ont été calculés afin de guider le plongeur-photographe dans les prises de vues orientées correctement et assurer un taux de recouvrement adéquat (> 70%) pour une reconstruction correcte. Tous les modèles 3D des paysages récifaux ont été géoréférencés à l'aide de points de calage positionnés sur le fond, visibles sur les photos et géolocalisés à l'aide d'un GPS en surface. Ensuite, les reconstructions 3D ont été réalisées avec l'aide des logiciels de photogrammétrie Pix4D et Agisoft Metashape.

Les analyses quantitatives des modèles 3D (colonies) ont permis la quantification de la capacité de refuge des colonies coralliennes. Les analyses physiques sur des modèles numériques d'élévations et écologiques sur les orthomosaïques (paysages récifaux) ont permis la caractérisation de la complexité structurelle de l'habitat et des communautés benthiques avec des descripteurs quantitatifs. Les analyses on été réalisées à l'aide des logiciels QGIS, Global Mapper et Meshlab, 3ds Max, *R* (langage).

3. Quantification de la capacité de refuge des colonies et paysages récifaux

La quantification de la capacité de refuge (volume) des colonies coralliennes et paysages récifaux est une étape fondamentale pour estimer le potentiel des écosystèmes à soutenir la biodiversité. Ce chapitre de Thèse vise à quantifier le volume de refuge fournis par des colonies de corail individuelles. Au total, 120 modèles 3D de colonies ont été examinés représentant 4 morphologies majeurs des coraux bioconstructeurs : branchue, massive, columnaire et tabulaire. Trois paysages récifaux ont également été modélisés. À l'échelle de la colonie, les mesures de diamètre, de surface plane, de surface 3D et de volume du refuge ont été calculées. À l'échelle des paysages récifaux, le diamètre et la surface plane de chaque colonie ont été calculés sur les orthomosaïques et ces dernières ont été utilisées pour estimer la capacité de refuge. La complexité de la surface et le volume de refuge des colonies permettent de déduire la taille des refuges des différentes morphologies coralliennes. Les modèles linéaires développés ont montré une haute précision dans l'estimation du volume de refuge à partir des mesures 2D. Les descripteurs quantitatifs tels que le pourcentage relatif de refuge par morphologie, l'abondance des colonies coralliennes, « l'indice de refuge de Shannon » ont révélé des différences dans la composition du refuge l'échelle du paysage.

La conclusion principale de cette étude est que la surface plane et le diamètre des colonies de corail sont de bons proxies pour estimer le volume de refuge. Ces nouveaux descripteurs permettent de quantifier la capacité de refuge (une mesure 3D) à l'aide de mesures 2D. Ces nouveaux proxies sont particulièrement pertinents pour les scientifiques et les gestionnaires, et relativement faciles à mettre en œuvre dans la mesure où ces mesures 2D sont largement prises en compte dans les programmes de suivis de récifs coralliens.

4. La photogrammétrie sous-marine révèle des nouvelles relations entre les traits de l'habitat et les groupes des poissons qui fournissent des fonctions clés dans les récifs coralliens

Le maintien des fonctions clés des récifs coralliens est vital pour la persistance de ces écosystèmes et de leurs biens et services dans l'Anthropocène. Ainsi, l'identification et quantification des caractéristiques physiques et biologiques qui assurent ces fonctions sont des étapes essentielles pour la conservation de ces écosystèmes remarquables. Ce chapitre de Thèse présente une étude qui combine la photogrammétrie sous-marine avec des suivis des peuplements des poissons afin d'explorer comment les caractéristiques des paysages récifaux influencent l'abondance, la biomasse et la structure fonctionnelle des assemblages de poissons de récifs. Parmi les 22 descripteurs quantitatifs de l'habitat calculés, sept ont été retenus, pour le pertinence et pour l'absence de corrélations entre eux : la complexité de la surface, la capacité de refuge total, « l'indice de refuge de Shannon », la couverture corallienne et l'abondance de colonies branchues, massives et tabulaires. Des analyses canoniques des correspondances ont montré que ces sept descripteurs pouvaient expliquer 63 % de la biomasse des poissons et 70 % de leur abondance. Cinq fonctions clés assurées par les assemblages de poissons ont été corrélées de manière significative avec ces descripteurs de l'habitat : l'herbivorie-bioérosion, la production secondaire, l'assimilation du plancton, la prédation et le broutage des polypes/poissons corallivores. Cette approche basée sur des traits fonctionnels permet une évaluation cohérente des liens entre ces descripteurs dans un large éventail de localités. Cette étude nous a permis de conclure que les caractéristiques des récifs quantifiées par photogrammétrie sous-marine fournissent des outils abordables et des données pertinentes pour informer à la fois sur l'habitat et la structure des communautés de poissons des écosystèmes coralliens.

5. Quelle méthode pour quel objectif ? Etude comparative de la méthode LIT (*Line Intercept Transect*) et des trois méthodes issues de la photogrammétrie pour le suivi des récifs coralliens

Le choix des méthodes écologiques pour l'étude des récifs coralliens est crucial pour répondre de façon efficace aux questions de gestion et de conservation de ces écosystèmes. Dans le contexte actuel de crise mondiale des récifs coralliens, de nombreux chercheurs consacrent leurs efforts à l'optimisation de programmes de suivi de ces écosystèmes. Ce chapitre de Thèse présente une étude comparative de quatre méthodes écologiques de suivi des récifs, une méthode traditionnellement utilisée pour le suivi de communautés benthiques, Line Intercept Transect (LIT- GCRMN) et trois méthodes dérivées de la photogrammétrie sous-marine, en examinant notamment leurs performances relatives. Des estimations de la couverture corallienne par le LIT *in situ* et des évaluations numériques en reproduisant deux méthodes traditionnelles sur les orthomosaïques, le LIT et les photoquadrats, ainsi que des analyses surfaciques sur les mêmes orthomosaïques ont été réalisés. La complexité structurelle des sites a été calculée, en utilisant des descripteurs physiques à partir des modèles numériques d'élévation (MNE). De plus, une analyse comparative de ces méthodes en termes d'information écologique obtenue et de l'expertise et des temps requis est proposée.

La comparaison de l'estimation du recouvrement corallien par ces méthodes a montré que les pourcentages les plus élevés sont issus du LIT *in situ*, le LIT numérique et les photoquadrats ont obtenu des pourcentages équivalents et l'analyse surfacique sur les orthomosaïques a donné les estimations de pourcentage les plus faibles, mais les plus précises (plus faible dispersion des valeurs). Dans l'ensemble, les estimations du recouvrement corallien, indépendamment de la méthode utilisée, confirment la tendance à la baisse de ce recouvrement dans les récifs réunionnais. En résumé, la comparaison des estimations du recouvrement corallien, des expertises et temps nécessaires et des informations scientifiques spatio-temporelles obtenues, a relevé que les analyses surfaciques sur les orthomosaïques et MNE représentait la méthode la plus efficace. La méthode des photoquadrats, produisant plus qu'un seul descripteur, a pris plus de temps que le LIT *in situ* et le LIT sur les orthomosaïques, cependant, leurs estimations de recouvrement corallien ont été équivalentes. La méthode LIT *in situ* reste la méthode qui demande le moins de temps, et reste la plus efficace pour les identifications taxonomiques précises (au niveau de l'espèce notamment). En revanche, elle est la plus limitée en termes de descripteurs et restreinte en terme de représentativité de l'écosystème.

6. Discussions, conclusions et perspectives

Le rôle de la structure tridimensionnelle des récifs coralliens est une question majeure depuis les premières études écologiques de ces écosystèmes remarquables. Les limitations techniques pour quantifier cette complexité structurelle et développer des descripteurs adaptés ont freiné les progrès dans ce domaine. Actuellement, les avancées technologiques permettent de mener des recherches innovantes, qui permettent de décloisonner de répondre à de nouvelles considérations spatio-temporelles, qui complètent les connaissances actuelles appliquées aux programmes de suivi écologique et de conservation des récifs. L'efficacité de ces programmes repose sur deux grands types de suivi : les suivis écologiques et les suivis socio-économiques (Wilkinson et al. 2003, Williams and Graham 2019). Les travaux de cette thèse ont abordé des questions écologiques, plus spécifiquement sur le développement de descripteurs quantitatifs de la structure tridimensionnelle des habitats des récifs coralliens à différentes échelles spatiales. Le Chapitre 3 présente de nouveaux descripteurs quantitatifs du volume de refuge des colonies coralliennes, développés à partir des modèles 3D issus de la photogrammétrie. Le Chapitre 4 présente également des descripteurs de l'habitat qui représentent des traits des paysages récifaux cartographiés. Ces nouveaux descripteurs visent à produire de nouvelles connaissances dans une approche basée sur des traits fonctionnels de l'écosystème corallien et d'explorer les relations de ceux-ci avec des processus écologiques clés des récifs. Ainsi, les résultats peuvent être intégrés dans des analyses multivariés pour le suivi écologique des récifs et peuvent contribuer à des approches multifactorielles pour leur gestion.

L'étude des digues (structures artificielles) n'a pas pu être approfondie suffisamment pour faire l'objet d'un chapitre de thèse, principalement en raison de contraintes de temps de durée de la Thèse. Cependant, les principaux résultats ont été présentés dans la discussion générale et montrent la pertinence des outils photogrammétriques pour le suivi physique et écologique de ces structures. Les modèles 3D, les modèles numériques d'élévation (MNE) et les orthomosaïques ont été générés, les descripteurs physiques de l'habitat ont été calculés à partir des MNE, mais les analyses écologiques sur les orthomosaïques n'ont pas pu être réalisées, faute de temps. Les relevés biologiques *in situ* (suivi des communautés benthiques et peuplements de poissons) ont mis en évidence un assemblage particulier de poissons juvéniles sur la digue la plus récente (D4-NRL), ce qui n'est pas le cas pour l'ancienne digue de Port Est, et qui suggère que des nouvelles structures immergées peuvent potentiellement agir comme une "nurserie" temporaire pour les premiers stades de vie de certains groupes de poissons. Par rapport aux communautés benthiques, la digue la plus ancienne a montré un fort pourcentage de recouvrement corallien (40,3%). En revanche, la communauté benthique de la digue la plus récente (D4-NRL) présente un recouvrement élevé en gazons algaux (95%), bien qu'une colonisation de coraux opportunistes du genre *Pocillopora* (2%) ait observée. Concernant les descripteurs physiques, la complexité de surface était plus élevée au site D4-NRL, mais le site D-PE présentait des dimensions fractales légèrement plus supérieures. Ces résultats, qui doivent être confirmés par d'autres études complémentaires, suggèrent un potentiel de ces structures artificielles pour offrir de nouveaux habitats structurellement complexes qui peuvent promouvoir le développement de nouvelles communautés récifales dans des environnements modifiés par l'homme. En effet, aujourd'hui une nouvelle génération des mesures de restaurations (e.g. récifs artificielles, projet HYPER3D) et de protection des côtes (e.g. Reguero et al. 2018) sont guidées et enrichies par des connaissances issues des recherches innovantes sur les caractéristiques tridimensionnelles des habitats. Dans ce contexte la photogrammétrie sous-marine est un outil particulièrement adapté pour le suivi précis de la dynamique des communautés benthiques et leurs modifications temporelles. Cet aspect appliqué est notamment intéressant pour le domaine des aménageurs littoraux et dans la conception des mesures d'évitement, de réduction ou de compensation (ERC) qui sont souvent exigées par les lois environnementales françaises et/ou internationales.

En ce qui concerne les outils opérationnels développés, les protocoles photogrammétriques ont permis des reconstructions 3D de haute précision (résolution <1 cm) tout à fait adaptées à la réalisation de mesures et d'analyses 3D proposés pour les deux échelles d'étude. Au total, 120 modèles 3D de colonies coralliennes isolées ont été reconstruits sur 170 colonies échantillonnées (70,5 %), ainsi tous les modèles 3D de paysages de récifs et des digues ont été correctement reconstruits à 100 %. Les principales limites de cette technique sont associées aux conditions de visibilité dans l'eau, une bonne visibilité étant indispensable pour obtenir des reconstructions de bonne qualité ; les possibles artefacts sur les orthomosaïques aux sites en forte pente ou très complexes qui conduisent à une sur ou sous - estimation des surfaces sur les orthomosaïques et le coût financier (matériel photographique et informatique) associés au déploiement de cette méthode.

Ensemble, les protocoles opérationnels et les analyses écologiques développées au cours de cette thèse ont permis une nouvelle activité d'ingénierie pour les études environnementales des sociétés Creocean OI et Geolab. Notamment, le projet REBIOMA-3D qui a été sélectionné pour le financement Life4Best 2020-2021 (https://www.life4best.org), une subvention de la Commission européenne en collaboration avec l'OFB (Office Français de la Biodiversité) et l'AFD (Agence Française du Développement), qui soutient des actions de terrain à petite échelle pour la conservation de la biodiversité et le développement durable dans les régions ultrapériphériques de l'Union Européenne. REBIOMA-3D représente l'application directe des méthodes et outils développés pendant la thèse visant à soutenir les gestionnaires de récifs coralliens et d'autres organismes de conservation. Il s'agit également du premier résultat commercial de ces nouveaux services opérationnels.

Les aspects commerciaux et concurrentiels de la photogrammétrie sous-marine ont été abordés pour donner une vision sur le développement au niveau national où cette technique a été particulièrement développée au cours des cinq dernières années, à l'exception de la COMEX (Compagnie d'Expertises Maritime) qui utilise et développe cette technique depuis plusieurs décennies notamment dans les milieux d'eaux profondes. À l'heure actuelle, le pôle d'innovation de la COMEX a développé un système pour des révélés photogrammétriques, ORUS 3D, qui peut être déployé de 0 à 10.000 mètres de profondeur. Elle représente ainsi une référence dans le domaine au niveau national. Dans le domaine académique, des collaborations avec des programmes internationaux permettent aux instituts et laboratoires de recherche français de connaître et d'appliquer cette nouvelle technologie pour la recherche sur les récifs. En ce qui concerne l'UMR Entropie, le laboratoire a initié les recherches dans ce domaine en accueillant ce programme de doctorat en 2017. L'Ifremer (Institut français de Recherche pour l'Exploitation de la Mer) mène un projet depuis 2018 dans les récifs réunionnais pour le déploiement des technologiques photogrammétriques dans des zones profondes avec des ROVs. Plus globalement à l'heure actuelle, dans l'hexagone ainsi que dans les pays et territoires d'outre-mer, la photogrammétrie sous-marine est principalement utilisée pour des recherches scientifiques. Dans le domaine privé, à notre connaissance, sauf exceptions des deux structures (COMEX, Andromède), la technique est encore au niveau d'expérimentation et la plupart des sociétés ne l'utilisent pas de manière opérationnelle. En générale les potentiels d'application de la photogrammétrie suscite un grand intérêt pour les représentants français des sciences marines fondamentales et appliquées. Plus particulièrement sur la région ouest de l'Océan Indien où il n'existe, à notre connaissance, aucune entreprise qui offre le même type de services que Creocean-OI aujourd'hui, ce qui lui confère un avantage concurrentiel.

En conclusion, les chapitres 3 et 4 ont présenté de nouveaux descripteurs quantitatifs de l'habitat, qui peuvent être suivis dans le temps pour évaluer les changements potentiels de structure à une échelle spatiale fine. La quantification des volumes de refuge des colonies coralliennes a représenté un grand défi en termes de relevés photogrammétriques sur le terrain et d'analyses 3D. En contrepartie, ces nouveaux descripteurs quantifient l'une des principales fonctions de l'écosystème, le refuge offert par les colonies de coraux Scléractiniaires, et peuvent ainsi orienter la gestion des récifs vers des objectifs d'amélioration des aspects fonctionnels de ces écosystèmes. De manière complémentaire, les descripteurs d'habitat à l'échelle des paysages récifaux ont mis en évidence des relations avec des fonctions clés du récif assurées par des groupes de poissons. Ces nouvelles évidences peuvent compléter l'évaluation des fonctions clés et de la capacité de résilience de l'écosystème récifal, ce qui est particulièrement pertinent dans la période actuel de changement rapide de ces écosystèmes. Enfin, le Chapitre 5 a porté sur une étude comparative des méthodes de suivi benthique des récifs coralliens entre une méthode traditionnellement utilisé (LIT, Line Intercept Transect) et des méthodes photogrammétriques. Ce chapitre présente les informations et données que ces nouvelles méthodes apportent, leurs avantages et désavantages avec le but d'orienter les chercheurs et les gestionnaires dans la sélection des méthodes de suivi écologique les plus adaptées à leurs objectifs et à leurs ressources.

Ensemble, les descripteurs quantitatifs développés dans cette Thèse permettent d'élargir les connaissances sur les caractéristiques 3D de l'habitat et la complexité structurelle des récifs, les liens entre les communautés benthiques des récifs et les peuplements des poissons associés, ainsi que des fonctions clés assurées par ces écosystèmes. La comparaison des méthodes de suivi écologique de récifs a permis d'examiner l'opérabilité de ces nouveaux outils. Toutes les informations issues des investigations de ce programme doctoral sont particulièrement pertinentes dans l'actuel défi de conservation des récifs du 21^{e} siècle, elles apportent de nouveaux éléments à considérer dans les plans de gestions et la conception des mesures de conservation.

Chapter 1. General introduction

1.1 Structural complexity of ecosystems and coral reefs

Structural complexity can be defined as the three-dimensional structure of an ecosystem. This composite characteristic is determined by three main elements: abiotic structures like mineral components and topography, biotic structures resulting from the activity of engineer organisms, and the age of the ecosystems (Margalef 1963; Loya 1972; Jones et al., 1994; Richardson et al., 2017a). Also known as habitat complexity, this factor has been well studied in ecology, with several investigations describing its influence on different population level attributes (Kovalenko et al., 2012; Fig. 1.1). In fact, this characteristic plays a key role in the dynamics of natural ecosystems (prey-predator interactions, population oscillations, etc.), influencing the associated biodiversity, space-size heterogeneity, and patterns (shelter, habitat). It also enhances the productivity, stability, and resilience of the ecosystems. Thus, structural complexity primarily defines the shelter capacity and habitat quality for a given area of an ecosystem. This central role in ecosystem functioning, and its influence on the associated biodiversity and successional processes, has been demonstrated in terrestrial (e.g. Tews et al., 2004), freshwater (e.g. Kalacska et al., 2018) and marine ecosystems (e.g. Graham and Nash 2013).

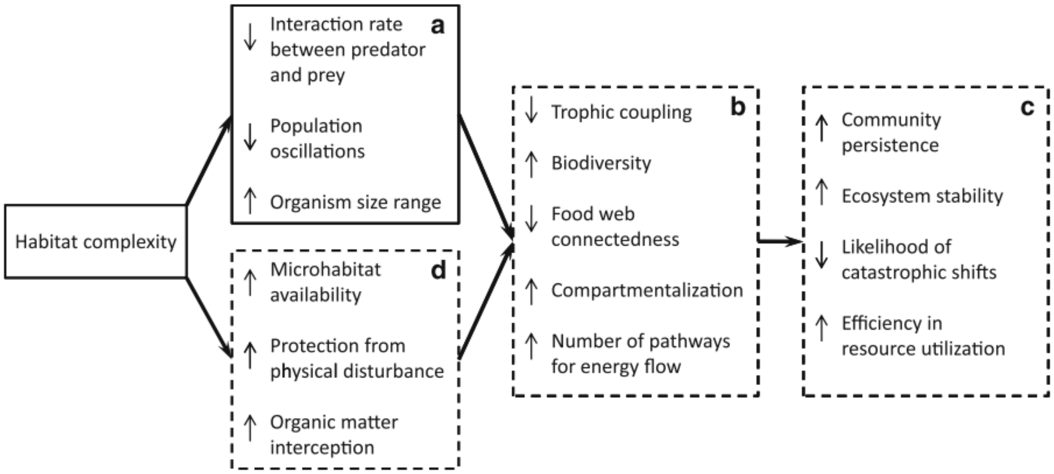


Figure 1.1 Effects of habitat complexity on population level attributes. Some are well documented (a), while little is known about the ensuing effects on community and ecosystem attributes (b, with exception of biodiversity), their emergent properties (c), and potential underlying mechanisms (d). An upward arrow indicates an increase and a downward arrow a decrease. Extracted from Kovalenko et al. (2012).

From a landscape perspective, the structural complexity of ecosystems is largely modeled from the number, size, age, frequency of distribution, and spatial arrangement of biological and abiotic structures. In a terrestrial ecosystem like a tropical forest, old trees, large snags or scrubs are the main contributing elements. In coastal and marine ecosystems, a large swath of organisms and topographic elements determine structural complexity, from the trees and submerged roots of mangrove forests and the mineral platforms of rocky shores, through to the plants and algae providing refuge in seagrass or kelp forests, and reef-building corals shaping the coral reef architecture in response to natural constraints (e.g. luminosity and hydrodynamism) (Fig. 1.2).

Figure 1.2 Habitat complexity and associated biodiversity of natural ecosystems: (a) Tropical forest (b) Mangrove forest (c) Rocky shore platform (d) Kelp forest (e) Seagrass and (f) Coral reefs. Artwork by Verónica Alvarado: @nique_illustration *(https://www.patreon.com/nique_illustration)*

Coral reefs: one of the greatest three-dimensional ecosystems

Tropical coral reefs represent one of the most complex three-dimensional bioconstructions on Earth. Scleractinian corals are the major engineer organisms of these ecosystems (Loya 1972; Wild et al., 2011), thanks to their capacity to build calcium carbonate structures. Coral colonies are the primary elements in coral reefs, with their diverse growth forms, spatial arrangement and relative abundance shaping the reefscape architecture (Zawada et al., 2010). They are also a major contributor to the shelter capacity of reefs, providing habitat and refuge from physical stress, competition and predation to a multitude of reef organisms (e.g. fishes, crustaceans, mollusks; Hixon and Beets 1993; Richardson et al., 2017b). Several studies describe a positive correlation between habitat complexity and reef fish assemblage attributes (i.e. biomass, abundance, diversity) (Gratwicke and Speight 2005; Wilson et al., 2016). Habitat complexity underpins ecological functioning, the resilience and the long term stability of associated biodiversity of coral reef ecosystems (Peterson et al., 1998; Alvarez-Filip et al., 2013; Darling et al., 2017; Magel et al., 2019). Indeed, the effects of reef flattening on reef ecosystem function, biodiversity (loss in species richness, abundance, and biomass) and associated environmental services have been observed in numerous studies led in the Caribbean region particularly affected by this process (Alvarez-Filip et al., 2009; Newman et al., 2015). For instance, the loss in structural complexity of reefs can induce a coral-algal phase shift, when reefs initially dominated by corals shift into an alternative, algal-turf dominated state. These algal-turf dominated reefs are associated with reef flattening, compromising key maintenance ecosystem services such as fisheries production, shoreline protection, and cultural services (Tebbet et al., 2020). Acknowledging that coastal and marine environments are getting flatter, Airoldi et al. (2008) investigated how habitat loss affects species diversity and can induce environmental and biotic homogenization, facilitating the invasion of opportunistics and/or invasives species (Fig. 1.3).

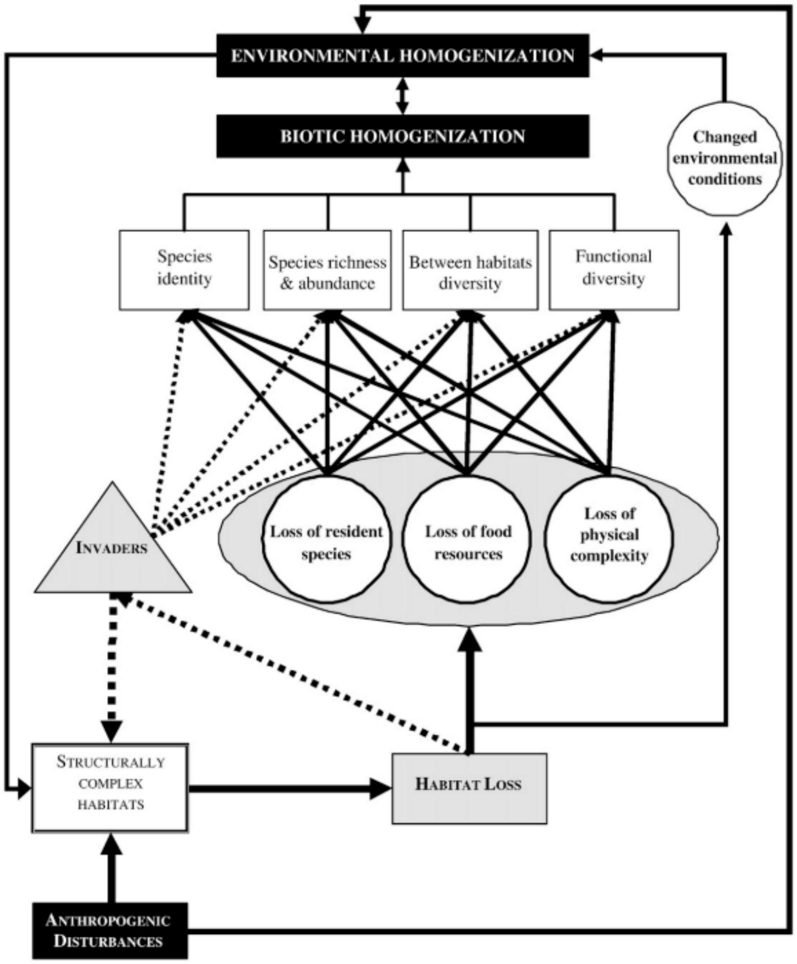


Figure 1.3 Diagram representing links between habitat loss and patterns of diversity, the possible feedbacks between these different processes, and the overall resulting biotic and environmental homogenization. Extracted from Airoldi et al. (2008).

Coastal protection offered by the back reef through wave energy dissipation is a major ecosystem service directly related to structural complexity. Despite the importance of reef infrastructure services and benefits, they are rarely assessed and managed. Among the few studies focused on this, Harris et al. (2018) concentrated their efforts on developing the Reef Health Index (RHI), combining vertical reef growth rates and wave dissipation models (Fig. 1.4). The authors argued the critical importance of reef complexity for coastal regions in the near future. Indeed, healthy and well-developed coral reef ecosystems keep the shoreline in equilibrium and stable as demonstrated by Reguero et al. (2018) for the Grenada coasts. Their study examined the protective function of coral reefs by monitoring shoreline erosion and coastal flooding exposed to wave dissipation models. The findings also support the conception of reef restoration solutions to mitigate coastal erosion and flooding. Both studies concluded that the degradation of reef structural complexity explains shoreline erosion better, and has more of a determining role in coastal protection, than future sea-level rise. Another important risk factor for the maintenance of structurally complex and healthy coral reefs is the intensification of the frequency of severe coral bleaching episodes, causing high rates of coral mortality (particularly for branching species) and thus weakening the reef carbonate structure, which then becomes more vulnerable to erosion from storms and waves (Bastidas et al., 2012; Eakin et al., 2019; Magel et al., 2019).

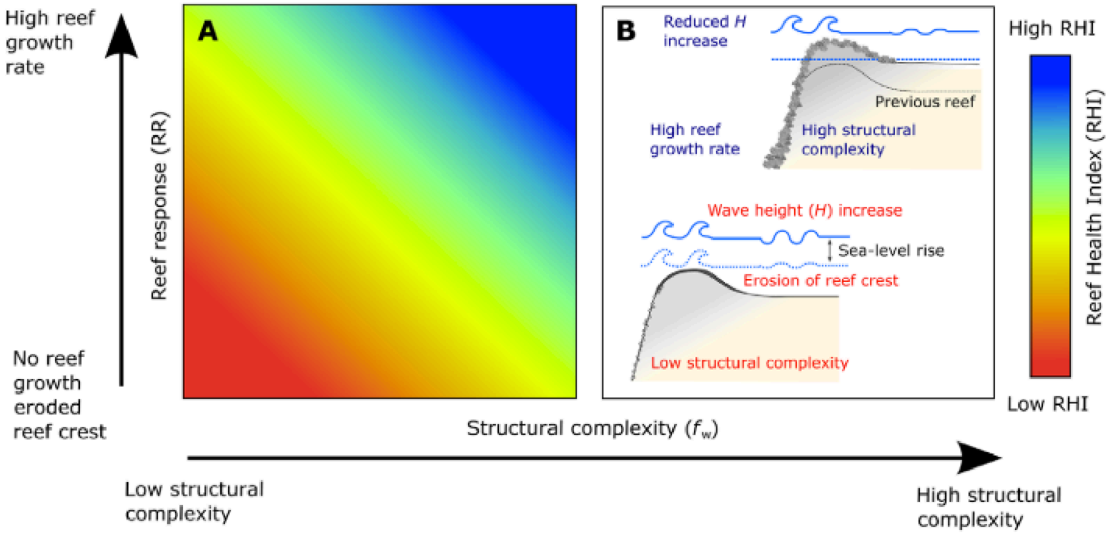


Figure 1.4 Conceptual diagrams showing the Reef Health Index (A) and two scenarios of reef structural complexity, vertical reef accretion and coastal protection (B). Extracted from Harris et al. (2018).

In this context, including the quantification of structural complexity and habitat changes in monitoring programs is essential to improve the stewardship of coral reefs and the maintenance of their goods and services. Keystone habitat structures are defined as distinct structures that have a disproportionate contribution to ecological diversity and process to their abundance, providing shelter or services crucial for other species (Tews et al., 2004; Kerry and Bellwood 2015; Wilson et al., 2019). In fact, the presence of keystone structures seems to be a determining factor in the definition of protected areas, and structural complexity could ameliorate evaluating the effectiveness of marine protected areas. In this sense, Rees et al. (2018) demonstrated that the inclusion of this variable in their analyses enhanced the explanation of the variability of fish abundance up to 50%. The authors recommended quantifying structural complexity to better understand ecological changes in seascapes. Concerning environmental management, other experiments have shown that the enhancement or maintenance of reef structural complexity, at different spatial scales, improves the potential of coral recruitment, the preservation of reef ecosystem functions and maximizes coral restoration (Rogers et al., 2014; Yanovski and Abelson 2019). From the review study conducted by Baine (2001), structural complexity is considered as one of the most important aspects for artificial reef purpose and design.

Despite the evidences and the recommendations cited above, a worldwide review of coral benthic community monitoring methods (Hill and Wilkinson 2004) reveals that only three out of fifteen methods used globally encompassed a single descriptor of structural complexity, the linear rugosity of the reef. Most use coral cover as the main parameter to describe and survey sessile benthic communities (Obura et al., 2019). Such coarse evaluations lack important information as they neglect the functional characteristics that coral communities strongly depend on, such as the relative abundance of different coral colony structures and other components that determine a reef's structural complexity (González-Barrios and Alvarez-Filip 2018). As coral reef ecosystems are critically threatened, rapid improvement of assessment methods to better characterize their structure and dynamics is necessary to implement efficient conservation measures (Ferrari et al., 2016; House et al., 2018). Quantification of habitat complexity is thus relevant for both fundamental research and applied sciences. Its temporal and spatial monitoring of reef ecosystems would allow tracking the ecological changes linked to manmade impacts and intensifying natural events (e.g. storms, bleaching). Assessing coral reef functioning is an emerging priority for conservation issues and reef researches (e.g. Hughes et al., 2017a; Bellwood et al., 2019a,b). New descriptors of habitat complexity can provide significant progress in the (re) definition or adaptation of conservation measures and environmental compensation actions. Such information would help illuminate and advocate conservation targets to decision-makers, sea planning actors and environmental managers.

1.2 Methods to quantify structural complexity of coral reef ecosystems

Quantitative measures of morphology, topography or bathymetry across different scales are the major components of the geomorphology of Earth systems. Geomorphometry is the science based on quantitative measurements of terrain morphology (i.e. slope, rugosity, aspect) and discrete landforms. It is founded in geosciences, mathematics, and computer concepts (Lecours et al., 2016). In coral reef ecosystems, first assessments of reefscapes' geomorphology and measurements of structural complexity were conducted by Goreau (1959), describing reef profiles (Fig. 1.5a, b) and coral growth forms characteristic of different reef zones, from the back reef to the inshore zones (Fig. 1.5c). This study highlighted the importance of scleractinian corals as major contributors in reef architecture. Later, in 1972, Risk was inspired by terrestrial ecology, and the underlying relationship between foliage height diversity and species diversity of birds, to measure the structural complexity of reefs as the ratio of a flexible chain draped over the reef (L-Fig. 1.5d) to the length of a straight line transect (D-Fig. 1.5d); he called this measure the *rugosity*. He also demonstrated the relationship between this rugosity measure and the diversity of reef fishes. Since then, *"the chain method"* was largely adopted as the main method to quantify structural complexity of coral reefs (Luckhurst and Luckhurst 1978; Hill and Wilkinson 2004).

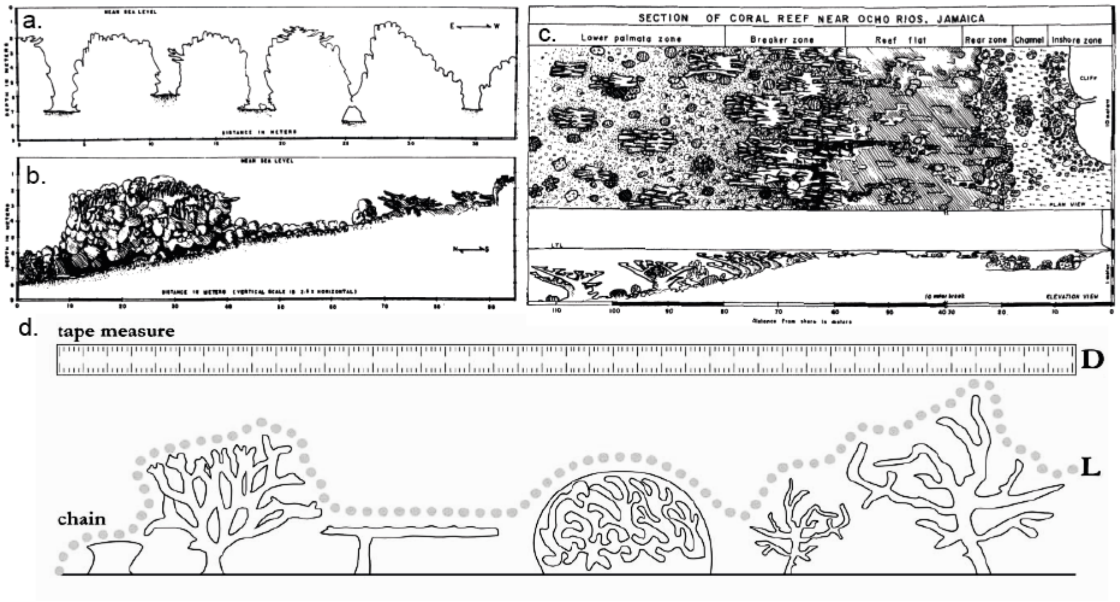


Figure 1.5 Cross sectional (a) and longitudinal transects (b) of reef buttress zone and detailed plan view of the crest and back reef zones (c) of Jamaican reef. Adapted from Goreau (1959). Chain-tape method used to calculate the rugosity (d). Adapted from Hill and Wilkinson (2004).

As a composite feature, reef habitat complexity is also assessed combining different substrata characteristics and measurements (e.g. depth, rugosity, number of holes, volumes of holes, corals morphologies, coral cover, percentage of different coral morphologies). This multifactorial approach allows better identification of the relationship between habitat and reef biodiversity (e.g. fishes, crustaceans…) (Martin-Smith 1993; Chabanet et al., 1997; Friedlander and Parrish 1998). However, Jones and Syms (1998) argues that common observations and experimental methodologies are necessary to clearly evaluate the general importance of fish-habitat interactions.

In the early eighties, another method to quantify structural complexity was developed with a mathematical approach. The fractal dimension theory was used to describe coral reef topography and investigate the complexity observed at different scales of these ecosystems. Fractal dimension can be defined as the ratio between the scale and detail of a habitat, providing a statistical index comparing how the detail in a pattern changes with the scale at which it is measured. This concept, long discussed in the mathematical field, was brought to light in 1967 by *"The Coastline paradox"* article (Mandelbrot 1967), which cited a previous works of L.F. Richardson. This method provided new ecological insights and contributed to the understanding of multiscale natural phenomena (Bradbury and Reichelt 1983; Mark 1984). Sugihara and May (1990), provided different applications of fractals (scale, measurements and hierarchy) in ecological systems. Thus, the fractal dimension of habitat could be represented by corals, algal or other complex organisms, and their influence on the abundance, biomass and prey-predator relation in fish communities could then be investigated (e.g. Crowder and Cooper 1982; Gee and Warwick 1994). In the late nineties, Herzfeld and Overbeck (1999) used a multifractal approach to design methods and algorithms for the calculation of surface characteristics and reproduce geophysical data of seafloors (Fig. 1.6). This developed simulation-software package exemplifies a case study that marks the beginning of new tools for monitoring marine ecosystems using high-performance numeric processing and applying innovative technologies to quantify the components of marine geomorphology. However, important parameters influencing the structural complexity quantification are the spatial scale and the accuracy of its measurement (e.g. Fig. 1.6 seafloor scale-dependent reconstructions). Knudby and LeDrew (2007) focused their study on this influence, demonstrating that structural complexity measurements unpredictably change across spatial scales and arguing that this should be particularly considered in reef studies. In a recent study, Yanovski et al. (2017) confirmed this importance and presumed that differences in levels of structural complexity have specific ecological implications. In fact, depending on the scale of the study, the structural complexity does not have the same ecological significance regarding the associated biodiversity.

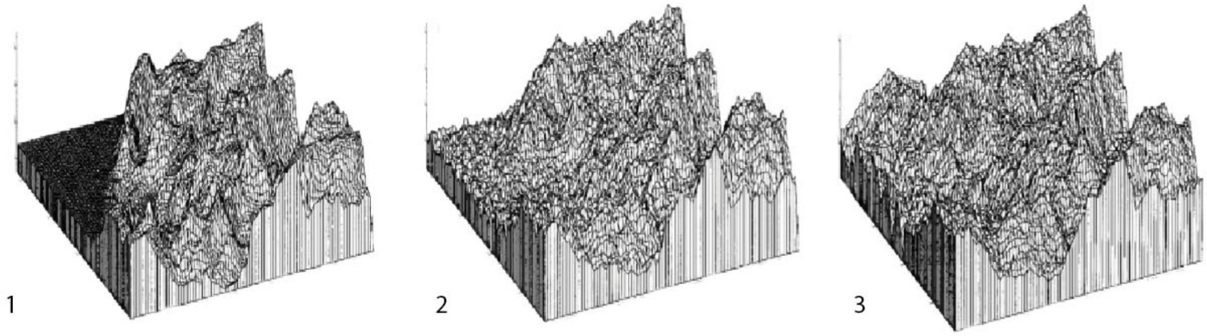


Figure 1.6 Scale-dependent interpolations using the Shepard method to reproduce geophysical data, low (1) to high (3) resolutions. Adapted from Herzfeld and Overbeck (1999).

Novel methods to quantify structural complexity and monitoring technologies

Since 2000, scientists increasingly adopted new technologies that allow creating bathymetric reconstructions and better quantification of the structural complexity of coral reefs. Among them, Airborne Lidar (Light Detection and Ranging) technology is used to reconstruct the bathymetry of coastal zones and reef environments. This powerful tool can map large areas, and with ideal conditions (very clear waters, low wind and swell), it can detect up to 50 meters of depth. The reconstructions allow spatial analyses from meters to hundreds of meters, computing terrain morphometric descriptors of surface, slope, plan curvature, surface complexity and fractal dimension (from the Lidar grid) (e.g. Pittman et al., 2009; Zawada and Brock 2009). Using this method, Wedding et al. (2008) found that rugosity measures from the *in situ* chain-tape method was equivalent to 4m resolution of Lidar grid. Despite the limits of the resolution scale reported (approx. 1m), some studies demonstrated the relationship between structural complexity descriptors from Lidar method and reef fishes descriptors (e.g. biomass and abundance of species) and recommended Lidar methods for conservation and management goals. However, the associated financial costs to Lidar survey field campaigns largely limit the applications of this technology. Another weakness of this method is associated with the poor penetration of the laser in the water. In fact, water turbidity and waves frequent in field conditons can produce artifacts and limit the detection level, omitting some parts of the reef in the mapping.

Focusing on the fine-scale measurement of reef structural complexity, Dustan et al., (2013) described an accurate *in situ* method to obtain a digital reef rugosity (DRR), using pressure measurements with a digital level gauge instrument (typically used to track groundwater or stream levels). This method provides a better resolution than chain-tape traditional method but is underused in reef studies. Other technologies were developed for fine-scale quantification using geo-referenced stereo imagery allowing bathymetric reconstructions at centimeter resolutions. Friedman et al. (2012) used the data collection by Autonomous Underwater Vehicles (AUVs) and Remote Operated Vehicles (ROVs) equipped with imagery systems (stereo cameras pointed downward to the seafloor) and proposed it as a new method to calculate virtual area-based rugosity, using stereo-derived 3D models (Fig. 1.7). The authors highlighted that the calculations of digital terrain reconstructions are more robust in terms of measurments, easily repeatable (due to georeferencing), and have the potential to survey extended areas in a non-invasive way, as there is no contact with benthic components. Price et al. (2019), confirmed this potential using ROV video to describe benthic communities in deep waters (795-740 m) of a canyon branch in the Whittard Canyon system. Acoustic technologies such as sonar or multi-beam echosounder are widely used for the production of fine-scale seascape maps at large extents often used for deep zones. Proudfoot et al. (2020) proposed this tool to improve the understanding of seafloor ecological processes and support marine biodiversity conservation strategies. This technology has also been tested to map reef reliefs, however Zurk et al. (2006) noting that the quality of the reconstructions produced can be affected by sampling underwater conditions and processing artifacts of the beam shape, position of the boat, or wave motion.

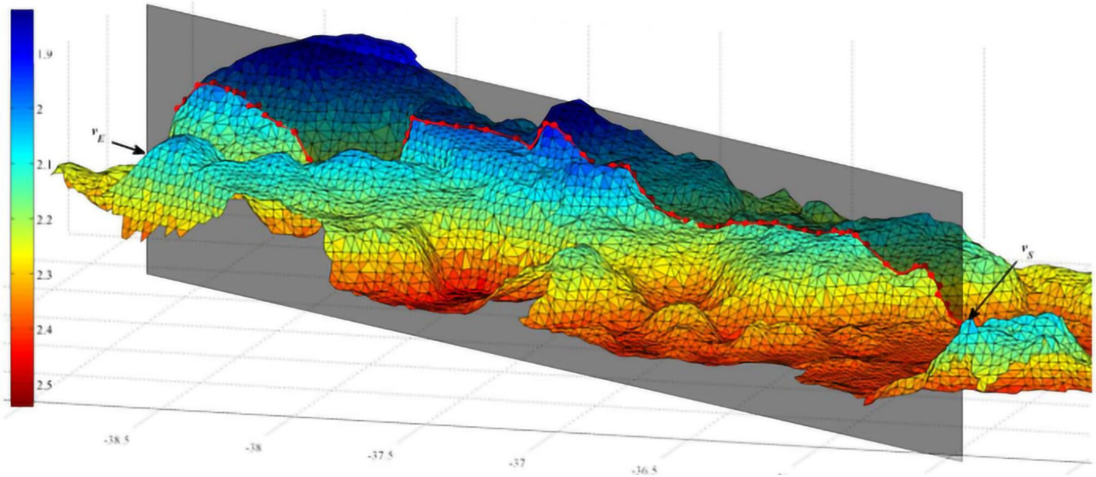


Figure 1.7 Virtual chain 'draped' to a 3D terrain reconstruction (red line). Virtual area-based rugosity is calculated by dividing the sum of the area of triangles by the area of their orthogonal projections. Extracted from Friedman et al. (2012).

Over the last decade, the application of Structure from Motion (SfM) photogrammetry, which allows creating high-resolution 3D models from overlapping photographs, has become an effective and powerful method used in quantitative benthic reef studies (e.g. Storlazzi et al., 2016; Leon et al., 2014; Burns et al., 2015a; Price et al., 2019). SfM photogrammetry allows reconstructing the bathymetry and digital profiles of coral reefs with at least a <1cm resolution, two orders of magnitude greater than Lidar data and one order of magnitude greater than sonar data. It also has the advantage of coming at no additional field cost and with lower requirements, in terms of hardware, software, and salary time, than traditional remote sensing methods (Storlazzi et al., 2016). SfM photogrammetry is also applied with aerial data collection (e.g. Unmanned Aerial Vehicule or drone) to the 3D mapping of shallow reefs. Casella et al. (2016) findings showed that in good weather conditions the resolution of such 3D reconstructions are equivalent to the Lidar method. Multispectral and hyperspectral methods are also powerful technologies that allow mapping and can reveal structural complexity of reef environments and their possible changes (e.g. Silver 2019; Bajjouk et al., 2019).

Today, as described above, a large panel of methods is available to quantify structural complexity of reef ecosystems. The choice between these methods depends study goals, budget and affordability, and the tool's efficiency.

1.3 Photogrammetry science and underwater applications

The history of photogrammetry and fundamental principles

Photogrammetry is the science of obtaining reliable information about the properties of objects and the environment by recording, measuring, and interpreting photographic images. Derived from Greek, the word photogrammetry is composed of *photos* – meaning "light", *gramma* – meaning "drawing", and *metrein* – meaning "measurement". Figure 1.8 presents a brief illustrated history of photogrammetry summarizing the principal concepts and key periods in the development of the technique. The fundamental principle of photogrammetry is triangulation, the process of determining the location of a point by measuring angles of triangles from known locations (Fig. 1.9a), a concept developed by Leonardo da Vinci in 1480. The science was developed through the following centuries with the advances of projective geometry science and accelerated with the advent of photography (1837-8). In the middle of the nineteenth century, A. Lussedat used photographs to compile topographic measurements (1849), and first aerial photography was recorded (~1860). At the end of the century, the biologist Boutan successfully captured the first underwater photography in 1893 after technical tests led by Thompson in 1856. In the same year, the term photogrammetry is used for the first time by Meydenbauer, using the technique for documenting cultural heritage (Albertz 2001). At the beginning of the twentieth century, the International Society for Photogrammetry and Remote Sensing (ISPRS) was founded (1910). Over the following century, aerial, terrestrial, and underwater applications of photogrammetric techniques were widely developed, notably in the second half of the twentieth century. In the 60's, an automated orthophotographic system correlating stereo imagery was developed by the brothers Hobrough, and Roberts L. submitted his Ph.D. thesis in 1963 *"Machine Perception of Three Dimensional Solids"* at MIT. In the eighties**,** Levoy and Whitted wrote a paper introducing point cloud data *"The Use of Points as a Display Primitive"* (Levoy and Whitted 1985)**.** Since 1990, with the onset of digital photography and improvement of digital processing performances, the field of photogrammetry has expanded and is now largely applied in many cultural, scientific, industrial and diverse domains.

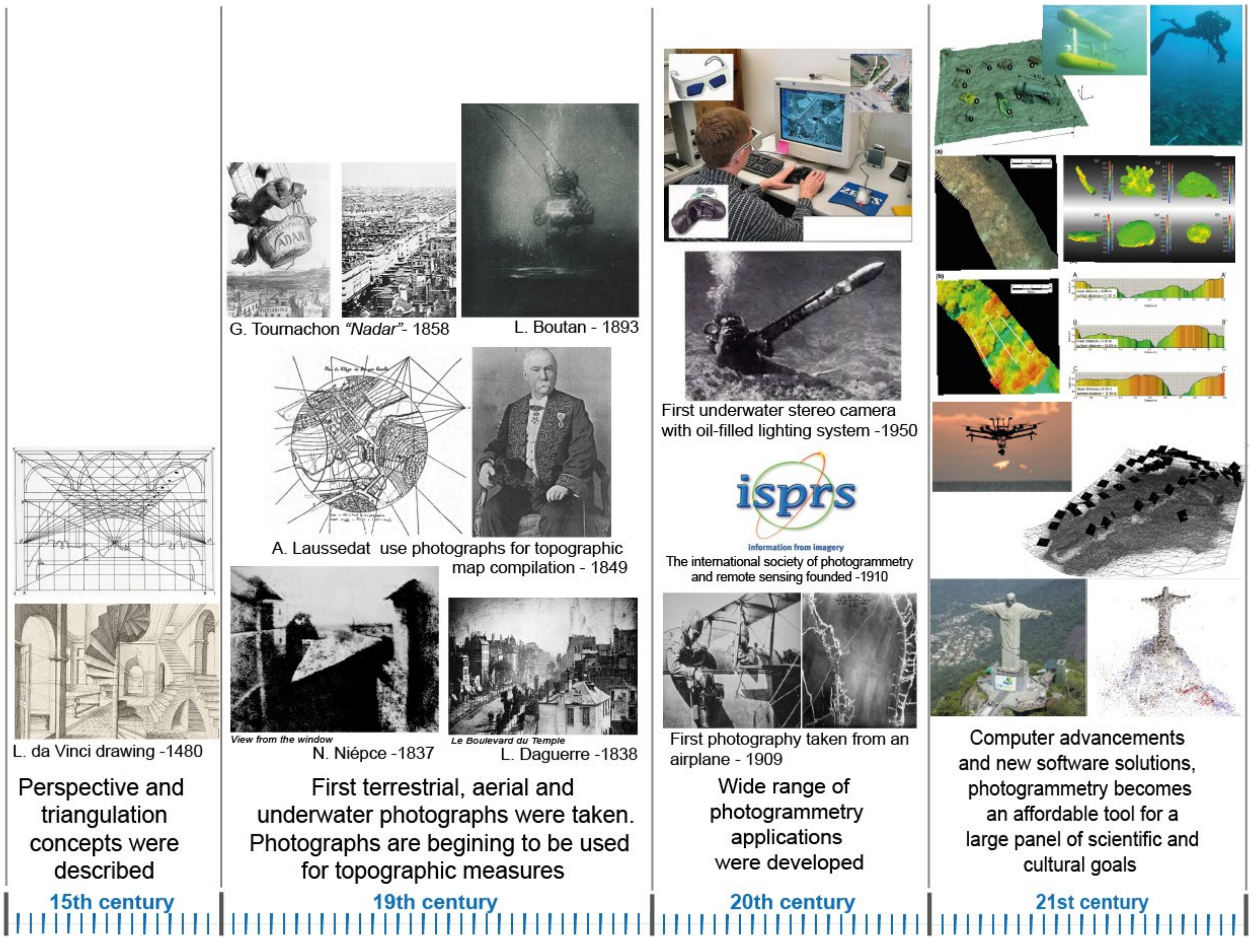


Figure 1.8 Brief illustrated history of photogrammetry.

Another major contribution in this field was the development of the Structure from Motion technique (SfM), which allows the reconstruction of three-dimensional objects from a series of 2D images with a high degree of overlap (Fig. 1.9b, c.). Unlike traditional photogrammetry, SfM does not require knowledge of the 3D location, orientation of the camera or accurate 3D information of control points in the scene prior to reconstructing the scene geometry (Cullen et al., 2018). Today, photogrammetric software solutions allow users to create 3D models from a series of photographic images (Fig. 1.9d, e). In the natural sciences field, photogrammetry applications aim at quantifying physical features and calculating measurements of organism and environments. Geosciences particularly benefit from SfM photogrammetry applications, advancements in computer performances and the development of geomatic fields (Westoby et al., 2012). While SfM photogrammetry is just one branch of photogrammetry, photogrammetry will hereinafter be used to refer to SfM photogrammetry, for simplification purposes.

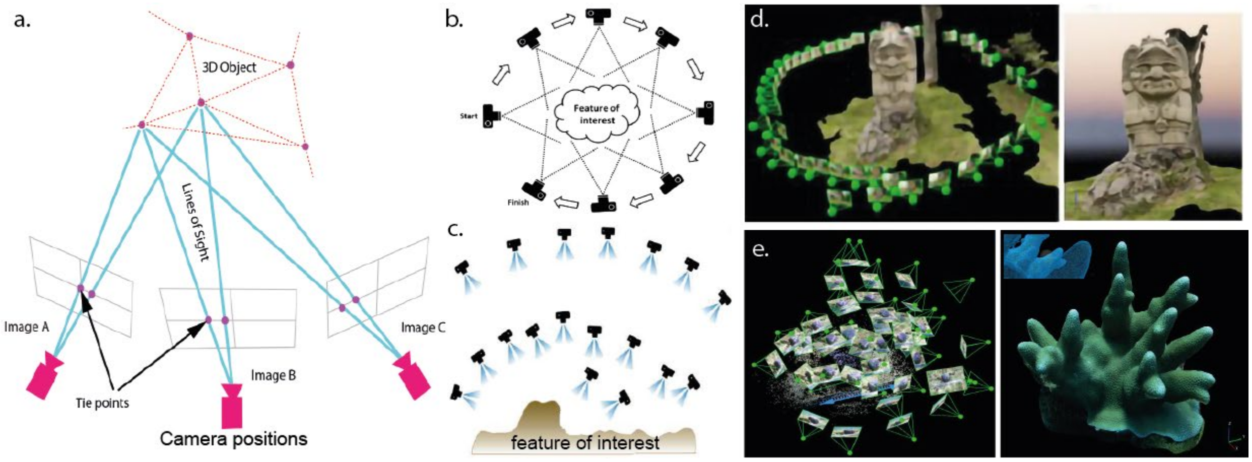


Figure 1.9 Illustration of the principle of triangulation used to calculate the location of specific points from known locations (a) (source: http://geokatse.gtk.fi). Structure from Motion technique requires multiple overlapping photographs to 3D reconstructions (b, c), extract from Westoby et al. (2012) and Micheletti et al. (2015). Examples of 3D SfM photogrammetric reconstructions on cultural heritage conservation fields (d) extract from Tavera et al. (2019); and on coral colony reconstruction performed in this Thesis (e).

The photogrammetry workflow and underwater field applications

The photogrammetry workflow to generate 3D models from the captured images is as follows:

- Image acquisition: photographs collected from the object or zone (Fig. 1.9b, c). Depending on the complexity or the extent area of the study, it is often necessary to follow a protocol to ensure the correct overlap between images.
- Camera calibration and sparse cloud generation: identical features between different images are detected and matched with the scale-invariant feature transform algorithm (SIFT) (Lowe 2004). Square bundle adjustment algorithms (Triggs et al., 2000) are then used to find the positions of the images based on these matches. These two steps result in a 3D sparse cloud, reflecting the most prominent features of the scene and the relative position of the images used to generate it.
- Point cloud densification: the sparse cloud is condensed by multi-view stereo and dense matching algorithms, using redundant information to weaken the influence of occlusion and noise (Shao et al., 2016). The result is a dense point cloud, a 3D model composed of a multitude of points with 3D coordinates derived from the triangulation of the positions in their original images.

Generating high resolution outputs from the 3D - dense point cloud:

- Mesh: 3D model composed of vertices, edges and faces that define the polyhedral shape of the object. Most meshing technics are based on Delaunay triangulation (Shewchuck 2002) or combine approaches with other methods (e.g. advancing-front method).
- Digital elevation model (DEM): grid of the elevations of a continuous surface projected to a plane of projection (any reference datum or geographic coordinate system). DEMs are often used to produce relief maps. The accuracy of this data is determined primarily by the resolution (the distance

between sample points), commonly known as ground sampling distance (GSD) by resolution or pixel.

- Orthomosaic: a single image product is mosaicked from an image collection, where the geometric (lens) distortion is corrected and the perspective is rectified (orthorectification) and projected on a projection plane (orthographic view). This can then be used as a map of an area.

These photogrammetric outputs (point cloud, mesh, DEM, orthomosaic) provide the possibility to perform a large panel of measurements and mapping analyses for a large range of studies and industrial applications. For instance, successive point clouds and DEMs of the same environment are relevant data for temporal surveys, allowing detection and quantification of changes in physical features in GIS or 3D software. Orthomosaics, representing an accurate map of the studied areas, can be used to quantify 2D metrics (i.e. surfaces, distances) as well as others spatial and ecological descriptors (e.g. patterning of elements/organisms). Mesh can be used to quantify metrics such as volumes, surfaces, and rugosities of objects/organisms.

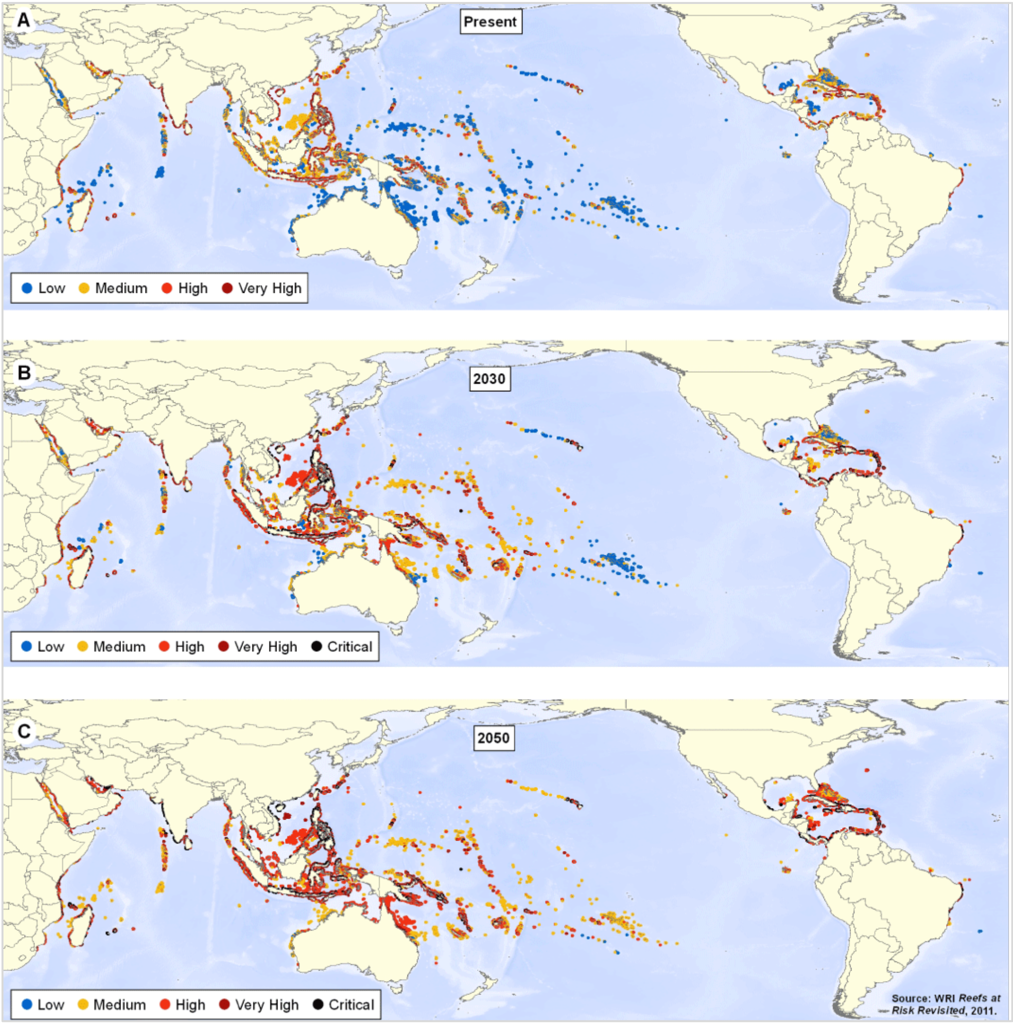
Underwater photogrammetry initially started for industrial applications procedures such as offshore structure inspection techniques (e.g. Leatherdale and Turner 1983). Archeology researchers also pioneered adopting this technique to map study areas and compute quantitative descriptions of structures and objects (Drap et al., 2013). In the marine biology field, Bythell et al. (2001) applied underwater photogrammetry to measure the surface of coral colonies and lead morphometric analyses, Cappelletto and Agudo-Adriani (2017) proposed this technique as an alternative to traditional biological morphology methods. Indeed, 3D reconstructions from photogrammetry have been demonstrated to allow accurate *in-situ* measures such as volume, surface area, or other biological morphometric measures (i.e. height, branch length and spacing, cavity width) of epibenthic organisms (e.g. Cocito et al., 2003; Abdo et al., 2006). As photogrammetry applications increased, several studies validated and tuned underwater photogrammetry methods. Among them, Troisi et al. (2015) compared the quality of 3D-reconstruction between dry and underwater environments, determining that water turbidity is an important parameter that induces noise in the models; they also discussed the settings of the camera depending on seawater conditions. Young et al. (2017) compared 3D modeled objects to their known dimensions and highlighted the high accuracy and precision of photogrammetric reconstructions (metrics varied <3%). In a similar study, Raoult et al. (2017) determined the reliability of surface and volume measurements of 3D coral boomy models between observers and over the time, detecting errors from 12% to 15% in measurements. Ferrari et al. (2016), compared *in-situ* and 3D model measurements, revealing high accuracy for small scales (with <1mm error of the surface area) and the accuracy of 85.3% +/- 6% (CI) at the transect scale. Other experiments determined associated errors as a function of image overlap, morphological community composition, surface rugosity and environmental conditions (e.g. Bryson et al., 2017; Rossi et al., 2019). Considering fieldwork aspects, several photographic equipment were tested and different protocols were proposed for image acquisition campaigns (e.g. Burns et al., 2015a; Guo et al., 2016; Pizarro et al., 2017; Youg et al., 2017). Regarding software solutions, Burns and Delparte (2017) studied the differences in accuracy of 3D modeling of coral reef habitats at three spatial scales and between two commercial photogrammetric software. Other studies investigated the cost-time efficiency of the method (e.g. Young et al., 2017; Marre et al., 2019).

In summary, this wide array of studies reflects a rigorous development of the underwater photogrammetry technique, validating its corresponding relevance in the applications for studying and surveying coral reefs.

1.4 Coral reef conservation issues, reef survey technologies, and photogrammetric tool contributions

Coral reefs are among the most biologically diverse and productive ecosystems worldwide; occupying only 0.1% of the Earth's surface yet supporting more than 25% of marine life. Five-hundred million people depend on and benefit from goods and services provided by reef ecosystems (e.g. fisheries, coastal protection, tourism), which support vibrant economies and businesses in tropical and sub-tropical regions. The annual economic value of reef ecosystems is estimated at $3.4 billion, with flood protection alone being $94 million every year (Moberg and Folke 1999; NOAA Office for Coastal Management). Despite these contributions, coral reefs are among the most threatened ecosystems, facing intensifying anthropic pressures (e.g. overfishing, coastal development, agricultural runoff), thermal stress and ocean acidification. Combinations of these threats show that most reefs are at a very high or critical risk of degradation in the near future if the efficiency of management actions is not improved and there is no reduction of local and global threats (Burke et al., 2011; Fig. 1.10).

Urgency in the enhancement of management efficiency is the greatest challenge of the twenty-first-century reef's conservation. In the last two decades, new reef assessment technologies have been devoted to efforts improving the ecological, spatial and temporal constraints of traditional methods (D'Urban et al., 2020). Understanding that this technology is not the end-goal, but rather a tool to provide scientists, will increase the ability to collect information safer, faster, and with greater accuracy and/or quantity (Obura et al., 2019). In a review study by Madin et al. (2019), authors argue that emerging technologies can play a pivotal role in tackling many of the critical issues facing coral reef conservation science and practice. Yet, maximizing the impact of these technologies requires addressing several significant barriers including lack of awareness of technologies and tools, prohibitive cost, lack of transferability across systems and/or scales, lack of technical expertise, and lack of accessibility.



Source: WRI *Reefs at Risk Revisited*, 2011.

Figure 1.10 Risk at reef in the present (A), 2030 (B) and 2050 (C) (Burke et al., 2011).

Underwater photogrammetry technology and the applications in coral reef ecological studies are now considered as an efficient and non-invasive tool to describe reef organisms and monitor spatial and temporal changes of reef ecosystems thanks to simple field protocols, useful generated output (i.e. point clouds, meshes, DEMs, orthomosaics) and the accuracy of measurements made possible. At the organism level, photogrammetry has been used to: examine coral skeletons and conduct precise taxonomic identifications from 3D models (e.g. Gutiérrez-Heredia et al., 2015); quantify several metrics of coral colonies (i.e. surface, volume, slope, curvature, surface complexity) and compare them across different morphologies (e.g. Burns et al., 2015b; Figueira et al., 2015); study coral anomalies (e.g. Burns et al., 2016b); and quantify erosion and growth rates of coral colonies (Ferrari et al., 2017b; Rossi et al., 2019). At the reefscape level, new descriptors have been developed to describe reef benthic communities (e.g. volume, surface complexity, fractal dimension, slope, abundance and distribution patterns of organisms), while standard descriptors such as coral cover can also be precisely calculated (e.g. Burns et al., 2015a, b; Palma et al., 2017; Fukunaga et al., 2019).

The high resolution of photogrammetry outputs is one of the strengths of this method, allowing three-dimensional features to be measured at the appropriate scale with respect to the reef macrofauna (e.g.

corals, fishes, crustaceans) (Storlazzi et al., 2016). In fact, the scale of measurement should preferably match the typical body size of the organisms whose habitat is being investigated. This is not the case for remote sensing technologies and methods were the resolution of their outputs (maps and images) are not directly related to the scale of most reef organism and ecology studies (Knudby and LeDrew 2007). Photogrammetric mapping instead allows fine scale measurements (<1m) and thus has been proposed as an adapted and innovative tool to assess reef biodiversity (e.g. Barde et al., 2018; Price et al., 2019), with an increasing number of studies showing the links between benthic descriptors and fish assemblages (e.g. González-Rivero et al., 2017; Agudo-Adriani et al., 2019). Focusing on the benthic communities, reef zones mapped by photogrammetry are also increasingly used to describe coral communities and their dynamics (e.g. Hernández-Landa et al., 2020). Monitoring the changes in morphological composition of reefs can illuminate changes in their structural complexity and thus assess the evolution of "habitat quality" facing increased disturbances (Denis et al., 2017). Suitably, high-resolution three dimensional mapping by photogrammetry can be quantitatively analysed at multi-spatial scales to predict the evolution of morphological features and the structural complexity of reef ecosystems (Burns et al., 2019; Carlot et al., 2020). Indeed, photogrammetry has already been applied to assess the impact of disturbances on the 3D reef structure. Burns et al. (2016a) quantified structural reef changes after several disturbances including hurricane, bleaching, and tropical storms, using volumetric comparison of point clouds of the reef. This type of photogrammetric survey illustrates this technique's contribution for coral reef surveys, allowing users to obtain quantitative information for multiple spatial and temporal scales that is often largely limited using traditional ecological tools, due to practical constraints and unadapted descriptors (D'Urban et al., 2020). Yet, it is important to consider in the estimates the possible associated errors that could arise from the quality of the photographic equipment, the environmental conditions, the overlap of images, and software performances. In fact, Bryson et al. (2017) established that their measurements could be biased up to 7.5% due to environmental conditions during any particular survey. However, the photogrammetry technique enables unlocking new spatial and temporal ecological issues, which in turn can help redefine conservation targets.

Regarding the potential applications for environmental consultancy and the rehabilitation or restoration fields, photogrammetry has been used to design and monitor artificial reefs and other underwater structures or coastal installations (e.g. Gautier-Debernardi et al., 2017; Abadie et al., 2018). All the advantages listed above exemplify the technique as an efficient and adapted tool to habitat surveys and environmental rehabilitation solutions. Overall, the information gained from photogrammetric data analyses contributes to the description of life-trait-based approaches of coral reef ecosystems. These approaches help enhance our understanding of reef ecosystem health, functioning, and resilience, while contributing to improving conservation programs (Ferrari et al., 2016; Fukunaga et al., 2019). Photogrammetry is likely to become a standard sampling tool for mapping and monitoring coral reefs in the coming years thanks to their affordability (Obura et al., 2019; D'Urban et al., 2020). In summary, the multitude of studies have shown the performance and relevant contributions of photogrammetry in coral reef assessments and particularly for monitoring the structural complexity of these environments. In this context, my Ph.D. thesis proposes to develop new quantitative habitat descriptors of coral reefs using 3D modeling by photogrammetry, to investigate ecological and functional aspects of these descriptors and discuss the efficiency of the developed tools for benthic surveys.

1.5 General objectives and Thesis outline

1.5.1 Thesis research questions, technical goals, and cross-cutting objectives

The research questions of the present thesis are divided into three objectives:

Objective 1. Development of new quantitative descriptors for coral reef habitats from 3D photogrammetric models

- Which descriptors precisely quantify the capacity and diversity of shelter of coral colonies?
- Which habitat descriptors of reefscapes can be calculated from photogrammetric outputs?

Objective 2. Ecological analyses of reef habitat descriptors and associated biodiversity

- Which are the most relevant habitat descriptors to characterize habitat complexity and to monitor reefscapes?
- Which habitat descriptors are most related to fish groups ensuring key functions of coral reef ecosystems?

Objective 3. Comparison between one traditional reef benthic monitoring method and innovative photogrammetric methods

- What are the strengths and weaknesses of photogrammetry methods compared with the traditional monitoring method?

From these three principal objectives, a major technical goal of the Thesis is proposed:

- Develop easy to deploy and reproducible photogrammetric protocols to produce three-dimensional models adapted to the two study scales: (i) coral colony (two cubic meters or less), (ii) reefscape and artificial structure (hundreds of square meters).

Accurate photogrammetric outputs (i.e. 3D models, DEM, orthomosaics) are necessary to correctly perform physical and ecological analyses and answer the research questions exposed above.

Crosscutting objective:

- Use 3D models and visuals as an effective communication tool to explain research objectives, ecological analyses and results of the Thesis. I propose to participate in conferences and awareness actions addressed to audiences including the general public, students, and stakeholders in marine environment domains, among others.

1.5.2 Thesis outline

The outline of the thesis is based on the development of underwater photogrammetry protocols and new coral reef habitat descriptors, the validation of links between these habitat descriptors and key functional processes ensured by associated fish assemblages, and the comparison of three photogrammetric methods and one traditional method for reef benthic monitoring. Chapter 2 focuses on the material and methods section, presenting the study sites, the developed photogrammetric protocols, and ecological methods. Chapter 3, 4, and 5 are related to articles (in review or submitted). Chapter 6 includes general discussions on the operability of tools developed, the results, and a brief discussion of sites studied. This final chapter also presents the limits, conclusions and perspectives of this Thesis (Fig. 1.11).

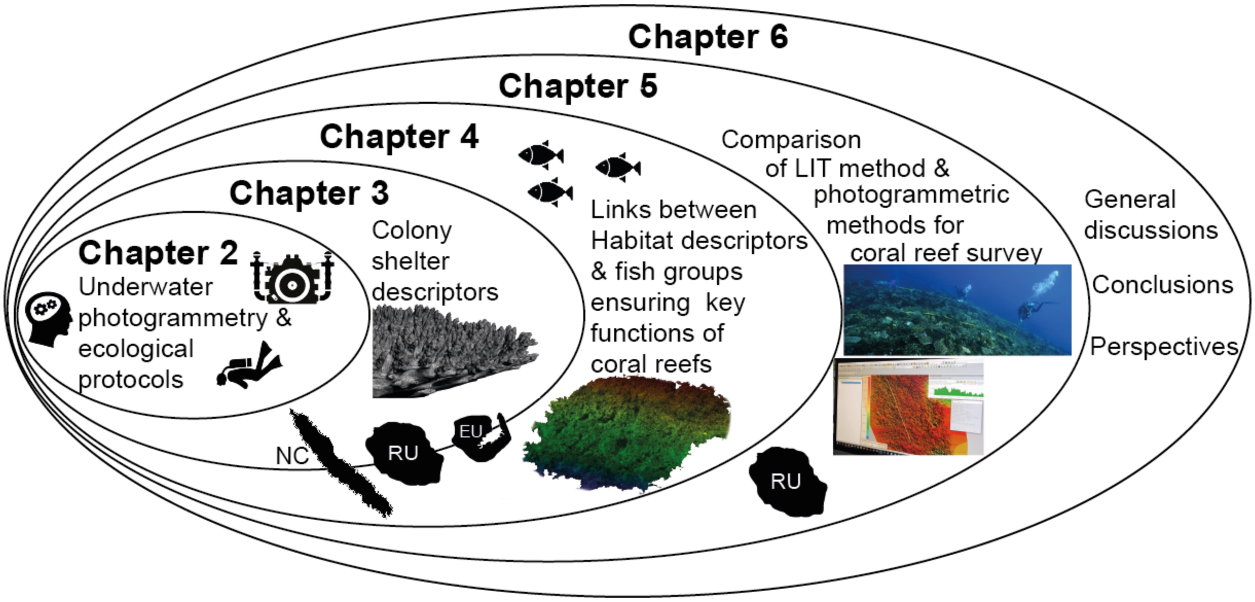


Figure1.11 Diagram representing the interconnection of Thesis chapters and the studies conducted to reach the overall Thesis objectives. Abbreviations for study sites: EU= Europa Island, NC= New Caledonia, RU= Reunion Island.

Chapter 2 describes the materials and methods used for the overall experiences conducted in this Thesis. I present: the description of the study sites and the detail of the study scales; the underwater photogrammetric protocols and the general workflow used throughout the study; the photographic equipment and computing resources, and the principles to calculate physical and biological descriptors.

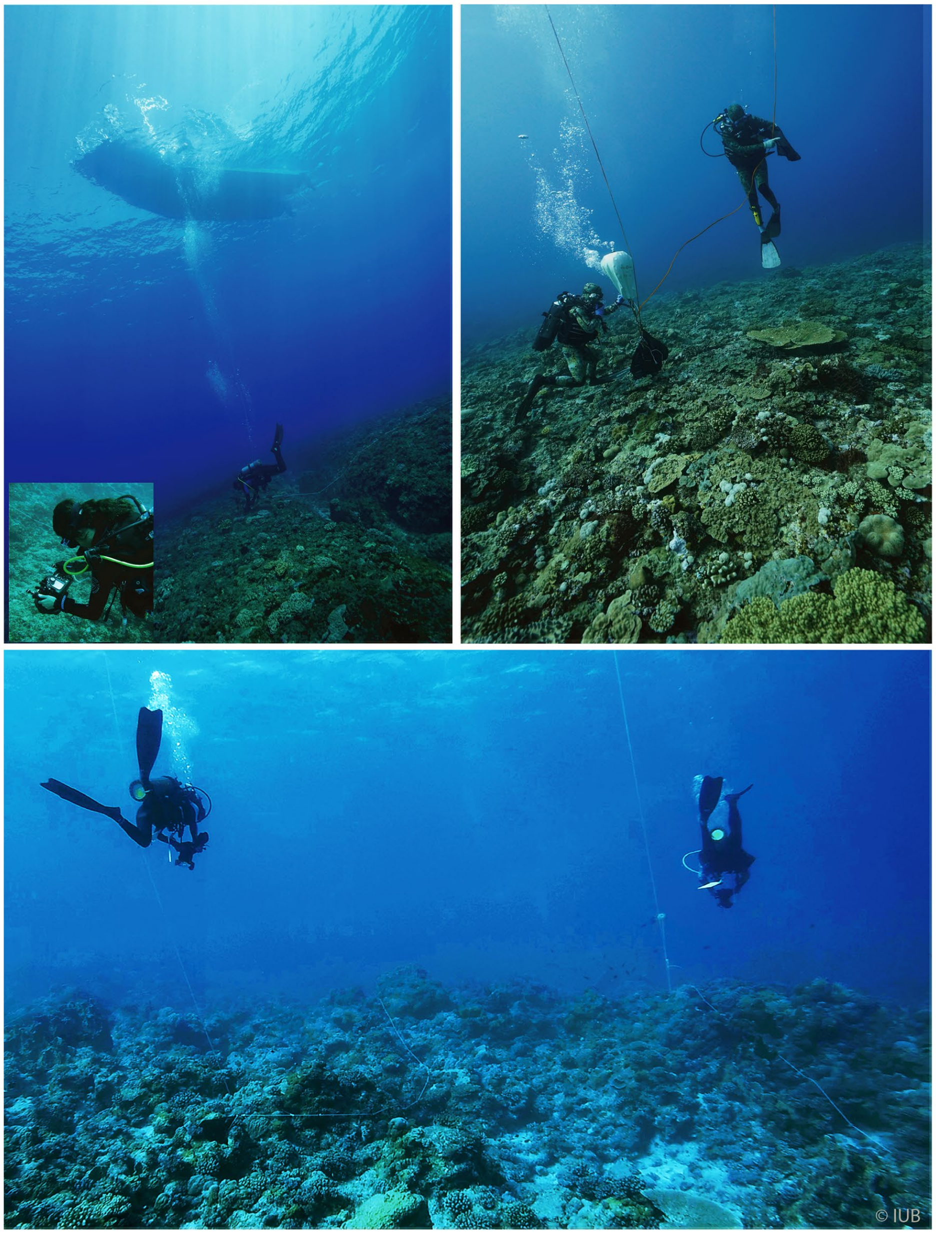
Chapter 3 aims at developing a new habitat descriptor to quantify the shelter capacity (volume) of corals colonies of various growth forms (i.e. branching, columnar, massive, tabular). Predictive models to estimate the shelter capacity from 2D measurements (i.e. diameter, planar area and surface) are also presented and applied at the reefscape scale. Shelter capacity and new diversity shelter index are compared across three study sites.

Chapter 4 investigates new habitat descriptors of reefscapes and their possible relationships with associated fish assemblages using a trait-based approach. First, the study presents an analysis among habitat descriptors and selects the most relevant/least redundant. Second, the investigation examines the relationships between habitat descriptors and functional groups of fishes representing core processes of reef ecosystems and management interests.

Chapter 5 focuses on comparing a traditional benthic monitoring method, the Line Intercept Transect (LIT), with three photogrammetric methods for coral cover estimations and required technical and human resources for deployment. Overall, the information clarifies the strengths and weaknesses and offers recommendations and perspectives for coral reef monitoring methods.

Chapter 6 lays out general discussion of this Thesis, targeting methodological developments, fundamental and conservation aspects, and operational applications. First, I discuss the new quantitative tools developed for monitoring benthic communities of coral reefs, the shelter volumes, the habitat descriptors at a reefscape scale and the links with fish assemblages that assure some core process of reef ecosystems. I relate the development of this work with the trait-based and multifactorial approaches in reef management. Second, I present the operability of the tools developed, discussing the results of the two breakwater sites surveyed and offering some elements of applying the new photogrammetric skills in the engineering activities for the company that hosted this Ph.D. To complement this business portion, I list the principal companies and actors at the national level that are interested in this technique or can apply photogrammetry technology to their offered services to study marine environments. I then discuss scale issues for reef benthic monitoring and some limitations of this work and present actual solutions to confronting these limitations. Finally, I present the conclusions of the study and the perspectives.

Chapter 2. Material and Methods



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2.1 Study sites

The study was conducted in three French overseas territories: Europa Island (Scattered Islands), Reunion Island, both in the Western Indian Ocean, and the archipelago of New Caledonia in the Southwest Pacific Ocean (Fig. 2.1).

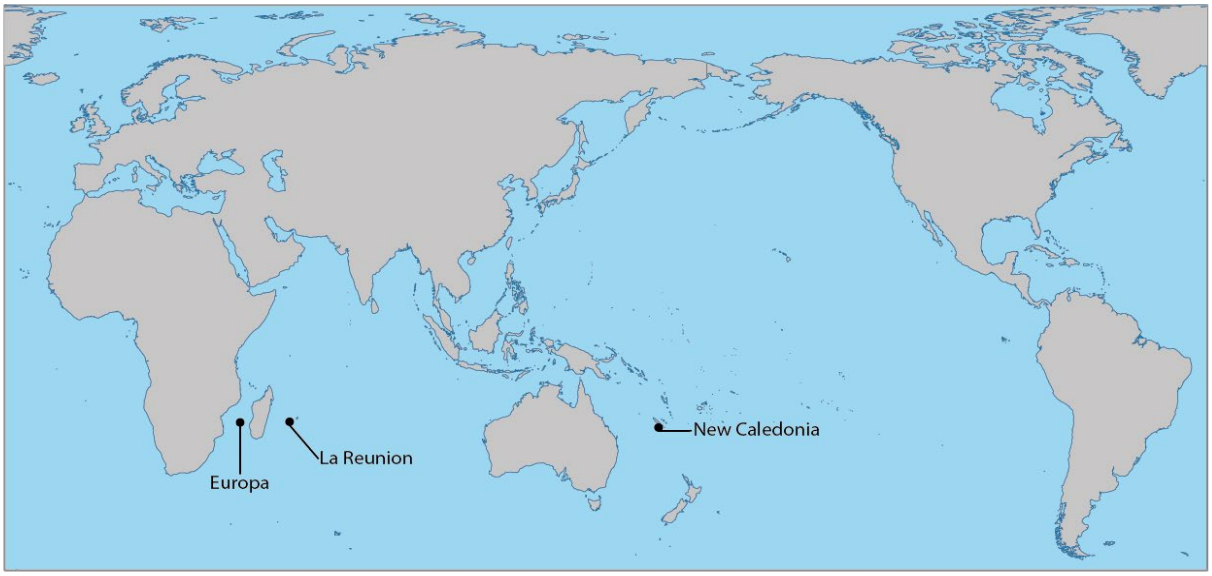


Figure 2.1 Location of the study sites on the world map.

The study sites represent different geomorphologies of tropical coral reefs: outer reef slopes (the majority of our sites), inner reefs, and reef flats (specifically for the sampling of coral colonies). Outer reef slope is the main representative of coral reef ecosystems and is both widely studied by the scientific community and targeted by conservation actions (Mumby et al., 2008). Coral communities on underwater lava flows and artificial structures (coastal breakwaters) were investigated with the aim of developing operational tools that could be deployed on these types of ecosystems.

In total, 22 outer reef slope sites were studied: nine in Europa Island, five in Reunion Island, and eight in New Caledonia, as well as two coral community sites and two breakwaters in Reunion. The depth of sites varied from 8 to 15 m on outer reef slopes and underwater lava flows, and from 3 to 8 m for breakwaters. Three reef flat zones (< 3 m depth) at Reunion and two inner reefs (~10 m depth) at New Caledonia were also explored to collect images of specific coral colony forms. The summary of the study site information is presented in Table 2.1. For all study sites, these were the first reef photogrammetric surveys to be carried out.

In Chapters 3, 4 and 5, we used and combined data from one or more study sites relevant to the respective objective.

2.1.1 Europa Island

Europa Island is a Scattered Island and belongs to the French Southern and Antarctic Lands (Terres Australes et Antarctiques Françaises, TAAF), located in the south of the Mozambique Channel. The coral reefs of Europa Island are of the most remarkable and preserved reefs of the region. The territory of the island has been surveyed since 1975 and special measures for implementing a Marine Protected Area took place in 2009. It also belongs to the RAMSAR Convention on Wetlands of International Importance, especially as Waterfowl Habitat, since 2011. Fishing is banned in its waters and other human activities, such as tourism, are highly regulated.

The study was conducted on nine sites of outer reef slopes (Fig. 2.2), attempting the largest representation of reefs in terms of structural complexity. At each of the nine sites, a photogrammetric protocol was deployed to survey the reefscape. Two sites were additionally surveyed to sample isolated coral colonies. The fieldwork was conducted in April 2018 thanks to the collaboration established with the CORCOPA project (BEST 2.0 program). The data and results were shared between collaborators to accomplish the scientific and visual awareness goals of the project.

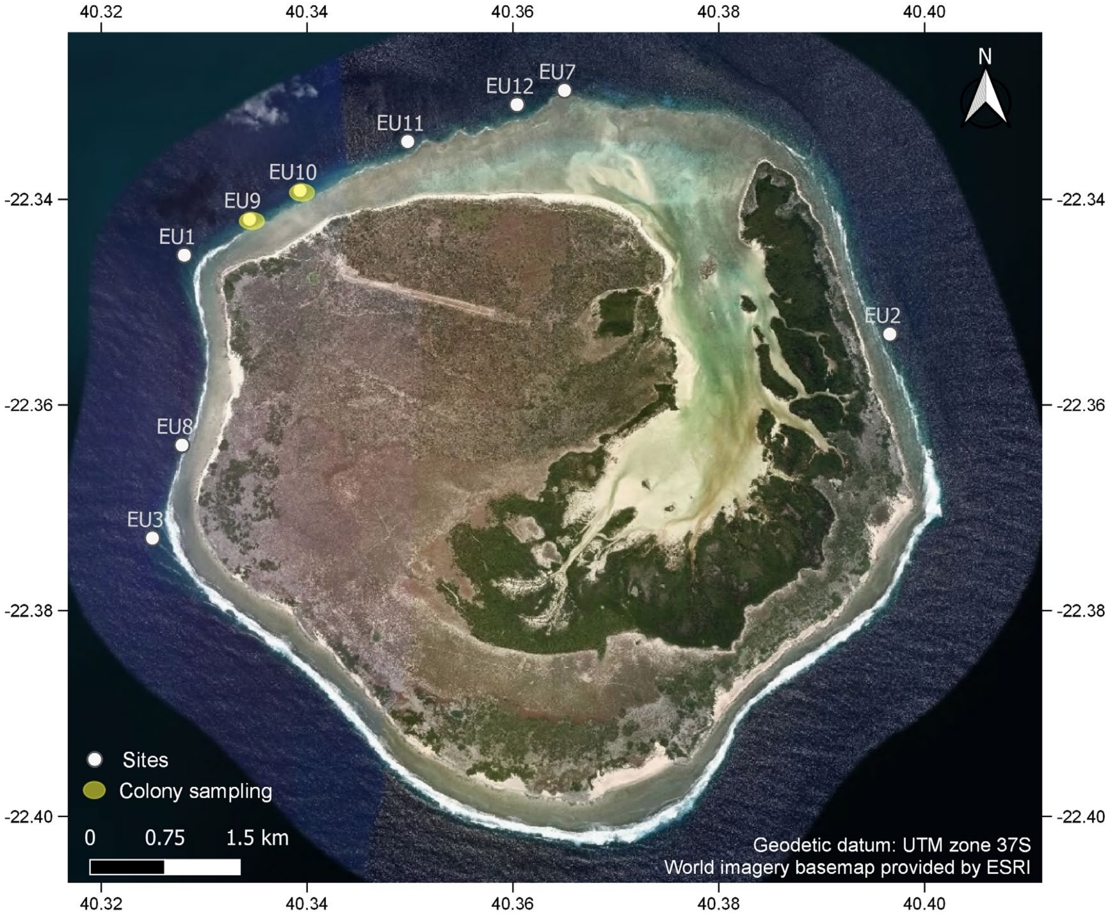


Figure 2.2 Location of study sites in the outer reef slopes of Europa Island. White circles indicate reefscape samplings; yellow zones indicate coral colony sampling areas.

2.1.2 Reunion Island

Reunion is a volcanic island belonging to the Mascarene archipelago, which is located in the southwest Indian Ocean. Since 2006, the island has a Marine Protected Area covering a large portion of the reef zones and regulating human activities. The study sites were selected to represent three geomorphologies: coral reefs (outer reef slopes [ORS] and reef flats in the west coast), basaltic spur (coral communities on underwater lava flows in the east coast [RLF]), and artificial structures (breakwaters in the north coast [AS]) (Fig. 2.3). We attempted to represent a wide variety of structural complexity across all sites.

Coral reefs of Reunion are composed of young and very heterogeneous coral communities (island age ~3 million years, reef age ~8,000-12,000 years old) (Chabanet et al., 2001). The studied sites on the outer reef slopes and reef flats are situated in two different reef complexes: TRC, SAL and SBL in the Saint Gilles/ La Saline complex and COR and GEN in the Saint-Leu complex, all sites being located in the MPA.

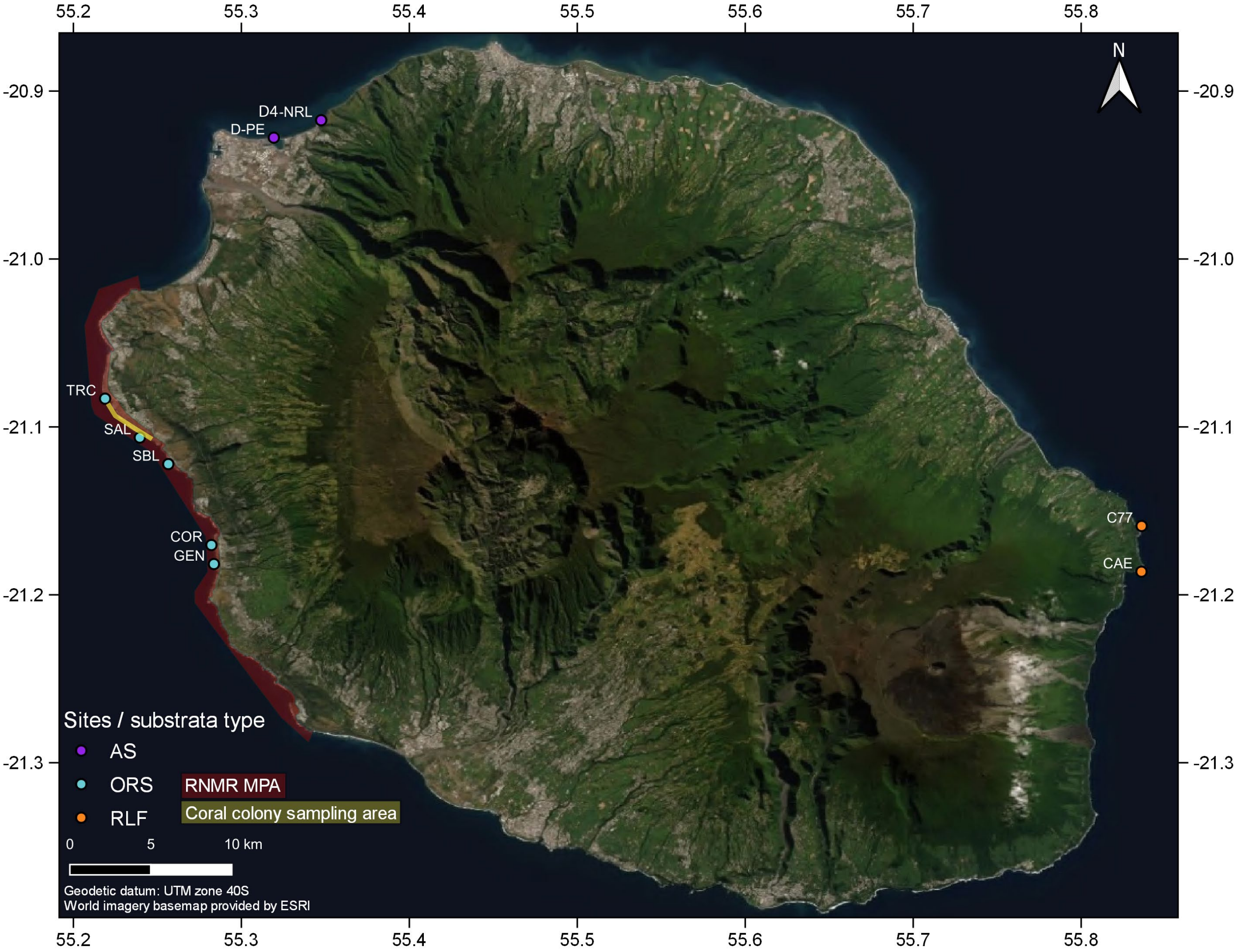


Figure 2.3 Location of the study sites around Reunion Island. Filled circles indicate the reefscape studied and the yellow zone the area explored for coral colonies. The circle colors indicate the type of substrate: AS for Artificial Structures (breakwaters), ORS for Outer Reef Slope and RLF for coral communities on underwater Lava Flows.

The reef communities on underwater lava flows (RLF) depend principally on the age and hardness of the lava (Schleyer et al., 2016). The C77 site dates from volcanic activity in 1977 and CAE site is a centennial lava flow. None of these sites have specific protection status.

All the reef communities of the island are highly exposed to stressors both natural (i.e. cyclones and austral swells) and anthropic (island population = ~1 million mostly located on the west coast and near seaside zones).

Regarding the coastal installations, the breakwaters sites were selected in this study primarily to test the feasibility of the fieldwork and photogrammetric reconstruction on various types of sites and thus its applicability for environmental monitoring and structure inspection. These operational applications were of great interest to both of the engineering companies: the environmental consultancy Creocean OI, hosting this Ph.D. program, and Geolab, technical partners of the project.

Two sites were chosen based on the date when the infrastructure was submerged and the existing environmental monitoring program. The first site was a section of a breakwater just outside the Port East harbor (D-PE) built in 2005, which has been ecologically monitored since 2009 (Pers. com. Garnier R.; Creocean-OI, 2016). The second site was a portion of a breakwater of a highway (D4-NRL) being built at the time of our study that was submerged in April 2018, seven months prior to our survey. While asking for authorization to access the construction site, we witnessed great interest by the construction company representatives for both the industrial and ecological applications of photogrammetric monitoring.

The fieldwork was conducted from March 2017 to November 2018.

2.1.3 New Caledonia

New Caledonia is an archipelago located in the southwest Pacific Ocean. It is composed of numerous islands and belongs to the "Coral Sea". Recently, the French government created the biggest Marine Protected Area in the region (Nature Park of the Coral Sea - 2014), showing the importance of preserving marine ecosystems and their resources. The high diversity and conservation status of coral reef ecosystems hosted in the New Caledonia territory was the main reason to expand the study in this region. The outer reef slopes situated around the Dumbea pass (M'Béré reef and Aboré great reef) in the southwest part of the archipelago were studied. The selection of the sites followed the same considerations as for Europa and Reunion; eight sites were selected to obtain the largest contrast of structural complexity. Four sites are located in the integral Marine Protected Area (Aboré great reef [AB]) while the other four have no specific protection measures (M'Béré reef [MB]). Two inner reef areas at the Boulari pass were also explored, sampling specific colony forms (Fig. 2.4).

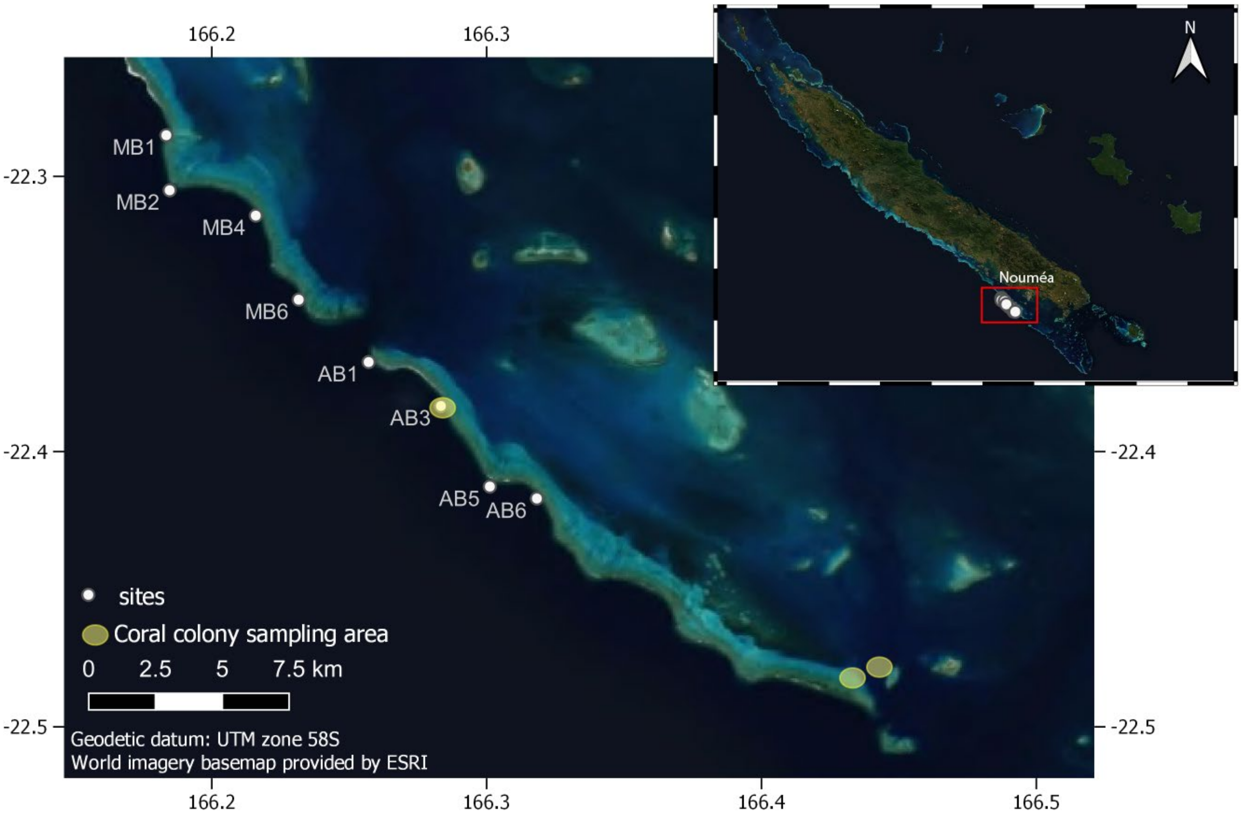


Figure 2.4 Location of the study sites in outer reef slopes of M'Béré (MB) and Aboré (AB) reefs. The white circles indicate the surveyed reefscapes and the yellow zones the areas surveyed for coral colonies.

Table 2.1 Summary of the information for study sites: type of ecosystem, geomorphology of substrata, sampling scale implemented and protection status. Site code: CAE= *"Caesari"*, C77= *"Coulée 77"*, COR= *"La Corne"*; GEN= *"Gendarmerie"*; HER= *"l'Hermitage"*, SAL= *"La Saline"*; SBL= *"Souris Blanche"*; TRC = *"Trois Bassins"*; BOU = *"Boulari"*

Island	Site code	Type of ecosystem	Geomorphology	Scale	MPA
Europa	EU1	Coral reef	Outer reef slope	Reefscape	YES
Europa	EU2				
Europa	EU3				
Europa	EU7				
Europa	EU8				
Europa	EU9		Outer reef slope	Reefscape	
				Coral colony	
Europa	EU10		Outer reef slope	Reefscape	
				Coral colony	
Europa	EU11		Outer reef slope	Reefscape	
Europa	EU12		Outer reef slope	Reefscape	
Reunion	CAE	Coral community	Underwater lava-flow	Reefscape	NO
Reunion	C77			Coral colony	
Reunion	COR	Coral reef	Outer reef slope	Reefscape	YES
				Coral colony	
Reunion	GEN		Outer reef slope	Reefscape	
Reunion	SAL		Outer reef slope	Reefscape	
				Coral colony	
Reunion	SBL		Outer reef slope	Reefscape	
Reunion	TRC		Outer reef slope	Reefscape	
Reunion	D-PE	Breakwater	Artificial structure	Seascape	NO
				Coral colony	
Reunion	D4-NRL			Seascape	
Reunion	HER-TBS	Coral reef	Reef flat	Coral colony	YES
New Caledonia	AB1	Coral reef	Outer reef slope	Reefscape	YES
New Caledonia	AB3		Outer reef slope	Reefscape	
				Coral colony	
New Caledonia	AB5		Outer reef slope	Reefscape	
New Caledonia	AB6		Outer reef slope	Reefscape	
New Caledonia	MB1		Outer reef slope	Reefscape	NO
New Caledonia	MB2		Outer reef slope	Reefscape	
New Caledonia	MB4		Outer reef slope	Reefscape	
New Caledonia	MB6		Outer reef slope	Reefscape	
New Caledonia	BOU1		Inner reef	Coral colony	YES
New Caledonia	BOU2		Inner reef	Coral colony	

2.2 Study scales and ecological methods

2.2.1 Coral colony scale

Coral colonies were sampled aiming to represent the principal growth forms of Scleractinian corals following Veron (2000): branching, columnar, encrusting, foliaceous, massive, and tabular. Only living corals with a diameter ≥ 10 cm were considered. The fieldwork consisted of one-hour dives on outer reef slopes or inner reefs and two hours of snorkeling on reef flats. Colonies were haphazardly selected, attempting to represent the largest range of colony size for each growth form. Chapter 3 focused on this study scale, examining three-dimensional features of coral colonies.

2.2.2 Reefscape scale

Reefscapes were composed of all outer reef slopes and coral communities on lava flows sites, representing a large array of coral reef structural complexity and habitat diversity. The photogrammetric protocol was conceived to cover an area of 250 m^2 (20 × 12.5 m patch) at a depth ranging from 9 to 15 m. Two additional ecological assessments, a fish survey and an in-situ benthic assessment, were deployed at the reefscape scale:

Fish survey: two methods were used to assess reef fish assemblages:

- In Reunion, the Underwater Visual Census (UVC) (Labrosse et al., 2002) was performed by an expert biologist diver along three 5 x 30 m belt-transects.
- In Europa and New Caledonia, video footage was recorded and analysed following the methodology presented in Elise et al. (2019b).

The fish surveys were conducted to respond to the second main goal of the thesis. Chapter 4 focuses on the relationship between reef fish assemblages and reefscape descriptors.

In-situ benthic assessment LIT method: in the Line Intercept Transect method, 3 transects of 20 m of length were deployed to benthic assessments following the Global Coral Reef Monitoring Network protocol – SWIO (Obura, 2014).

Reproductions of two traditional methods for benthic assessment, Line Intercept Transect and Photoquadrats, on photogrammetric outputs were also conducted to answer the third main goal of the thesis. Chapter 5 focuses on comparing the different benthic survey methods applied in this Thesis.

2.2.3 Coastal installations: breakwaters

Two photogrammetric protocols were deployed to monitor breakwater structures: For D-PE, the same protocol used for the reefscapes was applied to cover an area of 350 m^2. For D4-NRL, we adapted an existing protocol to a surveyed area of 650 m^2. The two additional ecological assessments were deployed:

- Fish surveys: the Underwater Visual Census (UVC) (Labrosse et al., 2002) was performed by an expert biologist diver along three 5 x 30 m belt-transects.

- In-situ benthic assessment LIT method: in the method of Line Intercept Transect, 3 transects of 20 m of length were deployed to benthic assessments following the Global Coral Reef Monitoring Network protocol – SWIO (Obura, 2014).

Though the breakwaters case study is not presented in a specific chapter, the main results, being the illustration of photogrammetric outputs and biological surveys, are presented in general discussions.

2.3 Photogrammetric equipment, underwater test and informatics resources

2.3.1 Photographic equipment

In selecting the photographic equipment, the aim was the highest quality of photogrammetric outputs (within the limits of the financial budget). I used the following photography equipment and underwater accessories in this study (Fig. 2.5):

- Camera: Sony Alpha 7II - 24MP full frame sensor (24x36mm) with a high-speed SD card of 32 Gb
- Lens: Sony FE 16-35 mm F4
- Housing: Nauticam NA-A7II
- Dome: Nauticam 180 mm glass dome port

Figure 2.5 Photographic equipment used for photogrammetric survey (camera, lens, housing, and dome port).

2.3.2 Underwater tests

We conducted two *in situ* underwater tests to determine the settings for image acquisition and to ensure the correct three-dimensional reconstructions:

- Photography resolution and depth-field range: taking the same image but changing the sensitivity (ISO value) and aperture f lens (ø f-number), we analysed the sharpness and the neatness of the objects in the images (Fig. 2.6).
- Photogrammetric reconstructions quality: 3D reconstructions of different growth forms of coral colonies were performed to identify the principal limitation related to the complexity of the coral morphologies (Fig. 2.7).

At the same time, other parameters influencing the quality of reconstructions were studied. Environmental constraints, luminosity on the scene, and turbidity of water were noted, and the colors, size of scale bars, and ground control points (GCP) were tested. The goal was to determine the most adequate field conditions and the most adept materials to carry out photogrammetric fieldwork.

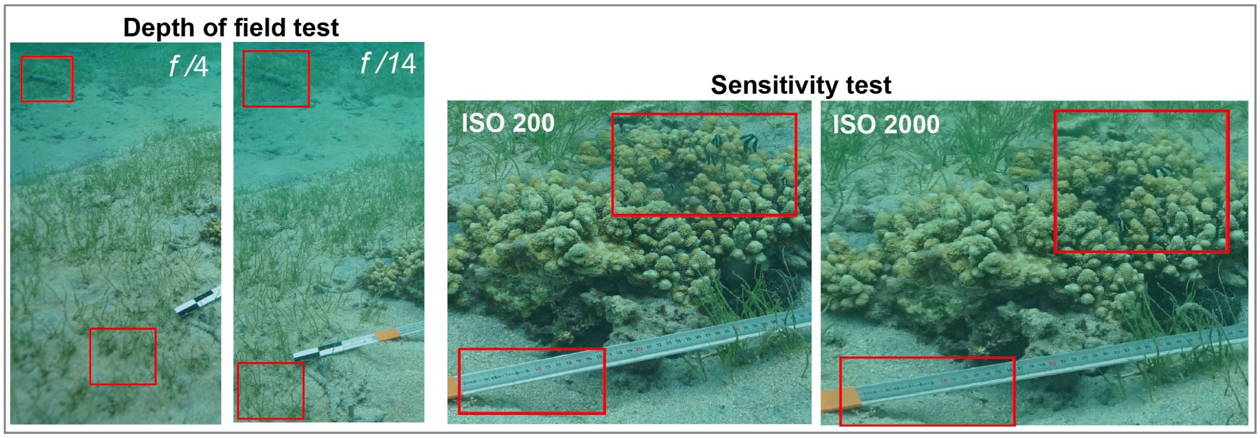


Figure 2.6 Camera settings tests: Depth of field test (left) and sensitivity test (right) performed to identify the best camera settings for underwater photogrammetry. The red squares indicate the comparison zones.

Considering the high apertures (f) of the lens, the image has a good sharpness throughout the scene (red rectangle in seagrass and rubble zones). Lower sensitivities (ISO) showed a better definition (resolution) of the objects in the image (i.e. more details on coral colony and numbers in the scale bar). From this test, the settings retained to use in the photogrammetric acquisitions were: an aperture of f 9, shutter speed fixed to a 1/250seg minimum and sensitivity ISO values with a maximum of 1000. The lens was fixed to 16mm in reefscapes and breakwaters and 24mm for colonies. However, the settings could be adapted on a case-by-case basis according to the field conditions (luminosity and turbidity); for example, higher sensitivities for poor lighting conditions.

The photogrammetric reconstruction quality tests allowed us to evaluate the problems and limitations in the image acquisitions and 3D reconstructions (Fig. 2.7). For highly complex structures, such as branching, foliaceous or tabular colonies, more photos taken at different angles were necessary to ensure adequate overlap of images. Theoretical calculations were done to determine other parameters related to image acquisition: the minimum distance to the interest feature (e.g. colony or substrata), the minimum overlap percentage of the images, the real focal distance of the lens in underwater conditions, and the image deformations related to the dome port (diameter and material of dome port [glass or acrylic]). It is important to note that all these aspects studied above permitted the estimation of appropriate spatial resolution for 3D models in the ecological analyses. The spatial resolution for 3D models is either calculated by the size of triangles composing a mesh or inferred by the density of points in the model (faces, points and edges). For the 2D outputs (digital elevation models and orthomosaics), the spatial resolution, known as Ground Sampling Distance (GSD), is the distance between two consecutive pixel centers measured in the ground (centimeter.pixel^{-1}). For instance, a GSD of 5 cm means that one pixel in the image represents linearly 5 cm on the ground (5 × 5 = 25 square centimeters). A GSD of 10 m means that one pixel in the image represents linearly 10 m on the ground (10 × 10 = 100 square meters) (source: https://support.pix4d.com). Conceiving the two photogrammetric protocols allowed us to obtain fine reconstruction models of coral colonies, GSD < 1 cm.pixel^{-1} which allowed fine measurements of interest (e.g. surface and volume), and of reefscapes and breakwaters, at least 1 cm.pixel^{-1} of GSD as we aimed to study potential links between structural features of reefs and the associated macrofauna >1cm (fishes).

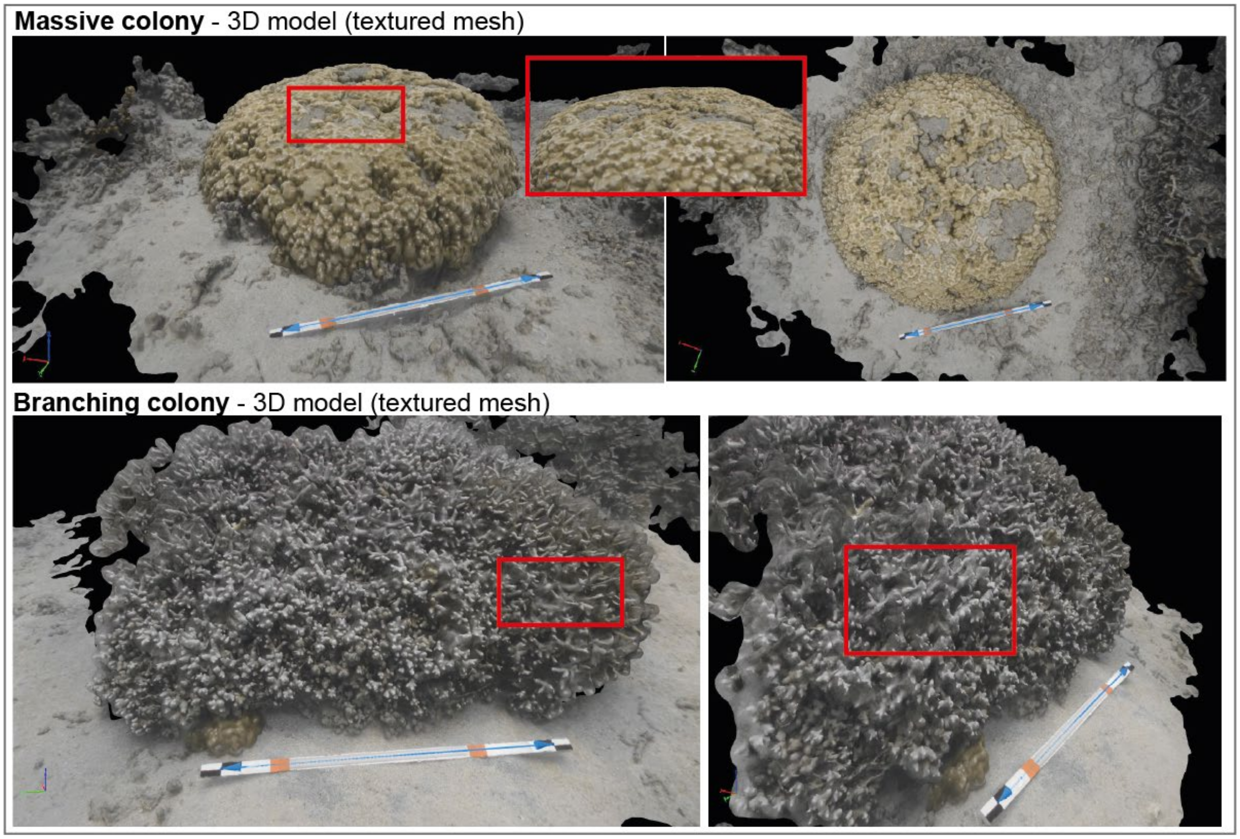


Figure 2.7 Photogrammetric reconstruction quality tests: 3D reconstructions of a massive colony (top) and branching colony (bottom). Meshes reconstructions were studied from different angles of the model (left and right images), red squares indicate the zones where the quality of reconstruction was evaluated.

2.3.3 Informatics resources

Powerful computing hardware was necessary for photogrammetric processing. The most important features to consider were a high-speed processor, a recent graphic card and enough RAM. The computer used in this Thesis was a laptop equipped with an Intel i7-770HQ processor, a Nvidia GTX1060 graphic card and 16Gb of RAM. This configuration was sufficient for most of the photogrammetric projects of this study. However, for time efficiency, some of the largest projects were processed by the technical partner (Geolab), which was equipped with higher performance computers.

Three-dimensional reconstructions and analyses were performed with photogrammetric software. At colony scale, three-dimensional measurements were performed to quantify the shelter volume and the surface of each colony (software used in Table 2.2). At reefscape scale, physical analyses were conducted on the digital elevation models to obtain 3 measurements: surface complexity, slope, and fractal dimension. Furthermore, ecological reef benthic assessments were achieved on the orthomosaics using quantitative habitat descriptors of coral communities (i.e. surface, abundance, and mean neighbour distances of colonies). Both biological and physical analyses were conducted with Geographic Information Systems (shown in Table 2.2).

Chapter 3 is dedicated to the study of shelter capacity (a new biological 3D descriptor) for both colony and reefscape scales. In Chapters 3, 4 and 5, the descriptors coming from digital elevation models and orthomosaic analyses are detailed and used for the respective studies proposed.

Table 2.2 Software used for three-dimensional reconstructions, physical and biological analyses. References of photogrammetric coral reef studies, which used the same software packages.

Software	Processing performed	Study scale	References studies
Agisoft Metashape Professional Edition	Photogrammetric reconstruction	Colony and breakwater	Burns et al., 2015a,b; 2016a,b; Burns and Delparte 2017; Palma et al., 2017; Price et al., 2019; Rossi et al., 2017; Carlot et al., 2020
Pix4D mapper Pro	Photogrammetric reconstruction	Reefscape	Raoult et al., 2017; Burns and Delparte 2017; Lowe et al., 2019
3ds Max	Mesh edition and 3D measurements	Colony	Gutiérrez-Hereida et al., 2015; Olinger et al., 2019; Lavy et al., 2015
MeshLab	Mesh edition and 3D measurements	Colony	No reference found
QGIS	Biological analyses on orthomosaics	Reefscape	Barde et al., 2018; Lecours et al., 2016
Global Mapper	Physical analyses on DEMs	Reefscape	No reference found
R (language)	Physical analyses on DEMs	Reefscape	Fukunaga et al., 2019

2.4 Photogrammetric protocols

To achieve the three key study objectives, two photogrammetric acquisition protocols were designed adapted to the two study scales: isolated coral colonies (of 2 cubic meters or less) and reefscapes (hundreds of square meters). In addition, we adapted a specific acquisition protocol for the complex case of breakwaters. All protocols were designed to ensure satisfactory overlap (> 70 %) of the content between consecutive images, ensuring a high-quality photogrammetric reconstruction.

We used scale bars to scale the photogrammetric outputs to their real dimensions, thus allowing accurate measurements. These aluminum bars, 50 cm or 1 m long with checkered patterns at the ends (Fig. 2.8),

were placed in or close to the surveyed area or object and captured in the photographs. Up to three scale bars were placed, depending on the area or object size. During the photogrammetric processing, the real dimensions of these scale bars were indicated in the software to scale the entire reconstruction.
When measuring reefscapes and breakwaters we used Ground Control Points (GCPs), as their geolocation and depth were important for follow-up analyses. Three to five of these small, 5x5 cm checkered metal plates (Fig. 2.8), were placed on the site and captured in the photographs. Their geographical coordinates were recorded with a GPS from the surface and their depth recorded with a diving computer. These coordinates and depth were then indicated in the photogrammetric software during processing to set the reconstruction at their real position on earth and for underwater depth.

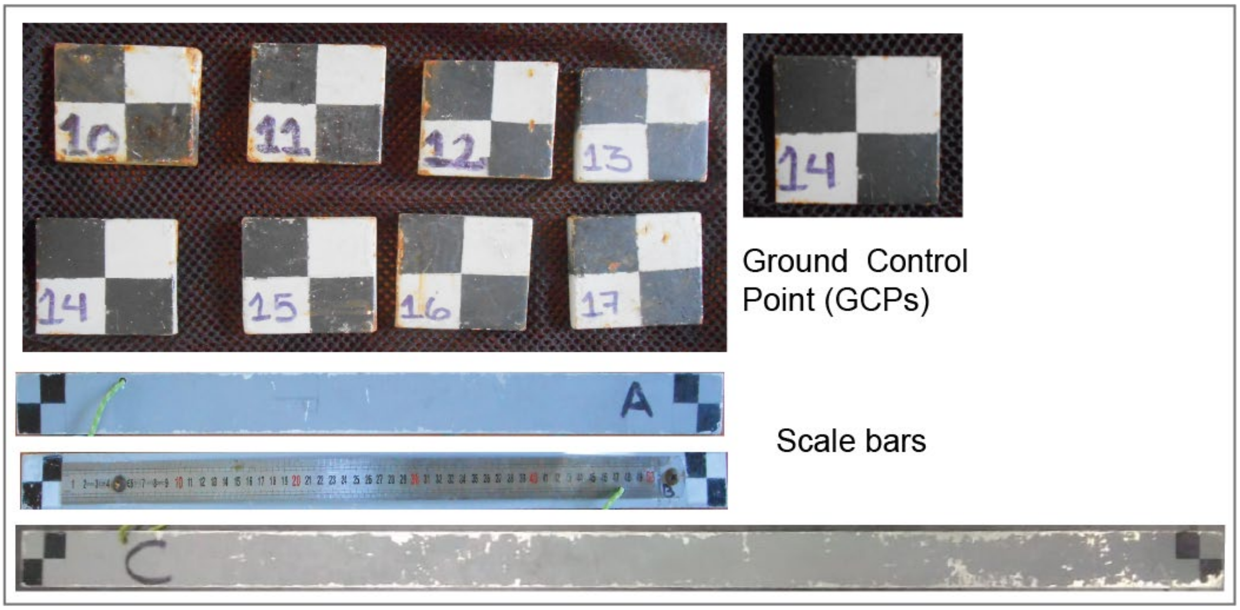


Figure 2.8 Scale bars and GCPs used for photogrammetric samplings

The photogrammetric protocols described where and how the photographer must take the images, according to the complexity of the study area or object, the underwater visibility, and the desired resolution of the photogrammetric outputs. For confidentiality reasons, I only present the general guidelines of the photogrammetric protocols developed.

In summary, the image acquisition process was carried out as follows:

- Colony scale: the images were collected via snorkeling or scuba diving. Photographs were taken from multiple angles, both nadir (i.e. pointing downwards) and oblique, and from two to four rings of different heights around the colony. At least one scale bar was placed close to each colony and captured in the images.
- Reefscape and breakwater scale: a diver collected the images in 60 minutes of scuba dive. Photographs were taken 3 m above the seafloor with nadir orientation (i.e. pointing downwards) and along several parallel lines. Additional oblique images were taken for highly complex components of the reefs. Three scale-bars (2 × 50cm, 1 ×100cm) and eight GCPs were placed across the study area.

Thus, the overall photogrammetric workflow can be decomposed in 6 key steps (Fig. 2.9):

1. Site preparation with scale bars and, for reefscapes and breakwater, GCPs
2. Image acquisition
3. Image calibration and sparse cloud generation
4. Scaling of the project and, for reefscapes and breakwaters, georeferencing
5. Dense point cloud and, for isolated coral colonies, mesh generation and exportation
6. Digital elevation model, orthomosaic generation, and exportation for reefscapes and breakwaters

Steps 1 and 2 composed of fieldwork while steps 3 through 6 were carried out on the computer and represented the process of the three-dimensional reconstructions and the export of photogrammetric outputs and 3D colony analysis (Fig. 2.9).

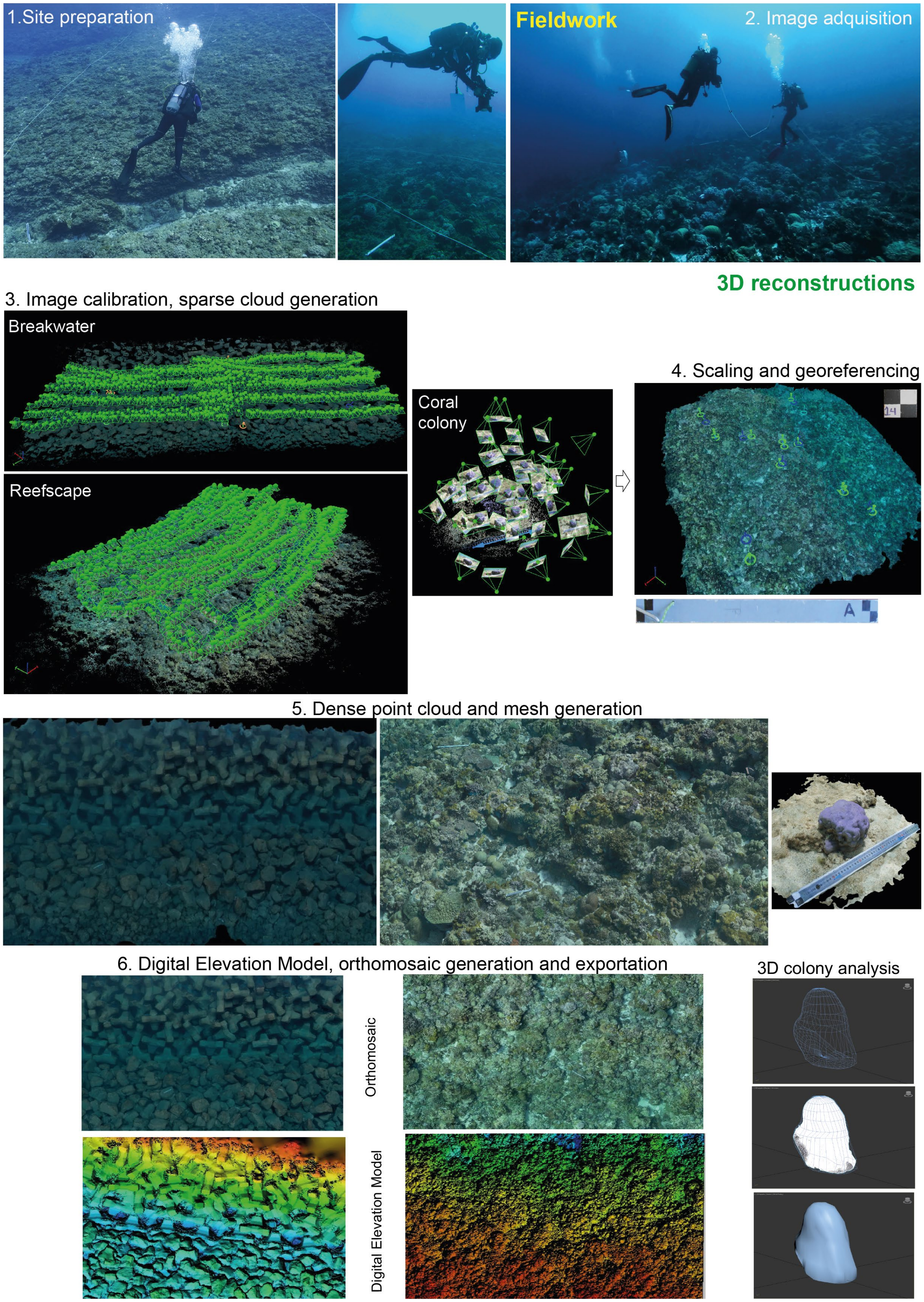
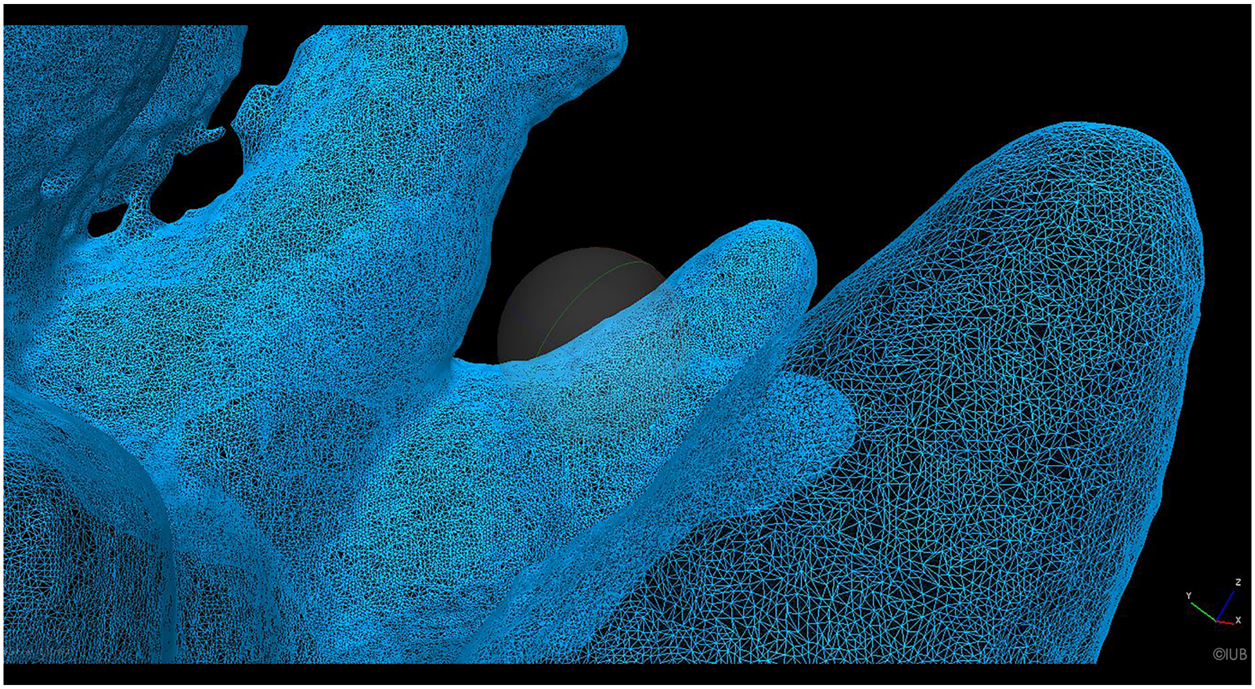


Figure 2.9 Key steps of photogrammetric workflow.

Chapter 3. Quantifying the shelter capacity of coral reefs using photogrammetric 3D modeling: from colonies to reefscapes



Inter-chapter

Following the Thesis objectives, in the first study I focused on quantifying shelter provision of reef-building corals. All colonies were sampled *in situ* and fieldwork was conducted in three islands that contrasted in terms of habitat complexity and anthropogenic pressures; thus the data set well represented four major growth forms of Scleractinian corals. I, along with technical partners, designed an underwater photogrammetric protocol to obtain the necessary resolution for 3D models. Agisoft Metashape software was used to conduct the 3D reconstructions and 3ds Max and MeshLab software were used for 3D analyses. Measurements of 2D and 3D features of coral colonies were then used to calculated shelter volume and infer shelter sizes by growth form. We then developed and fitted linear predictions models to quantify shelter capacity at reefscape scale using an automated R code. In this section I emphasized the importance of these new quantitative descriptors in coral reef conservation programs to better characterize the capacity of a reef ecosystem to support biodiversity.

Quantifying the shelter capacity of coral reefs using photogrammetric 3D modeling: from colonies to reefscapes

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Abstract

Structural complexity plays a key role in the functioning of coral reef ecosystems. Reef-building corals are major contributors to this complexity, providing shelter and food for numerous invertebrates and fish species. Both structural complexity and shelter capacity of reefscapes are determined by several components such as spurs and grooves, slope, caves and holes, vegetation and coral colonies. Quantifying the shelter capacity from coral colonies to reefscapes is a fundamental step to estimating ecosystem potential to support biodiversity. Here, we applied underwater photogrammetry to quantify shelter volumes provided by individual coral colonies. Overall, 120 3D models of coral colonies from branching, massive, columnar and tabular growth forms were studied. Three reefscapes were also 3D modeled. The study encompasses three Indo-Pacific Islands: Reunion, Europa and New Caledonia. At the colony level, measurements of diameter, planar area, surface and shelter volume were computed. At the reefscape, the diameter and planar area of each colony were extracted from orthomosaics and then used to estimate shelter capacity. Linear models had high accuracy for predicting shelter volume from 2D (diameter = 83.1%, R^2=0.95; planar area = 87.5%, R^2=0.95) and 3D (colony surface = 87.3 %, R^2=0.96) metrics. The surface complexity and the shelter volume of the colonies allowed inferring the size of shelters provided by coral growth forms. Quantitative descriptors (i.e. relative percentage of shelter by growth form, the abundance of coral colonies, "Shannon-Shelter Index") revealed reefscape-scale shelter differences.

Our major finding is that planar area and diameter of coral colonies are satisfactory proxies for estimating shelter volume. These new proxies allow 2D metrics to quantify 3D shelter provision, which can support scientists and managers in conservation actions since such metrics are widely used in monitoring programs. Future investigations on the relationships between shelter provision and reef biodiversity will improve the understanding of these complex ecosystems.

Keywords: coral reefs, reef-building corals, photogrammetry, 3D models, predictive models, shelter capacity, structural complexity, coral growth forms.

3.1 Introduction

Structural complexity of ecosystems is a well-studied field in ecology. This important feature is mainly determined by abiotic characteristics (i.e. mineral composition, topography), biotic structures resulting from the activity of engineer organisms, and ecosystem age (Margalef, 1963; Loya, 1972; Jones et al., 1994; Richardson et al., 2017a). The central role of structural complexity in ecosystem functioning and its influence on associated biodiversity and successional processes has been shown in terrestrial (Tews et al., 2004), freshwater (Kalacska et al., 2018) and marine ecosystems (Graham and Nash, 2013). In consequence studies increasingly recommended to prioritizing structurally complex habitats for conservation purposes (e.g. Rees et al., 2018; Fukunaga et al., 2019). Tropical reefs are among the most ecologically and structurally diverse ecosystems on the planet (Yanovski and Abelson, 2019). Representing only 0.1% of the oceans' surface, they host more than 25% of marine biodiversity. Yet, they are critically threatened by human impacts, natural catastrophes and climate change (Bozec et al., 2015; Hughes et al., 2017a; Cornwall, 2019).

As ecosystem engineers, scleractinian corals are the principal contributors to the structural complexity of tropical reefs (Wild et al., 2011). The spatial arrangement, morphology and abundance of living coral colonies largely shape the topographic complexity (Zawada et al., 2010) and shelter capacity of reefscapes (Richardson et al., 2017b), providing refuges from physical stress, competition and predation to a multitude of reef organisms (e.g. fishes, invertebrates) (Hixon and Beets, 1993). Shelter availability in coral reefs is also determined by the structures of dead coral colonies, the caverns or interstices in the reef matrix, and at larger scales, by the spurs and grooves, fissures, walls and reef slopes (Friedlander and Parrish, 1998). Vegetative components, such as erect macroalgae can also contribute to shelter capacity and provide key habitats for diverse communities of epifauna, juvenile and adult fishes (Fulton et al., 2019; Pu et al., 2019). Overall, structural complexity enhances the diversity and biomass of fish assemblages (Darling et al., 2017; Wedding et al., 2019), and provides ecosystem services such as fish productivity (Rogers et al., 2014) and coastal protection (Harris et al., 2018). While quantitative assessments of structural complexity have become an important topic in reef research over the last two decades (e.g. Bythell et al., 2001; Knudby and LeDrew, 2007), technical limitations have hindered progress in this field. New tools are now available thanks to novel technologies and advances in computing power (Burns et al., 2015a,b), but whereas these new technologies should increasingly complement coral reefs surveys (Obura et al., 2019), management applications are still lacking.

Photogrammetry is a non-invasive and efficient technique that uses images to create 3D models (Westoby et al., 2012). The high accuracy of 3D reconstructions provides a fine, cross-scale quantification of several embedded metrics from the coral colony to the entire reefscape (i.e. surfaces, volumes and fractal dimensions) (Figueira et al., 2015; Burns et al., 2015b). These measures are especially valuable for temporal monitoring (Fukunaga et al., 2019) and analyses of reef functional ecology. For instance, the assessment of 3D metrics improves the prediction of the structure of fish assemblages and can contribute to explain associated biodiversity (Price et al., 2019; Wedding et al., 2019). Moreover, using 2D metrics from images to estimate 3D metrics allows incorporation of three-dimensional aspects into reef monitoring (House et al., 2018).

Coral morphology, more commonly known as "growth form", is one of the most important life history traits of scleractinian corals (Darling et al., 2012) and an strong predictor of coral ecosystem functions

(Denis et al., 2017). For instance, Kerry and Bellwood (2012, 2015) highlighted the importance of particular corals (i.e. tabular growth forms) as keystone structures that disproportionally influence the abundance of large benthic fishes and thus whole ecosystem functioning, confirming the results of previous studies (Tews et al., 2004; Alvarez-Filip et al., 2011). Wilson et al. (2008) observed that pomacentrid fishes used different growth forms (i.e. tabular or branching) depending on their life stage. The relation between individual colony features and the functional characteristics at the reefscape scale was investigated for the first time by González-Barrios and Álvarez-Filip (2018). These authors proposed a quantitative coefficient (Reef Functional Index, RFI) that combines coral cover, structural complexity and calcification rate to evaluate reef-building functional contribution and structural complexity for Caribbean coral communities. However, this approach did not include a quantitative estimation of shelter volume provided by the different colony growth forms. The role of the diversity of shelter volumes provided by specific growth forms in structuring associated biodiversity and ecosystem functioning at the reefscape scale is yet to be fully understood and, above all, quantified. This could considerably enhance the evaluation of the potential of a reefscape to support biodiverse and productive assemblages (e.g. fishes, invertebrates, etc.) and facilitates the assessment of ecosystem services like coastal protection and resource provision (Graham, 2014; Harris et al., 2018).

Our study proposes a novel method to quantify the shelter volume provided by living colonies of scleractinian corals from individual colony to reefscape scales. Here, we used underwater photogrammetry to create 3D models of 120 coral colonies of varying growth forms and sizes. We quantified their shelter volume and surface complexity through 3D analyses and inferred the size of the shelters provided by each growth form. We then fitted predictive linear models of shelter volume based on either colony diameter and planar area (2D metrics) or colony surface (a 3D metric) for each major growth form of reef-building corals, enabling the use of 2D measures to estimate volumes. Finally, we applied these predictors at the scale of reefscapes (i.e. hundreds of m^2) to provide large-scale estimates of shelter volumes, overall and by coral growth form. We also evaluated the abundance and the size of coral colonies by growth form at the reefscape scale to further illustrate the wide range of possibilities offered by this new tool. In addition, we developed an R code to automate this process and make it easily usable by end users.

3.2 Material and Methods

3.2.1 Study sites

The study was conducted at three islands of the French oversea territories of the Indian and Pacific Oceans from March 2018 to April 2019, encompassing outer reef slopes and shallow reef flats to obtain a wide representation of coral growth forms and sizes. The reefscape study sites were chosen such as to maximize contrast in structural complexity and conservation status. Two sites are located in the western Indian Ocean, Reunion and Europa islands, and one in the Southwest Pacific Ocean, New Caledonia (Fig. 3.1).

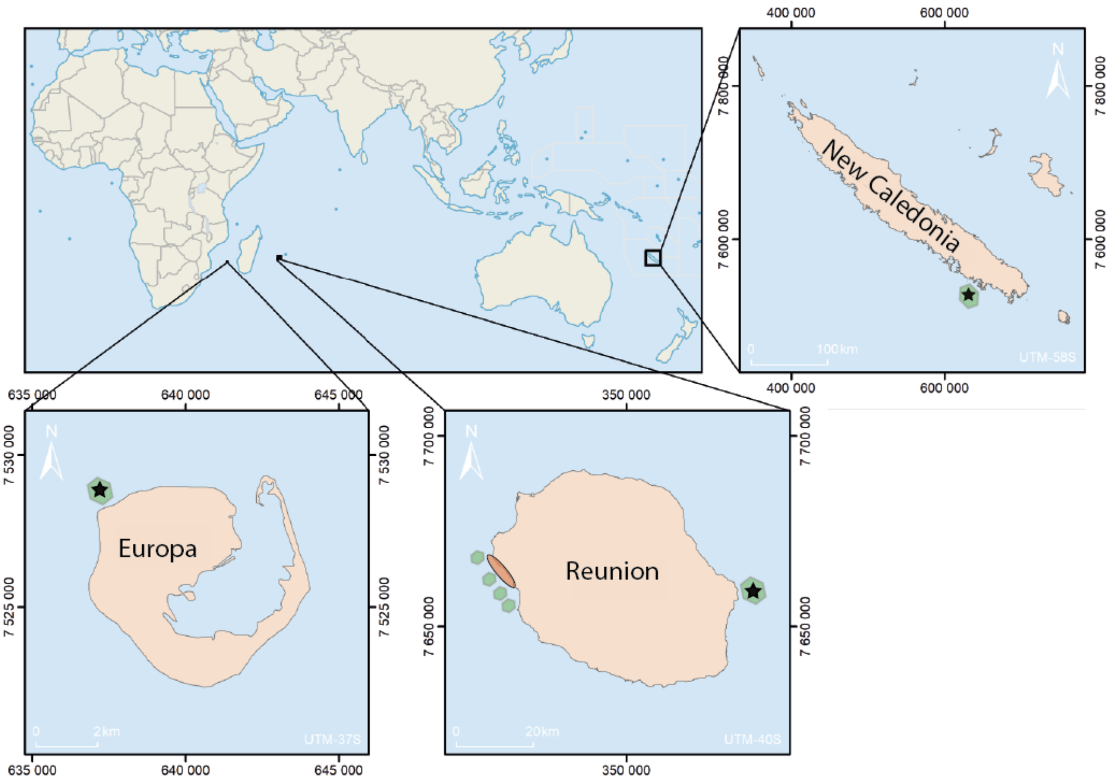


Figure 3.1 Map of study sites. Stars indicate reefscape study sites. Coral colony sampling sites are marked with a green hexagon for outer reef slopes and with an orange ellipse for reef flats.

3.2.2 Coral colony-level workflow

Image acquisition

In situ sampling was designed to obtain the largest range of growth forms and sizes of reef-building coral colonies. In this study, we considered only living corals with a diameter ≥ 10 cm. Colonies were categorized as: branching, columnar, massive and tabular as proposed by Veron (2000). Foliaceous/laminar growth forms were analysed but not considered in this study due to insufficient sample sizes (see appendix 3.1). Also, helmet-shaped growth forms were excluded since only two colonies were found at our study sites. Encrusting growth forms were not included for two reasons: 1) the 3D model analyses are not suitable, and 2) it was assumed that they have no internal shelter volume (colony shape matches the underlying substrate).

Colonies were sampled haphazardly during one-hour dives on outer reef slopes and during two hours of snorkeling on reef flats. The observer was equipped with a Sony Alpha 7II camera and a Sony FE16-35mm F4 lens in a Nauticam NA-A7II housing and 180mm glass dome port. Images were taken from multiple angles, both zenith (i.e. pointing downwards) and oblique, and from two to four circles at different heights around the colony. This underwater photogrammetry protocol was conceived to ensure appropriate overlap of photographic images for 3D reconstructions (>70 %). One scale bar was placed close to each colony and captured in the images for scaling the 3D model. The number of captured images depended on colony size and complexity (50 - 250 per colony). In total, 120 colonies were 3D-modelled for further analyses.

Coral colonies 3D reconstruction

For each colony, a 3D model was reconstructed using the photogrammetry software Agisoft Metashape Professional (version 1.5.0 build 7618) following five steps: (i) estimating image quality as function of the sharpness, exposure, focus, resolution and field depth of the images; (ii) aligning the cameras and generating a sparse point cloud calculated by the software (Fig. 3.2A); (iii) scaling the sparse cloud using the scale bar; (iv) building a dense point cloud, with depth information for each camera and densification algorithms (Fig. 3.2B); (v) building a 3D mesh, the points of dense cloud are connected to create triangles and define a shape (a polyhedral object). Mesh texture was processed, although this step it is not compulsory to perform the measures and 3D analyses (Fig. 3.2C). All models were oriented by the planar projection using the orthographic view (Fig. 3.2D), then isolated ("cleaning" coral colony model from other elements of reconstruction like reef foundation) and "closed" with Agisoft Metashape editing tools (mesh tool: Close Holes) (Figs. 3.2D, E). Finally, all models were exported for quantitative analysis and shelter volume computation.

Measurement of 2D and 3D metrics

For each colony 3D model, the planar area (i.e. 2D projected area) was calculated with the geographic information system (GIS) software Global Mapper (version 19.0), using spatial analysis tools from an orthographic projection of the 3D models (Figs. 3.3A, B). Then, the maximum diameter (henceforth called diameter) was computed using the open source GIS software QGIS (version 3.4.6 Madeira) applying the minimum enclosing circles tool (Fig. 3.3C). These parameters were calculated to obtain commons metrics at the colony and reefscape scale. Also, quantitative measure of the colony's external surface (Fig. 3.2F represented by a light blue line) and volume (V_c in Fig. 2F) were computed from the colony 3D models using the open source system for processing and editing 3D models, MeshLab (version 2016.12).

Three-dimensional analyses: shelter volume assessment and description

Three-dimensional analysis for shelter volume estimation (in dm^3) was performed using the 3D computer graphic program Autodesk-3ds Max2020. For each coral colony model, the process followed four steps: (i) creating a geode composed of 960 faces enveloping the colony (ii) shrinking the geode to the shape of the coral colony with the basis defined by the planar projection bounds (Fig. 3.2H), thus obtaining an "enclosing shape" (Fig. 3.2G); (iii) computating the "enclosing shape" volume (V_e) using MeshLab software; (iv) calculating the shelter volume (S) as the difference between the "enclosing shape" volume and the colony volume (V_c). The shelter volume ($S = V_e - V_c$) represents the empty space within the enclosing shape and the coral colony volume (Fig. 3.2H.)

Differences in the shelter provision by colonies across the four growth forms were described calculating: (i) the shelter size factor, as the ratio of the shelter volume to the surface of the colony; (ii) the surface complexity, as the ratio of the surface to the planar area of the colony. Both descriptors allow inferring the level of fragmentation/splitting of the shelter volume and the size of available spaces offered by the colony structure. Analyses of variance (ANOVA) and Tukey HSD post-hoc test were performed to test the differences across the four growth forms.

Construction of shelter predictive models

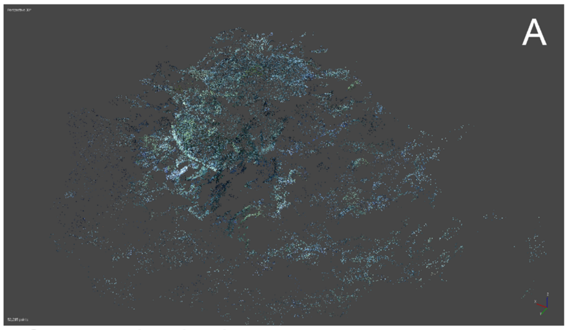
First, a Local Polynomial Regression (LOESS) smooth regression was fitted to view relationships between shelter volume and the three metrics previously computed (i.e. diameter, planar area, colony surface) without assumptions about the distribution or linearity of the data. Then, all data were log transformed and three log-log linear models of shelter volume (S, in dm^3) from 2D (diameter and planar area) and 3D (colony surface) metrics were estimated, taking into account the effects of site and growth form using the 'lm' function in R; adjusted-R^2 was calculated for each model. After log-log transformations, relationships between shelter volume and diameter, planar area and colony surface were viewed by study site (appendix 3.2). Analyses of covariance (ANCOVAs) and Tukey HSD post-hoc test evaluated the possible influence of site and growth form on the predictions.

These predictive models only consider the shelter provided by colonies with diameter ≥ 10 cm, corresponding to a minimal shelter volume prediction of 0.095 dm^3. This limitation rests upon two principal reasons: 1) only colonies with diameter ≥ 10 cm display a clear and defined growth form, and 2) technical limitations of image acquisition of small colonies in the field.

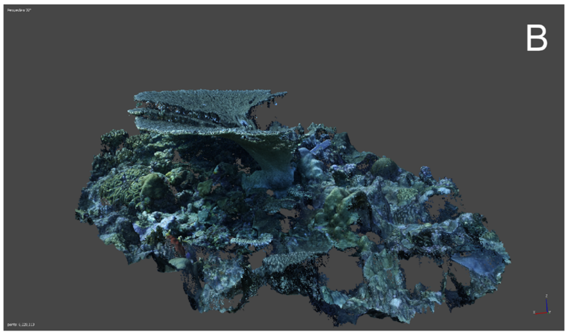
Third, predictor intervals (the uncertainty for a single specific outcome) and confidence intervals, both at 95%, were computed by bootstrap method. In addition, leave-one-out cross validations (LOOCV) were performed to test the fitness of the predictive models.

Data exploration and analyses were conducted with R sofware (R Core Team, 2019). To perform linear models, 'car' (Fox and Weisberg, 2019) and 'multicomp' (Hothorn et al., 2008) packages were used. Figures were produced using 'ggplot2' (Wickman, 2016) and 'ggpubr' (Kassambara, 2019) packages.

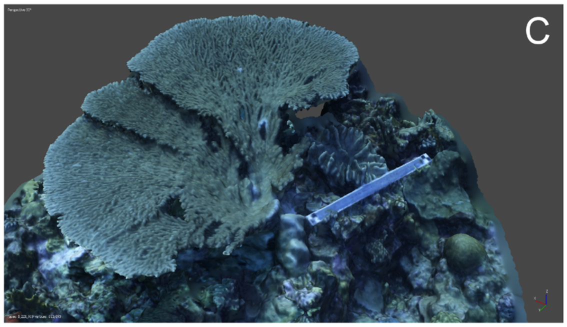
Steps of three-dimensional reconstructions



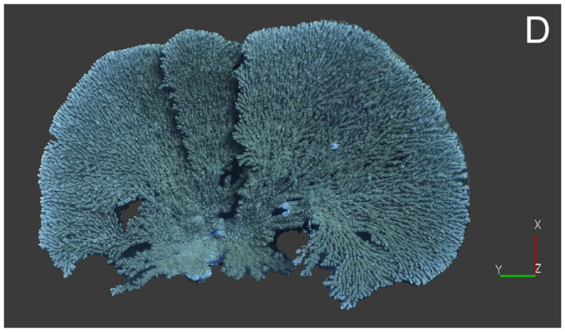
Sparce point cloud



Dense point cloud



3D model - mesh



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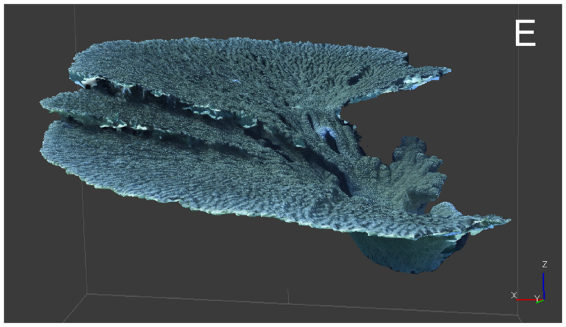
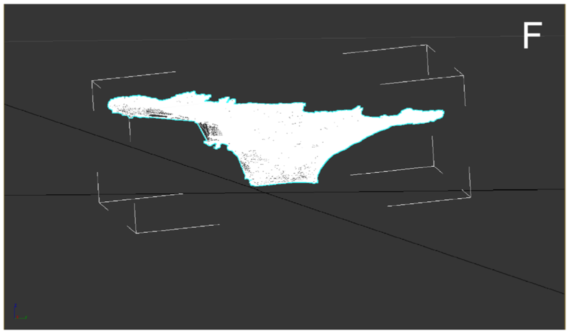
Isolated model - orthographic view

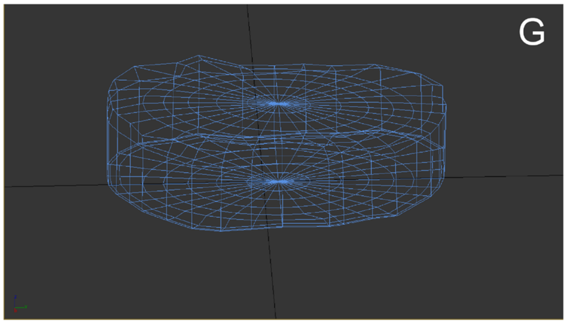
Steps of three-dimensional analyses



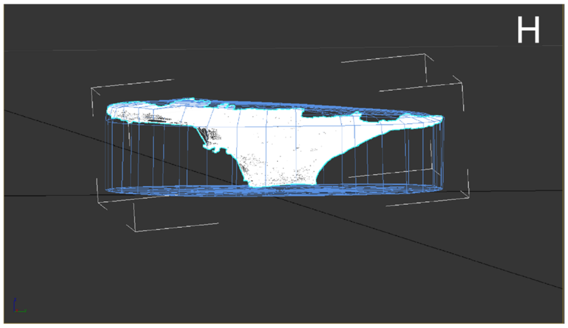
Isolated and closed model



Coral colony Surface & volume (Vc)

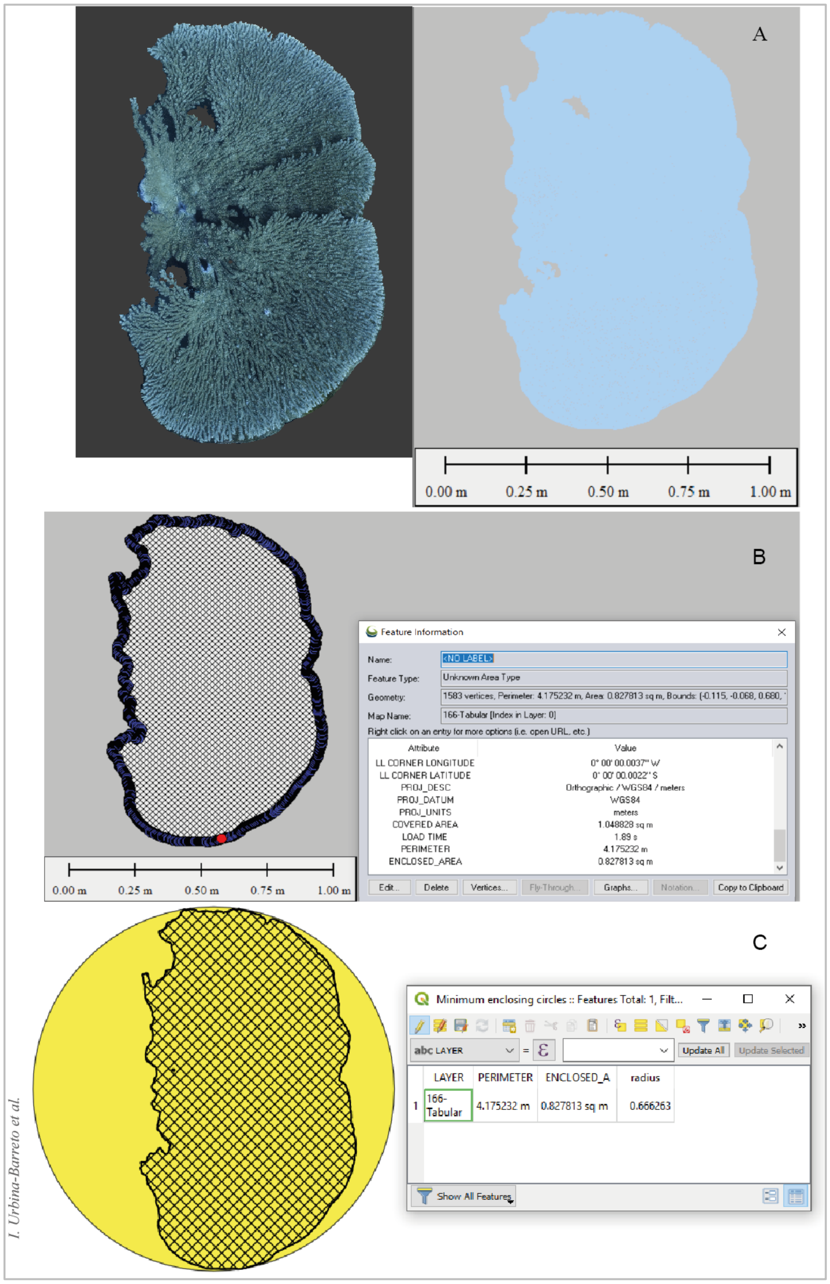


"Enclosing shape" (Ve)



Shelter volume S = Ve-Vc

Figure 3.2 Steps of 3D reconstruction in Agisoft Metashape (left column: A, B, C, D) and 3D analysis in Autodesk-3ds Max (right column: E, F, G, H) for a tabular coral colony model (appendices 3.3, 3.4, 3.5 for branching, columnar and massive colonies)



Name: <NO LABEL>
Feature Type: Unknown Area Type
Geometry: 1583 vertices, Perimeter: 4.175232 m, Area: 0.827813 sq m, Bounds: (-0.115, -0.068, 0.680,
Map Name: 166-Tabular [Index in Layer: 0]
Right click on an entry for more options (i.e. open URL, etc.)

Attribute	Value
LL CORNER LONGITUDE	0° 00' 00.0037" W
LL CORNER LATITUDE	0° 00' 00.0022" S
PROJ_DESC	Orthographic / WGS84 / meters
PROJ_DATUM	WGS84
PROJ_UNITS	meters
COVERED AREA	1.048828 sq m
LOAD TIME	1.89 s
PERIMETER	4.175232 m
ENCLOSED_AREA	0.827813 sq m

	LAYER	PERIMETER	ENCLOSED_A	radius
1	166-Tabular	4.175232 m	0.827813 sq m	0.666263

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Figure 3.3 Process to compute 2D metrics of coral colonies: orthographic view/projection (A), computation of planar area (B) and diameter (C).

3.2.3 Reefscape-level workflow

Image acquisition

Images of the three reefscapes were collected by scuba divers and using the same photographic equipment used for coral colonies; the underwater photogrammetry protocol was conceived to cover an area of 150m² (15 × 10 m patch) at ~15 m depth, following the method described in Elise et al. (2019b).

Images were taken along several parallel lines 3 m above, and oriented perpendicular to, the seafloor. Additional oblique images were taken for high-complexity reef components. In order to scale and georeference 3D models, three scale-bars and eight Ground Control Points (GCPs, metal pieces with checkered pattern) were placed across the study area. Geographical coordinates (x, y) and depth (z) were recorded with a GPS at the sea-surface and depth gauge from dive computer on the bottom, respectively. The number of captured images ranged from 750 to 1200 per site.

Reefscape 3D reconstructions

For each reefscape, a 3D model was reconstructed following the steps described in 2.2.2 with two additional steps: georeferencing and the generation of the orthomosaics (geometrically rectified photographic projection covering 150 m^2) for the future quantitative assessments.

Measurement of 2D metrics

On the orthomosaics, each coral colony was manually delineated as a polygon in QGIS and classified by growth form (Fig. 3.4). Some growth forms were not included in our dataset (i.e. foliaceous, helmet-shaped, encrusting forms) and were excluded from further analyses. The surface of each polygon was calculated with the QGIS command: area($geometry) in the field calculator tool. The maximum diameter was obtained for each polygon using the procedure presented for the coral colonies.

Application of shelter predictive models and calculation of descriptors at the reefscape scale

Planar area and diameter of each polygon delineated on the reefscape orthomosaics were then used to feed the predictive model and compute the corresponding shelter volume of each coral colony; a function in R code was developed to automatize this calculation (see in data availability). The overall shelter capacity (i.e. volume of shelter calculated for the entire reefscape) was obtained by summing the shelter volume estimate for all polygons; this analysis was also performed automatically using a code created in R programming language (R Core Team, 2019). In addition, we investigated the distribution of shelter volumes by growth form in a reefscape by adapting the Shannon index to shelter provider colonies as follows:
Shannon shelter index, $\boldsymbol{SSI = -\sum p_i \, log(p_i)}$
where pi = relative shelter volume of a given growth form.

To assess the importance of colony size in providing shelter volume, colonies were grouped into three size classes: small (diameter ≤ 30 cm), medium (30 < diameter < 60 cm) and large (diameter ≥ 60 cm) and their abundance calculated. Using abundances and shelter volumes, we estimated the mean colony shelter volume by growth form and the relative percentage of shelter volume by colony growth form and size for each reefscape.

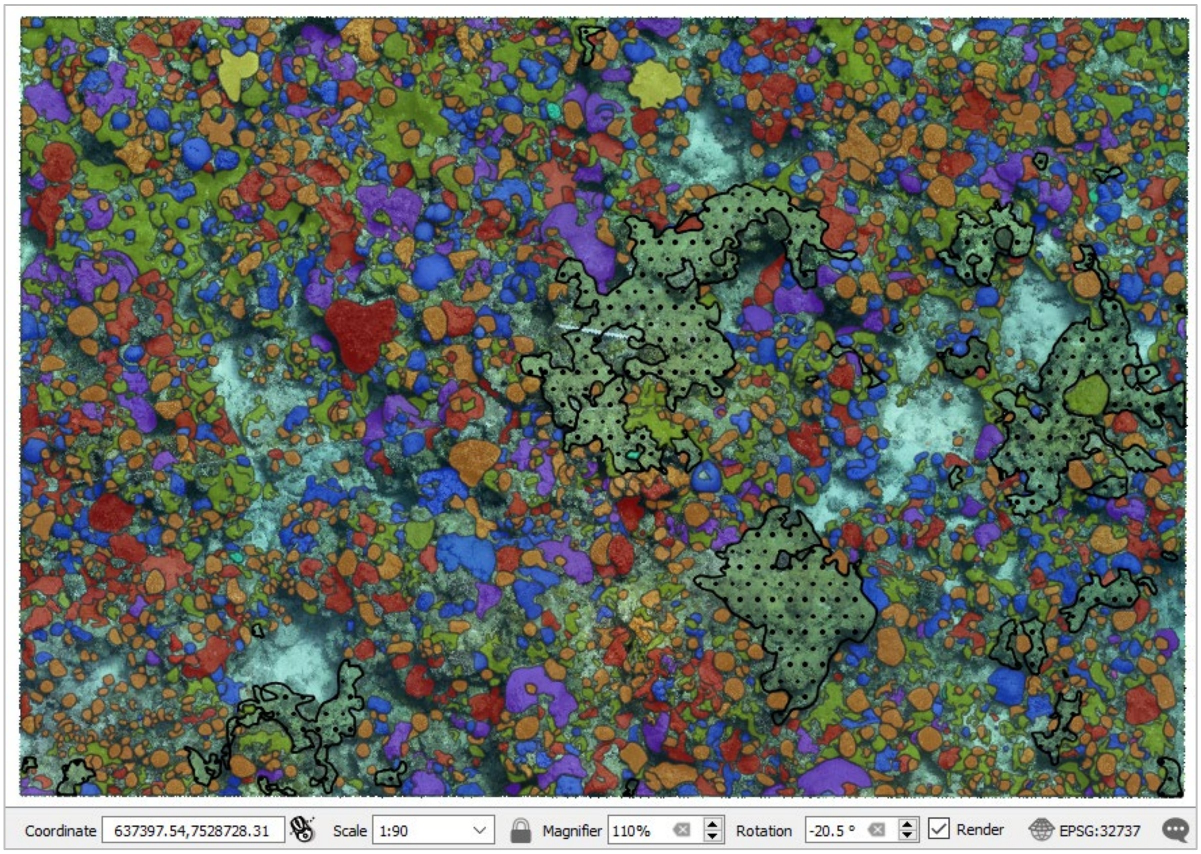
Coordinate 637397.54,7528728.31
Scale 1:90
Magnifier 110%
Rotation -20.5 °
☑ Render
EPSG:32737

Figure 3.4 Spatial analysis of Europa reefscape orthomosaic (150 m^2). Colors of polygons represent growth forms of coral colonies: branching (orange), columnar (cyan), encrusting (red), helmet-shaped (purple), massive (blue), tabular (yellow). Other categories like soft corals, algae, Milleporidae were also delineated but not considered in this study.

3.3 Results

3.3.1 Shelter quantification and predictive models

Our training database comprised 3D models of 120 colonies: 52 branching, 26 massive, 25 tabular and 17 columnar. Taxonomically, the four growth forms were Acropora spp. and Pocillopora spp. for branching colonies, mainly *Favia stelligera* for columnar colonies, Porites spp. for massive colonies and *Acropora hyacinthus* for tabular colonies (Appendix 3.6). While all growth forms were present at the three sites, most of the largest tabular colonies were found only in New Caledonia. We here present shelter predictive models based on diameter and planar area (Fig. 3.5-right) and corresponding equations (Table 3.1) and predictive model for colony surface in appendix 3.7.

The LOESS smooth regressions of shelter volume versus each of the three metrics showed linear relationships until approximately 60 cm in diameter, 2,500 cm^2 in planar area (Fig. 3.5-left) and 5,000 cm^2 in colony surface (Appendices 3.8) for tabular, columnar and branching growth forms, beyond these thresholds the relationships became exponential. For massive corals, relationships were almost linear throughout the size range (Fig.5-left). ANCOVA and Tukey tests showed that there was no site effect (Appendices 3.9, 3.10, 3.11).

Shelter volumes were strongly correlated with the diameter (R^2=0.95), planar area (R^2=0.95) and surface (R^2=0.96) of coral colonies (model summaries appendices: 3.12, 3.13 and 3.14). The accuracy of the volume predictions (LOOCV- test) was high for the planar area model (87.3%) and the surface model (87,3%) and somewhat lower for the diameter model (83.1%).

For all growth forms, the predicted shelter volume is scaled to colony diameter to the power of approximately 3, to colony planar area and colony surface to the power of 1.5 (Table 3.1, appendix 3.7). Only massive corals differed significantly from other growth forms for both metrics (colony diameter and planar area): M-T, M-C; M-B (all $p<0.001$, Tukey HSD-tests).

Table 3.1 Shelter volume for different coral growth forms predicted from colony diameter and planar area. Equations of the log-log linear models (log(y) = b + a log(x)) are shown. Different letter codes denote significant differences.

Growth form	Colony diameter (D)		Colony planar area (PA)	
Tabular	log(shelter) = -8.66 + 2.83 log(D)	a	log(shelter) = -8.32 + 1.50 log(PA)	a
Columnar	log(shelter) = -8.5 + 2.74 log(D)	a	log(shelter) = -7.37 + 1.34 log(PA)	a
Branching	log(shelter) = -9.41 + 3.00 log(D)	a	log(shelter) = -8.31 + 1.47 log(PA)	a
Massive	log(shelter) = -10.20 + 2.91 log(D)	b	log(shelter) = -9.69 + 1.49 log(PA)	b

While predictions of shelter volumes were generally accurate for all growth forms and metrics throughout the three study sites, this was not the case for the largest tabular colonies in New Caledonia (Appendix 3.15). The mean ground sample distance GSD (resolution.pixel^{-1}) of 3D models was 0.1 cm pixel^{-1}. Surface complexity was significantly greater for branching and columnar colonies than for massive and tabular colonies (ANOVA, F=14.1, $p<0.001$; Fig. 3.6 top). Shelter size factor was significantly higher for tabular colonies compared to branching, columnar and massive colonies (ANOVA, F=16.6, $p<0.001$; Fig. 3.6 bottom).

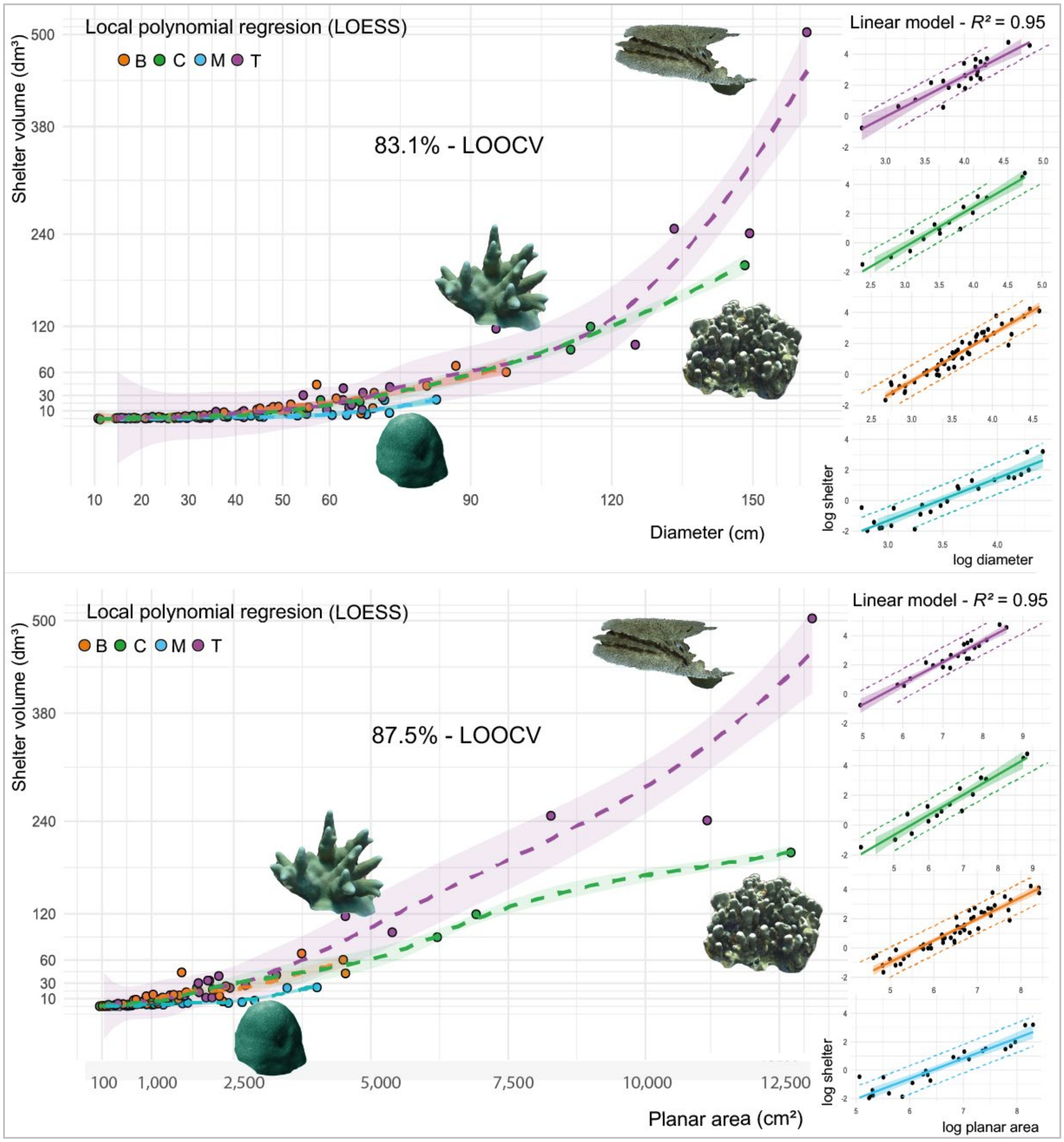

Figure 3.5 Shelter volume (dm^3) as a function of diameter (top) and planar area (bottom) for each growth form: B: Branching (orange); C: Columnar (green); M: Massive (blue); T: Tabular (purple) using local polynomial regression. Confidence intervals (95%) are represented by light colored bands. The right column shows log-log linear models with colors indicating growth forms. The confidence intervals (95%) are represented by light colored bands and prediction intervals (95%) are represented by dashed lines.

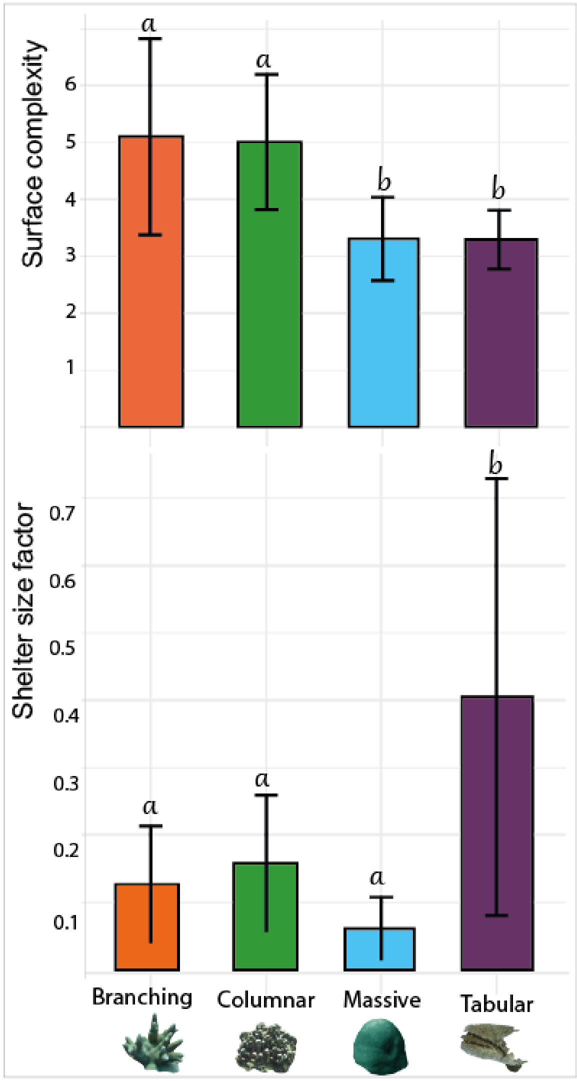

Figure 3.6 Mean (± SD) of surface complexity (top) and shelter size factor (bottom). Different letter codes denote significant differences (ANOVA, *p*<0.001).

3.3.2 Estimation of shelter volumes in reefscapes (150m²)

As planar area was the most accurate predictor of shelter volume, overall shelter capacity at the scale of reefscapes was calculated based on this metric. Total shelter volume in 150m² of reefscape provided by the coral colonies of four growth forms was highest in New Caledonia reef (1,810 dm³), intermediate at Europa (1,045 dm³) and lowest at Reunion (728 dm³). Reunion presented higher shelter volumes by columnar and tabular forms compared to Europa, while shelter volume provided by large tabular colonies was higher at New Caledonia compared to the other sites. Accuracy of shelter volume predictions varied according to growth form and reefscape and was highest for Reunion and lowest for New Caledonia (Fig. 3.7).

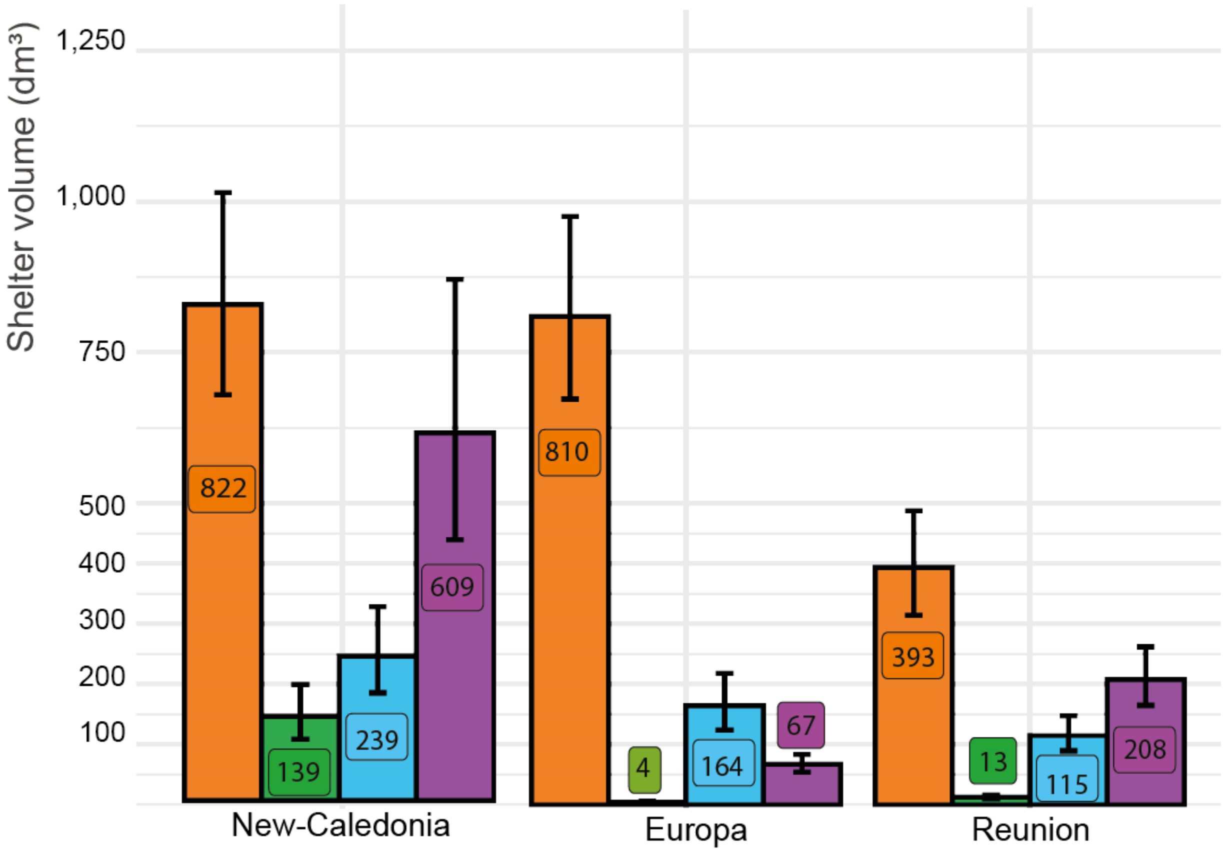

Figure 3.7 Predictions for mean shelter volumes (bars) for each reefscape from planar area of colonies by growth forms: B: Branching (orange), C: Columnar (green), M: Massive (blue) and T: Tabular (purple) with lower and upper prediction intervals (black line). Prediction values are indicated for each bar.

The distribution of shelter provided by corals in reefscapes was represented using the treemapping method (Fig. 3.8). Abundance of shelter providing colonies (branching, columnar, massive and tabular growth forms) was 918 in New Caledonia, 1,169 in Europa and 989 in Reunion. Tabular colonies were not abundant but they provided a significant volume of shelter. In contrast, massive colonies were widely represented but their contribution in shelter volume was lower than for other growth forms. The branching form was the principal shelter provider but also the most abundant growth form across the three reefscapes. Finally, the columnar growth form, despite providing high shelter volume, was poorly represented in the three reefscapes studied.

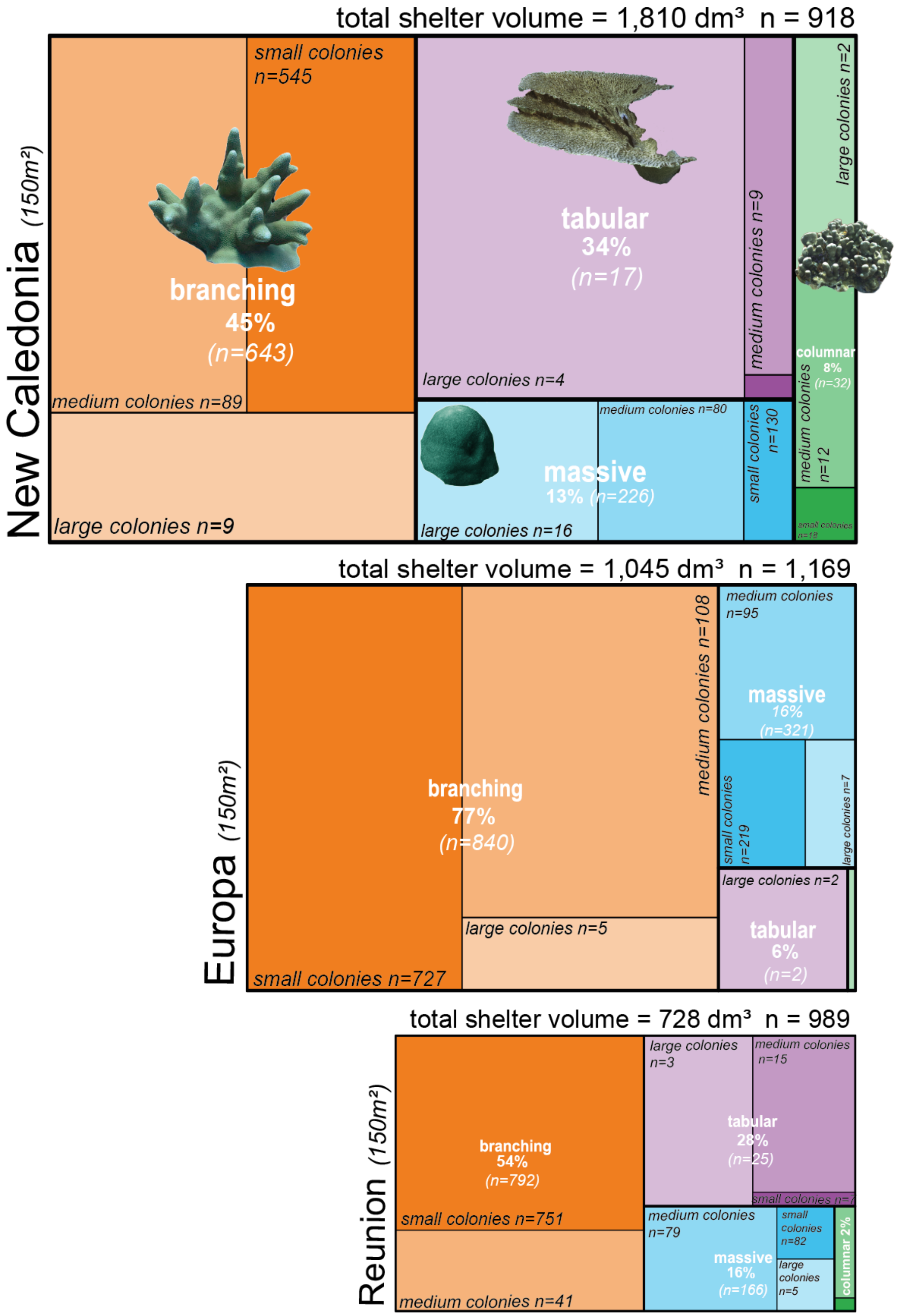

Figure 3.8 Treemap presentation of the overall shelter volume provided by corals and its distribution by colony growth form and size for each reefscape. Colors denote different growth forms: branching (orange scale), columnar (green scale), massive (blue scale) and tabular (purple scale). Rectangle size represents shelter volume provided by each colony size class: small colonies (diameter ≤30 cm) in dark tone, medium (30 < diameter <60 cm) and large colonies (diameter ≥ 60 cm) in light tone.

Tabular forms provided the highest mean shelter volume by colony followed by columnar, branching and massive forms (Table 3.2). It is important to note that this average is directly related to the relative abundance and size distribution of colonies (Table 3.3). Hence, New Caledonia exposes also the largest structures across all growth forms. New Caledonia's reefscape had the most balanced distribution of shelter providing colonies, i.e. the highest SSI, while SSI was higher at Reunion than at Europa (Table 3.2).

Table 3.2 Mean shelter volume per coral colony by growth forms and Shannon-shelter index at each reefscape, V_{Sh} = mean shelter volume (dm^3), n_{total} = total abundance of colonies by reefscape.

	Mean shelter volume by coral colony (V_{Sh} / n_{total})				Shannon-shelter index (SSI)
	Branching	Columnar	Massive	Tabular	
New Caledonia	822/643 = 1.27	139/32 = 4.35	239/226 = 1.05	609/17 = 35.85	0.51
Europa	810/840 = 0.96	2.72/4 = 0.68	164/321= 0.51	67/2= 33.56	0.29
Reunion	0.49	2.09	0.69	8.30	0.45

Table 3.3 Frequency of colony size classes by growth form and reefscape, S = small (diameter ≤ 30 cm), M = medium (30 < diameter < 60 cm) and L= large (diameter ≥ 60 cm)

	Branching			Columnar			Massive			Tabular		
	S	M	L	S	M	L	S	M	L	S	M	L
New Caledonia	545	89	9	18	12	2	130	80	16	4	9	4
Europa	727	108	5	6	-	-	219	95	7	-	-	2
Reunion	751	41	-	3	3	-	82	166	5	7	15	3

3.4 Discussion

We built predictive models of shelter volume provided by reef building corals from 2D and 3D metrics for four major growth forms. Training data for these metrics were obtained entirely from 3D models, reconstructed by photogrammetry of in situ coral colonies growing on fore reef slopes and shallow reef flats. The main outcome of this study was the ability to predict shelter volume, a 3D metric, from proxies like colony diameter, planar area or surface, which are 2D metrics. The accuracy of predictions was highest for planar area (87.5%), followed by surface (87.2%) and colony diameter (83.1%). These proxies will make shelter volume estimation largely accessible and will be useful for managers and stakeholders in setting measurable targets for reef conservation adapted to local conditions.

Over the last decade, several quantitative studies investigated the ecosystem roles of corals' morphological traits (e.g. Ferrari et al., 2016; Madin et al., 2016a; House et al., 2018; Zawada et al., 2019a). Such traits largely shape the structural complexity of reef habitats and determine the availability of niches, food, shelter and hydrodynamic conditions (i.e. current velocity, shear, turbulence) (Price et al., 2019), which in turn affect the associated biodiversity and functional process of reef ecosystems.

Thus, shelter provision is an important facet of coral reef ecology, and has often been estimated by counting holes and measuring overhangs to better understand the relationships with reef fish assemblages (Friedlander and Parrish 1998; Ménard et al., 2012). While few studies have attempted to quantify the shelter capacity of corals colonies, likely due to technical and technological limitations, Zawada et al. (2019a,b) did provide such quantitative measures using similar metrics (convex hull volume) to study the morphology of coral skeletons.

Our predictive models showed differences in shelter provision across the four growth forms. For a given size, tabular colonies provided highest shelter volumes, followed by columnar, branching and massive growth forms in decreasing order. Growth form also determines the size and form of provided spaces, with highest values of colony surface complexity corresponding to lowest values of the Shelter size factor and thus smaller sized shelters. Massive colonies were an exception in having low values of surface complexity combined with small-sized shelters. Indeed, massive colonies of our data set present protuberances and small grooves contributing to their shelter volume. It should be noted here that massive colonies that have a space at their basis were classified as 'helmet-shaped' forms and were not included in our data set. Thus, two growth forms may have an identical shelter capacity but not necessarily the same spatial shelter distribution or shelter quality. For instance, branching corals will provide a greatly fragmented volume, which will favor small organisms, whereas a tabular coral of similar shelter volume will provide protection for larger organisms. Knowing that fish size (Kulbicki et al. 2015) is an important determinant of other life-history traits such as diet or home range, the relative proportions of the various forms of corals will influence the structure of fish assemblages and their associated ecological processes (Jones and Syms, 1998; Kerry and Bellwood, 2012, 2015 ; Pereira and Munday, 2016, Darling et al., 2017). Hence, knowing the structure of shelter capacity of reefs may expand our understanding of ecosystem functioning.

The differences in shelter capacity among reefscapes were directly related to the coral growth forms present, their abundance and size distributions at the study sites. Indeed, combinations of sizes and growth forms of colonies have been used as morpho-functional groups to better describe the architecture of coral reefs and their associated biodiversity and services (Alvarez-Filip et al., 2013; González-Barrios and Álvarez-Filip, 2018). For the three reefscapes studied, branching and tabular colonies were the major shelter providers, these coral morphologies have been particularly studied and reported as possible keystone reef structures in relation to the habitat or refuge for reef fishes (Noonan et al., 2012 and Kerry and Bellwood, 2015). Reunion reef has the lowest shelter capacity. Its young age together with strong natural pressures (e.g. episodic austral and cyclonic swells) and higher human impacts (island population ~850,000) could explain the lower abundance and smaller size of the coral colonies found there. In contrast, New Caledonian reef offers the highest shelter capacity, mean shelter volume by colony and the most balanced combination of shelter providers (i.e., highest SSI). Among the three study sites, this reef is probably the most developed and least degraded (Marine Protected Area) and closest to the center of tropical marine biodiversity, the Indo-Australian archipelago. These factors may explain the diversity and abundance of various growth forms and the presence of large colonies. The environmental setting at Europa is comparable to that at New Caledonia but some growth forms that were excluded from our analysis (i.e. helmet-shaped, foliaceous/laminar) were well represented in this reefscape. As a consequence, we have likely underestimated its shelter capacity provided by the coral colonies as well as its Shannon-shelter index. Also, the Europa reefscape presents steeper slope than at

New Caledonia and Reunion, which may affect the representation of structures on the orthomosaics. Indeed, sites presenting high structural complexity and/or steeply sloping sites are more impacted by the orthographic projection than flatter sites. In fact, the structures present in slopes or steep areas are underrepresented when projected. Consequently, the planar areas of colonies and the shelter estimations were probably underestimated, here particularly at Europa. Despite our knowledge of this possible bias, we were unable to investigate it. This points to two of our study's limitations, which needs to be considered in case of further correlation analyses with associated biodiversity. Furthermore, the training database could be enriched with new data (measurements), including new morphologies, to improve the robustness of the predictive models.

Relationships between shelter volume and the colony diameter, planar area or surface correspond to the allometric growth of reef building corals: for all growth forms (branching, columnar, massive and tabular), the shelter volume is scaled to diameter to the power of 3 and to planar area to the power of ~1.5. These allometric scaling rules indicate that shelter provision by the principal growth forms of reef building corals follow the same principles of biological design of multicellular organisms (West et al., 2002). Our results are consistent with the findings of Dornelas et al. (2017), demonstrating that reef building corals have allometric rather than isometric growth rates. As in the present study, Dornelas and colleagues used the planar area to quantify coral growth (a 3D feature of colonies like shelter volume) and worked with morphologic groups rather than species that would allow more precise differentiation among groups. Now, shelter capacity of branching, columnar, massive and tabular colonies can be included and used in combination with size and growth rates to improve the predictions of habitat changes (Burns et al. 2019).

Conclusions and perspectives for coral reef conservation

Taken together, our findings contribute to the quantification of structural complexity and the shelter availability of reef ecosystems. Using a morpho-functional approach, we focus on reef building coral colonies as one of the major components providing habitat on reefs (for macrofauna/organisms >1 cm). Yet, the orientation of coral colonies used to calculate shelter volumes were based on their orthographic projections, while growth orientations are more variable depending on environmental characteristics (i.e. the habitat complexity, slope, light field), thus inducing possible bias in our estimates of shelter capacities. This point was noted on tabular growth form at New Caledonia which have shown lower accuracy of shelter predictions. This may be due to some uncontrolled and/or unquantified morphological features such as the number of plates in the colony structure, but also the height of the colony table with respect to the sea floor and the tilt compared to zenith. This aspect should be further investigated to improve the accuracy of predictive models of shelters capacities. Also, the inclusion of other components contributing to the shelter availability of reefs, like grooves and spurs, holes and overhangs, dead coral structures, the internal cavities of the reef and vegetative component should improve the estimation of the overall shelter capacity of reefscapes. Nevertheless, our results advanced the description and quantification of the structural complexity considered to be a fundamental feature of habitats and reef-communities (Graham and Nash, 2013; Richardson et al., 2017a; Agudo-Adriani et al., 2019).

The major conclusion of the study is that planar area and diameter of coral colonies are satisfactory proxies for estimating shelter volume. Since planar area is an accessible and commonly used metric in coral reef monitoring and diameter can be inferred from commonly surveys methods such as Line Intercept Method (e.g. Zawada et al. 2019b), shelter volume estimators have important potential applications for conservation purposes. Indeed, shelter volume quantification is feasible, especially with automated computation with a simple function in R code, and could be used to estimate the shelter capacity of reefscapes in spatial and temporal surveys. Further analyses are needed to evaluate the 2D-3D relationships for other coral growth forms. Additionally, it is still necessary to enhance the data training (more colonies models) to tune these predictors at other localities covering a wider geographical range, aiming to provide universal and accurate formulas which would make estimations of shelter provision by corals easier on large spatial and temporal scales. Shelter provision data will be an important complement to existing monitoring programs, helping in the forecast of recovery and resilience of reef ecosystems, and providing critical data for reef management.

Authors' contributions

IUB, RP, MA conceived the ideas; IUB, RP, VM, LP, MA, ED designed methodology; IUB, VM, LF, JPQ and RG collected the data; IUB, RP, VM and LF performed 3D models; IUB, FC, RP, SE performed data handling and analysed the data; IUB, MK, SE, HB, LP and MA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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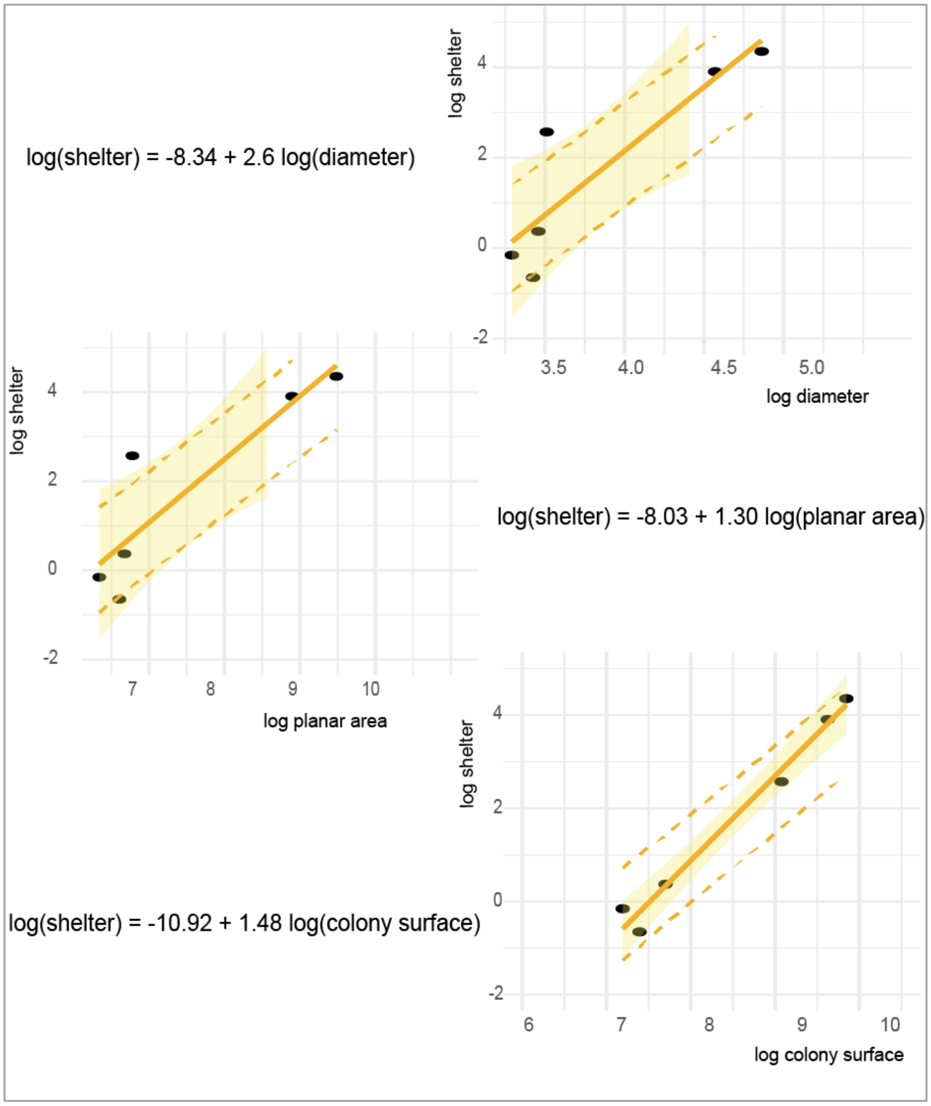
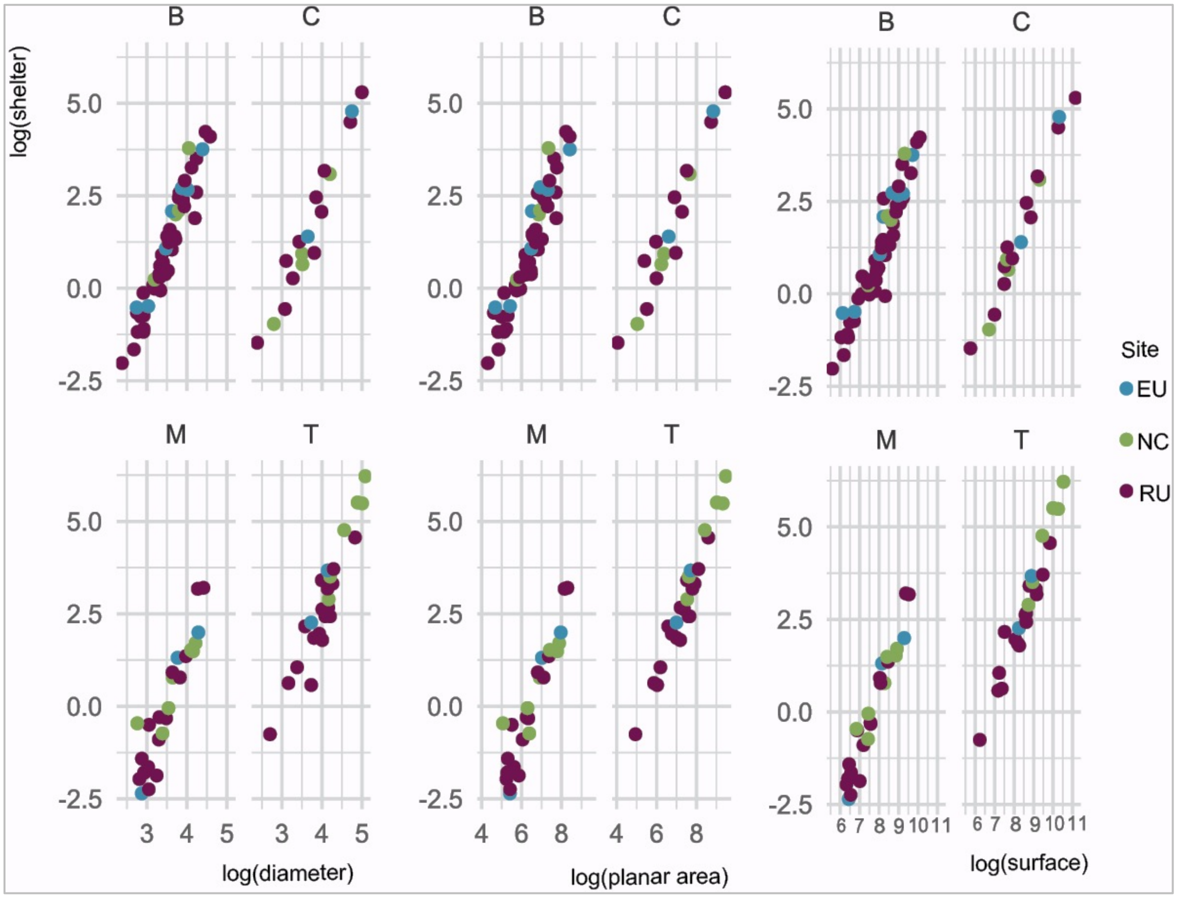
Appendices - Chapter 3

Appendix 3.1



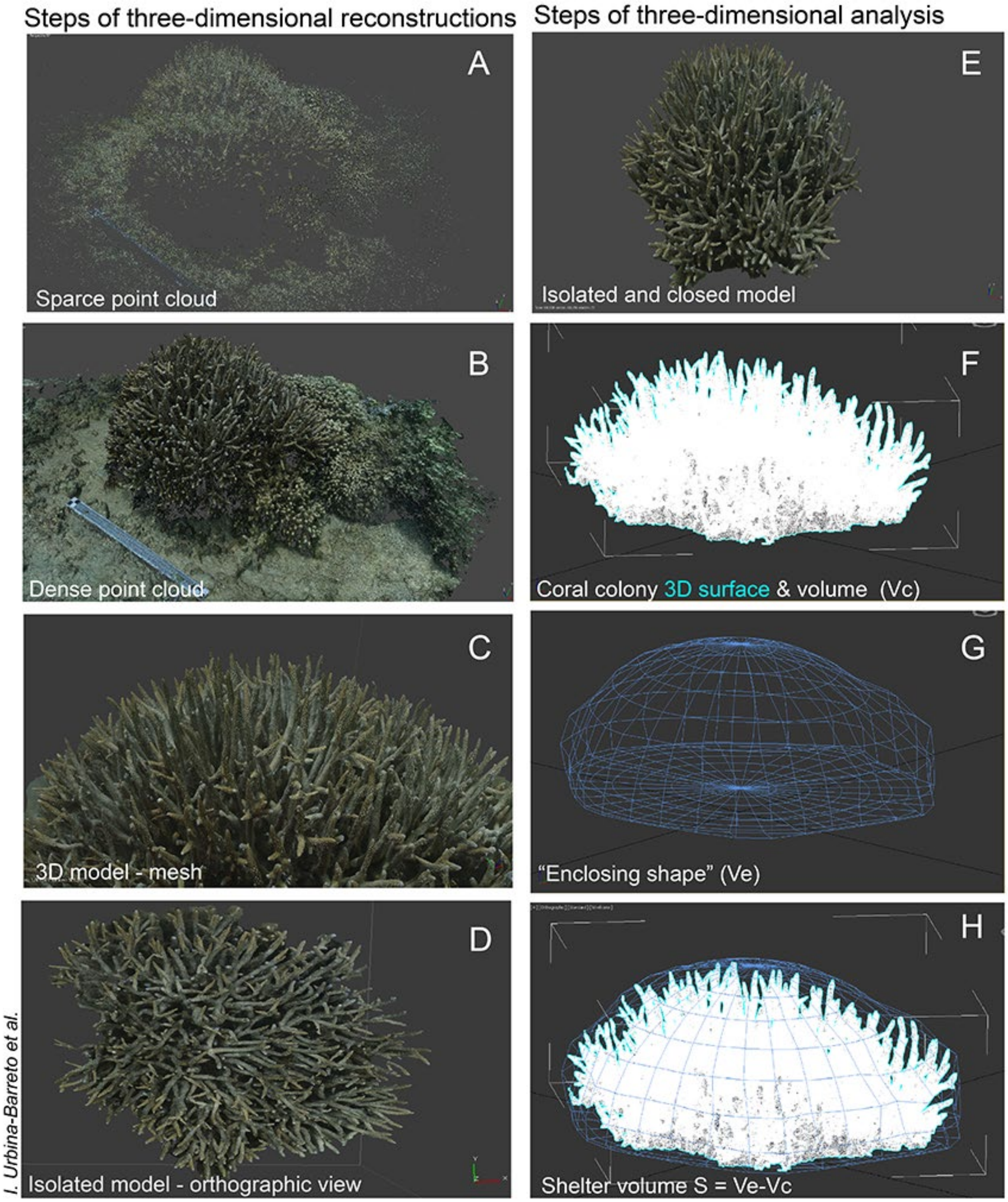
Log-log linear models for Foliaceous/laminar form. The confidence intervals (95%) are represented by light coloured region and prediction intervals (95%) are represented by dashed line.

Appendix 3.2



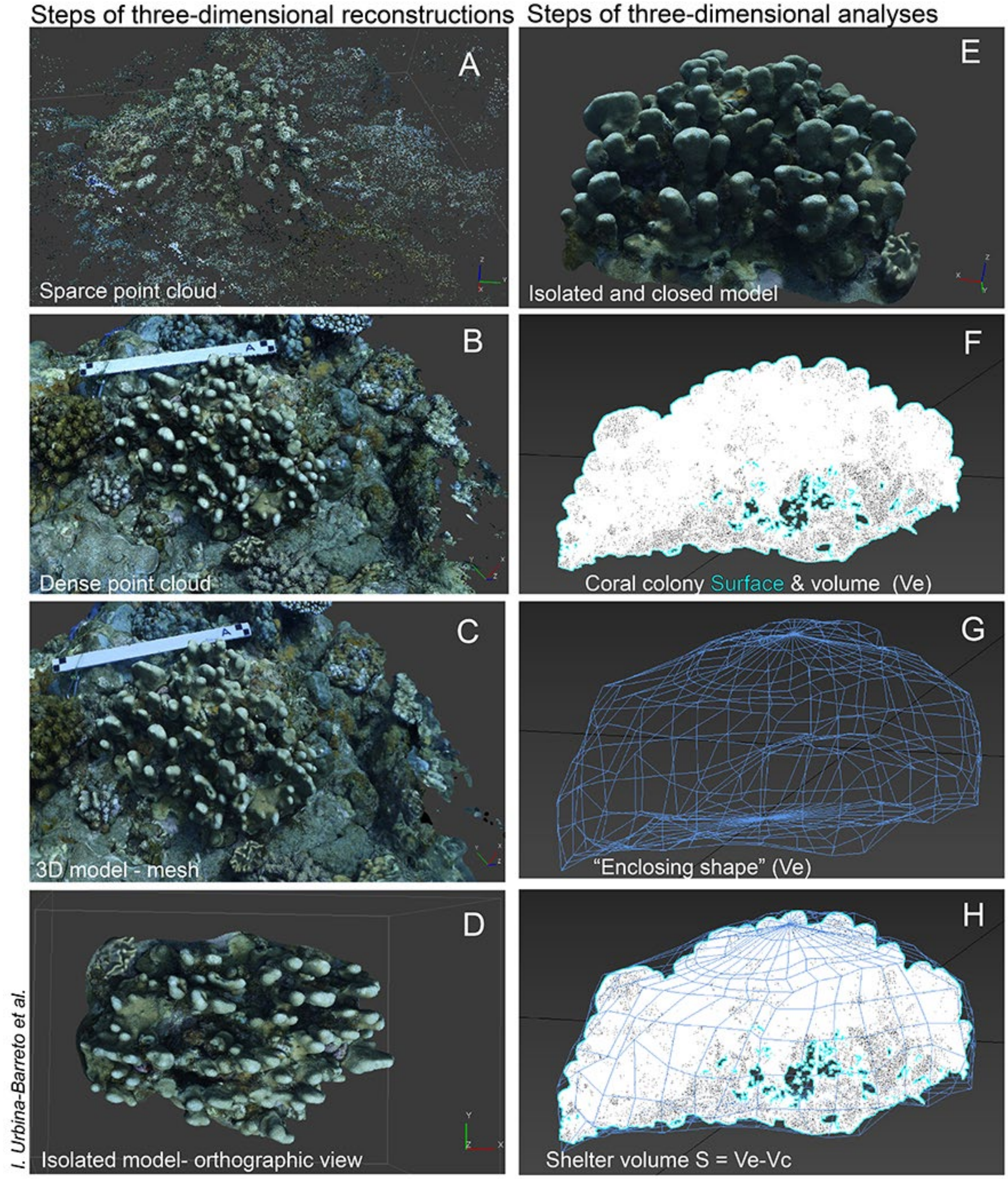
Relationship between shelter volume and diameter (left column), planar area (middle column) and surface (right column) for each growth form (B = branching, C = columnar, M= Massive, T = Tabular). Colours indicate study sites blue = Europa (EU), green = New Caledonia (NC) and purple = La Reunion (RU).

Appendix 3.3



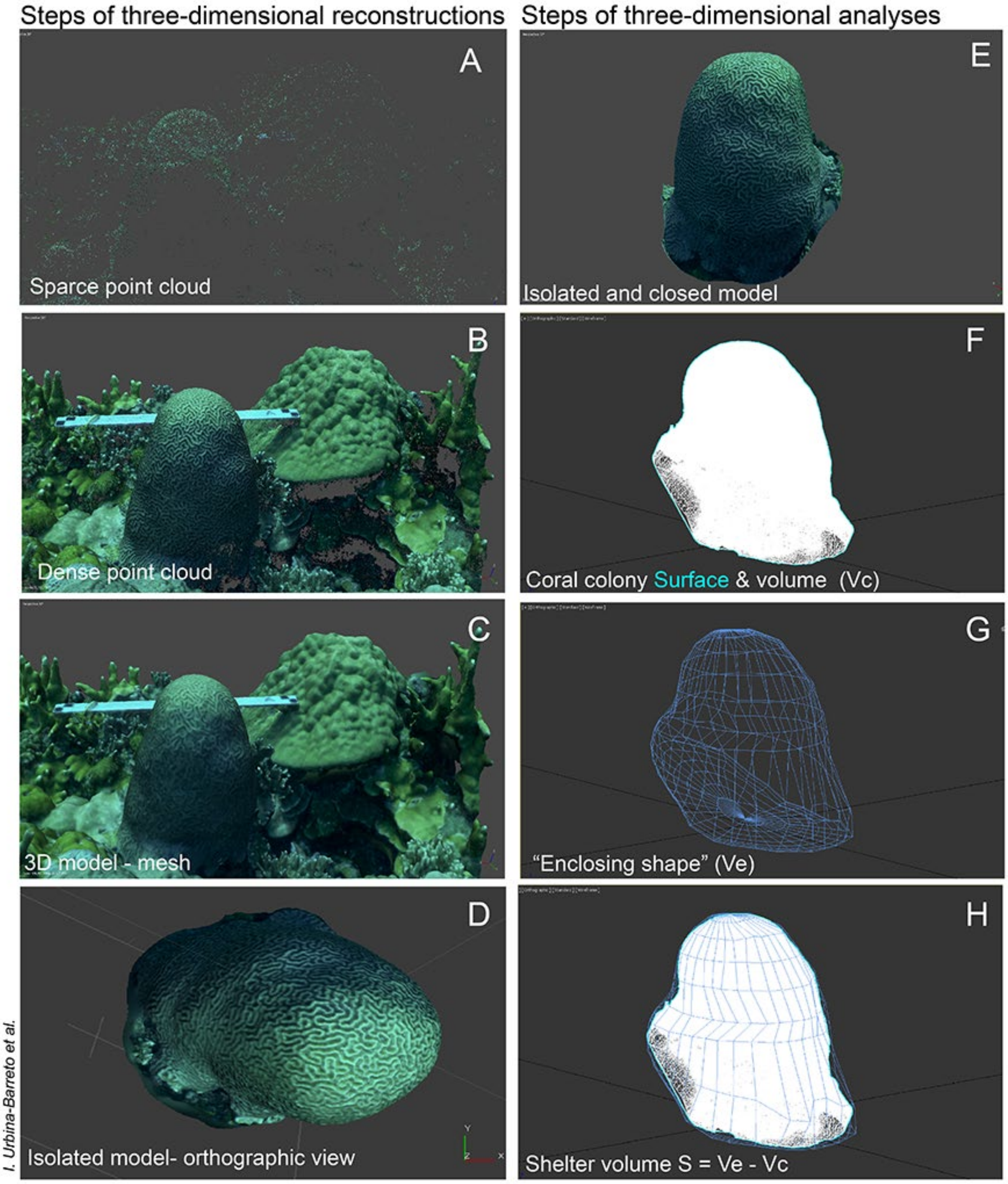
Steps of 3D reconstruction in Agisoft Metashape (left column: A, B, C, D) and 3D analysis in Autodesk-3ds Max (right column: E, F, G, H) for a branching coral colony model

Appendix 3.4



Steps of 3D reconstruction in Agisoft Metashape (left column: A, B, C, D) and 3D analysis in Autodesk-3ds Max (right column: E, F, G, H) for a columnar coral colony model

Appendix 3.5



Steps of 3D reconstruction in Agisoft Metashape (left column: A, B, C, D) and 3D analysis in Autodesk-3ds Max (right column: E, F, G, H) for a massive coral colony model

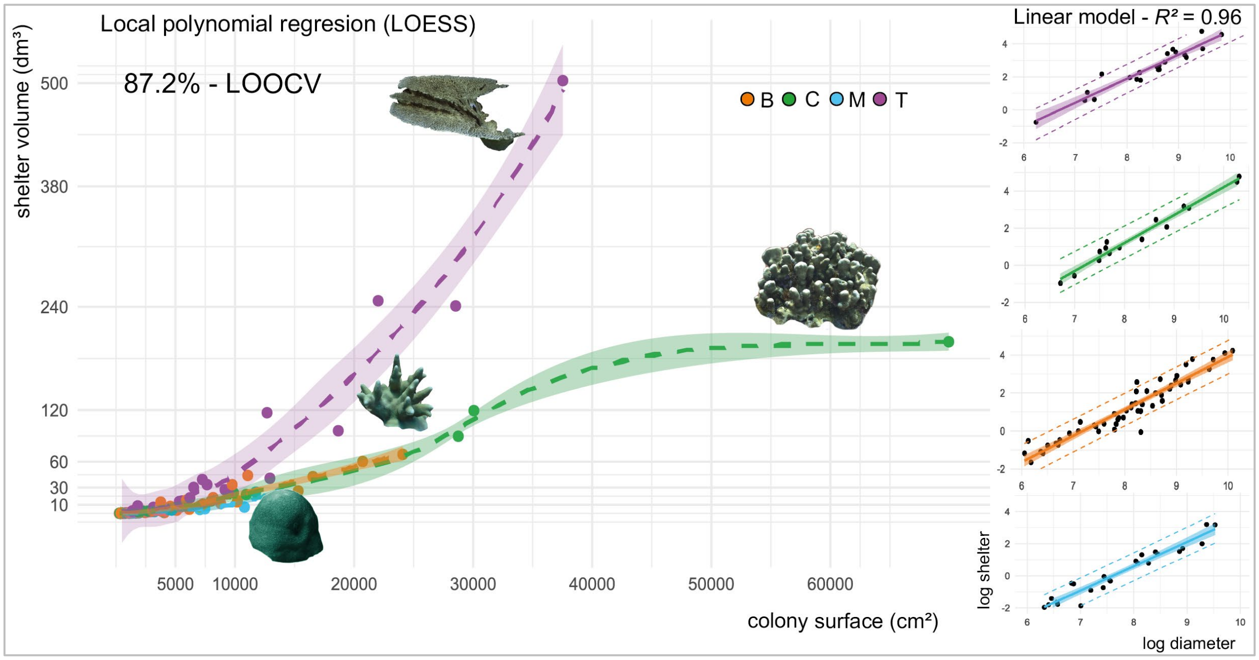
Appendix 3.6 Genus of scleractinian corals represented in the four growth forms.

Genus	B	C	M	T	Total
Acropora	20	0	0	25	45
Astreopora	0	0	1	0	1
Favia	0	10	1	0	11
Favites	0	0	1	0	1
Goniopora	0	1	0	0	1
Isopora	1	0	0	0	1
Leptoria	0	1	1	0	2
Lobophylia	0	0	3	0	3
Montipora	0	1	0	0	1
Platygyra	0	0	5	0	5
Pocillopora	20	0	0	0	20
Porites	11	3	14	0	28
Scaphophylia	0	1	0	0	1
Total	52	17	26	25	120

Appendix 3.7 Summary of log-log linear model equation for colony surface model

Growth form y = -b+ax	Colony Surface
Tabular	-10.58 + 1.55x
Columnar	-9.88 + 1.39x
Branching	-9.88 + 1.38x
Massive	-11.94 + 1.56x

Appendix 3.8



Shelter volume (dm^3) as a function of colony surface for each growth form: B: Branching (orange); C: Columnar (green); M: Massive (blue); T: Tabular (purple) using local polynomial regression. Confidence intervals (95%) are represented by light coloured region. The right column shows log-log linear models with the same colours indicating growth forms. The confidence intervals (95%) are represented by light coloured region and prediction intervals (95%) are represented by dashed line.

Appendix 3.9

ANCOVAS and Tukey test results – Diameter

Diameter	Df	SumSq	MeanSq	Fvalue	Pr(>F)
log(Diam)	1	378.2	378.2	1728.058	<2.00E-16***
site	2	0.7	0.3	1.492	0.2302
G_F	3	25.1	8.4	38.273	2.34e-16***
log(Diam):site	2	0.1	0.1	0.236	0.7903
log(Diam):G_F	3	0.4	0.1	0.541	0.6554
site:G_F	6	2.0	0.3	1.553	0.1694
log(Diam):site:G_F	6	3.6	0.6	2.717	0.0176*
Residuals	96	21.0	0.2		
> TukeyHSD					
$G_F	diff	lwr	upr	padj	
C-B	-0.04515557	-0.3868931	0.2965820	0.9857435	
M-B	-1.07460906	-1.3684100	-0.7808081	<10-7***	

T-B	0.04215327	-0.2555393	0.3398458	0.9825736
M-C	-1.02945349	-1.4109735	-0.6479335	<10-7***
T-C	0.08730884	-0.2972160	0.4718337	0.9337685
T-M	1.11676233	0.7741345	1.4593902	<10-7***
$site	diff	lwr	upr	padj
NC-EU	-0.22770183	-0.6042075	0.14880380	0.3247576
RU-EU	-0.22133036	-0.5335123	0.09085161	0.2150938
RU-NC	0.006371467	-0.2653481	0.27809100	0.9982835

Appendix 3.10 ANCOVAS and Tukey test results – Planar area.

Planar area	Df	SumSq	MeanSq	Fvalue	Pr(>F)
log(Surf2D)	1	369.6	369.6	1741.703	<2e-16***
site	2	0.4	0.2	0.963	0.3853
G_F	3	34.4	11.5	53.996	<2e-16***
log(Surf2D):site	2	0.0	0.0	0.005	0.9948
log(Surf2D):G_F	3	0.3	0.1	0.546	0.6522
site:G_F	6	2.2	0.4	1.698	0.1297
log(Surf2D):site:G_F	6	3.8	0.6	2.964	0.0107*
Residuals	96	20.4	0.2		
> TukeyHSD					
$G_F	diff	lwr	upr	padj	
C-B	0.0740917	-0.2624187	0.4106021	0.9391307	
M-B	-1.1982136	-1.4875207	-0.9089066	<10-7***	
T-B	0.1794934	-0.1136457	0.4726325	0.3829650	
M-C	-1.2723053	-1.6479898	-0.8966210	<10-7***	
T-C	0.10540167	-0.2732416	0.4840450	0.8857270	
T-M	1.37770705	1.0403199	1.7150942	<10-7***	
$site	diff	lwr	upr	padj	
NC-EU	-0.1470651	-0.5178119	0.2236816	0.6137134	
RU-EU	-0.1780106	-0.4854176	0.1293963	0.3561342	
RU-NC	-0.0309455	-0.2985089	0.2366179	0.959090	

Appendix 3.11 ANCOVAS and Tukey test results – Surface.

Colony surface	Df	SumSq	MeanSq	F	valuePr(>F)
log(Surf3D)	1	385.1	385.1	2346.807	<2e-16***
site	2	0.5	0.2	1.477	0.2334
G_F	3	25.3	8.4	51.392	<2e-16***
log(Surf3D):site	2	0.7	0.4	2.282	0.1076
log(Surf3D):G_F	3	0.5	0.2	0.994	0.3992

site:G_F	6	1.2	0.2	1.250	0.2878
log(Surf3D):site:G_F	6	2.0	0.3	2.001	0.0729
Residuals	96	15.8	0.2		
> TukeyHSD					
$G_F	diff	lwr	upr	padj	
C-B	0.03653938	-0.2593637	0.3324424	0.9882968	
M-B	-0.5943996	-0.8487955	-0.3400038	0.0000001	
T-B	0.7449456	0.4871802	1.0027111	0.0000000	
M-C	-0.6309390	-0.9612889	-0.3005892	0.0000156	
T-C	0.70840629	0.3754546	1.0413580	0.0000014	
T-M	1.33934532	1.0426713	1.6360193	<10-7***	
$site	Diff	lwr	upr	padj	
NC-EU	0.0411118	-0.2848962	0.36711985	0.9515586	
RU-EU	-0.1094897	-0.3798014	0.16082176	0.6011461	
RU-NC	-0.1506016	-0.3858777	0.08467437	0.2843482	

Appendix 3.12 Model summary for diameter, S = shelter, G_F = growth form, lm(formula = log(S) ~ G_F + G_F:log(Diam) - 1, data = dataColDes, y = T)

Residuals	Min	1Q	Median	3Q	Max
	-1.30845	-0.28232	0.00615	0.34267	1.68229
Coefficients	Estimate	Std. Error	t value	Pr(>|t|)	
Branching	-9.4137	0.4963	-18.97	<2e-16***	
Columnar	-8.5023	0.6703	-12.68	<2e-16***	
Massive	-10.1712	0.6670	-15.25	<2e-16***	
Tabular	-8.6567	0.7632	-11.34	<2e-16***	
Branching:log(Diam)	3.0026	0.1397	21.49	<2e-16***	
Columnar:log(Diam)	2.7433	0.1776	15.44	<2e-16***	
Massive:log(Diam)	2.9091	0.1888	15.41	<2e-16***	
Tabular:log(Diam)	2.8253	0.1853	15.24	<2e-16***	
Signif. codes: 0 ‘***’ ; 0.001 ‘**’ ; 0.01 ‘*’ ; 0.05 ‘.’ ; 0.1 ‘ ’					
Residual standard error: 0.5005 on 112 degrees of freedom					
Multiple R-squared: 0.9565, Adjusted R-squared: 0.9534					
F-statistic: 307.7 on 8 and 112 DF, p-value: < 2.2e-16					

Appendix 3.13 Model summary for planar area, S = shelter, G_F = growth form, lm(formula = log(S) ~ G_F + G_F:log(2Dsurf) - 1, data = dataColDes, y = T)

Residuals	Min	1Q	Median	3Q	Max
	-1.18001	-0.33250	-0.01446	0.28770	1.64037
Coefficients	Estimate	Std. Error	t value	Pr(>|t|)	

Branching	-8.31476	0.44804	-18.56	<2e-16***
Columnar	-7.36926	0.59728	-12.34	<2e-16***
Massive	-9.68956	0.62502	-15.50	<2e-16***
Tabular	-8.31958	0.71329	-11.66	<2e-16***
Branching:log(Surf2D)	1.47120	0.06883	21.37	<2e-16***
Columnar:log(Surf2D)	1.34389	0.08689	15.47	<2e-16***
Massive:log(Surf2D)	1.49873	0.09553	15.69	<2e-16***
Tabular:log(Surf2D)	1.50184	0.09475	15.85	<2e-16***

Signif. codes: 0 ‘***’ ; 0.001 ‘**’ ; 0.01 ‘*’ ; 0.05 ‘.’ ; 0.1 ‘ ’

Residual standard error: 0.4961 on 112 degrees of freedom

Multiple R-squared: 0.9572, Adjusted R-squared: 0.9542

F-statistic: 313.5 on 8 and 112 DF, p-value: < 2.2e-16

Appendix 3.14 Model summary for colony surface, S = shelter, G_F = growth form, lm(formula = log(S) ~ G_F + G_F:log(Surf3D) - 1, data = dataColDes, y = T)

Residuals	Min	1Q	Median	3Q	Max
	-1.61886	-0.28027	-0.00803	0.26618	1.12229
Coefficients	Estimate	Std.Error	tvalue	Pr(>|t|)	
Branching	-9.88164	0.44587	-22.16	<2e-16***	
Columnar	-9.88379	0.64101	-15.42	<2e-16***	
Massive	-11.94103	0.64375	-18.55	<2e-16***	
Tabular	-10.58829	0.74197	-14.27	<2e-16***	
Branching:log(Surf3D)	1.37662	0.05515	24.96	<2e-16***	
Columnar:log(Surf3D)	1.39024	0.07605	18.28	<2e-16***	
Massive:log(Surf3D)	1.56317	0.08357	18.70	<2e-16***	
Tabular:log(Surf3D)	1.55944	0.08536	18.27	<2e-16***	

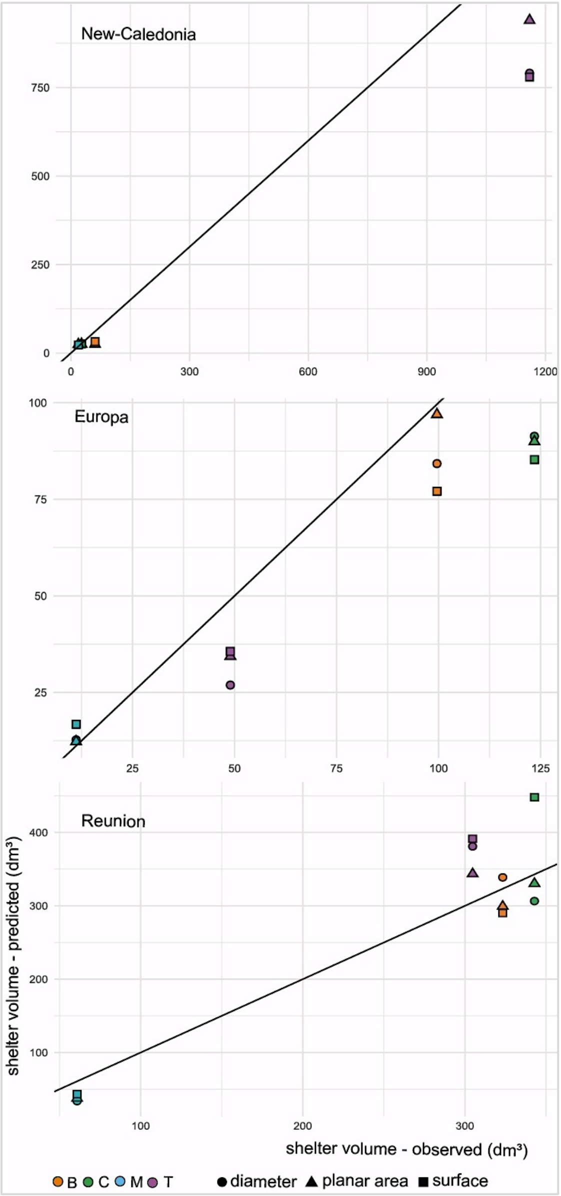
Signif. codes: 0 ‘***’ ; 0.001 ‘**’ ; 0.01 ‘*’ ; 0.05 ‘.’ ; 0.1 ‘ ’

Residual standard error: 0.4281 on 112 degrees of freedom

Multiple R-squared: 0.9682, Adjusted R-squared: 0.9659

F-statistic: 425.7 on 8 and 112 DF, p-value: < 2.2e-16

Appendix 3.15



Observed shelter volumes (n=120) versus predicted shelter volumes based on our training data from three metrics (represented by different symbols) for each colony and growth form B: Branching (orange), C: Columnar (green), M: Massive (blue), T: Tabular (purple).

Chapter 4. Underwater photogrammetry reveals new links between the habitat traits and fishes that ensure key coral reef functions

Inter-chapter

In Chapter 3 I presented new quantitative descriptors for shelter capacity of coral colonies and reefscape estimates. Differences of shelter composition were described using the abundance and size distribution of colonies, and the diversity of shelter was described adapting the Shannon index to these new descriptors. The availability of shelter and habitat complexity in reef ecosystems directly influences their associated fish groups. Links between benthic communities and biodiversity attributes (e.g. fish abundance, biomass or diversity) have arisen since the beginning of ecological studies. In Chapter 4, I used photogrammetry outputs (digital elevation models and orthomosaics) to map reefs and calculate other new physical and ecological habitat descriptors. I investigated the links between these new habitat descriptors and specific fish groups, this trait–based approach allowing identification of key ecosystem functions ensured by fish assemblages and reefscape traits. In this chapter I highlighted the contribution of the underwater photogrammetry method to better describe reefs ecosystems and its potential for conservation planning.

Underwater photogrammetry reveals new links between the habitat traits and fishes that ensure key coral reef functions

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In review in *Ecological applications*.

Urbina-Barreto I., Elise S., Bruggemann J. H., Pinel R., Kulbicki M., Vigliola L., Mou-Tham G., Guilhaumon F., Mahamadaly V., Facon M., Bureau S., Peignon C., Dutrieux E., Garnier R., Penin L., Adjeroud M. (2020). Underwater photogrammetry reveals new links between the habitat and fish community structures that ensure key functions of coral reefs.

Abstract

Maintaining key ecosystem functions of coral reefs is vital for the persistence of these ecosystems and their goods and services in the Anthropocene. Identifying the physical and biological features that ensure these key functions is a critical step to supporting healthy reefscapes. Underwater photogrammetry by Structure from Motion (SfM) allows the definition of novel habitat descriptors that may be particularly relevant in assessing these ecosystems physical and biological features. Here, we combined this new technology with fish surveys to explore how reefscape traits shape abundance, biomass and functional structure of reef fish assemblages at three environmentally contrasted islands of the Indo-Pacific. Twenty-two habitat descriptors were computed from Digital Elevation Models (DEM) and described based on ecological analyses on orthomosaics. Reef fish assemblages were assessed in the same areas, at 24 reefscapes of Europa Island, Reunion Island and New Caledonia archipelago.

While strong correlations existed among the 22 habitat descriptors, only seven were marginally correlated and presented low Variance Inflation Factor (VIF) values, signifying the most complementary descriptors: surface complexity, total shelter, Shannon Shelter Index, total coral cover, and abundance of branching, massive and tabular colonies. Canonical correspondence analyses showed that these seven habitat descriptors could explain 63% of reef fish biomass and 70% of their abundance. Five key functions ensured by fish assemblages were significantly correlated with the seven habitat descriptors: herbivory-bioerosion, secondary production, plankton assimilation, predation and coral feeding.

Reefscape traits quantified from underwater photogrammetry tools provide easily available data to inform both habitat and fish community structure in coral reef ecosystems. This functional trait-based approach allows consistent assessment of the links between these descriptors in a wide range of localities. Considering the global coral reef crisis and the increasing availability of world-reef photogrammetric surveys, this new technology should be key to bringing solutions to 21st-century conservation issues.

Keywords: Anthropocene, coral reefs, digital elevation model (DEM), fish assemblages, habitat descriptors, key ecosystem functions, orthomosaic, photogrammetry, shelter capacity, structural complexity.

4.1 Introduction

Over the last two decades, life history traits of corals and reef fishes have been increasingly considered to improve the understanding of their ecosystem roles (Bellwood et al., 2004; Darling et al., 2012; Mouillot et al., 2014; Madin et al., 2016a). Indeed, identifying and maintaining key ecosystem functions that sustain coral reefs could help determine their persistence, and that of the goods and services they provide, in the near future (Hughes et al., 2017a; Bellwood et al., 2019a,b). Trait-based approaches for corals have been proposed to improve proxies for key biological and ecological processes and already help fill data gaps by prioritizing easily measurable traits (Madin et al., 2016a; McWilliam et al., 2018; Zawada et al., 2019a). Yet, visually based, traditional survey methods continue to focus on measuring live coral cover to inform conservation strategies (Hill and Wilkinson 2004; Obura et al., 2019).

New technologies such as LIDAR and drone imagery (Collin et al., 2018; Wedding et al., 2019), 3D scanning (Reichert et al., 2016) and photogrammetry (Burns et al., 2015a) allow the computation of novel biological and physical parameters at extended spatial scales. In particular, photogrammetry by Structure from Motion (SfM) allows creation of 3D models from overlapping images and has become a powerful affordable tool for three-dimensional topographic modeling and its geoscience applications (Westoby et al. 2012). Beyond 3D models, photogrammetry can provide Digital Elevation Models (DEM, digital representation of a continuous surface with terrain elevation data) and orthomosaics (mosaicked image geometrically corrected such that the scale is uniform). These photogrammetric outputs can be analyzed to calculate several ecological (e.g. coral cover, shelter volume, colony size and abundance) and physical (e.g. surface, slope, structural complexity, fractal dimension) reefscape metrics (e.g. Figueira et al., 2015; Casella et al., 2016; Urbina-Barreto et al. under review). R codes have been developed to facilitate their application for scientists and managers (Fukunaga et al., 2019; Urbina-Barreto et al. under review), and the accessibility of this information has led a wide use of photogrammetry for the study of coral reef ecosystems in the last few years (e.g. Burns et al., 2015a,b; Bryson et al., 2017; Price et al., 2019). These novel habitat descriptors represent reefscape traits that could be particularly relevant for research on coral reef ecosystems as they allow assessing physical features, as well as biological and functional aspects. To date, few studies have investigated the relationships among these new habitat descriptors and their associations with biodiversity.

Relationships between visually evaluated benthic features and the overall structure of reef fish assemblages have been amply described (e.g. Chabanet et al., 1997; Friedlander et al., 2003; Longo et al., 2015). Other authors have examined the associations between benthic components and the presence or abundance of certain fish species or families highlighting the importance of certain coral growth forms (i.e. morphology) for habitat and diet of specialist species (Bozec et al., 2005; Wilson et al., 2008; Kerry and Bellwood 2012). Meanwhile, the importance of particular functions ensured by fishes for ecosystem stability and resilience has been demonstrated (e.g. Bellwood et al., 2003; Green and Bellwood 2009). Fish assemblages have been increasingly studied from a functional point of view, through functional entities (FEs), which are defined by shared life-history traits (e.g. diet, size class, mobility, schooling, etc.: see Guillemot et al., 2011), and considered to represent proxies for the functions ensured by groups of species. This approach was implemented for vulnerability assessments facing global threats (e.g. Graham et al., 2011a), identification of management targets (e.g. McClanahan 2014) and for worldwide biogeographic analyses (e.g. Mouillot et al., 2014). Other authors have investigated the links between fish functional groups and visually evaluated habitat features (Floeter et al., 2007; Alvarez-Filip et al., 2011; Pinca et al., 2012; Richardson et al., 2017a).

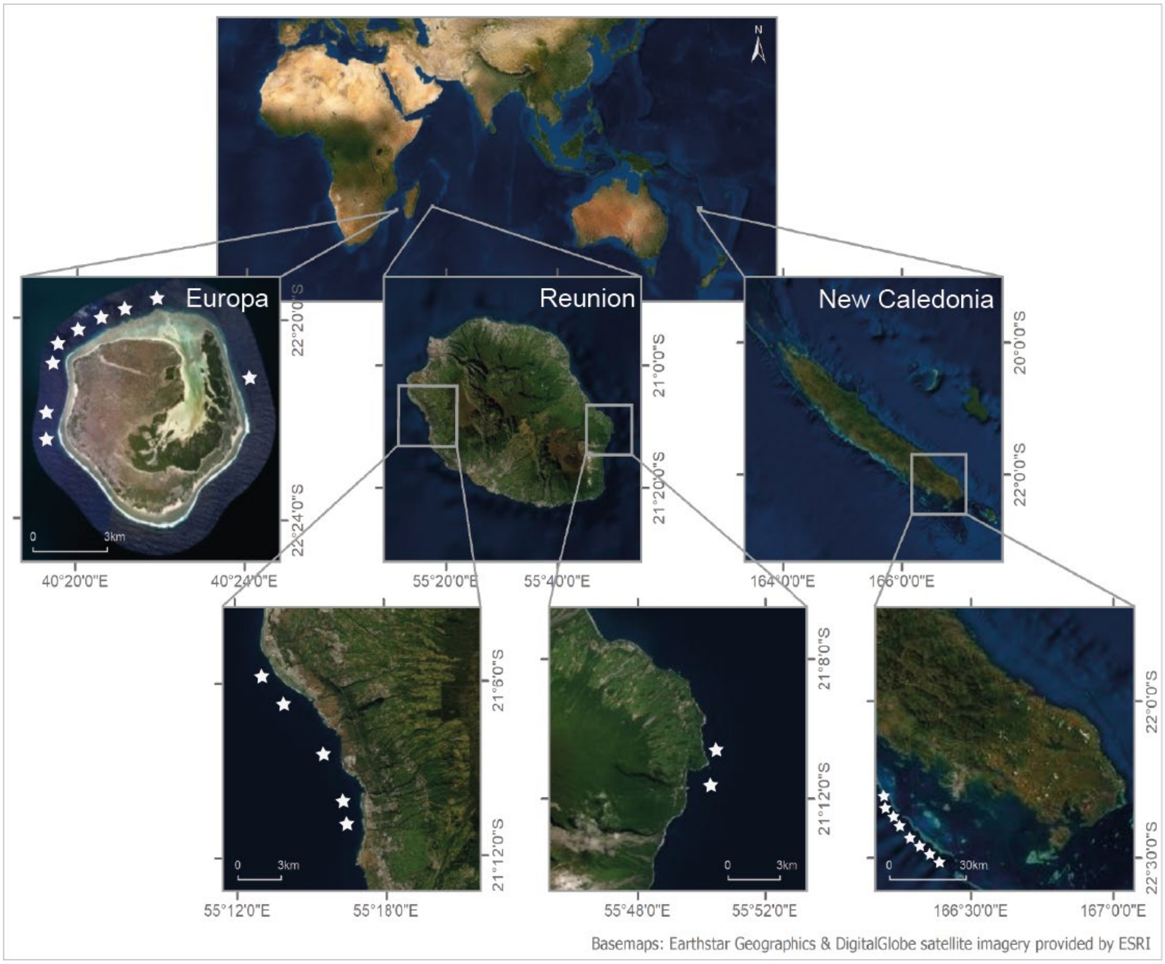
The taxonomic composition of coral reef fish assemblages shows marked differences from one region to the next. For example, Pinca et al. (2012) found only 1% of the species common to all the assemblages across 18 archipelagoes in the south and central Pacific, which suggest, that the taxonomical approach may not be adapted for large scale studies within highly diversified regions. In contrast, the functions ensured by corals and fishes are relatively similar worldwide (Mouillot et al. 2014, McWilliam et al. 2018), which can greatly facilitate the comparison of functional structures and fish-habitat relationships at large spatial scales. Upscaling the spatial scale of surveys, together with a focus on functioning by considering coral growth forms and fish FEs, has strong potential to enhance global coral reef management conservation (Hoegh-Guldberg et al., 2018; Bellwood et al., 2019a,b). However, exploration of the links between new quantitative habitat descriptors provided by the novel monitoring technologies, and the structure of fish assemblages has been limited to a few species or coarse taxonomic descriptors, such as overall diversity or biomass (González-Rivero et al., 2017; Wedding et al., 2019). Only Agudo-Adriani et al. (2019) examined such relationships by combining taxonomic and functional descriptors of fishes (trophic groups), highlighting the importance of multiple habitat attributes and the need for further investigations. In particular, identifying habitat features (beyond coral cover) that promote biodiversity and ensure functional fish assemblages could dramatically help the detection and conservation of favorable reef areas, and provide guidelines for the restoring impacted zones. In the context of accelerating worldwide ecological disruption of coral reef ecosystems, conservation programs and management sciences urgently need composite accurate information to enhance conservation actions that promote a greater regeneration of these ecosystems (Duarte et al., 2020). As such, new descriptors could complement current programs that use physical and biological aspects to estimate the resilience or vulnerability of coral reef ecosystems (e.g. Reef Resilience Network - www.reefresilience.org).

Here, we explored: (i) the complementarity and redundancy among new quantitative habitat descriptors obtained by photogrammetry; (ii) the relationships between these descriptors and the diversity, abundance and biomass of key fish functional groups and vulnerable species. In answering these questions, we aim to contribute to improving the stewardship of coral reef ecosystems.

4.2 Material and Methods

4.2.1 Study sites

Our study was conducted from April 2018 to April 2019 at 24 outer reef slopes sites around three islands: Europa and Reunion in the South-West Indian Ocean, and New Caledonia in the South-West Pacific Ocean (Fig.4.1). It encompasses coral reefs with strong environmental contrasts (i.e. habitat complexity, exposure to austral and cyclonic swell) and variable anthropogenic pressure (i.e. fishing, touristic activities, island population).



Basemaps: Earthstar Geographics & DigitalGlobe satellite imagery provided by ESRI

Figure 4.1 Location of the 24 study sites (white stars) disposed on the outer reef slopes of Europa, Reunion, and New Caledonia. At Reunion, sites on the east coast were located on lava flows.

4.2.2 Three-dimensional reconstructions and assessment of reefscape traits

Reefscapes at the 24 sites were 3D modeled by photogrammetry, following the workflow proposed by (Urbina-Barreto et al. under review). Images were collected in scuba dive and to cover an area of 150m^2 (15 × 10 m patch) at ~14 m depth. Mean overlap among images was ~70%. The mean resolution of the models (i.e. Ground Sampling Distance) was 0.13 cm/pixel and the mean reprojection error was 0.25 pixel. Digital Elevation Models (DEMs) and orthomosaics were generated and clipped to a plane area of 150 m^2 in Global Mapper v19.0 software (Blue Marble Geographics, 2019) to perform physical and ecological analyses. Scleractinian coral colonies were delineated as polygons on the orthomosaics using the open source GIS software QGIS (version 3.4.6 Madeira, QGIS Development Team, 2019), considering an individual as a colony growing independently from its neighbor (Loya 1972). Each colony was classified by growth forms following Veron (2000): branching, columnar, encrusting, foliaceous, helmet-shaped, tabular, massive and free-living. Other benthic organisms (i.e. soft corals, Milleporidae, crustose coralline algae) and abiotic components (i.e. sand and rubble) were delineated but not analysed here (Appendix

4.1). To measure the main reefscape traits at each study site (Table 4.1; Fig. 4.2), habitat descriptors were computed as follows:

DEM descriptors: Surface complexity (i.e. the ratio of 3D surface/2Dsurface), fractal dimension and mean slope were computed with R program (R Core Team, 2019) applying the code developed by Fukunaga et al. (2019).

Surface descriptors: Planar area was computed for each delineated colony using the command area($geometry) in QGIS, with surfaces totaled by growth form.

Mapping descriptors: Total abundance of colonies and abundances by growth form were computed by totaling the number of corresponding polygons using QGIS. Nearest neighbor distances were computed using the centroid of each polygon by measuring its distance to the centroid of the nearest polygon of similar growth form. Measurements (in meters) were averaged by site and growth form (Appendix 4.2).

3D descriptors: Shelter volumes provided by branching, columnar, massive and tabular colonies were calculated using the predictive models proposed by Urbina-Barreto et al. (under review). The total shelter capacity was computed as the sum of all shelters provided by these four growth forms. A Shannon Shelter Index (SSI) was computed to reflect the diversity of shelters available at each site following the expression: $\boldsymbol{SSI = -\sum p_i \, log(p_i)}$ with pi = relative shelter volume of a given growth form.

Table 4.1 Main reefscape traits and corresponding units by groups of habitat descriptors.

Groups of descriptors	**Reefscape traits**	**Units**
DEM descriptors (from DEM analyses)	Surface complexity (3D/2D surface)	Ratio - no units
	Fractal dimension (FD64 from Fukunaga et al. 2019)	Index - no units
	Mean slope	Degrees (°)
Surface descriptors (from orthomosaics analyses)	Surface of living coral cover by growth form and total coral cover	Square meters (m^2)
Mapping descriptors (from orthomosaics analyses)	Abundance of colonies by growth forms and total abundance	Number = n
	Mean distance to nearest neighbor by growth forms	Meters (m)
3D descriptors (from shelter predictive models)	Volume of shelter by growth forms or total	Cubic decimeter (dm^3)
	Shannon Shelter Index (SSI)	Index - no units

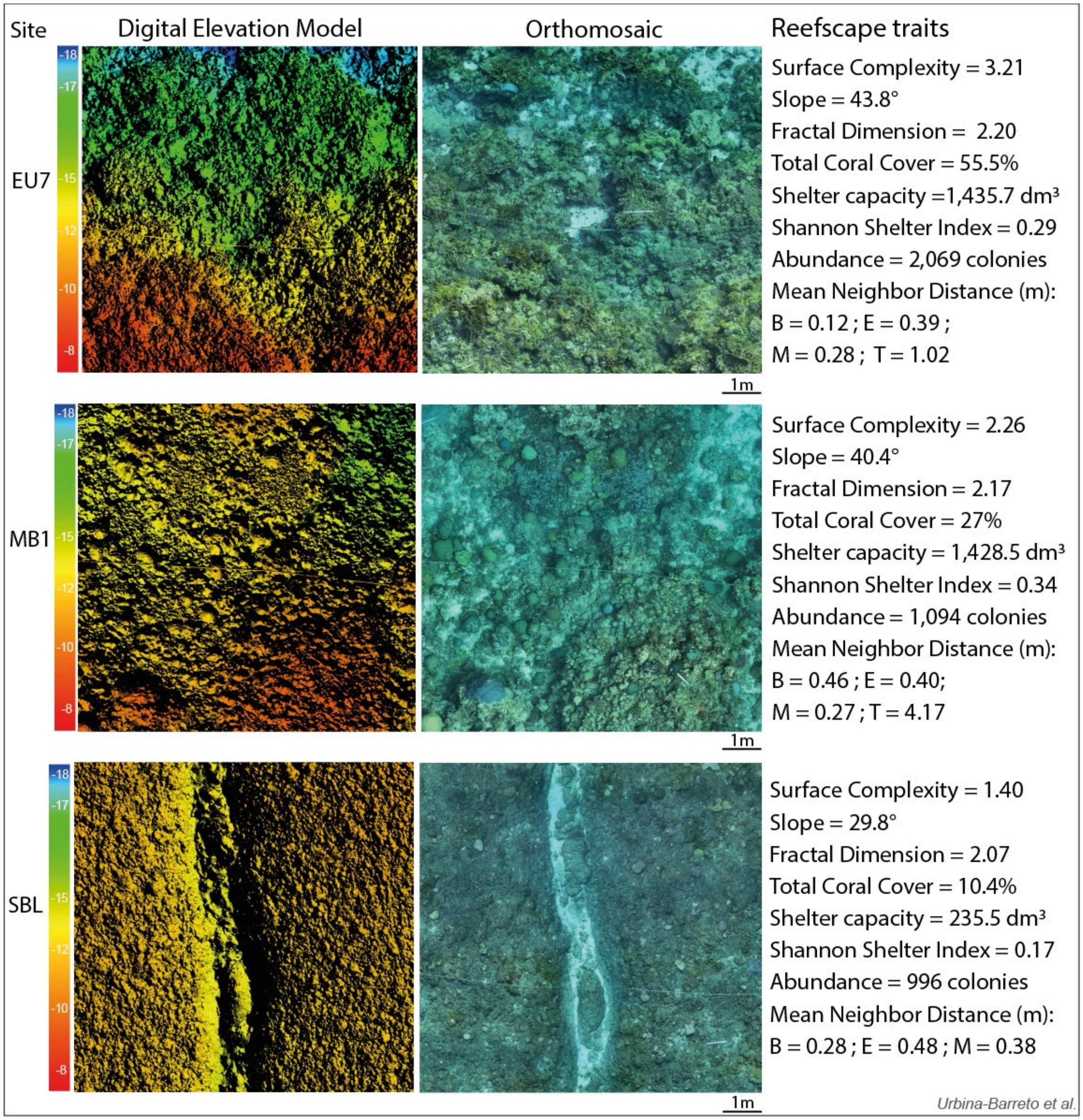


Figure 4.2 Reefscape traits at three study sites: EU7 most complex reef (Europa), MB1 moderately complex reef (New Caledonia) and SBL less complex reef (Reunion). An area of the Digital Elevation Model and corresponding orthomosaic is shown to illustrate each site. B = branching, E = encrusting, M = massive, T = tabular.

4.2.3 Fish assemblage evaluation and definition of functional entities

Fish assemblages were evaluated by remote underwater stereo-video footage at Europa Island and New Caledonia sites, following the methodology presented in Elise et al. (2019b). At each Reunion Island site, Underwater Visual Census (UVC; e.g. Labrosse et al., 2002) was performed along three 5 x 30 m belt-transects, averaging fish assemblage descriptors for each transects; the 150 m^2 survey area is approximately equivalent to the spatial coverage of a video station. For both methods, all detectable species were recorded and their abundance and length estimated. Their biomass was then evaluated using available length-weight coefficients (FishBase 2019).

Life-History Traits (LHT) were compiled for each species according to the classification used in Mouillot et al. (2014), with five traits considered: diet, species size class, schooling, adult home range, and level in the water column. Diet was divided into six categories (HD: herbivores-detritivores, OM: omnivores, SI: sessile invertebrate feeders, MI: mobile invertebrate feeders, PK: plankton feeders, FC: piscivores). Species size, based on maximum recorded total length (FishBase 2019), was divided into six size classes (S1: <7 cm, S2: 7-15 cm, S3: 16-30 cm, S4: 31-50 cm, S5: 51-80 cm and S6: >80 cm). Schooling was divided into solitary species (Sol), species living in pairs (Pair), species living in small groups (Small G: 3-20 fish on average in a group), medium size groups (MedG: 20-50 fish) and large groups (LargeG: >50 fish). Adult home range was divided into sedentary species (Sed), mobile species (Mob - staying within the same reef for several days), and very mobile (VMob - constantly moving around usually changing reefs within a day). Height in the water column was divided into species staying on the bottom (Bottom- benthic), species hovering just above the bottom (Low- demersal) and species hovering high above the reef (High- pelagic).

Functional entities (annotated "FEs") were defined as the combinations of two LHT (e.g. Diet-Size, Size-Schooling). The ten types of LHT combinations resulted in 195 FEs in our dataset. Among them five were selected as potential contributors to several key processes that promote coral reef functioning and fish productivity (Harborne et al., 2017; Brandl et al., 2019; Morais and Bellwood 2019): grazers (i.e. including both scraping and grazing species described in Green and Bellwood 2009), planktivores, predators (i.e. tertiary consumers), and preys (i.e. secondary producers). In addition, we retained a FE mainly represented by Chaetodontidae (i.e. butterflyfishes), a family that includes species relying partially to exclusively on coral for food (Pratchett 2005) (Table 4.2). The six selected FEs grouped 133 species in total, amongst which 16 were redundantly classified in two FEs (Appendix 4.3). The diversity of species within each FE, as well as the abundance and biomass (log-transformed) of the individuals representing each FE, were then computed.

Finally, two additional variables of particular interest for management were created. Commercial interest (CI) was divided in two categories: high and medium/low. Vulnerability to fishing (VUL) was divided in three categories: high, medium, low. Information was compiled using criteria from fisheries information systems (fishery yields and fish catches)

Table 4.2 Key ecosystem processes and potential corresponding fish FEs and families.

Key ecosystem process	Functional Entity	Main families represented in the FE
Herbivory-bioerosion	HD-S4 (grazers)	Acanthuridae (herbivory), Scarinae (herbivory and bioerosion)
Secondary production	Sed-Low (preys)	Blennidae, Chaetodontidae, Labridae, Pomacentridae, Pseudanthias sp.
	S2-Small G (preys)	Labridae, Pomacentridae
Plankton assimilation	S3-Vmob (planktivores)	Caesionidae
Predation	S6-Sol (predators)	Carcharhinidae, Serranidae
Coral feeding	Sed-Pair (coral feeders)	Chaetodontidae

4.2.4 Statistical approaches

Spearman's rank correlation tests were used to explore the relationships among all habitat descriptors. Non-collinear habitat descriptors, with correlation coefficients <0.7 and Variance Inflation Factor (VIF) values <3.5 were retained for subsequent analyses.

Canonical Correspondence Analyses (CCA) were performed to examine the associations between fish assemblages and habitat descriptors. Two independent CCA were conducted, considering taxonomic matrices of abundance and biomass of fish assemblages. To test model significance and determine the contribution of each habitat descriptor in explaining variance, ANOVA permutation tests (under reduced model, permutations=999) for each CCA were performed.

We then examined the Pearson correlations between the FEs contributing to key ecosystems processes (grazers, planktivores, coral feeders, predators and preys) and the main habitat descriptors. We retained the habitat descriptor most correlated to either diversity, abundance, biomass or log(biomass) of each of the key FEs. In addition, we looked for correlations with the diversity, abundance and biomass of commercially important species and species vulnerable to fishing.

4.3 Results

4.3.1 Habitat descriptors

For representativeness we only retained the 22 habitat descriptors present at more than 15 sites and representing at least 3% of the surface of each site.

Surface complexity, fractal dimension and mean slope were all strongly correlated (Spearman rank ρ >0.9, top-left black triangle in Fig. 4.3), while these DEM descriptors were only marginally correlated (ρ <0.7) with other habitat descriptors. Abundance of colonies, surface and shelter capacity were positively correlated for all coral growth forms (ρ >0.75; black triangles on the left of Fig. 4.3), except for the abundance and shelter capacity of branching corals. These descriptors were negatively correlated to the mean distance to nearest neighbor, in particular for massive and encrusting forms. Total coral cover was strongly correlated (ρ >0.8) with surface and abundance of encrusting forms. Total shelter capacity was marginally correlated with the shelter provided by tabular colonies (ρ = 0.67), and strongly correlated with the shelter provided by branching colonies (ρ = 0.77). Shannon Shelter Index (SSI) had the weakest correlations with all other habitat descriptors. Seven habitat descriptors representing the four main groups of reefscape traits were marginally correlated (ρ <0.7) and presented low multicollinearity (VIF values <3.5): surface complexity, total shelter capacity, coral cover, SSI and abundance of massive, abundance of tabular and abundance of branching colonies (dashed black rectangles in Fig. 4.3). These were selected to perform the CCA.

Regarding differences between localities, the surface complexity and abundance of massive colonies were significantly lower at Reunion than at Europa (Kruskal-Wallis and post-hoc Dunn's tests, p <0.05), while total shelter capacity was significantly lower at Reunion than at New Caledonia (Kruskal-Wallis and post-hoc Dunn's tests, p <0.05). Total coral cover was significantly lower at Reunion than at Europa and New Caledonia (Kruskal-Wallis and post-hoc Dunn's tests, p <0.001). No significant differences were detected among the three localities for SSI and the abundance of branching and tabular colonies (Kruskal-Wallis tests, p >0.1).

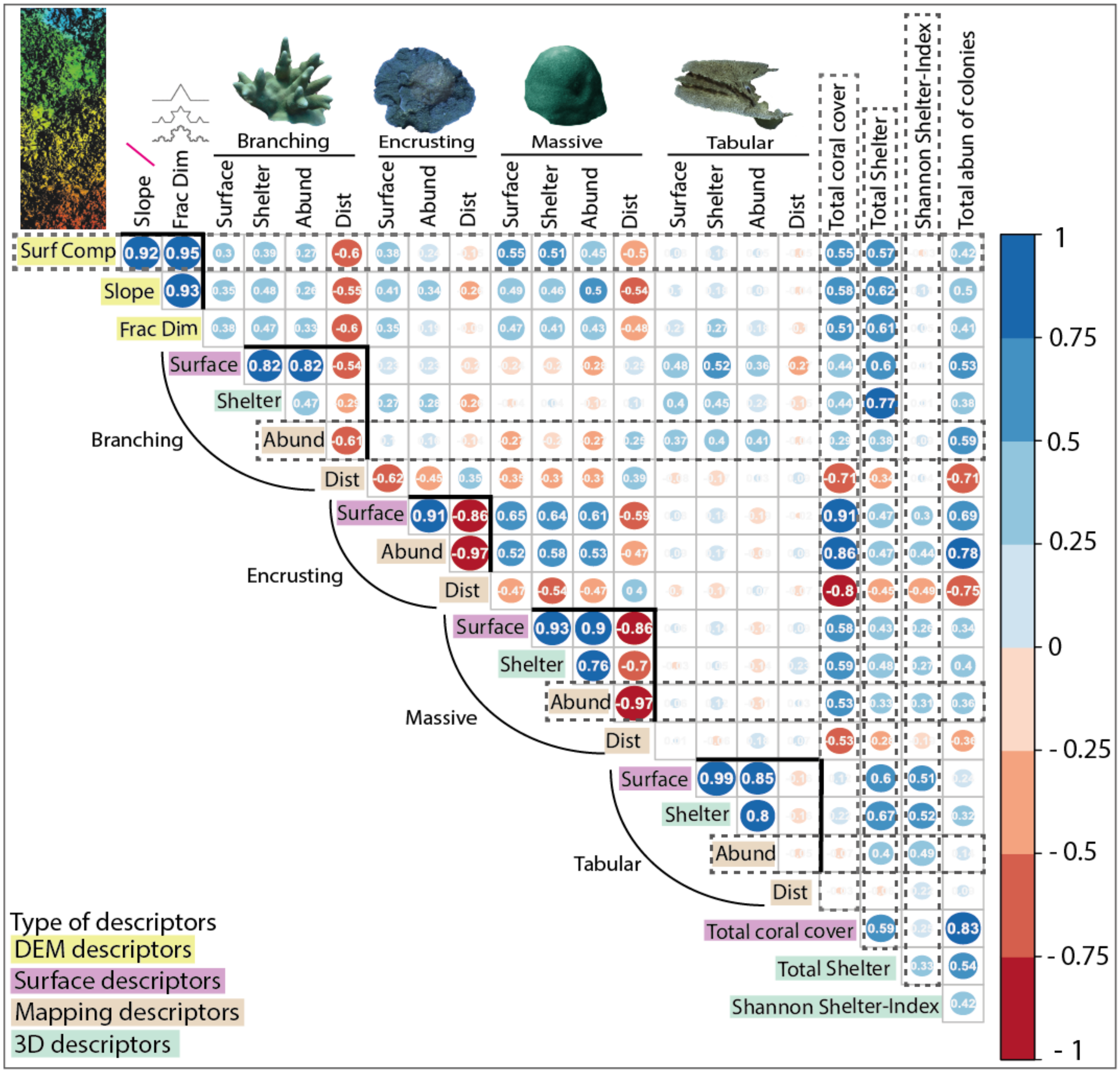


Figure 4.3 Results of Spearman's rank correlation tests among habitat descriptors. Size and color of circles represent the strength of correlation (blue for positive and red for negative). Color codes in boxes indicate the type of descriptors. Thick black lines (triangles) indicate correlations among DEM habitat descriptors for a given growth form. Dashed rectangles shows the habitat descriptors selected to perform the CCA. Abbreviations: Surf Comp = surface complexity, Frac Dim = fractal dimension, Abund = abundance of colonies, Dist = mean distance to nearest neighbor

4.3.2 Relationships between habitat descriptors and fish assemblages

A total of 331 fish species representing 45 families and 117 genera were recorded. All species were included to compose the matrices of abundance and biomass for the Canonical Correspondence Analyses, which revealed that surface complexity most explained the variance in the distribution of both biomass and abundance of fishes. The other six habitat descriptors (abundance of branching, massive and tabular colonies, total coral cover, total shelter, SSI) also contributed significantly in explaining biomass distribution (Table 4.3). Overall, the CCA model was highly significant (ANOVA test $p < 0.001$) with the first three axes explaining 62.9 % of biomass variance by the seven habitat descriptors. In contrast, the significance of CCA on abundance distribution was lower (ANOVA test $p < 0.1$) but the total proportion of abundance variance explained by the first three axes was higher (70.4 %). Only surface complexity and the abundance of massive colonies contributed significantly to explaining this variance (Table 4.3).

Table 4.3 Summary of the CCA performed on the matrices of abundance and biomass of fish species. Significance of the models and for the seven habitat descriptors are indicated: '***': $p < 0.001$; '**': $p < 0.01$; '*': $p < 0.05$; '.': $p < 0.1$; 'NS': not significant-test

	Signif.	**Axis 1**	**Axis 2**	**Axis 3**
Fish species abundance	.			
Surface complexity	**	0.7355	0.5989	0.1306
Abundance branching	NS	0.0258	-0.3167	0.2504
Abundance massive	*	0.5061	-0.3241	0.4503
Abundance tabular	NS	-0.5456	0.1451	0.4003
Total coral cover	NS	0.6990	-0.1684	0.5760
Total shelter	NS	0.0610	-0.0398	0.2155
Shannon Shelter Index	NS	-0.5570	0.1346	0.7347
Summary statistic for ordination axes				
Eigenvalue		0.6989	0.6057	0.4001
Proportion explained		0.2887	0.2503	0.1653
Fish species biomass	***			
Surface complexity	***	0.5655	-0.6586	0.4010
Abundance branching	**	-0.4779	-0.2928	-0.2589
Abundance massive	.	0.2136	0.0514	-0.1800
Abundance tabular	**	-0.7556	-0.4111	0.0892
Total coral cover	*	0.5411	-0.2474	-0.2607
Total shelter	.	0.0647	0.0436	0.2101
Shannon Shelter Index	**	-0.3398	0.2212	-0.0226
Summary statistic for ordination axes				
Eigenvalue		0.7069	0.6527	0.4845
Proportion explained		0.2410	0.2225	0.1652

Both planktivore biomass and grazer diversity were positively correlated with surface complexity (Figs. 4.4a, c). The biomass of large predators was correlated with total shelter (Fig. 4.4b). Prey biomass was strongly correlated with total coral cover, while their diversity was correlated with the diversity of shelters (Shannon Shelter Index) (Figs. 4.4f, d). The biomass of butterflyfishes was positively correlated with the abundance of massive colonies (Fig. 4.4e). Concerning the species with high vulnerability to fishing, their biomass and diversity were positively correlated with the surface complexity and total shelter (Fig. 4.4g, h).

There were also differences between localities, with four out of the six fish FEs examined ("S6-Sol", "Sed-Pair", "Sed-Low", "HD-S4"), having significantly lower biomass (or diversity) levels at Reunion than at Europa and New Caledonia (Kruskal-Wallis and post-hoc Dunn's tests, $p < 0.01$). The diversity of the FE "S2-SmallG" (i.e. prey) was not significantly different between Reunion and Europa, but was significantly higher in New Caledonia (Kruskal-Wallis and post-hoc Dunn's tests, $p < 0.001$). The biomass of planktivores was not significantly different among the three localities (Kruskal-Wallis test, $p = 0.27$). The biomass levels at Reunion were significantly lower than at Europa or New Caledonia, and their diversity was significantly lower at Reunion than at New Caledonia, which in turn was significantly lower than at Europa (Kruskal-Wallis and post-hoc Dunn's tests, $p < 0.001$).

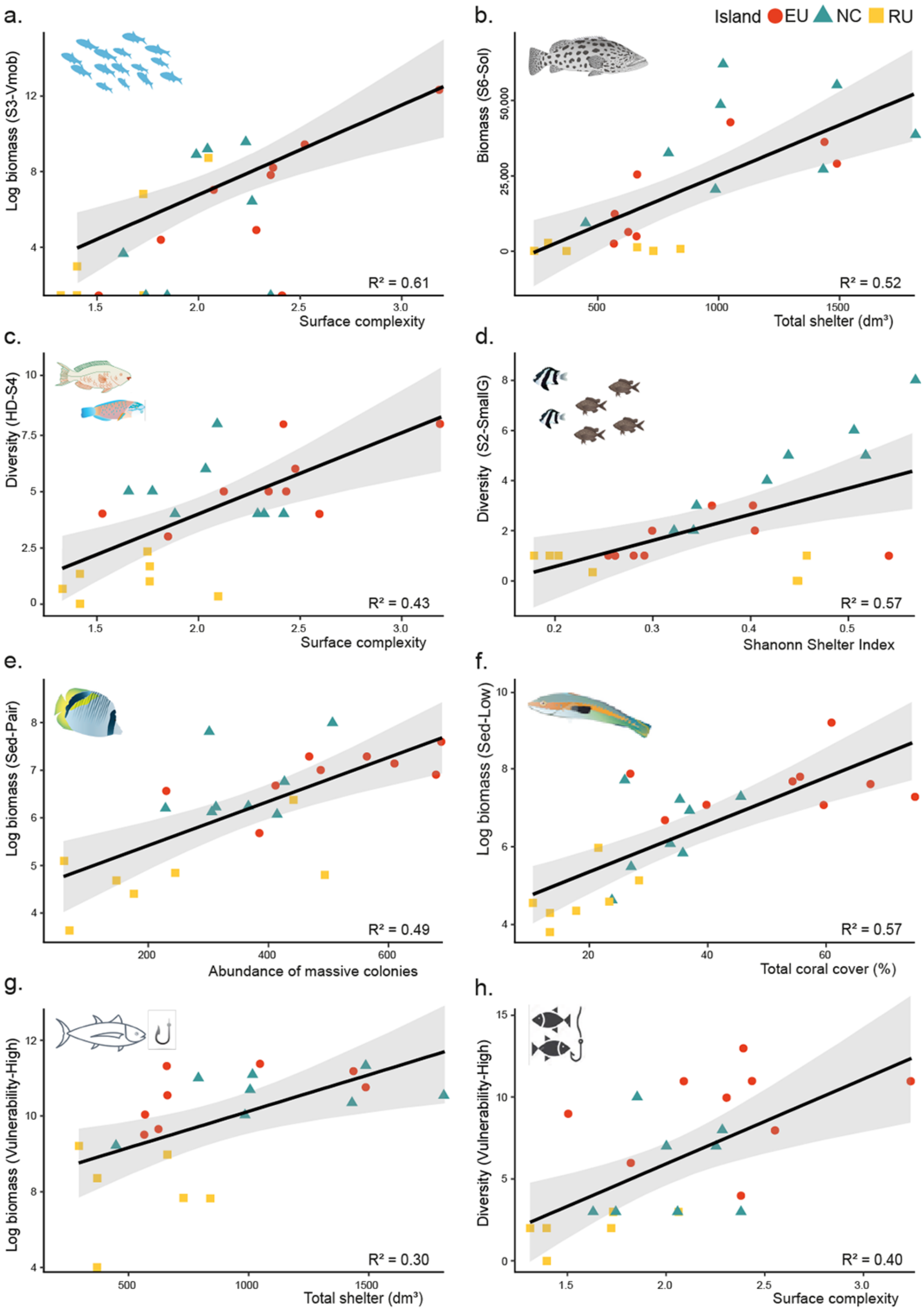


Figure 4.4 Relationships between habitat descriptors and: key FEs (a to f), biomass and diversity of fish species highly vulnerable to fishing (g, h). Fish icons from figures a to f, courtesy of IAN Integration and Application Network http://ian.umces.edu/imagelibrary/.

4.4 Discussion

Habitat descriptors

Hitherto, reef benthic communities and coral reef health have often been characterized using coral cover as the main metric (Loya 1972; Hill and Wilkinson 2004; Graham et al., 2011b; Obura et al., 2019). However, the need to evaluate the spatial complexity of these structurally highly diverse ecosystems has already been identified and various methods have been tested to this end: using chains following substrate contours (Risk 1972), counting holes, or visually estimating complexity on semi-quantitative scales (e.g. Friedlander and Parrish 1998; Gratwicke and Speight 2005; Johansen et al., 2008). More recently, new descriptors have been defined, such as surface complexity, volume compactness, top-heaviness, Reef Functional Index, shelter volume and Shannon Shelter Index (e.g. Burns et al., 2015a; González-Barrios and Álvarez-Filip 2018; Zawada et al., 2019b; Urbina-Barreto et al., under review). Today, underwater photogrammetry allows accurate quantification of these descriptors (e.g. Figueira et al., 2015; Burns et al., 2019; Carlot et al., 2020) and enables the assessment of new reefscape traits such as the mapping descriptors presented here.

Identifying the redundancies and complementarities among habitat descriptors, and examining the role of habitat traits in structuring associated biodiversity (i.e. corals, fishes, crustaceans, algae, etc.), can improve the assessment and understanding of coral reef biodiversity distribution and ecosystem functioning. Fukunaga et al. (2019) led one of the first studies focused on examining the redundancies among novel DEMs descriptors (i.e. slope, fractal dimension, platform and profile curvature, and surface complexity), identifying fractal dimension as the most appropriate for reef benthic surveys. Our study confirms some of their results, as all DEM descriptors (slope, fractal dimension and surface complexity) were strongly interrelated. In contrast, correlations between DEM descriptors and other habitat descriptors were much weaker, highlighting the complementary information provided by these additional descriptors. In fact, coral cover and surface complexity were only marginally correlated, probably because the influence of coral cover on complexity largely depends on the growth forms present (Graham and Nash 2013; Gonzalez-Barrios and Alvarez-Fillip 2018).

Regarding the 3D descriptors, shelter capacities of branching and tabular colonies were most strongly correlated with total shelter capacity, likely because these growth forms are the major shelter providers (Urbina-Barreto et al., under review). The Shannon Shelter Index was the least correlated with all other descriptors, once more underscoring the complementary information also provided by this descriptor. Across all morphologies, strong correlations between surface and shelter descriptors can be explained because shelter calculation is based on the surface area of coral colonies. Nonetheless, total shelter and total coral cover were less correlated due to the contribution of encrusting corals, a growth form that provides little shelter. For the same reason, surface area of encrusting corals was strongly correlated with total coral cover. Overall, surface area of corals and abundance were highly correlated at the growth form level, whereas Hernández-Landa et al. (2020) found that this was not necessarily the case at the species level.

Concerning mapping descriptors, abundance of colonies and mean distance to the nearest neighbor offer new relevant metrics in reefscape assessments. The evaluation of colony size and frequency distributions can provide valuable information about benthic community dynamics and recruitment at different spatial scales (Adjeroud et al., 2016; Jouval et al., 2019; Hernández-Landa et al., 2020). Furthermore, colony density and their spatial arrangement provide an indication of habitat fragmentation and spatial connectivity at coral community scale. Such properties at the scale of seascapes (e.g. Olds et al., 2012; Proudfoot et al., 2020) have been related to the resilience capacity of coral reefs (e.g. Mumby and Hastings 2008). Future investigations on these aspects at the scale of benthic communities could help better explain reef species associations and distributions, and also to assess the impacts of natural or manmade disturbances.

Relationship between habitat descriptors and fish assemblage structure

CCA showed that the taxonomic structure of fish assemblages in terms of biomass, and to a lesser extent abundance, was well explained by seven of our habitat descriptors. The higher significance of habitat descriptors in explaining biomass variance could probably be linked to the integration by biomass of both abundance and size distribution, the latter being related to the available diversity in shelter sizes. While these results support the relevance of the selected habitat descriptors, the CCA performed on the taxonomic structures did not allow further examination of the relationships between these descriptors and specific fish species traits. To explore such relationships, we considered Functional Entities (FEs) that grouped species that potentially support similar key functions (or contribute to similar core processes) in the ecosystem.

Most studies examining fish-habitat relationships have identified coral cover to increase the overall diversity, abundance and biomass of fish assemblages (e.g. Bell and Galzin 1984, Alvarez-Filip et al., 2011, McClanahan et al., 2011). Our results indicate that this is particularly true for sedentary small-bodied fishes (i.e. prey such as Pomacentridae) that dwell among or within coral colonies of diverse growth forms (Wilson et al., 2008; Pratchett et al., 2008; Alvarez-Filip et al., 2011). Likewise, multiple studies have found surface complexity, often measured or named as structural or habitat complexity, to be positively correlated to diversity, abundance and biomass of fishes (e.g. Friedlander et al., 2003; Gratwicke and Speight 2005; Graham and Nash 2013). Thus, both coral cover and surface complexity are relevant for the study of such coarse descriptors of fish assemblages.

Few authors have investigated the relationships between habitat complexity and finer-grained categories of fishes (e.g. trophic groups) or predatory-prey mechanisms (e.g. Beukers and Jones 1997; Kovalenko et al., 2012; Kerry and Bellwood 2015). Here we found that the diversity of grazers was related to surface complexity, consistent with the findings of Graham and Nash (2013) and Darling et al. (2017) who highlighted the positive influence of structural complexity on the presence of Scarinae and herbivores respectively. This could be explained by the fact that their diversity helped maintain cropped turf algae and thus promote the coral recruitment, growth and survival (Burkepile and Hay 2008; Graham et al., 2013). The resulting increase in the number and size of coral colonies (except encrusting growth forms) could in turn contribute to enhance the structural complexity and the provision of shelter that these fishes depend on, especially at night (Grutter et al., 2011). This positive feedback between herbivorous fishes (including browsers, grazers and scraper-excavators) and reef structural complexity has been described by Graham et al. (2006) and Hoey and Bellwood (2011).

Steep outer reef slopes are generally associated with high habitat complexity (this study; Darling et al., 2017; Fukunaga et al., 2019). Planktivores often reach high abundance on steep reef slopes of high complexity where the proximity to deep water promotes coastal upwelling and the advection of nutrients and zooplankton (Pinca et al., 2012; Darling et al., 2017; Morais and Bellwood 2019). This is consistent with what was observed in the present study (i.e. all but one species of the FE "S3-Vmob" are planktivores).

Understanding how shelter availability shapes the structure of fish assemblages is a fundamental and recurrent question in coral reef ecology, but the lack of standardized methods to quantify shelters has made this endeavour challenging (e.g. Friedlander and Parrish 1998; Gratwicke and Speight 2005; Johansen et al., 2008). Our study demonstrated that photogrammetry could fill this gap thanks to the recently developed metrics presented here (i.e. Shannon Shelter Index - SSI, shelter capacity of particular growth forms, total shelter capacity; Urbina-Barreto et al. under review). Indeed, we found that the diversity of prey was correlated with the availability of a panel of shelter types (i.e. holes and crevices of varying sizes) created by the diversity of coral growth forms and their interlinking, as quantified by the SSI. In addition, we found that the biomass of large solitary species (i.e. tertiary consumers) was correlated with total shelter capacity, the latter being mostly dependent on the shelter provided by tabular and branching growth forms. Thus, high biomass of tertiary consumers could result from the simultaneous availability of shelter provided by tabular colonies coral colonies (Kerry and Bellwood 2012, 2015) and branching growth forms that offer shelter to their prey (Wilson et al., 2008), which is consistent with the findings of Agudo-Adriani et al. (2019). These findings suggest that the diversity of shelters, including high contributions from tabular and branching growth forms, could be the feature of habitat complexity that ensures high fish productivity (Rogers et al., 2014), by maintaining high diversity and abundance of prey, and the associated high abundance of predators (Hein and Gillooly 2011).

The correlation between the biomass of Chaetodontidae (i.e. butterflyfishes) and the abundance of massive colonies was an unexpected and surprising result of the study. Butterflyfishes are usually considered to be mainly associated with Acropora dominated habitats (e.g. Emslie et al., 2010) and we did not find mention of such relationship in the literature. Although the association with massive corals could be due to statistical coincidence, it may be valuable to further investigate this observation.

Perspectives for coral reef conservation

The habitat descriptors scores, as well as the biomass and diversity of key functional groups of fishes, were globally lower at Reunion sites. They were not significantly different between Europa and New Caledonia, except for the diversity of species vulnerable to fishing, perhaps because Europa is a nearly pristine reef. The lower levels of fish and habitat descriptors at Reunion were likely due to higher anthropogenic pressure (population/km^2 of reef: ~350 in Reunion; ~15 in New Caledonia; <1 in Europa). However, reef fish assemblages were surveyed with a different method in Reunion, and our sampling design did not allow us to disentangle the potential effects of locality and the fish assessment method, calling for further investigation to confirm these results. Nonetheless, highly significant positive correlations between key fish functional groups and habitat descriptors were found across the three islands, suggesting that these relationships may still be valid for a wide range of localities. This illustrates the added value of functional approaches for management, as comparing surveys over large spatial scales represents an essential step for implementing efficient conservation strategies (Hughes et al., 2017a; Hoegh-Guldberg et al., 2018; McWilliam et al., 2018).

Moreover, maintaining ecosystem functions, including high biomass of key fish functional groups, is increasingly recognized as a conservation priority (MacNeill et al., 2015; Bellwood et al., 2019a,b). As such, identifying the main habitat features that support high biomass levels is of major interest to define conservation targets, especially when relationships are consistent across distant localities. Here, we illustrated the complementarity of several new habitat descriptors for improving our knowledge of the drivers of fish assemblage structure. While the panel of novel habitat descriptors may not be necessary for inferring coarse fish assemblage descriptors, their complementarity appeared fundamental to understand several specific aspects of coral reef functioning. This improved understanding of habitat-scale structure and limiting factors for key functional groups of fishes, along with the consideration of natural variability across environmental gradients (Heenan et al., 2020), can significantly contribute to refining multifactorial approach studies aimed at identifying sustainable trade-offs between human exploitation and ecosystem maintenance (i.e. coral reef "bright spots"; Cinner et al., 2016). Furthermore, the biomass and diversity of species highly vulnerable to fishing were correlated to total shelter and surface complexity, which reinforces the interest of including these descriptors in evaluations, for example on the exploitation levels and maintenance of fishable stocks.

Monitoring the key habitat descriptors identified in this study could also orientate ecosystem restoration actions, such as habitat regeneration or rebuilding. These could be guided by the increasing availability of 3D healthy reef models worldwide (e.g. "100 island challenge" http://100islandchallenge.org), which constitute baselines of reef architecture in a diversity of environmental and geographic contexts. Depending on the habitat features that could be expected at a given site, deficits in specific reefscape traits could be identified and counteracted by adapted interventions (e.g. translocation of coral colonies of a particular growth form). Photogrammetry further offers opportunities for innovative conservation surveys and awareness actions by generating visually attractive supports (i.e. 3D models, DEMs, orthomosaics).

To summarize, we quantified reefscape traits using different types of habitat descriptors (DEM, Surface, 3D or Mapping). Surface complexity, total shelter, coral cover, Shannon Shelter Index, and abundance of tabular, branching and massive colonies were identified as the most complementary descriptors. While such complex relationships need to be explored through larger datasets, our results suggest that these reefscape traits support essential fish groups particularly those ensuring trophic processes. This is of principal interest in fine-tuning conservation goals like the enhancement of coral reef resilience, and we suggest to considering these new habitat descriptors as candidates for EOVs (Essential Ocean Variables) in reef monitoring programs (Obura et al., 2019). In fact, the panel of habitat descriptors could be assessed at large spatial scales using Remotely Operated Vehicles or Autonomous Underwater Vehicles (Friedman et al., 2012; Ferrari et al., 2016; Obura et al., 2019; Price et al., 2019), and the data curation and analysis will likely be increasingly automated with the development of Artificial Intelligence (e.g. Hopkinson et al., 2020; Mohamed et al., 2020). As conservation targets in the 21st-century are numerous and improved stewardship of coral reefs and marine ecosystems is urgent (Madin et al., 2019; Cinner et al., 2020; Duarte et al., 2020), using 21st-century technology to optimize the efficiency of coral reef monitoring programs may be a way to meet the challenges.

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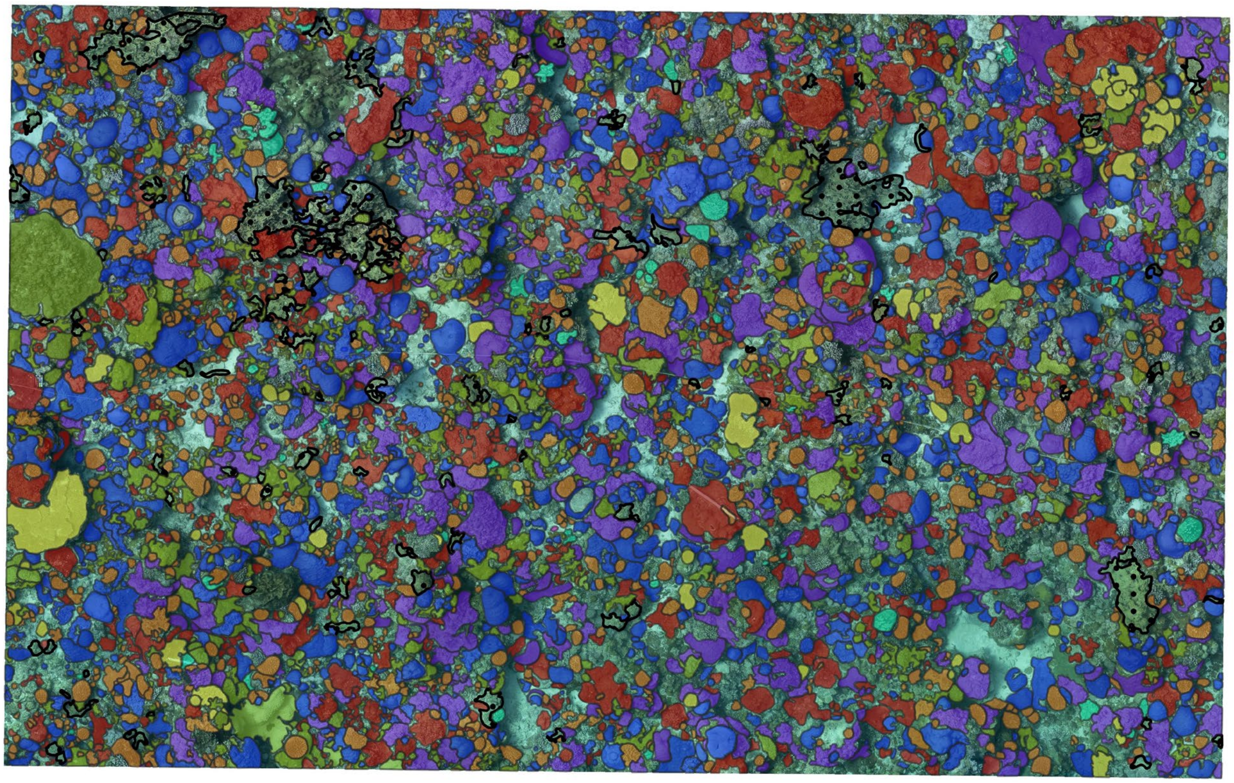
Author's contribution

IUB, SE, MA conceived the ideas; IUB, RP, LV, SE, HB, VM, LP, MA, ED designed methodology; IUB, VM, SE, LV, MF, SB, CP and RG collected the data; IUB, RP and VM performed 3D models; IUB, SE, FG, GM performed data handling and analyzed the data; IUB, SE, HB, MK, LP and MA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

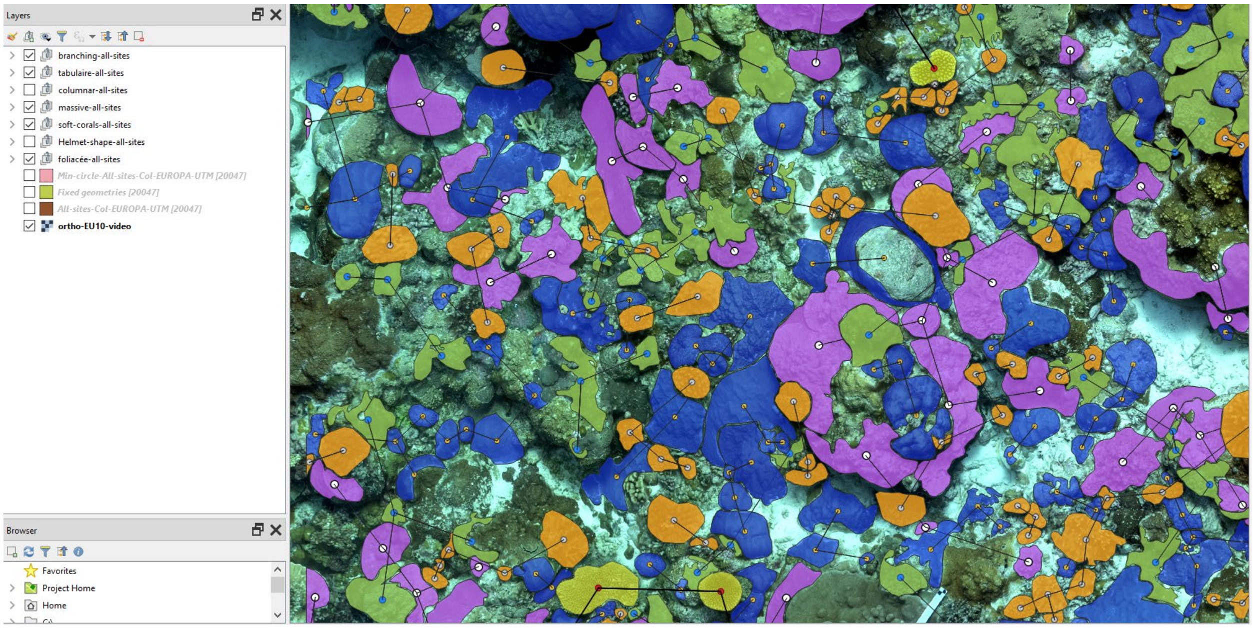
Appendices - Chapter 4

Appendix 4.1



Classification of benthic features on orthomosaic of site EU10. Colors of polygons represent coral growth forms and other benthic components: massive (blue), orange (branching), red (encrusting), turquoise (columnar), violet (helmet-shaped), yellow (tabular), green (soft corals), black pointed area (Milleporidae), light blue (sand). There was no rubble present at this site.

Appendix 4.2



Zoom from nearest neighbor distance computation in a reefscape orthomosaic from Europa. Colors represent growth forms of coral colonies: branching (orange), helmet-shaped (purple), massive (blue), tabular (yellow) and soft corals are showed in green polygons. Vectors between centroids show the distance of the nearest neighbor colony on each own by growth form.

Appendix 4.3

Life History Traits of the fish species observed in this study. Particular FEs targeted for analyses.

Family	Genus-species	Diet	Size	Home range	Schooling	Level water	HD-S4	Sed-Low	S2_ Small G	S3-Vmob	S6-Sol	Sed-Pair	TOTAL
Acanthuridae	*Acanthurus_albipectoralis*	PK	S4	VMob	MedG	Low							
Acanthuridae	*Acanthurus_dussumieri*	HD	S5	Mob	SmallG	Bottom							
Acanthuridae	*Acanthurus_leucosternon*	HD	S5	VMob	Sol	Bottom							
Acanthuridae	*Acanthurus_lineatus*	HD	S4	Sed	Sol	Bottom	X						X
Acanthuridae	*Acanthurus_nigricauda*	HD	S4	Mob	SmallG	Bottom	X						X
Acanthuridae	*Acanthurus_pyroferus*	HD	S3	Sed	Sol	Bottom							
Acanthuridae	*Acanthurus_sp*	HD	S3	Sed	SmallG	Bottom							
Acanthuridae	*Acanthurus_thompsoni*	PK	S3	VMob	MedG	Low				X			X
Acanthuridae	*Acanthurus_triostegus*	HD	S3	VMob	LargeG	Bottom				X			X
Acanthuridae	*Acanthurus_xanthopterus*	HD	S5	Mob	MedG	Bottom							
Acanthuridae	*Acanthurus_nigrofuscus*	HD	S3	Sed	SmallG	Bottom							
Acanthuridae	*Acanthurus_tennentii*	HD	S4	Mob	SmallG	Bottom	X						X

Acanthuridae	*Ctenochaetus_binotatus*	OM	S3	Sed	Sol	Bottom							
Acanthuridae	*Ctenochaetus_cyanocheilus*	HD	S3	Sed	SmallG	Bottom							
Acanthuridae	*Ctenochaetus_striatus*	OM	S3	Sed	MedG	Bottom							
Acanthuridae	*Ctenochaetus_truncatus*	OM	S3	Sed	SmallG	Bottom							
Acanthuridae	*Naso_annulatus*	PK	S6	VMob	MedG	High							
Acanthuridae	*Naso_brevirostris*	OM	S5	VMob	LargeG	Low							
Acanthuridae	*Naso_elegans*	HM	S4	Mob	SmallG	Bottom							
Acanthuridae	*Naso_hexacanthus*	PK	S5	VMob	LargeG	High							
Acanthuridae	*Naso_lituratus*	HM	S4	Mob	SmallG	Bottom							
Acanthuridae	*Naso_sp*	PK	S5	VMob	LargeG	High							
Acanthuridae	*Naso_unicornis*	HM	S5	Mob	SmallG	Bottom							
Acanthuridae	*Naso_vlamingii*	PK	S5	VMob	SmallG	Low							
Acanthuridae	*Zebrasoma_desjardinii*	HM	S4	Mob	Pair	Bottom							
Acanthuridae	*Zebrasoma_gemmatum*	HD	S3	Sed	Sol	Bottom							
Acanthuridae	*Zebrasoma_scopas*	HD	S4	Mob	SmallG	Bottom	X						X
Acanthuridae	*Zebrasoma_veliferum*	HM	S4	Mob	Pair	Bottom							
Anthiinae	*Pseudanthias_evansi*	PK	S2	Sed	LargeG	High							
Atherinidae	*Atherinidae_spp*	PK	S2	VMob	LargeG	High							
Aulostomidae	*Aulostomus_chinensis*	FC	S5	Mob	Sol	Low							
Balistidae	*Balistapus_undulatus*	IM	S3	Mob	Sol	Bottom							
Balistidae	*Balistoides_conspicillum*	IM	S4	Mob	Sol	Bottom							
Balistidae	*Balistoides_viridescens*	IM	S5	Mob	Sol	Bottom							
Balistidae	*Melichthys_niger*	PK	S4	VMob	MedG	High							
Balistidae	*Melichthys_vidua*	OM	S4	VMob	SmallG	High							
Balistidae	*Odonus_niger*	PK	S4	VMob	MedG	High							
Balistidae	*Sufflamen_bursa*	IM	S3	Sed	Sol	Bottom							
Balistidae	*Sufflamen_chrysopterum*	IM	S3	Sed	Sol	Bottom							
Balistidae	*Sufflamen_sp*	IM	S4	Sed	Sol	Bottom							
Bleniidae	*Plagiotremus_tapeinosoma*	IM	S2	Sed	Sol	Low		X					X
Blennidae	*Aspidontus_taeniatus*	IM	S2	Sed	Sol	Low		X					X
Blennidae	*Cirripectes_sp*	HD	S3	Sed	Sol	Bottom							
Blenniidae	*Aspidontus_sp*	OM	S3	Sed	Sol	Low		X					X
Blenniidae	*Atrosalarias_fuscus*	HD	S3	Sed	Sol	Bottom							
Blenniidae	*Exallias_brevis*	IS	S2	Sed	Sol	Bottom							
Blenniidae	*Meiacanthus_atrodorsalis*	IM	S2	Sed	Pair	Low		X				X	XX
Blenniidae	*Blenniidae_spp*	HD	S2	Sed	Sol	Bottom							
Blenniidae	*Plagiotremus_laudandus*	FC	S2	Sed	Sol	Low		X					X
Caesionidae	*Caesio_lunaris*	PK	S4	VMob	LargeG	High							
Caesionidae	*Caesio_teres*	PK	S4	VMob	LargeG	High							
Caesionidae	*Caesio_xanthonota*	PK	S4	VMob	LargeG	High							
Caesionidae	*Pterocaesio_marri*	PK	S4	VMob	LargeG	High							
Caesionidae	*Pterocaesio_pisang*	PK	S3	VMob	SmallG	High				X			X
Caesionidae	*Pterocaesio_sp*	PK	S3	VMob	LargeG	High				X			X
Caesionidae	*Pterocaesio_tile*	PK	S3	VMob	LargeG	High				X			X

Caesionidae	*Pterocaesio_trilineata*	PK	S3	VMob	LargeG	High				X			X
Caracanthidae	*Caracanthus_madagascariensis*	OM	S1	Sed	SmallG	Bottom							
Carangidae	*Caranx_lugubris*	FC	S6	VMob	SmallG	High							
Carangidae	*Caranx_melampygus*	FC	S6	VMob	SmallG	High							
Carangidae	*Caranx_sp*	FC	S6	VMob	SmallG	High							
Carcharhinidae	*Carcharhinus_amblyrhynchos*	FC	S6	VMob	SmallG	Bottom							
Carcharhinidae	*Carcharhinus_galapagensis*	FC	S6	VMob	SmallG	High							
Carcharhinidae	*Carcharhinus_leucas*	FC	S6	VMob	Sol	Bottom					X		X
Carcharhinidae	*Carcharhinus_melanopterus*	FC	S6	VMob	Sol	Bottom					X		X
Carcharhinidae	*Triaenodon_obesus*	FC	S6	VMob	Sol	Low					X		X
Chaetodontidae	*Chaetodon_auriga*	IS	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_bennetti*	IS	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_ephippium*	OM	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_falcula*	IM	S3	Sed	SmallG	Bottom							
Chaetodontidae	*Chaetodon_flavirostris*	OM	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_guttatissimus*	IS	S2	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_interruptus*	OM	S3	Sed	SmallG	Bottom							
Chaetodontidae	*Chaetodon_kleinii*	OM	S3	Sed	Pair	Low		X				X	XX
Chaetodontidae	*Chaetodon_lineolatus*	IS	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_lunula*	IS	S3	Sed	Pair	Low		X				X	XX
Chaetodontidae	*Chaetodon_lunulatus*	IS	S2	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_madagaskariensis*	IM	S2	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_melannotus*	IS	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_mertensii*	OM	S2	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_meyeri*	IS	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_ornatissimus*	IS	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_pelewensis*	IS	S2	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_plebeius*	IS	S2	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_reticulatus*	IS	S3	Sed	Pair	Low		X				X	XX
Chaetodontidae	*Chaetodon_trifascialis*	IS	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_trifasciatus*	IS	S2	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_ulietensis*	OM	S2	Sed	Pair	Low		X				X	XX
Chaetodontidae	*Chaetodon_unimaculatus*	IS	S3	Sed	SmallG	Bottom							
Chaetodontidae	*Chaetodon_vagabundus*	IM	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Chaetodon_xanthocephalus*	OM	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Forcipiger_flavissimus*	IM	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Forcipiger_longirostris*	IM	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Hemitaurichthys_polylepis*	PK	S3	Mob	LargeG	Low							
Chaetodontidae	*Hemitaurichthys_zoster*	PK	S3	Mob	LargeG	Low							
Chaetodontidae	*Heniochus_acuminatus*	PK	S3	Sed	Pair	Low		X				X	XX
Chaetodontidae	*Heniochus_monoceros*	IM	S3	Sed	Pair	Bottom						X	X
Chaetodontidae	*Heniochus_singularius*	IS	S3	Sed	Pair	Bottom						X	X
Cirrhitidae	*Cirrhitichthys_falco*	IM	S1	Sed	Sol	Bottom							

Cirrhitidae	*Cirrhitichthys_oxycephalus*	IM	S2	Sed	Sol	Bottom							
Cirrhitidae	*Cirrhitops_fasciatus*	IM	S2	Sed	Sol	Bottom							
Cirrhitidae	*Paracirrhites_arcatus*	IM	S3	Sed	Sol	Bottom							
Cirrhitidae	*Paracirrhites_forsteri*	FC	S3	Sed	Sol	Bottom							
Engraulidae	*Stolephorus_sp*	PK	S1	VMob	LargeG	High							
Ephippidae	*Platax_orbicularis*	OM	S5	VMob	SmallG	Low							
Fistulariidae	*Fistularia_commersonii*	FC	S6	VMob	SmallG	Low							
Gobiidae	*Gobiidae_spp*	IM	S1	Sed	Sol	Bottom							
Gobiidae	*Vanderhorstia_ornatissima*	IM	S2	Sed	Sol	Bottom							
Haemulidae	*Plectorhinchus_obscurus*	IM	S6	Mob	Sol	Low					X		X
Haemulidae	*Plectorhinchus_sp*	IM	S6	Mob	Sol	Low					X		X
Holocentridae	*Myripristis_murdjan*	PK	S5	Mob	SmallG	Low							
Holocentridae	*Myripristis_sp*	PK	S4	Mob	SmallG	Low							
Holocentridae	*Sargocentron_caudimaculatum*	IM	S3	Mob	Sol	Low							
Kyphosidae	*Kyphosus_cinerascens*	HM	S5	VMob	MedG	Low							
Labridae	*Anampses_caeruleopunctatus*	IM	S4	Mob	Pair	Bottom							
Labridae	*Anampses_femininus*	IM	S3	Mob	SmallG	Bottom							
Labridae	*Anampses_lineatus*	IM	S2	Mob	SmallG	Bottom			X				X
Labridae	*Anampses_meleagrides*	IM	S3	Mob	Sol	Bottom							
Labridae	*Anampses_neoguinaicus*	IM	S3	Mob	SmallG	Bottom							
Labridae	*Anampses_sp*	IM	S3	Mob	SmallG	Bottom							
Labridae	*Anampses_twistii*	IM	S3	Mob	Sol	Bottom							
Labridae	*Bodianus_anthioides*	IM	S3	Mob	Sol	Bottom							
Labridae	*Bodianus_axillaris*	IM	S3	Mob	Sol	Bottom							
Labridae	*Bodianus_bilunulatus*	IM	S5	Mob	Sol	Bottom							
Labridae	*Bodianus_diana*	IM	S3	Mob	Sol	Bottom							
Labridae	*Bodianus_loxozonus*	IM	S4	Mob	Sol	Bottom							
Labridae	*Bodianus_macrourus*	IM	S4	Mob	Sol	Bottom							
Labridae	*Bodianus_mesothorax*	IM	S3	Mob	Sol	Bottom							
Labridae	*Bodianus_perditio*	IM	S5	Mob	Sol	Bottom							
Labridae	*Cheilinus_chlorourus*	IM	S4	Mob	Sol	Bottom							
Labridae	*Cheilinus_oxycephalus*	IM	S3	Sed	Pair	Bottom						X	X
Labridae	*Cheilinus_sp*	IM	S4	Mob	Sol	Bottom							
Labridae	*Cheilinus_trilobatus*	IM	S4	Mob	Sol	Bottom							
Labridae	*Cheilinus_undulatus*	IM	S6	Mob	Sol	Bottom					X		X
Labridae	*Cheilio_inermis*	FC	S4	VMob	Sol	Low							
Labridae	*Cirrhilabrus_exquisitus*	PK	S2	Sed	MedG	Low		X					X
Labridae	*Cirrhilabrus_punctatus*	PK	S2	Sed	MedG	Low		X					X
Labridae	*Coris_aygula*	IM	S6	Mob	Sol	Bottom					X		X
Labridae	*Coris_cuvieri*	IM	S4	Mob	Sol	Bottom							
Labridae	*Coris_dorsomacula*	IM	S4	Mob	Sol	Bottom							
Labridae	*Coris_sp*	IM	S3	Mob	Sol	Bottom							
Labridae	*Epibulus_insidiator*	FC	S5	Mob	Sol	Low							

Labridae	*Gomphosus_caeruleus*	IM	S4	Mob	Sol	Bottom							
Labridae	*Gomphosus_varius*	IM	S3	Mob	Sol	Bottom							
Labridae	*Halichoeres_cosmetus*	IM	S2	Mob	Sol	Bottom							
Labridae	*Halichoeres_hortulanus*	IM	S3	Mob	Sol	Bottom							
Labridae	*Halichoeres_marginatus*	IM	S3	Mob	Sol	Bottom							
Labridae	*Halichoeres_nebulosus*	IM	S2	Mob	SmallG	Bottom			X				X
Labridae	*Halichoeres_ornatissimus*	IM	S3	Mob	Sol	Bottom							
Labridae	*Halichoeres_sp*	IM	S3	Mob	Sol	Bottom							
Labridae	*Hemigymnus_fasciatus*	IM	S5	Mob	Sol	Bottom							
Labridae	*Hemigymnus_melapterus*	IM	S4	Mob	Sol	Bottom							
Labridae	*Hemigymnus_sp*	IM	S4	Mob	Sol	Bottom							
Labridae	*Hologymnosus_sp*	IM	S4	VMob	Sol	Bottom							
Labridae	*Iniistius_pavo*	IM	S4	Sed	Sol	Low		X					X
Labridae	*Labrichthys_unilineatus*	IS	S3	Sed	Sol	Bottom							
Labridae	*Labroides_bicolor*	IM	S2	Sed	Pair	Bottom						X	X
Labridae	*Labroides_dimidiatus*	IM	S2	Sed	Pair	Bottom						X	X
Labridae	*Labropsis_xanthonota*	IS	S2	Sed	Sol	Bottom							
Labridae	*Macropharyngodon_bipartitus bipartitus*	IM	S2	Sed	Pair	Bottom						X	X
Labridae	*Macropharyngodon_cyanoguttatus*	IM	S2	Mob	SmallG	Bottom			X				X
Labridae	*Macropharyngodon_sp*	IM	S2	Sed	Pair	Bottom						X	X
Labridae	*Labridae_spp*	IM	S3	Mob	Sol	Bottom							
Labridae	*Novaculichthys_taeniourus*	IM	S3	Sed	Pair	Low		X				X	XX
Labridae	*Oxycheilinus_digramma*	IM	S4	Mob	Sol	Low							
Labridae	*Oxycheilinus_sp*	FC	S3	Mob	Sol	Bottom							
Labridae	*Oxycheilinus_unifasciatus*	FC	S4	Mob	Sol	Low							
Labridae	*Pseudocheilinus_evanidus*	IM	S2	Sed	Sol	Bottom							
Labridae	*Pseudocheilinus_hexataenia*	IM	S2	Sed	SmallG	Bottom			X				X
Labridae	*Pseudocheilinus_octotaenia*	IM	S2	Sed	Sol	Bottom							
Labridae	*Pseudocheilinus_sp*	IM	S2	Sed	Sol	Bottom							
Labridae	*Pseudodax_moluccanus*	OM	S3	Mob	Sol	Bottom							
Labridae	*Stethojulis_albovittata*	IM	S2	Mob	SmallG	Bottom			X				X
Labridae	*Thalassoma_amblycephalum*	PK	S3	Mob	SmallG	Low							
Labridae	*Thalassoma_genivittatum*	IM	S3	Mob	SmallG	Bottom							
Labridae	*Thalassoma_hebraicum*	IM	S3	Mob	SmallG	Bottom							
Labridae	*Thalassoma_jansenii*	IM	S3	Mob	SmallG	Bottom							
Labridae	*Thalassoma_lunare*	IM	S4	Mob	SmallG	Bottom							
Labridae	*Thalassoma_lutescens*	IM	S3	Mob	SmallG	Bottom							
Lethrinidae	*Gnathodentex_aureolineatus*	IM	S3	Mob	LargeG	Bottom							
Lethrinidae	*Lethrinus_atkinsoni*	IM	S4	VMob	MedG	Bottom							
Lethrinidae	*Lethrinus_obsoletus*	IM	S5	Mob	SmallG	Bottom							
Lethrinidae	*Lethrinus_olivaceus*	FC	S6	VMob	Sol	Bottom					X		X
Lethrinidae	*Lethrinus_sp*	IM	S5	VMob	Sol	Bottom							
Lethrinidae	*Monotaxis_grandoculis*	IM	S5	Mob	Sol	Low							
Lutjanidae	*Aphareus_furca*	FC	S5	VMob	SmallG	Low							

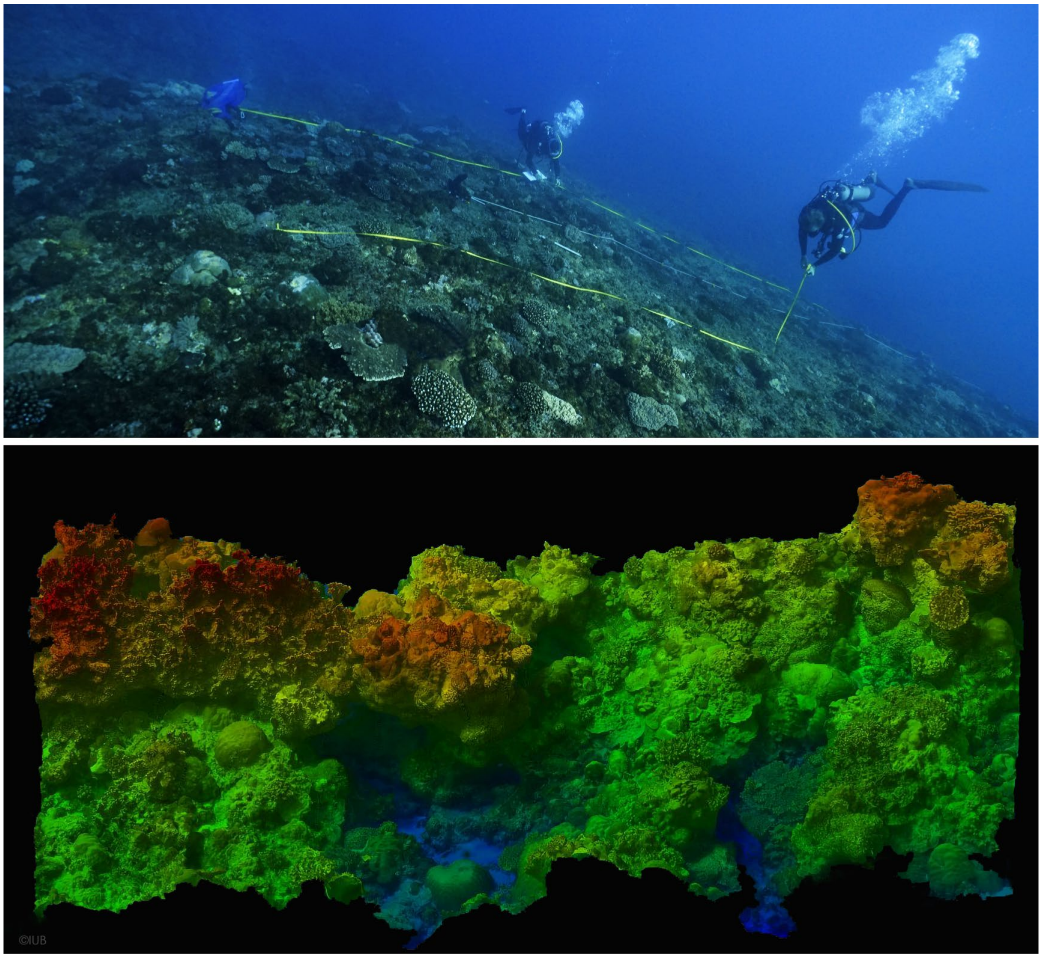
Lutjanidae	*Aprion_virescens*	FC	S6	VMob	SmallG	Low							
Lutjanidae	*Lutjanus_argentimaculatus*	FC	S6	Mob	MedG	Low							
Lutjanidae	*Lutjanus_bohar*	FC	S6	Mob	MedG	Low							
Lutjanidae	*Lutjanus_fulvus*	FC	S4	Mob	SmallG	Low							
Lutjanidae	*Lutjanus_gibbus*	FC	S4	Mob	MedG	Low							
Lutjanidae	*Lutjanidae_spp*	FC	S4	Mob	Sol	Low							
Malacanthidae	*Malacanthus_brevirostris*	IM	S4	Sed	Pair	Low		X				X	XX
Malacanthidae	*Malacanthus_latovittatus*	IM	S4	Sed	Pair	Low		X				X	XX
Monacanthidae	*Amanses_scopas*	IS	S3	Mob	Sol	Bottom							
Monacanthidae	*Cantherhines_dumerilii*	IS	S4	Mob	Pair	Bottom							
Monacanthidae	*Cantherhines_sp*	OM	S3	Mob	Sol	Bottom							
Monacanthidae	*Cantherhines_sp1*	IS	S4	Mob	Pair	Bottom							
Monacanthidae	*Oxymonacanthus_longirostris*	IS	S2	Sed	Pair	Bottom						X	X
Monacanthidae	*Pervagor_alternans*	OM	S3	Sed	Sol	Bottom							
Monacanthidae	*Pervagor_aspricaudus*	OM	S2	Sed	Sol	Bottom							
Monacanthidae	*Pervagor_sp*	OM	S2	Sed	Sol	Bottom							
Mullidae	*Mulloidichthys_vanicolensis*	IM	S4	Mob	SmallG	Bottom							
Mullidae	*Mullidae_spp*	IM	S4	Mob	SmallG	Bottom							
Mullidae	*Parupeneus_barberinus*	IM	S5	Mob	Sol	Bottom							
Mullidae	*Parupeneus_cyclostomus*	FC	S4	Mob	Sol	Bottom							
Mullidae	*Parupeneus_macronemus*	IM	S4	Mob	SmallG	Bottom							
Mullidae	*Parupeneus_multifasciatus*	IM	S4	Mob	SmallG	Bottom							
Mullidae	*Parupeneus_pleurostigma*	IM	S4	Mob	Sol	Bottom							
Mullidae	*Parupeneus_sp1*	IM	S4	Mob	SmallG	Bottom							
Mullidae	*Parupeneus_sp2*	IM	S4	Mob	SmallG	Bottom							
Mullidae	*Parupeneus_trifasciatus*	IM	S4	Mob	SmallG	Bottom							
Muraenidae	*Gymnothorax_flavimarginatus*	FC	S6	Sed	Sol	Bottom					X		X
Muraenidae	*Gymnothorax_meleagris*	FC	S6	Sed	Sol	Bottom					X		X
Muraenidae	*Gymnothorax_sp*	FC	S5	Sed	Sol	Bottom							
Muraenidae	*Muraenidae_spp*	FC	S5	Sed	Sol	Bottom							
Nemipteridae	*Scolopsis_bilineata*	FC	S3	Mob	Pair	Bottom							
Ostraciidae	*Ostracion_cubicus*	OM	S4	Mob	Sol	Bottom							
Ostraciidae	*Ostracion_sp*	OM	S4	Mob	Sol	Bottom							
Pempheridae	*pempheris_sp*	PK	S3	Sed	MedG	Low		X					X
Pomacanthidae	*Apolemichthys_trimaculatus*	IS	S3	Sed	SmallG	Bottom							
Pomacanthidae	*Centropyge_bispinosa*	HD	S2	Sed	Pair	Bottom						X	X
Pomacanthidae	*Centropyge_flavissima*	HD	S2	Sed	Pair	Bottom						X	X
Pomacanthidae	*Centropyge_heraldi*	HD	S2	Sed	SmallG	Bottom			X				X
Pomacanthidae	*Centropyge_multispinis*	HD	S2	Sed	Pair	Bottom						X	X
Pomacanthidae	*Centropyge_sp*	HD	S2	Sed	Pair	Bottom						X	X
Pomacanthidae	*Centropyge_tibicen*	HD	S3	Sed	SmallG	Bottom							
Pomacanthidae	*Genicanthus_melanospilos*	PK	S3	Sed	SmallG	Low		X					X
Pomacanthidae	*Genicanthus_watanabei*	PK	S2	Sed	SmallG	Low		X	X				XX
Pomacanthidae	*Pomacanthus_chrysurus*	IS	S4	Sed	Sol	Bottom							

Pomacanthidae	*Pomacanthus_imperator*	IS	S4	Sed	Sol	Bottom							
Pomacanthidae	*Pomacanthus_sexstriatus*	IS	S4	Sed	Pair	Bottom						X	X
Pomacanthidae	*Pygoplites_diacanthus*	IS	S3	Sed	Sol	Bottom							
Pomacentridae	*Abudefduf_whitleyi*	PK	S2	Sed	LargeG	Low		X					X
Pomacentridae	*Amblyglyphidodon_leucogaster*	PK	S2	Sed	SmallG	Low		X	X				XX
Pomacentridae	*Chromis_chrysura*	PK	S2	Sed	LargeG	Low		X					X
Pomacentridae	*Chromis_dimidiata*	PK	S2	Sed	MedG	Low		X					X
Pomacentridae	*Chromis_iomelas*	PK	S2	Sed	SmallG	Low		X	X				XX
Pomacentridae	*Chromis_lepidolepis*	PK	S2	Sed	MedG	Low		X					X
Pomacentridae	*Chromis_margaritifer*	PK	S2	Sed	SmallG	Low		X	X				XX
Pomacentridae	*Chromis_nigrura*	PK	S1	Sed	MedG	Low		X					X
Pomacentridae	*Chromis_sp*	PK	S2	Sed	MedG	Low		X					X
Pomacentridae	*Chromis_ternatensis*	PK	S2	Sed	MedG	Low		X					X
Pomacentridae	*Chromis_vanderbilti*	PK	S1	Sed	LargeG	Low		X					X
Pomacentridae	*Chromis_weberi*	PK	S2	Sed	MedG	Low		X					X
Pomacentridae	*Chromis_xanthura*	PK	S3	Sed	LargeG	Low		X					X
Pomacentridae	*Chrysiptera_taupou*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Dascyllus_reticulatus*	PK	S2	Sed	MedG	Bottom							
Pomacentridae	*Dascyllus_trimaculatus*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentridae_spp*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Neoglyphidodon_sp*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Plectroglyphidodon_dickii*	OM	S2	Sed	Sol	Bottom							
Pomacentridae	*Plectroglyphidodon_imparipennis*	OM	S1	Sed	Sol	Bottom							
Pomacentridae	*Plectroglyphidodon_johnstonianus*	HD	S2	Sed	Sol	Bottom							
Pomacentridae	*Plectroglyphidodon_lacrymatus*	OM	S2	Sed	Sol	Bottom							
Pomacentridae	*Pomacentrus_brachialis*	PK	S2	Sed	SmallG	Low		X	X				XX
Pomacentridae	*Pomacentrus_lepidogenys*	PK	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentrus_nagasakiensis*	PK	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentrus_nigromanus*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentrus_sp*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentrus_sp1*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentrus_sp2*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentrus_sulfureus*	OM	S2	Sed	SmallG	Bottom			X				X
Pomacentridae	*Pomacentrus_vaiuli*	OM	S2	Sed	Sol	Bottom							
Pomacentridae	*Pomachromis_richardsoni*	PK	S1	Sed	MedG	Low		X					X
Pomacentridae	*Stegastes_fasciolatus*	HD	S3	Sed	Sol	Bottom							
Pomacentridae	*Stegastes_sp*	HD	S2	Sed	SmallG	Bottom			X				X
Pseudochromidae	*Pseudochromis_sp*	IM	S2	Sed	Sol	Bottom							
Ptereleotridae	*Nemateleotris_magnifica*	PK	S2	Sed	Pair	Low		X				X	XX
Ptereleotridae	*Ptereleotris_evides*	PK	S2	Sed	MedG	Low		X					X
Ptereleotridae	*Ptereleotris_heteroptera*	PK	S2	Sed	Pair	Low		X				X	XX
Scaridae	*Calotomus_carolinus*	HM	S5	Mob	Sol	Bottom							
Scaridae	*Chlorurus_microrhinos*	HD	S5	Mob	SmallG	Bottom							

Scaridae	*Chlorurus_sordidus*	HD	S4	Mob	SmallG	Bottom	X						X
Scaridae	*Chlorurus_strongylocephalus*	HD	S5	Mob	SmallG	Bottom							
Scaridae	*Hipposcarus_harid*	HD	S5	Mob	MedG	Bottom							
Scaridae	*Scarus_altipinnis*	HD	S5	Mob	LargeG	Bottom							
Scaridae	*Scarus_caudofasciatus*	HD	S4	Mob	Sol	Bottom	X						X
Scaridae	*Scarus_chameleon*	HD	S4	Mob	Sol	Bottom	X						X
Scaridae	*Scarus_dimidiatus*	HD	S4	Mob	SmallG	Bottom	X						X
Scaridae	*Scarus_forsteni*	HD	S5	Mob	Sol	Bottom							
Scaridae	*Scarus_frenatus*	HD	S4	Mob	Sol	Bottom	X						X
Scaridae	*Scarus_ghobban*	HD	S5	Mob	SmallG	Bottom							
Scaridae	*Scarus_globiceps*	HD	S4	Mob	Sol	Bottom	X						X
Scaridae	*Scarus_longipinnis*	HD	S4	Mob	Sol	Bottom	X						X
Scaridae	*Scarus_niger*	HD	S4	Mob	Sol	Bottom	X						X
Scaridae	*Scarus_psittacus*	HD	S4	Mob	MedG	Bottom	X						X
Scaridae	*Scarus_rubroviolaceus*	HD	S5	Mob	Sol	Bottom							
Scaridae	*Scarus_scaber*	HD	S4	Mob	MedG	Bottom	X						X
Scaridae	*Scarus_schlegeli*	HD	S4	Mob	Sol	Bottom	X						X
Scaridae	*Scarus_sp*	HD	S4	Mob	SmallG	Bottom	X						X
Scaridae	*Scarus_sp1*	HD	S4	Mob	SmallG	Bottom	X						X
Scaridae	*Scarus_tricolor*	HD	S3	Mob	Sol	Bottom							
Scombridae	*Scomberomorus_commerson*	FC	S6	VMob	Sol	High					X		X
Serranidae	*Aethaloperca_rogaa*	FC	S5	Mob	Sol	Bottom							
Serranidae	*Cephalopholis_argus*	FC	S5	Sed	Sol	Bottom							
Serranidae	*Cephalopholis_miniata*	FC	S4	Sed	Sol	Bottom							
Serranidae	*Cephalopholis_nigripinnis*	FC	S3	Sed	Sol	Bottom							
Serranidae	*Cephalopholis_sp*	FC	S5	Sed	Sol	Bottom							
Serranidae	*Cephalopholis_sp1*	FC	S5	Sed	Sol	Bottom							
Serranidae	*Cephalopholis_sp2*	FC	S5	Sed	Sol	Bottom							
Serranidae	*Cephalopholis_urodeta*	FC	S3	Sed	Sol	Bottom							
Serranidae	*Epinephelus_fasciatus*	FC	S4	Mob	Sol	Bottom							
Serranidae	*Epinephelus_fuscoguttatus*	FC	S6	Mob	Sol	Bottom					X		X
Serranidae	*Epinephelus_hexagonatus*	FC	S3	Mob	Sol	Bottom							
Serranidae	*Epinephelus_macrospilos*	FC	S5	Mob	Sol	Bottom							
Serranidae	*Epinephelus_merra*	FC	S4	Mob	Sol	Bottom							
Serranidae	*Epinephelus_polyphekadion*	FC	S6	Mob	Sol	Bottom					X		X
Serranidae	*Epinephelus_sp*	FC	S5	Mob	Sol	Bottom							
Serranidae	*Epinephelus_sp1*	FC	S5	Mob	Sol	Bottom							
Serranidae	*Epinephelus_tauvina*	FC	S5	Mob	Sol	Bottom							
Serranidae	*Epinephelus_tukula*	FC	S6	Mob	Sol	Bottom					X		X
Serranidae	*Gracila_albomarginata*	FC	S4	VMob	Sol	Low							
Serranidae	*Grammistes_sexlineatus*	FC	S3	Sed	Sol	Low		X					X
Serranidae	*Plectropomus_laevis*	FC	S6	Mob	Sol	Bottom					X		X
Serranidae	*Plectropomus_leopardus*	FC	S6	Mob	Sol	Bottom					X		X
Serranidae	*Pseudanthias_pictilis*	PK	S2	Sed	LargeG	Low		X					X

Serranidae	*Pseudanthias_squamipinnis*	PK	S2	Sed	LargeG	Low		X					X
Serranidae	*Variola_albimarginata*	FC	S5	Mob	Sol	Bottom							
Serranidae	*Variola_louti*	FC	S6	Mob	Sol	Bottom					X		X
Siganidae	*Siganus_corallinus*	HD	S4	Mob	Pair	Bottom	X						X
Siganidae	*Siganus_stellatus*	HM	S4	Mob	Pair	Bottom							
Siganidae	*Siganus_puellus*	OM	S4	Mob	Pair	Bottom							
Siganidae	*Siganus_sp*	HD	S3	Mob	Pair	Bottom							
Sphyraenidae	*Sphyraena_forsteri*	FC	S5	VMob	LargeG	High							
Synanceiidae	*Synanceia_verrucosa*	FC	S4	Sed	Sol	Bottom							
Synodontidae	*Synodus_variegatus*	FC	S4	Mob	Pair	Bottom							
Tetraodontidae	*Arothron_meleagris*	IS	S4	Mob	Sol	Bottom							
Tetraodontidae	*Arothron_nigropunctatus*	IS	S4	Mob	Pair	Bottom							
Tetraodontidae	*Canthigaster_valentini*	OM	S2	Sed	Pair	Bottom						X	X
Zanclidae	*Zanclus_cornutus*	OM	S3	Mob	SmallG	Low							

Chapter 5. Which method for which purpose? A comparison of Line Intercept Transect and underwater photogrammetry for coral reef surveys



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Inter-chapter

In Chapters 3 and 4 I presented new quantitative habitat descriptors from underwater photogrammetry methods as well as ecological insights for the study of coral reef ecosystems. Taking into account the relevance of this new method and these descriptors, in Chapter 5 I focused on a technical and scientific comparison of one of the methods traditionally used for coral reef surveys (Line Intercept Transect) and the new photogrammetric methods applied in this Thesis. Ecological methods are the principle tools managers use to survey the spatial and temporal evolution of reefs. Considering the global reef crisis, new technologies and reef assessment methods better describing the ecosystems (i.e. extent and resolution) will likely revolutionize the ways to monitor them. This chapter constitutes one of the first case studies to evaluate the efficiency of these deployed methods. The benefits and disadvantages are presented for each method, evaluating efficiency in terms of scientific outputs, representativeness of the ecosystems, and expertise and time resources.

Which method for which purpose? A comparison of Line Intercept Transect and underwater photogrammetry for coral reef surveys

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Abstract

Selecting effective ecological methods for coral reef surveys is crucial for responding to pressing conservation issues. Facing the current global coral reef crisis, numerous researchers devote their efforts to optimize reef surveys. Here, we comparer four ecological methods for reef surveys, identifying the relative performance between traditionally used Line Intercept Transect (LIT) and three methods derived from underwater photogrammetry: LIT on orthomosaics, photoquadrats from orthomosaics, and surface analyses on orthomosaics at two different scales. Five outer reef slopes and two coral communities on underwater lava-flows were studied at Reunion Island. Coral cover was estimated in situ using LIT and through digital reproduction of two conventional methods on orthomosaics, LIT and photoquadrats. Surface analysis was also achieved on the same orthomosaics. The structural complexity of the sites was evaluated by calculating physical descriptors from digital elevation models. We also compared the methods in terms of scientific outputs, and requirements for human expertise and time.

Comparison estimated coral cover among methods indicated that a higher percentage resulted from LIT in situ, whereas digital LIT and photoquadrats showed lower but equivalent estimations. Surfaces analyses on orthomosaics produced the lowest, and most accurate cover estimations (i.e. lowest sample dispersion). The sites harboring the highest structural complexity showed the highest coral cover. In summary, the comparisons of coral cover estimates, resources required, and attainable spatio-temporal scientific information indicated that surface analysis on the orthomosaics was the most efficient method. Photoquadrats were more time-consuming than both in situ and digital LIT, but provided equivalent coral cover estimations as the latter method and offered more than a single descriptor. The LIT in situ method remains the least time-consuming and most efficient for specific taxonomic identifications but is also the most limited both in terms of potential descriptors for estimates and in the representativeness of the ecosystem.

Key words: coral cover, LIT, orthomosaic, reef survey methods, structural complexity, underwater photogrammetry.

5.1 Introduction

Coral reef survey methods were introduced in the second part of the twentieth century thanks to the development of technologies (e.g. scuba diving equipment and underwater photography) allowing direct access and direct observation of underwater marine ecosystems (Goreau 1959; Loya 1972; Riedl 1980; Dahl 1981). Since then, investigations have evaluated the relevance of these ecological methods and descriptors to monitor reef benthic communities. Quantitative (i.e. Line Intercept Transect Method [LIT], Point Intercept Transect Method [PIT], photoquadrats, video transect) and semi-quantitative (i.e. Dahl quotation, Medium Scale Approach [MSA]) methods have provided the basis of reference studies in benthic reef ecology (Loya 1978; English et al., 1997). Over the last 60 years, a large group of studies have compared these survey methods in terms of accuracy and effectiveness (e.g. Weinberg 1981; Ohlhorst et al., 1988; Lam et al., 2006; Dumas et al., 2009; Facon et al., 2015). Numerous handbooks have been published to support both scientists and managers in selecting the best method corresponding to their specific objectives, including ecological, conservation, and management purposes (e.g. Dahl 1981; Hill and Wilkinson 2004; Obura and Grimsditch 2009).

Over the last decade, new coral reef descriptors and innovative operational tools for monitoring reef ecosystems have been developed and made more accessible (e.g. Burns et al., 2015a, 2019; Hedley et al., 2016; Madin et al., 2016b; Elise et al., 2019a, 2019b; Zawada et al., 2019a,b; Urbina-Barreto et al., 2020 under review). Compared to traditional survey methods, these tools aimed to better understand reef communities and their ecological functioning by optimizing data collection, improving the scale surveyed, and enhancing the quantity and quality of information obtained. The urgency of preserving coral reef ecosystems has become critical in the current context of global climate change, as the increasing frequency and magnitude of human impacts and natural stresses (e.g. cyclones, bleaching events) accelerates the worldwide decline of coral reef ecosystems (Bellwood et al., 2004; Pendleton et al., 2016; Williams et al., 2019). Three aspects of coral reef monitoring methods are of particular interest for study: (i) observer bias and standardization of information (e.g. Caldwell et al., 2016; Flower et al., 2017); (ii) observation scale (e.g. González-Rivero et al., 2014; Wedding et al., 2019); (iii) accessibility for managers in technical and financial aspects and considering social factors (Gilbert and Quod 2018; Darling et al., 2019). In a recent study, Obura et al (2019) reviewed and analyzed coral reef monitoring methods, assessment technologies, and management perspectives in the near future. They stated that hard coral cover is the most standard variable because of its historical reported data, while they recognize that this single descriptor is insufficient to evaluate reef health and to base conservation measures. In addition, the authors specify that data sharing and maximizing global coverage of coral reef information are essential aspects to improve reef conservation and management.

As a matter of fact, the choice of ecological monitoring methods and descriptors is critical in coral reef conservation programs. Thus, survey methods should be adapted to respond to specific conservation purposes. Today, new technologies provide new operational tools and methods for reef surveys. Among them, photogrammetry by structure from motion (SfM) is a technique that allows three-dimensional reconstruction of coral reefs and generates outputs such as 3D models, Digital Elevation Models (DEM, i.e. digital representation of a continuous surface with terrain elevation data) and orthomosaics (i.e. mosaicked images geometrically corrected such that the scale is uniform), which have led to quantitative monitoring of biological and physicals features of ecosystems over time (e.g. Fukunaga et al., 2019; Price et al., 2019; Carlot et al., 2020). These new techniques and methods, likely to become new standards for reef surveying in the coming years (Obura et al., 2019; D'Urban et al., 2020), allow us to confront the challenging conservation targets of the twenty-first century (Kenchington 2018, Duarte et al., 2020).

Here, we applied four reef benthic survey methods, the traditional Line Intercept Transect method (LIT) and three photogrammetric methods (LIT on orthomosaics, photoquadrats from orthomosaics, and surface analyses at two different scales on orthomosaics), to estimate the coral cover at seven sites in Reunion Island. We aimed to: 1) compare the estimations of percent coral cover obtained by each method; 2) demonstrate the possibility to reproduce LIT and photoquadrats methods from photogrammetric outputs (orthomosaics); 3) Compare scientific outputs and required resources (expertise and time) of each method, and identify their advantages and disadvantages. Finally, we present the opportunities and perspectives of the operational application of these methods for conservation managers, fundamental research studies, and environmental consultancies.

5.2 Materials and methods

5.2.1 Study sites

The study was conducted in five outer reef slopes and two underwater lava-flow sites on Reunion Island, an island of the Mascarene Archipelago in the Western Indian Ocean region. The five reefs were located in two reef complexes on the west coast; from north to south, three sites were in Saint-Gilles/La Saline (noted: W-RS sites) and two in Saint-Leu (noted: W-RL sites). The two sites with coral communities on underwater lava-flows were located on the east coast (noted: E-RF sites) (Fig.5.1).

Reunion Island reefs are composed of young and very heterogeneous coral communities (island age ~3 million years) (Chabanet et al., 2001). The studied underwater lava-flows dated at 1977 for C77 and over 100 years old for CAE. They are characterized by successional communities that colonized the substrata after volcanic activities (Schleyer et al. 2016). The fieldwork took place from March to August 2018 at depths varying from 8 to 15 m.

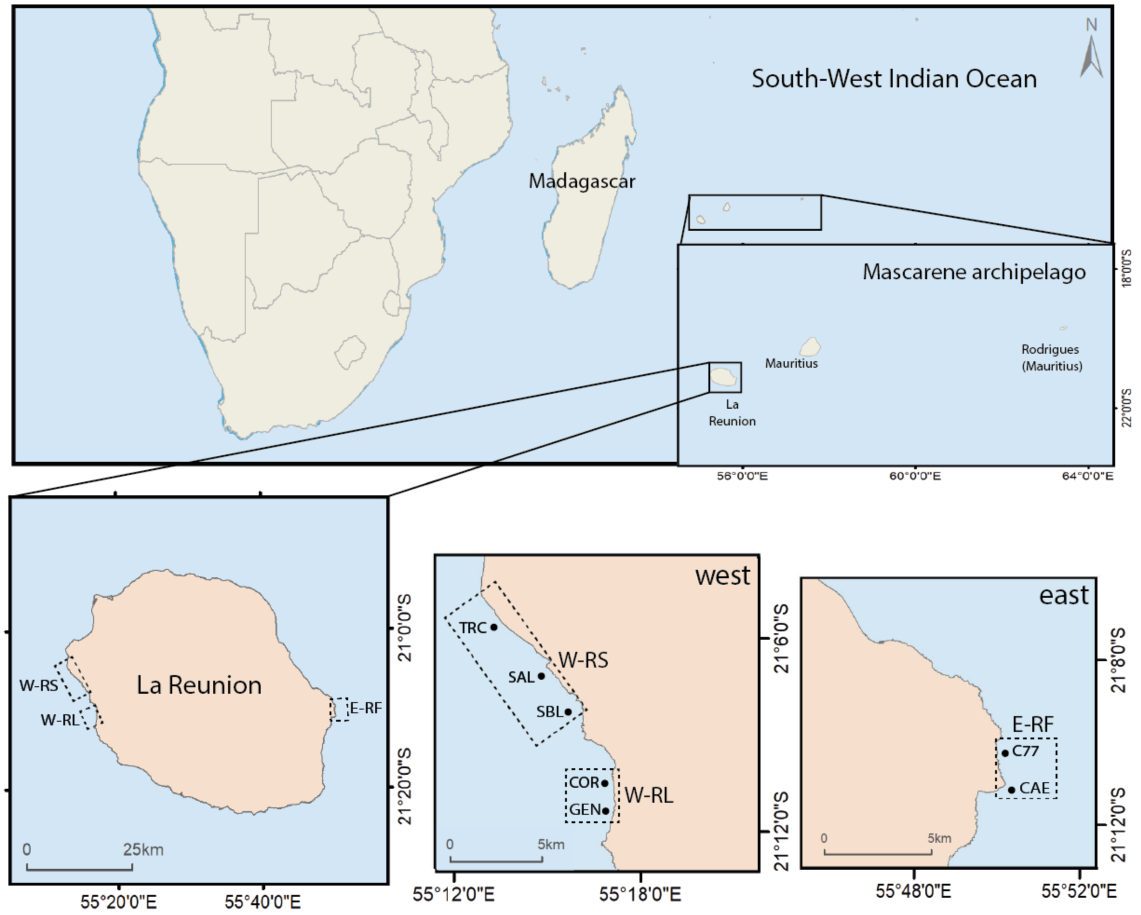

Figure 5.1 Map of the study sites. Reef complexes are indicated in dashed squares. On the west coast, W-RS (Saint-Gilles/La Saline reef complex): TRC, SAL, SBL; W-RL (Saint-Leu reef complex): COR and GEN; on the east coast, E-RF (lava-flow reefs): C77 and CAE.

5.2.2 Coral cover estimation methods

Traditional method, in-situ assessment

The Line Intercept Transect (LIT- in situ) method was conducted by scuba divers following the Global Coral Reef Monitoring Network protocol – SWIO (Obura 2014) (Fig. 5.2.A). Three transects of 20 m long, spaced at least 5 m were deployed at each site. An expert diver identified benthic categories per segment along each transect. The percent coral cover was then calculated adding the total length of segments classified as Scleractinian corals (hard corals) and dividing it by the total transect length.

Photogrammetric methods, digital assessments

Reefscapes at the seven sites were 3D modelled by photogrammetry. Images were collected by scuba divers and covered an area of 250 m^2 on underwater lava-flow sites (C77, CAE) and 500 m^2 on outer reef slope sites (COR, GEN, SAL, SBL, TRC). The mean overlap among images was ~70%. For each site, an

orthomosaic and a digital elevation model (DEM) were generated, the mean reprojection error was 0.25 pixel, and mean resolution (i.e. Ground Sampling Distance) was 0.13 $cm.pixel^{-1}$.
From the orthomosaics, digital assessments estimated the percent coral cover (Fig. 5.2.B). Two methods, LIT (Fig. 5.2.B.1) and photoquadrats (Fig. 5.2.B.2), were digital reproductions of traditionally used methods for benthic surveys that were here performed on the orthomosaics generated by photogrammetry. The other estimation method consisted of segmenting surfaces and classifying benthic communities on the same orthomosaic (Fig. S1), which was then clipped into two sampling units: $40m^2$ ×3 (Fig. 5.2.B.3) and $150m^2$ ×3 (Fig. 5.2.B.4). All methods used the same benthic classification as the LIT in-situ method. Sampling and digital assessment were executed as follows:

<u>Line Intercept Transect on Orthomosaics</u>: the same pattern for LIT in situ method was replicated on the orthomosaics (i.e. 20 m × 3 Fig. 5.2.B.3). The digital assessment was executed using the open source geographic information system software QGIS (version 3.1) by the same expert diver that carried out the in-situ method. Computations of length segments were performed using QGIS command: $length with the field calculator tool. Coral cover was calculated as described in for LIT *in-situ.*

<u>Photoquadrats from orthomosaics</u>: 10 photoquadrats of 1 m^2 each, spaced 50 cm apart, were extracted along each of the three transects created for the LIT orthomosaic method (Fig. 5.2.B.2). Thirty photoquadrats were exported from the orthomosaic and benthic classification was conducted in CPCe software (Kohler and Gill 2006) following Dumas et al. (2009). A stratified point sampling was chosen: each photoquadrat was divided into 9 cells (3 columns and 3 rows), with one point classified per cell (i.e. 9 total points were classified per photoquadrat). The software then directly calculated the mean total percent coral cover.

<u>Surface analyses on orthomosaics</u>: The benthic classification was done manually delineating each coral colony as a polygon in QGIS (Appendix 5.1). Then, the colony layer was clipped in three areas of 40 m^2 for all sites (Fig. 2.B.3) and three sampling areas of 150 m^2 for the five outer reef slopes (Fig. 5.2.B.4). Each polygon surface of scleractinian corals (hard coral) was calculated using the field calculator tool and the area($geometry) command in QGIS; the areas obtained were summed. The percent coral cover was finally calculated by dividing this summed area by the area of replicate (i.e. 40 or 150 m^2).

<u>Analyses on DEM, structural complexity descriptors</u>: for each site from the DEMs (Appendix 5.2), three descriptors of the structural complexity were computed running the R code developed by Fukunaga et al. (2019): surface complexity (i.e. the ratio of 2D to 3D surface), slope, and fractal dimension.

Two-way ANOVAs and Tukey multiple mean comparisons were performed to test the effects of site, method, and their interaction on coral cover estimations.

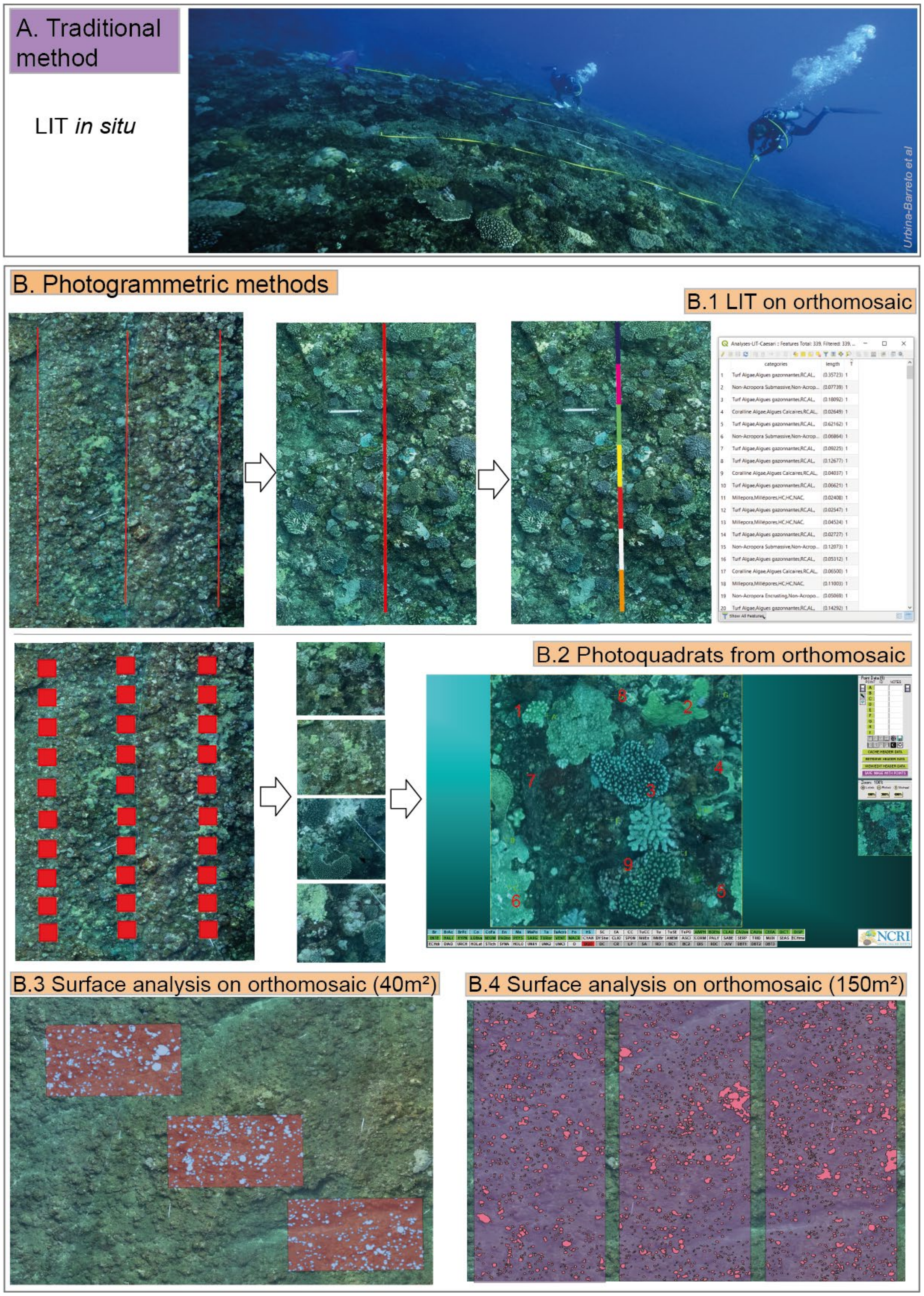

Figure 5.2 Illustration of the traditional method: LIT in situ, sampling distance 20 m ×3 (A) and the photogrammetric methods (B): LIT on orthomosaic, sampling distance 20 m ×3 (B.1); photoquadrats from orthomosaic, sampling area 1 m^2× 10× 3 (B.2); and surface analyses on orthomosaic: sampling area of 40 m^2 ×3 (B.3) and sampling area of 150 m^2 ×3 (B.4).

5.2.3 Description and comparison of traditional and photogrammetric methods

The methods listed above were compared in terms of scientific information obtained, human expertise and time required, advantages and disadvantages, and fields of application. Table 5.1 presents the comparison criteria. It is important to note the evaluation relied upon the experience of all collaborators in the study, representing a large array of scientists from fundamental academic research, applied sciences, and research and development in coral reef ecology. This ensured considering different interests and application targets when defining and evaluating the comparison criteria.

Table 5.1 Definition of each criterion used for the description and comparison of survey methods.

	Criterion		Definition
Method description	**Type of estimator**		Type of measurement used to estimate the descriptor (point, line, polygon)
	Sampling effort		Number and size of the samples used for one site
	Survey dimensions		Number of spatial dimensions represented by the sampling
	Attainable descriptors		List of descriptors possible to obtain from the field data with further analyses
	Limits for the taxonomic identification of Scleractinian corals		Maximum level of identification possible for Scleractinian corals. Other benthic organisms e.g. algae, sponges etc. were not considered in this evaluation
	Raw data		Type of data recorded on the field, on which are based all the analyses and which allow their reproduction
	Observer bias in biological analysis		Bias in the analyses due to subjective human observations and assessments
	Underwater equipment		Materials needed to deploy the method
	Computing equipment		Computer resources and software needed for the analyses
	Environmental constraints		Naturals conditions needed to realize fieldwork and collect the data
Human expertise and time required	**1. Planning**	**Protocol design**	Evaluation of human expertise and time required for the spatial scale of the present study: - The expert (i.e. marine biology specialist) and time required (estimated in days; 1 day = 7 hours)
		Sampling plan	
		Field tools	
	2. Fieldwork (for 1 site)	**Field Mob/Demob***	
		Field survey**	

	3. Office analyses	**Data handling**	- The technician (i.e. no specific skills in marine biology but with diver skills if fieldwork is scuba diving) and time required (estimated in days; 1 day = 7 hours).
		Processing model	
		Ecological analyses	
Review and perspectives	**Advantages and disadvantages**		Synthesis of identified advantages and disadvantages
	Field of applications		Potential organizations or domains for operational applications and perspectives envisioned

* **Field Mob/Demob:** overall time of preparation (mobilization and demobilization, including car and boats rides). ** **Field survey:** diving time.

5.3 Results

Estimations of percent coral cover were significantly different across sites and deployed methods (two-way ANOVA method × site $p < 0.05$; appendix 5.3). Regarding the differences among sites, the percent coral cover was significantly higher on underwater lava-flow sites (E-RF: C77, CAE) and on one outer reef slope site (W-RL: GEN), with the lowest percent covers estimated on SBL and TRC sites (W-RS) (two-way ANOVA $p < 0.001$; appendix 5.3; Tukey tests $p < 0.01$; appendix 5.4; Fig. 5.3).

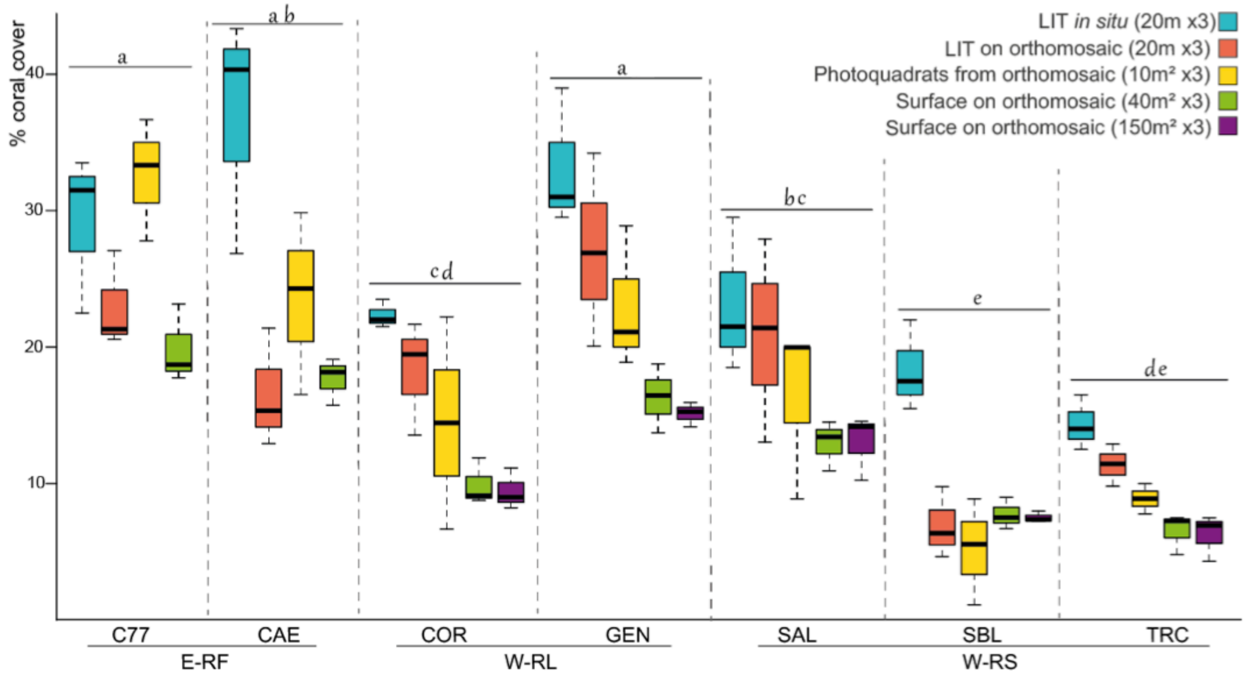

Figure 5.3 Percent coral cover by method across sites. Same letters (a, b, c, d or e) in top of boxplots/site means no significant differences between groups (two-way ANOVA and Tukey tests, $p<0.01$).

Concerning the differences between methods, the LIT in situ revealed the highest estimations of coral cover. Estimations provided by LIT on orthomosaic and photoquadrats from orthomosaic methods were significantly lower, but not significantly different among each other. Surface analyses on orthomosaics provided significantly lower estimations than the three other methods, while no significant differences were detected between the estimations from the two different sampling units of surface analyses (40 m^2 ×3 and 150 m^2 ×3) (two-way ANOVA $p <0.001$; appendix 5.3; Tukey tests $p <0.01$; appendix 5.5; Fig. 5.4). On each site, these two methods provided the lowest estimates except for SBL where photoquadrats and LIT on orthomosaics gave the lowest values, and for CAE, where LIT on orthomosaic also gave a lower value than surface analyses. In addition, the two surface analyses on orthomosaics revealed lower variability than other methods in estimating coral cover (Fig. 5.3).

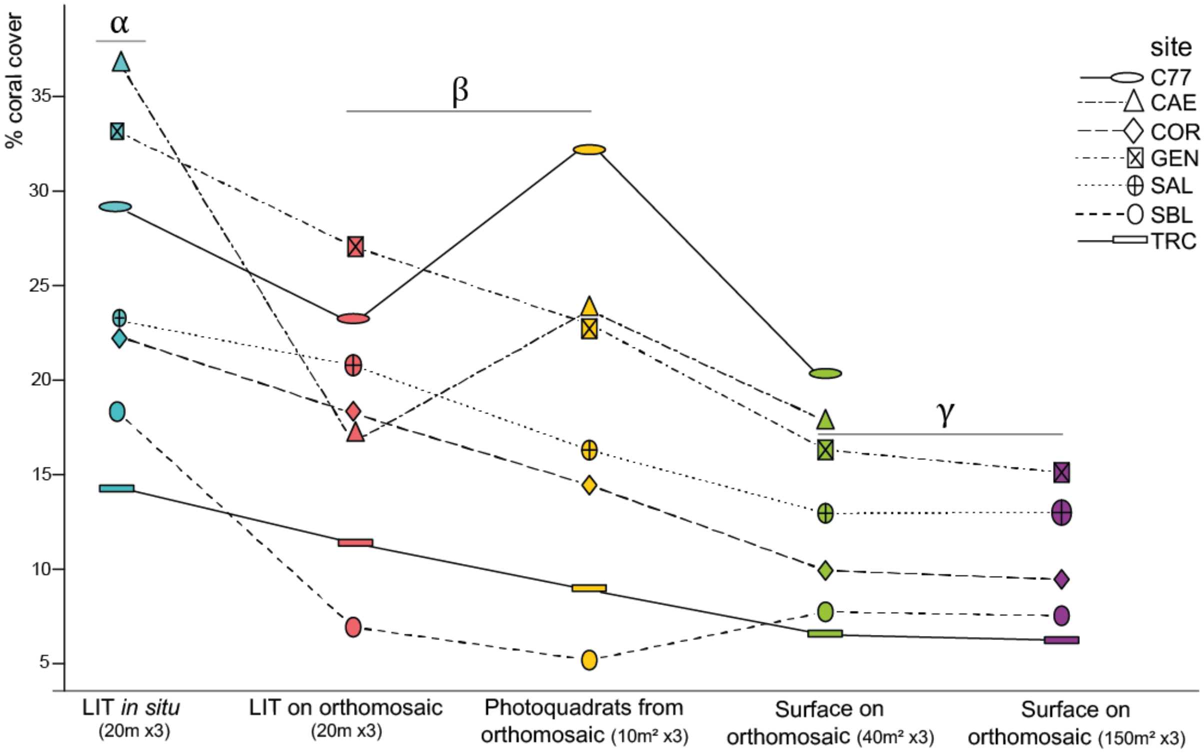

Figure 5.4 Method x Site interaction plot of percent coral cover estimations. Groups with the same Greek letters (α, β, γ) display no significant difference (two-way ANOVA and Tukey tests, $p<0.001$). Colors represent survey methods: LIT in-situ (turquoise); LIT from orthomosaic (pink), Photoquadrats from orthomosaic (yellow); surface analyses on orthomosaic sampling 40 m^2 ×3 (green); surface analyses on orthomosaic sampling 150 m^2 ×3 (purple).

Computing physical descriptors on DEMs allowed quantifying structural complexity characteristics (Table 5.2). CAE represented the most complex site, showing the highest surface complexity, slope, and fractal dimension values. COR, C77, and GEN showed similar structural complexity, higher than in SBL and SAL sites, with the two latter presenting similar values for the three physical descriptors. TRC was the least complex site, having the lowest values of all physical descriptors.

Table 5.2 Physical descriptors of the structural complexity: surface complexity, slope, and fractal dimension computed from each study site's DEM.

Site	Surface complexity	Slope (°)	Fractal dimension
CAE	2.05	38.02	2.15
COR	1.73	33.83	2.12
C77	1.73	33.39	2.13
GEN	1.72	34.23	2.13
SBL	1.40	29.37	2.07
SAL	1.40	29.84	2.08
TRC	1.32	24.59	2.07

In view of these results, we further investigated the possible influence of structural complexity (quantified by the three physical descriptors) on the differences of coral cover estimates among the LIT in situ and photogrammetric methods. The differences between LIT in situ and surface analyses on 40 m² ×3 were significantly correlated with the slope (Pearson correlation $R^2 = 0.68$; $p < 0.05$) and surface complexity (Pearson correlation $R^2 = 0.66$; $p < 0.05$), Fig. 5. The same trends were observed for LIT on orthomosaics, though not significantly (Appendix 5.6). This was not the case for the differences between LIT in situ and photoquadrats from orthomosaics, where the fractal dimension showed no correlation.

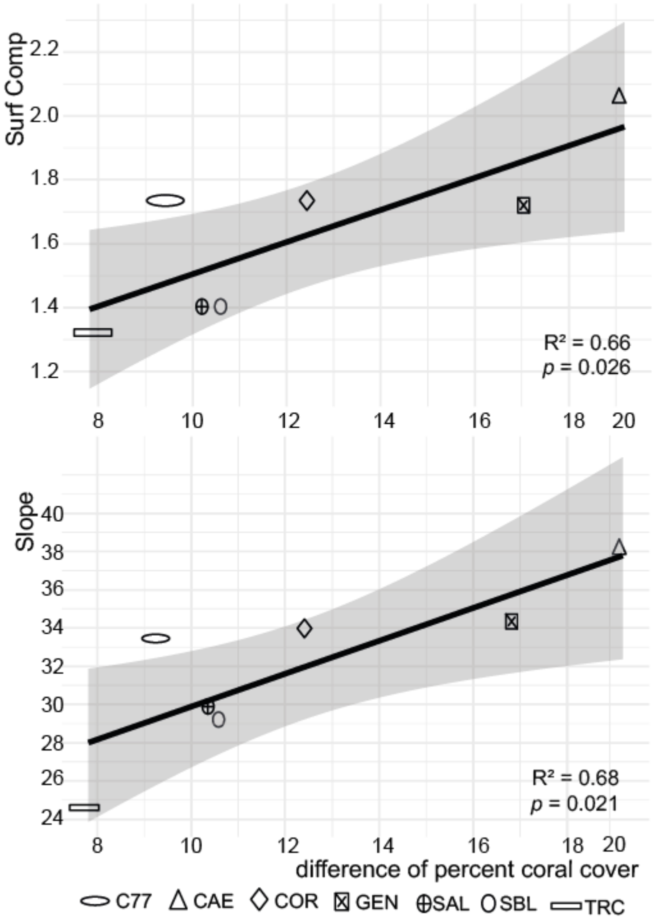

Figure 5.5 Correlation between the differences of percent coral cover = LIT in situ and surface analysis on 40 m² ×3 orthomosaic; structural complexity descriptors for surface complexity (top) and slope (bottom).

Table 5.3 Comparison of the survey methods deployed in this study. Abbreviations: NA = not applicable.

		Traditional method	**Photogrammetric methods**		
	Criterion	**LIT in situ**	**LIT on orthomosaic**	**Photoquadrats from orthomosaic**	**Surface analyses on orthomosaic and digital elevation model (DEM)**
Method description	**Brief description**	Method operated by biologist divers recording benthic categories (i.e. corals, algae, sponges, mineral substrate) along transects laid on substratum. Percent cover is obtained by dividing the total category length by the total transect length.	Photogrammetry by SfM is a technique that allows building 3D models from overlapping photographs. The main outputs from photogrammetry are 3D models (as point clouds and meshes), digital elevation models, and orthomosaics. Over the last decade, this technique has been adopted in the underwater domain to conduct quantitative coral reef studies and surveys.		
			Reproduction of LIT in situ survey method on an orthomosaic.	Reproduction of the traditional photoquadrat method, though frames are extracted from the orthomosaic. The classification of points allows estimating cover of different benthic categories.	Various spatial or biological analyses can be performed with GIS software, based on the outputs from photogrammetry.
	Estimator	Lines	Lines	Points	Polygons and measurements on elevation grids (DEM)
	Sampling effort	3 ×20 m transect (= 60 m)	3 ×20 m transect (= 60 m)	30 ×1 m^2 photoquadrats along 3 transects (= 30 m^2)	3× 40 m^2 or 3× 150 m^2 orthomosaic (=120 m^2; 450 m^2)
	Survey dimensions	2D	2D	2D	2D (orthomosaic) 2.5D (digital elevation model) 3D (if point cloud/mesh is used)

	Attainable descriptors	• Percent cover of benthic categories	• Percent cover of benthic categories	• Percent cover and frequency of benthic categories • Coral colony size and abundance • Distance between colonies	• Surface area and percent cover of benthic categories • Occurrence and frequency of benthic categories • Coral colony size and abundance • Distance between colonies • Surface complexity • Fractal dimension • Shelter capacity • Mean slope
	Limits for the taxonomic identification of Scleractinian corals	Species determination possible in most cases	Genus determination possible in most cases		
	Raw data	Length of segments for different benthic categories	Photographs		
	Observer bias in biological analysis	Medium (by the biologist diver)	Medium (by the biologist on computer)		
	Underwater equipment	GPS, measuring tape, Tablet, and pen	Photographic equipment, measuring tape, scale bars, GPS, and georeferencing targets		
	Computing equipment	No specific requirements	Computer with high processing power and photogrammetry software		
			Geographic Information System software	CPCe software and Geographic Information System software	Geographic Information System software
	Environmental constraints	Low swell and current	Sufficient lighting sources (natural or artificial) and low turbidity and swell		

Human expertise and Time required (1 study site)	**Criterion**		**Traditional Method**	**Photogrammetric methods**		
			LIT in situ	**LIT on orthomosaic**	**Photoquadrats from orthomosaic**	**Analyses on orthomosaic and digital elevation model (DEM)**
	1. Planning	Protocol design	NA	0.5 or 1.0 day for highly complex sites		
		Sampling plan	0.2 day - 1 person	0.5 day - 1 person		
		Field tools	NA	0.3 day - 1 person		
		Man-day	0.2 (Technician or expert)	1.3 (technician or expert) or 1.8 (technician or expert) for highly complex sites		
	2. Fieldwork	Mob/Demob	0.8 day - 2 persons	0.8 day - 2 persons		
		Field survey	0.2 day - 2 persons	0.2 day - 2 persons		
		Man-day	2.0 (1 technician + 1 expert)	2.0 (1 technician + 1 expert <u>or</u> 2 technicians <u>or</u> 2 experts)		
	3. Office analysis	Data handling	0.1 day - 1 person	0.7 day - 1 person *(Reproducing transects)*	1 day - 1 person *(Exporting frames)*	0.5 day - 1 person *(Selecting photographs)*
		Photogram-metry processing	NA	1 day - 1 person *(For ~800 photographs)*		
		Ecological analyses	0.1 day *(results handling)*	0.4 day - 1 person *(1.5 h for ecological GIS analysis + 1 h for length computation and results handling)*	0.3 day - 1 person *(0.3 h for CPCe analysis + 2 h for .csv exports and results handling)*	1.0 – 5.0 day(s) - 1 person *(According to targeted descriptors and the benthic cover of reef area - high coral cover involves more GIS analysis time)*
		Man-day	0.2 (1 expert)	2.1 (1 expert)	2.3 (1 expert)	2.5 to 6.5 (1 expert)

	Total estimation of human resources and time requirement by method E = expert T= technician	**2.4 man-days** (a) 1.2 E + 1.2 T or (b) 1.4 E + 1 T or (c) 2.4 E	**5.4 to 5.9 man-days** For a standard site: (a) 2.1 E+ 3.3 T or (b) 3.1 E+ 2.3 T or (c) 3.4 E + 2 T or (d) 4.1 E+ 1.3 T or (e) 4.4 E + 1 T or (f) 5.4 E	**5.6 to 6.1 man-days** For a standard site: (a) 2.3 E + 3.3 T or (b) 3.3 E + 2.3 T or (c) 3.6 E +2 T or (d) 4.3 E + 1.3 T or (e) 4.6 E+ 1 T or (f) 5.6 E	**5.8 to 10.3 man-days** For a standard site: (a) 2.5 E + 3.3 T or (b) 3.5 E + 2.3 T or (c) 3.8 E +2 T or (d) 4.5 E + 1.3 T or (e) 4.8 E+ 1 T or (f) 5.8 E
			Here, expert (E) requires biology, photogrammetry, and GIS skills		
Review and perspectives	**Advantages**	- Minimal equipment required - Less dependence on water conditions - Short time for office analyses	- Field work can be done by non-biologist - Availability of raw data for future analyses and repeatability - More accurate data (cm) and possibility for accurate long-term surveys - Approach allows obtaining numerous descriptors and gaining more information in terms of data quantity and quality - Sampling at a large spatial scale (seascape), which can be more representative		
	Disadvantages	- Field work must be done by an expert diver biologist - Only measures percent cover of the benthic categories of interest	- Requires good underwater conditions - Requires specific photographic and computing equipment and software - Requires skills or training for the photogrammetry processing and GIS analyses - No direct measurements (the photogrammetry processing must be complete before performing the analyses) - Orthomosaics of sites presenting high structural complexity and/or steep slope likely lead to underestimation of surfaces		
	Fields of application	- Marine area management	- Marine area management and industrial applications - Visually attractive outputs can be used for communication and awareness - Advances in artificial intelligence (AI) to automatize ecological analyses are promising and can promote new applications - Remotely Operated Vehicle and Autonomous Underwater Vehicle developments open perspectives for fieldwork optimization		

5.4 Discussion

Coral cover estimations

Reef communities of Reunion Island are exposed to recurrent natural (austral and cyclonic swells) and anthropogenic pressures (~350 inhabitants/km^2). Regardless of the method used, the percent coral covers of the two western reef complexes (5-35%) were similar to those assessed in the marine reserve (Bigot et al., 2016) encompassing these two complexes. When compared to the values reported in 2001 from the Global Coral Reef Monitoring Network program, these results confirm the declining trend of coral cover on Reunion's reefs over the last two decades (Chabanet et al., 2001). Focusing on the overall differences between sites, the outer, western reef slope sites (except GEN) had lower percent coral cover than lava-flow sites (eastern coast). Indeed, previous reports had indicated that reef lava-flow communities present high percent coral cover (Pinault et al., 2014; data compiled by Reef Check surveys 2017-2019; appendix 5.7; www.reefcheck.fr). These differences may be due to the lower anthropogenic pressures in this coastal zone (lower population density, appendix 5.8), despite the higher hydrodynamic conditions along the eastern coast. Furthermore, both lava-flow sites (C77, CAE) showed higher structural complexity (surface complexity, fractal dimension, and slope) than outer reef slopes, which can maintain the reef communities' functions, enhancing their resilience and promoting coral recruitment (Graham and Nash 2013; Adjeroud et al., 2016).

Concerning the differences among survey methods, the overall trends suggest that LIT in situ may overestimate percent coral cover. Our results are consistent with the findings of Leujak and Ormond (2007), who compared six methods of coral community surveys and found that LIT and Point Intercept Transect (PIT) methods overestimated principal benthic categories. Lam et al. (2006) also provided evidence of coral cover overestimation by PIT, especially at sites with scarce coral colonies. Regarding digital assessments on orthomosaics, no differences were detected between LIT on orthomosaic and photoquadrats from orthomosaics, suggesting that the linear and point sampling used (length and number) may be equivalent estimators in terms of the representativeness of coral cover and accuracy. Surface analyses on orthomosaics provided the lowest percent coral cover estimations across all methods and showed the lowest dispersion of estimates, thus being the most accurate. Despite the associated errors from the process to delineate polygons on orthomosaics, a polygon (the sampling unity of this method) is more representative than lines or points as a surface estimator. Consistent with this mathematical fact, low dispersions of estimates tend to confirm that surface analysis based on orthomosaics is the most accurate and consistent method in terms of coral cover estimation among the methods evaluated in this present study. However, a weakness of photogrammetric methods relates to the orthographic projection used to generate orthomosaics. While this does not affect flat sites, sites presenting high structural complexity and/or steep, sloping sites are more impacted by the orthographic projection, resulting in the underrepresentation of present structures when projected. Consequently, the surface of colonies is likely underestimated in these areas (Urbina-Barreto et al., 2020 in review). Results here confirmed this weakness, as the difference between cover estimates from LIT in situ and digital assessments (particularly for surface analyses on orthomosaics) increased with both the surface complexity and the slope of the sites. This indicates a limitation of orthomosaic-based methods, which can be problematic when comparing sites with considerable differences of slope or complexity. This underlines the need of further investigations to quantify underestimated cover related to the values of habitat complexity descriptors (e.g. surface complexity, slope). Such studies should improve these innovative photogrammetric methods.

The possible implications of our findings are of particular interest for coral reef conservation. Until now, coral reef studies have deployed different methods to map reef areas as accurately as possible, aiming to improve the descriptors and monitoring of coral communities (e.g. Goreau 1959; Weinberg 1981, Leujak and Ormond 2007; Casella et al., 2016; Fukunaga et al., 2019; Hernández-Landa et al., 2020). Scientists and managers often overlook the under or overestimation of coral cover, despite this being a crucial aspect for defining conservation targets and as those targets increasingly require integrating the results of numerous surveys at wide spatial scales (Hoegh-Guldberg et al., 2018). These implications should be better investigated, and calibration between survey methods should be developed, in particular for LIT and PIT, the most popular methods in conservation plans worldwide. For instance, Vallès et al. (2019) studied the transition between chain intercept transect (a method derived from LIT but using a chain instead of a taut measuring tape) and photoquadrat methods on Caribbean reefs and concluded that switching methods for coral surveys would be complicated, as almost all reef benthic categories would require different conversion procedures (i.e. specific mathematical adjustments). More comparative studies between traditional and photogrammetric methods for coral reef surveys are necessary to prepare for the likely transition to such methods, ensuring more accurate, long-term surveys of reef ecosystems at wide spatial scales without dismissing the fundamental historical data recorded over the last six decades.

Comparison of traditional and photogrammetric methods

Comparing the scientific information offered by each method illustrates that much more information can be derived from photogrammetric methods than from LIT in situ (Table 3). This conclusion is based on the fact that surface analyses can deliver more than eight highly comprehensive and high quality reef descriptors based on DEM and orthomosaic analyses, not to mention the analyses that could be performed on other photogrammetric outputs such as point clouds and meshes. The photoquadrat from orthomosaic method is a less comprehensive method, delivering only four descriptors, while LIT on orthomosaics only delivers a single descriptor (the percent cover of benthic categories), like the LIT in situ method. Furthermore, it is worth noting that the raw field data (i.e. photographs) allows the reproducibility of the analysis at a later stage or by different operators, whereas raw data collected from LIT in situ (or in any other in situ visual-based method) is subject to diver expertise. However, the photogrammetric methods require more equipment (photographic, computing, and software), and are more constrained by environmental conditions. Despite being more restrictive in terms of the information delivered, LIT in situ allows better taxonomic determination. Last but not least, it is important to note that photogrammetric methods allow quantifying 3D features such as the structural complexity (surface complexity, fractal dimension, slope, rugosity profiles), which is a fundamental characteristic promoting the biodiversity and productivity of coral reefs (e.g. Graham and Nash 2013; Price et al., 2019).

The human expertise required for the surveys varied throughout the operational steps of each method. The most important, in terms of practical aspects and applicability, is that the photogrammetric methods are independent of the presence of expert biologists for planning and implementing the survey operations and fieldwork, while the LIT in situ method requires an expert biologist to record the data on the field. On the other hand, no expert is required for post-acquisition analyses of data obtained by the LIT in situ method, unlike photogrammetric methods that call for an expert biologist for these tasks. Moreover, skills in photogrammetry and GIS are necessary to generate 3D models, handle photogrammetric outputs, and conduct ecological and spatial analyses.

Concerning the time required, the photogrammetric methods and ecological analyses need more preparation compared to the LIT in situ method, while the fieldwork time is comparable for all methods. In decreasing order, the total time used in this study for preparation, fieldwork and analyses was, by method: analyses on orthomosaics and DEM (5.8 to 10.3 man-days/site) > Photoquadrats from orthomosaics (5.6 to 6.1 man-days/site) > LIT on orthomosaics (5.4 to 5.9 man-days/site) > LIT in situ (2.4 man-days/site). As mentioned before, these results are directly correlated to the quantity and quality of the information produced.

Selection of survey method depending on conservation purposes

Overall, the comparisons of coral cover estimates, scientific outputs, and technical and human resources provided useful information for selecting which method could be more suited for a given reef monitoring program or conservation purpose, depending of available resources. Several studies have previously explored this question by comparing the means, fieldwork and accuracy across different benthic survey methods (e.g. Weinberg 1981; Ohlhorst et al., 1988; Beenaerts and Berghe 2007; Dumas et al., 2009; Facon et al., 2015). Taken together, our results allow us to conclude that surface analysis on orthomosaics is the most efficient method when considering the quantity and quality of data gathered and time expended, while the photoquadrat from orthomosaic method is an intermediate solution. Traditional LIT in situ remains the least time consuming method, efficient for specific taxonomic identifications, though also the most limited in terms of attainable descriptors and representativeness of the ecosystem. The reproduction of traditional methods from photogrammetric outputs (DEMs or orthomosaics), as proposed in the present study, is an innovative alternative to traditional reef survey methods that can be adapted for any coral reef study.

Confronting the global coral reef crisis, challenging conservation targets require the optimization of reef survey methods. New technologies can promote rapid advancements in reef science and support management programs to solve key issues facing coral reefs (Madin et al., 2019). In this context, our study represents a first step to launch the likely transition from traditional methods to novel and more accurate ones. We also provide new information to complement and optimize reef surveys, enhancing of the effectiveness of conservation programs. Photogrammetric tools can be of particular interest to coastal planners and decision-makers regarding the avoidance, reduction, or compensation measures often required by environmental laws for coastal and seascape works. Recently, Duarte et al. (2020) stated that improving conservation efficiency could allow a recovery of marine life (if major pressures are alleviated) and pointed out this action as an ethical and smart economic objective to achieve a sustainable future. To this end, new methods can provide relevant tools to progress in the fundamental reef research domain. Moreover, the development of artificial intelligence for classifying coral reef communities based on photogrammetry outputs (e.g. Hopkinson et al., 2020; Mohamed et al., 2020), multispectral and hyperspectral imagery (e.g. Parsons at al., 2018; Bajjouk et al., 2019; Li et al., 2019), and the automated data acquisition from Remotely Operated Vehicles and Autonomous Underwater Vehicles (Friedman et al., 2012; Obura et al., 2019; Hatcher et al., 2020) will likely revolutionize this field. Combined, these efforts will foster the application of these new methods in both research and coral reef conservation programs.

Authors' contributions

IUB, RG, RP, MA conceived the ideas; IUB, RG, RP, JPQ, LP, ED, MA designed the methodology; IUB, VM, JPQ, RG, SB collected the data; IUB, RP generated digital elevation models and orthomosaics; IUB, PD, CP, SE performed data handling and analyzed the data; IUB, RG, RP, JPQ, MF, PD, SE, ED, LP, MA evaluated the criteria methods; IUB led the writing of the manuscript with RP, LP and MA. All authors contributed critically to the drafts and gave final approval for publication.

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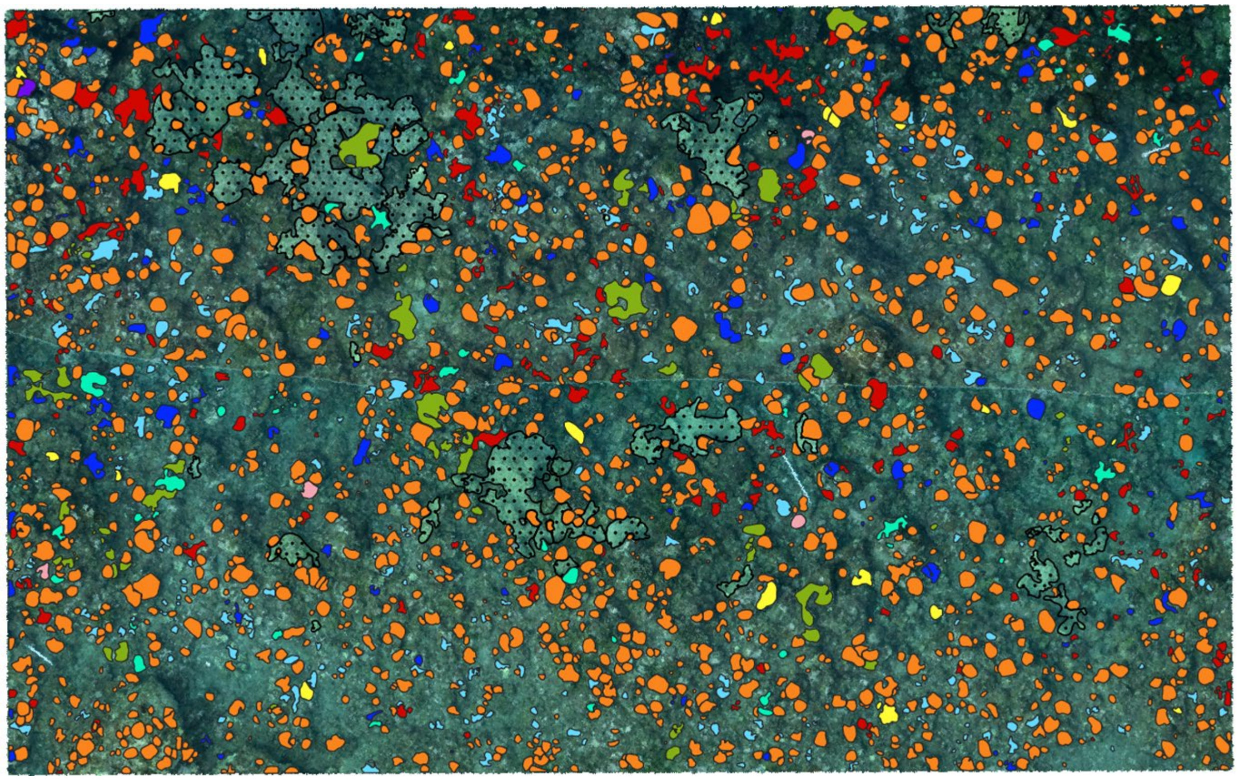
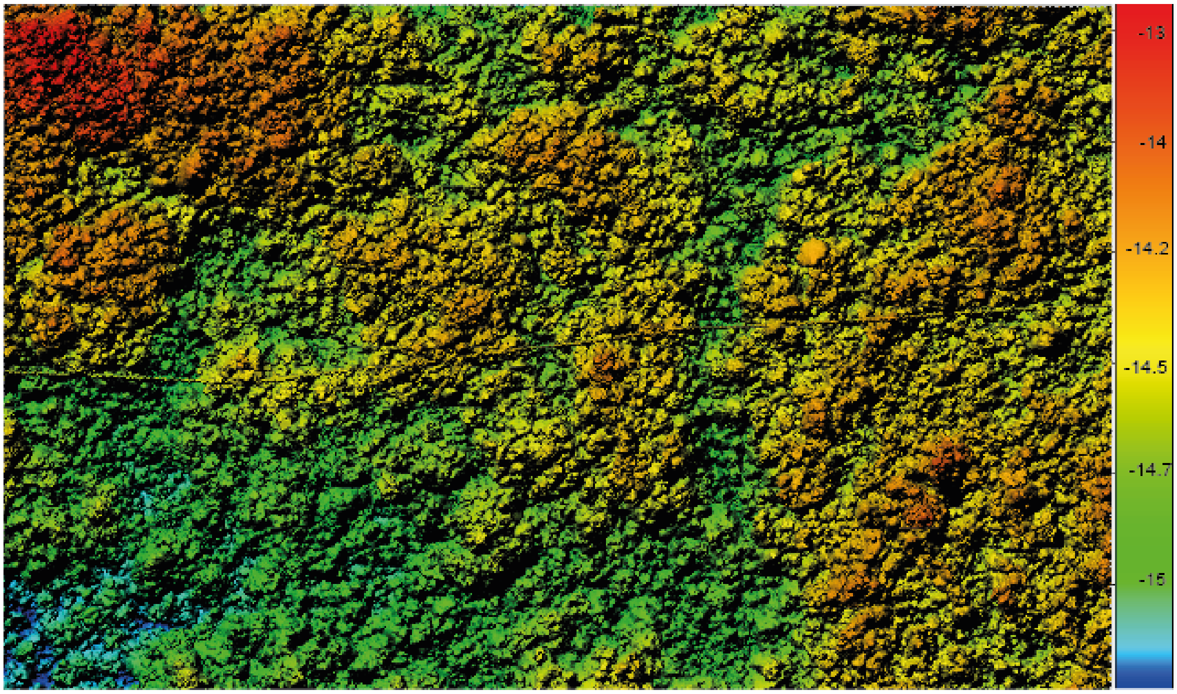
Appendices – Chapter 5

Appendix 5.1



Classification of the benthic communities on the C77 reefscape orthomosaic. Colors of polygons represent growth forms of coral colonies: branching (orange), columnar (cyan), encrusting (red), helmet-shaped (purple), massive (blue), and tabular (yellow). Other categories like soft corals (green) and Milleporidae (dotted area) were also delineated but not considered in this study.

Appendix 5.2



Digital Elevation Model of the C77 site. Structural complexity descriptors computed with R code: surface complexity, fractal dimension, and slope (visualization with GIS software-Global Mapper).

Appendix 5.3

Results of two-way ANOVAs on mean percent coral cover, factors: method and site, significance level code '*' p<0.05, '**' p<0.001, '***' p<0.0001. Results of tests for ANOVA assumptions: Levene's test for the homogeneity of variances and Shapiro-Wilk test on the ANOVA residuals.

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
method	4	2497	624.2	34,307	1.77e-15 ***
site	6	3448	574.6	31,582	< 2e-16 ***
method:site	22	831	37.8	2,077	0.012 *
Residuals	66	1201	18.2		
Levene's Test					
	Df	F valeu	Pr(>F)		
group	32	0.7218	0.8431		
	66				
Shapiro-Wilk normality test					
data: aov_residuals					
W = 0.97844	p-value = 0.1039				

Appendix 5.4

Tukey multiple comparisons of percent coral cover means with 95% family-wise confidence level, by site. Significance level code '*' p<0.001.

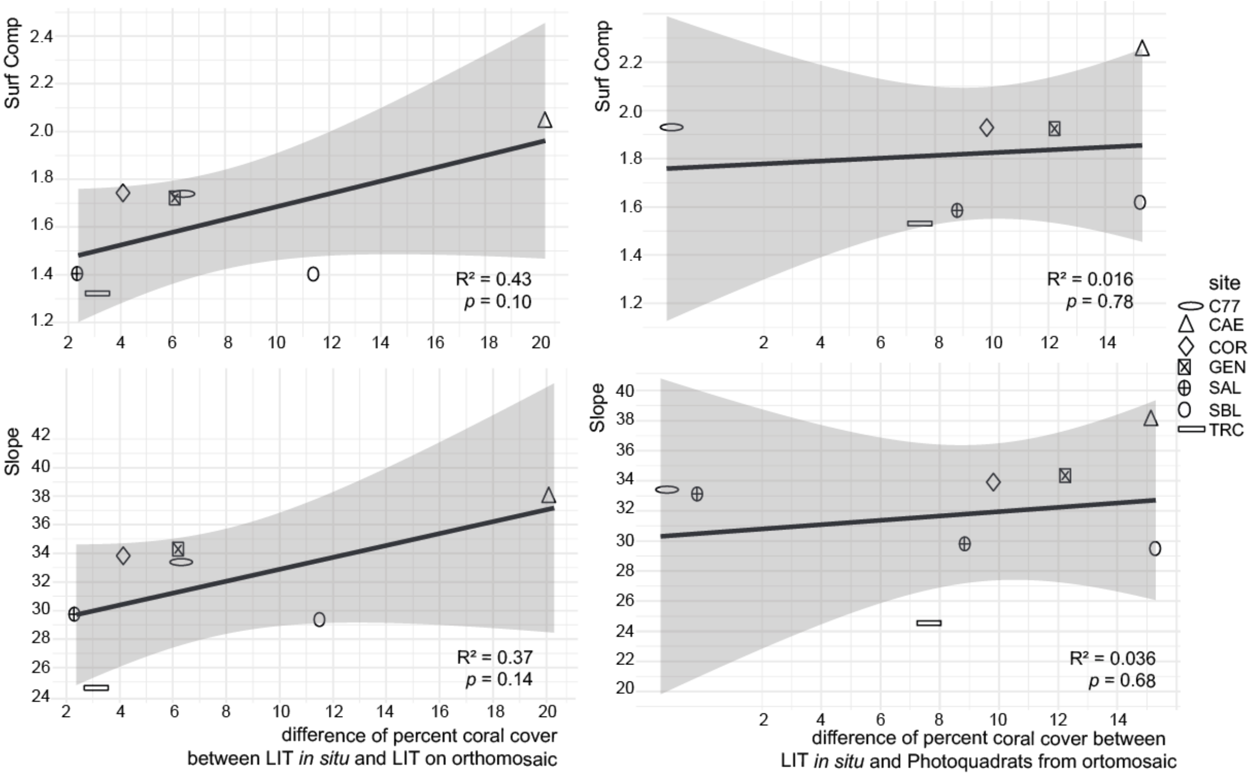
$site	diff	lwr	upr	p adj
CAE-C77	-2.3462417	-7.641986	2.94950316	0.826906
COR-C77	-9.6370436	-14.661028	-4.61305895	0.0000037*
GEN-C77	-1.5915436	-6.615528	3.43244105	0.9600248
SAL-C77	-7.276857	-12.300842	-2.25287228	0.0007552*
SBL-C77	-15.3720303	-20.396015	-10.34804562	0*
TRC-C77	-15.0442236	-20.068208	-10.02023895	0*
COR-CAE	-7.290802	-12.314787	-2.26681728	0.0007334*
GEN-CAE	0.754698	-4.269287	5.77868272	0.9992668
SAL-CAE	-4.9306153	-9.9546	0.09336938	0.0577813
SBL-CAE	-13.0257886	-18.049773	-8.00180395	0*
TRC-CAE	-12.697982	-17.721967	-7.67399728	0*
GEN-COR	8.0455	3.308842	12.78215817	0.0000479*
SAL-COR	2.3601867	-2,376472	7,09684484	0.7347267
SBL-COR	-5.7349867	-10.471645	-0.99832849	0.0081*
TRC-COR	-5.40718	-10.143838	-0.67052183	0.0152313
SAL-GEN	-5.6853133	-10.421972	-0.94865516	0.0089307*
SBL-GEN	-13.7804867	-18,517145	-9.04382849	0*
TRC-GEN	-13.45268	-18.189338	-8.71602183	0*
SBL-SAL	-8.0951733	-12.831832	-3.35851516	0.0000425*
TRC-SAL	-7.7673667	-12.504025	-3.03070849	0.0000933*
TRC-SBL	0.3278067	-4.408852	5.06446484	0.9999921

Appendix 5.5

Tukey multiple comparisons of percent coral cover means with 95% family-wise confidence level, by method. Significance level code '*' p<0.001

$method	diff	lwr	upr	p adj
LIT_ortho-LIT_in-situ	-7.63E+00	-11.323187	-3.939384	0.000002*
PhQ_ortho-LIT_in-situ	-7.63E+00	-11.324173	-3.94037	0.000002*
Surf_Ortho_40-LIT_in-situ	-1.23E+01	-16.028802	-8.644998	0*
Surf_Ortho_150-LIT_in-situ	-1.51E+01	-19.134505	-11.045954	0*
PhQ_ortho-LIT_ortho	-9.86E-04	-3.692887	3.690916	1
Surf_Ortho_40-LIT_ortho	-4.71E+00	-8.397516	-1.013713	0.0057758*
Surf_Ortho_150-LIT_ortho	-7.46E+00	-11.503219	-3.414668	0.0000226*
Surf_Ortho_40-PhQ_ortho	-4.70E+00	-8.39653	-1.012727	0.0057891*
Surf_Ortho_150-PhQ_ortho	-7.46E+00	-11.502234	-3.413683	0.0000227*
Surf_Ortho_150-Surf_Ortho_40	-2.75E+00	-6.797605	1.290946	0.3226446

Appendix 5.6



Correlation between the differences of percent coral cover = LIT in situ – LIT on orthomosaic, and the surface complexity (top-left) and the slope (bottom-left). Correlation between the differences of percent coral cover = LIT in situ – Photoquadrats from orthomosaic, and the surface complexity (top-right) and the slope (bottom-right).

Appendix 5.7

Proportion de corail bio-constructeur (HC) et de corail mou (SC) (moyenne sur la période sélectionnée)

Pente externe - 2 017 - 11/29/2017 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

2742 - Ste-Rose - Coulée 1977
Pente externe - 2 018 - 11/15/2018 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

2743 - Ste-Rose - Coulée 1977
Pente externe - 2 019 - 12/7/2019 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

2941 - Ste-Rose - Petit Tombant
Pente externe - 2 017 - 12/16/2017 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

2744 - Ste-Rose - Petit Tombant
Pente externe - 2 017 - 12/29/2017 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

2745 - Ste-Rose - Petit Tombant
Pente externe - 2 018 - 12/8/2018 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

2746 - Ste-Rose - Petit Tombant
Pente externe - 2 019 - 1/11/2020 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

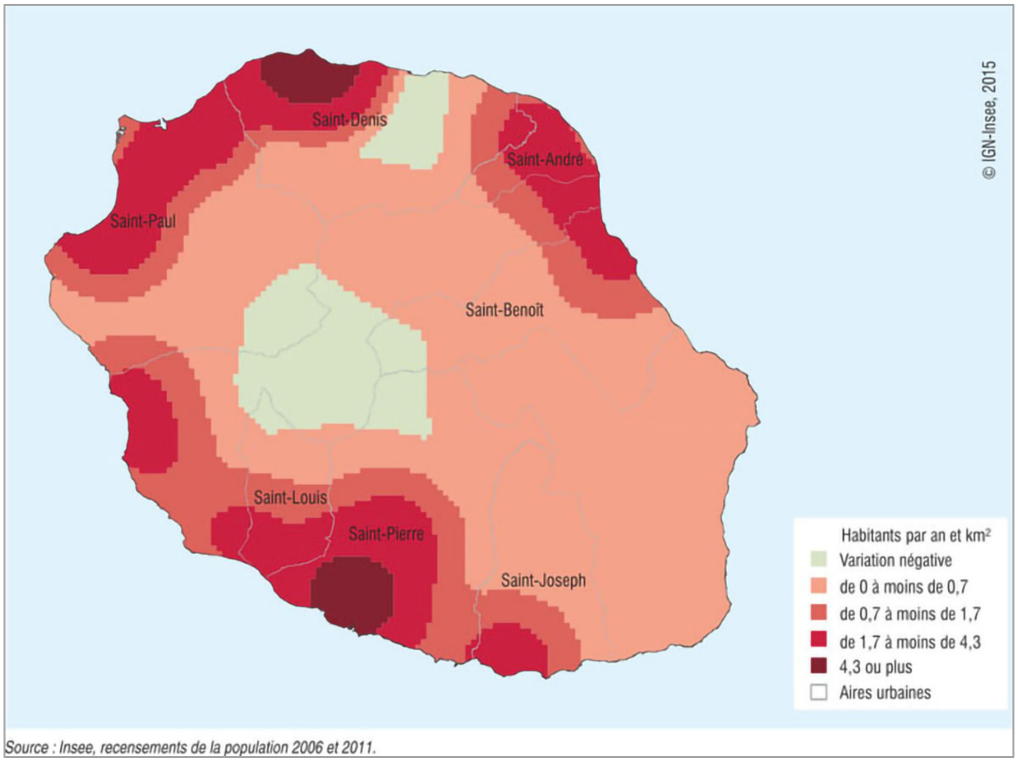
2740 - Ste-Rose - Roche Caesari
Pente externe - 2 018 - 11/14/2018 4:00 AM
Validation : OK -
Poissons : OK - Invertebrés : OK - Benthos : OK

Nombre moyen de Papillons sur 100m² en fonction de la couverture corallienne (HC). Les filtres n'agissent pas sur les valeurs affichées.

% du substrat recouvert par le Corail Dur (HC) (moyenne sur la période sélectionnée)

Percent coral cover (blue color) on underwater lava flow sites, Reef Check surveys 2017-2019.

Appendix 5.8



Source : Insee, recensements de la population 2006 et 2011.

Census of Reunion population 2006-2011 (source: Insee, https://www.insee.fr/).

Chapter 6. General discussion

6.1 Reef habitat descriptor advances

The role of the three-dimensional structure of coral reefs has been a major question since early reef ecological studies. Yet, technical limitations to quantify and develop adapted descriptors have hindered progress in this field. Today, technological advances allow addressing innovative research involving new spatial and temporal issues, complementing the current knowledge applied to reef monitoring and conservation programs. The efficiency of these programs is based on two main types of monitoring: ecological and socio-economic (Wilkinson et al., 2003; Williams and Graham 2019). This Thesis addressed the ecological issues, focusing on developing quantitative descriptors of the three-dimensional structure of coral reef habitats at different spatial scales. This new information aimed to produce new insights of these environments in a trait-based approach and explore the potential key ecological functions related to these new descriptors (Fig. 6.1, right). These findings can be integrated into multivariate analyses for reef ecological monitoring and contribute to multifactorial approaches in reef management. In the context of global environmental change, Pendleton et al. (2016) called for a new mesocosm-level approach to reef research (Fig. 6.1, left), highlighting the need to consider multiple factors and stressors in reef studies and monitoring. This is in contrast to most of the 20th century's management, which focused on one aspect, such as a single species, sector, activity or concern (Mcleod et al., 2019). Multifactorial approaches for reef studies and management are a logical way to better understand the dynamics of reef ecosystems and tune projections for their evolution. In this sense, resilience-based management prioritizes and adapts actions that sustain ecosystems and human well-being alike, using current and future drivers influencing reef ecosystem functions (e.g. physical changes like structure loss due to hydrodynamic forces, biological states like phase shifts to fleshy seaweed, natural pressures such as bleaching, or predator outbreaks such as *Acanthaster spp*.) (Bellwood et al., 2004; Lam et al., 2017; Mcleod et al., 2019). The habitat complexity of reefs is one of the key indicators used by this approach that compiles indicators to describe or quantify major reef functions (e.g. Reef Resilience Network: https://reefresilience.org). Also, Perry and Alvarez-Filip (2019) consider the maintenance of structurally complex habitats, reef-building and vertical reef accretion, and sand supply as key geo-ecological functions that underpin many goods and services that coral reefs provide society. In an earlier review, scientists did not classify habitat complexity in the first ten key resilience factors (McClanahan et al., 2012), instead including factors like recruitment or herbivory biomass, which are likely supported by highly complex structural habitats. In fact, the study presented in Chapter 4 demonstrated that the diversity of herbivorous fishes is positively correlated with the surface complexity and the Shannon Shelter Index.

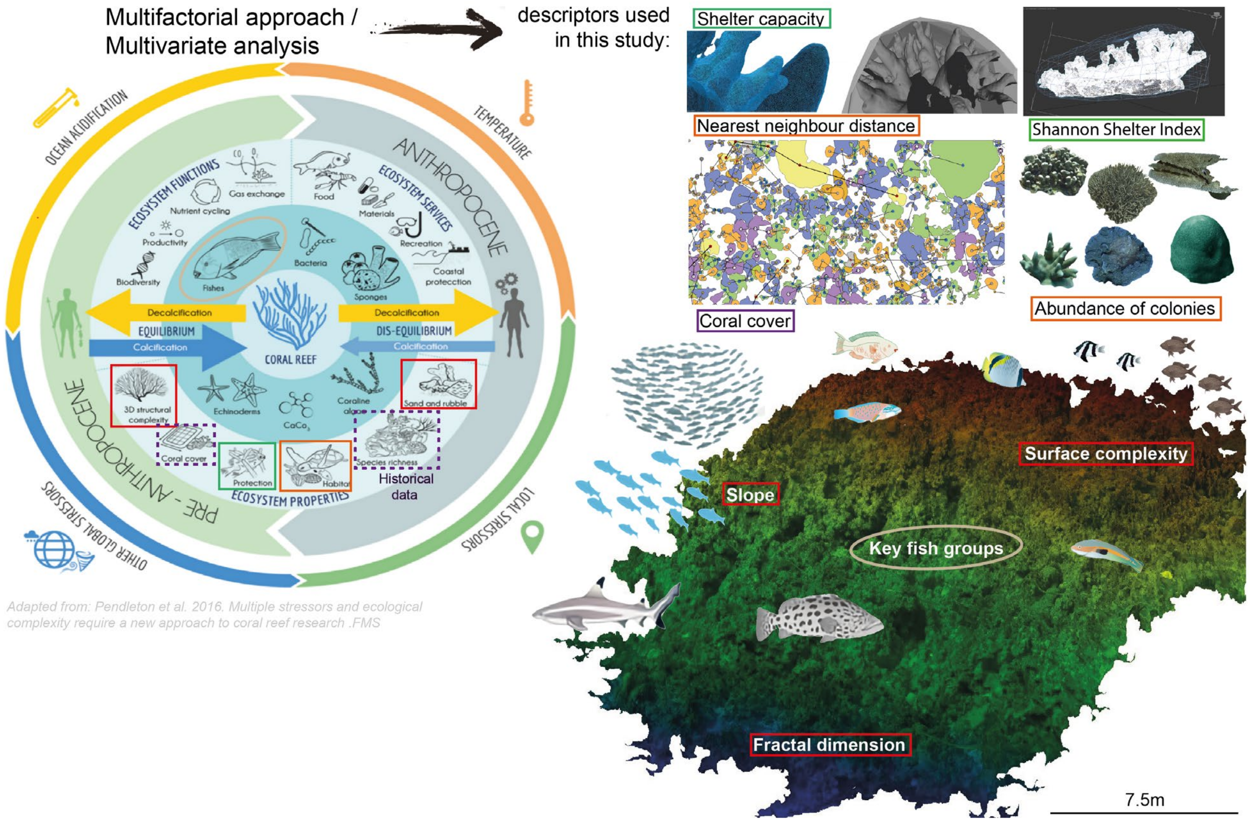


Figure 6.1 Conceptual framework describing ecological processes that contribute to coral reef growth and maintenance vs. the biological and anthropogenic factors that can work against these processes (left, adapted from Pendleton et al., 2016). Colors of squares and ellipse represent different ecosystem properties, the corresponding habitat descriptors developed, and key fish groups explored in this Thesis (right). Dashed squares indicate historical benthic data used in monitoring programs.

Nowadays, trait-based analyses and resilience-based management represent the most adapted and effective conservation approaches in the context of rapidly changing reef conditions in the Anthropocene (Bellwood et al., 2019a; Mcleod et al., 2019). Inspired by these two approaches developed over the last decade, this investigation applied an innovative technology, underwater photogrammetry, for the study of coral reefs. I chose a trait-based approach for benthic communities and associated fishes, the multivariate analyses allowing for fine descriptions of several properties and the core process of reef ecosystems. Thus, Chapters 3 and 4 present new quantitative descriptors of habitat that can be tracked over time to evaluate structural changes at a fine spatial scale. Quantifying the shelter volumes of coral colonies was challenging in terms of photogrammetric fieldwork and 3D analyses. Fortunately, these new colony descriptors quantify one of the major ecosystem functions that can guide management towards functional outcomes (Bellwood et al., 2019a,b). The descriptors of reefscape traits revealed the relationships between several key functions of coral reefs that are ensured by fish groups. These trait-based evidences can complement the assessment of the functional state and resilience of reef ecosystems in their current changing conditions (Fig. 6.1). Taken together, the developed descriptors offer a better, more integrated vision of reef benthic communities, their properties, and functions, potentially inducing new conservation actions. However, as mentioned above, coral reefs face other major pressures, including ocean acidification, thermal stress, and local stressors, that should be simultaneously considered to avoid dismissing relevant contributors to the ecological state and resilience of ecosystems (Burke et al., 2011; Pendleton et al., 2016; Williams and Graham 2019).

Coastal installations: 3D modeling of breakwaters structures

Concerning the breakwaters studied, the mapped zone of the D-PE breakwater was 350 m^2 and covered an over 20 year old station surveyed in the environmental monitoring program led by Creocean OI (Creocean-OI, 2016). The mapped zone of the D4-NRL breakwater was 650 m^2 and corresponded to a recent construction for the coastal highway connecting Reunion's capital (Saint-Denis) and the west of the island. Tetrapod structures used for construction were immersed six months before the photogrammetric survey. Figure 6.2 displays the generated 3D models, orthomosaics, and digital elevation models (DEMs). The physical habitat descriptors were calculated from DEMs, but the ecological analyses on the orthomosaics were not conducted, due to time limitations of the Ph.D. program.

Apropos of *in-situ* biological assessments, fish assessments on the D4-NRL breakwater showed a high presence of juvenile fishes (Table 6.1, Appendix 6.1). This particular juvenile fish presence may be due to three main factors: 1) the time of the survey, coinciding with the recruitment season (in the beginning of the austral summer, December 2018); 2) the refuge and habitat provided by the structural complexity of the new structures; 3) a low predation pressure in this zone, likely due to the absence of settled predator species explained by the recent age of this breakwater. However, these observations suggest that the structure can act as a temporal "nursery" for the earliest stages of some groups of fishes. In contrast, the presence of juvenile fish was not evidenced in the older breakwater (D-PE, Table 6.1). This may be explained by the season when the assessment was conducted (austral winter, August 2018), as well as the natural regulation of these groups by the trophic dynamics of the healthy coral communities that have developed over the last two decades. An evidence of this healthy state is the high coral cover of this breakwater (40.3%), the highest across all Reunion's study sites (including the outer reef slopes and lava-flows sites). On the other hand, unsurprisingly, the benthic community of the newer breakwater (D4-NRL) presented a rather high percentage of turf algae cover (95%), although initial colonization of pioneers and opportunistic Scleractinian coral families as Pocilloporidae (2%) was already observed. Concerning the physical descriptors, the surface complexity was higher in D4-NRL than D-PE, but the latter displayed slightly higher fractal dimensions, probably due to the diverse growth forms of developed coral communities. Combined, these findings suggest the potential of these artificial structures to offer new structurally complex habitats that can promote the development of novel reef communities in human-modified environments.

Table 6.1 Mean density of juvenile fish by families in breakwaters sites.

Family	**D-PE**		**D4-NRL**	
	Number/100 m²	*SD*	**Number/100 m²**	*SD*
Acanthuridae	0.0	*0.0*	5.3	*4.0*
Chaetodontidae	0.0	*0.0*	1.0	*1.7*
Labridae	0.0	*0.0*	4.7	*3.5*
Lutjanidae	0.0	*0.0*	33.0	*29.5*
Microdesmidae	0.0	*0,0*	10.0	*17.3*
Mullidae	0.7	*1.2*	3.0	*3.6*
Pomacentridae	2.3	*4.0*	96.7	*95.5*
Tetraodontidae	0.0	*0.0*	0.7	*1.2*

Inherently, an immerged structure in a submarine environment provides refuge for surrounding organisms. Consequently, the structure induces an *attraction effect* for biodiversity, particularly for some juvenile stages of fishes and crustaceans. This effect is well known and often used for fisheries and restoration goals (e.g. Wickham et al., 1973; Walters et al., 1991; Sandström et al., 2002; Santos et al., 2008). Likewise, these observations led to the conception of artificial reefs, often used as tools for compensation and restoration measures in environmental impact projects or fisheries management programs. Many experiences in this field have shown that the structural complexity of the artificial structures can significantly influence their success in terms of fish and organism assemblages (Tyler 2000; Pinault et al., 2010; Pinault 2013; Ehrenfeucht 2014). Better understanding of the main 3D-features of coral reef habitats promoting biodiversity (e.g. fishes, crustaceans, etc.) can help conceive novel artificial structures and provide new tools to restore degraded habitats.

Concerned by the global coral reef crisis, the scientific community and engineers have increased their investigations in the environmental restoration domain. Since 2000, the number of coral reef restoration projects worldwide has multiplied by four (Duarte et al., 2020). New technologies and innovative approaches can enhance the success rates for reef environments and other ecosystems. For instance, the HYPER3D project studies the successional colonization of six 3D printed artificial reefs immersed in the Mediterranean-sea (https://fondation-uca.org/projets/recifs-3d-hyper3d/). Other studies assessed the role of reef structural complexity to ameliorate coastal erosion and flooding for coastal protection (Reguero et al., 2018). Experiments like these can be reproduced in degraded coastal zones to promote new coral and fish recruitment, reinforcing the resilience of these ecosystems and enhancing the protection of the shorelines. The results of this Thesis, specifically the 3D models generated for coral colonies and reefscapes, can contribute to a new generation of artificial reefs. The photogrammetric tools and developed protocols are useful for accurate surveillance of the dynamics of benthic communities and their structural temporal changes. This can be of particular interest to coastal planners, decision-makers, and developers regarding the avoidance, reduction, or compensation measures often required by environmental laws for coastal and seascape works. Together, these types of initiatives and efforts can partially offset manmade impacts and relieve some stress induced by increasing natural pressures related to global climate change.

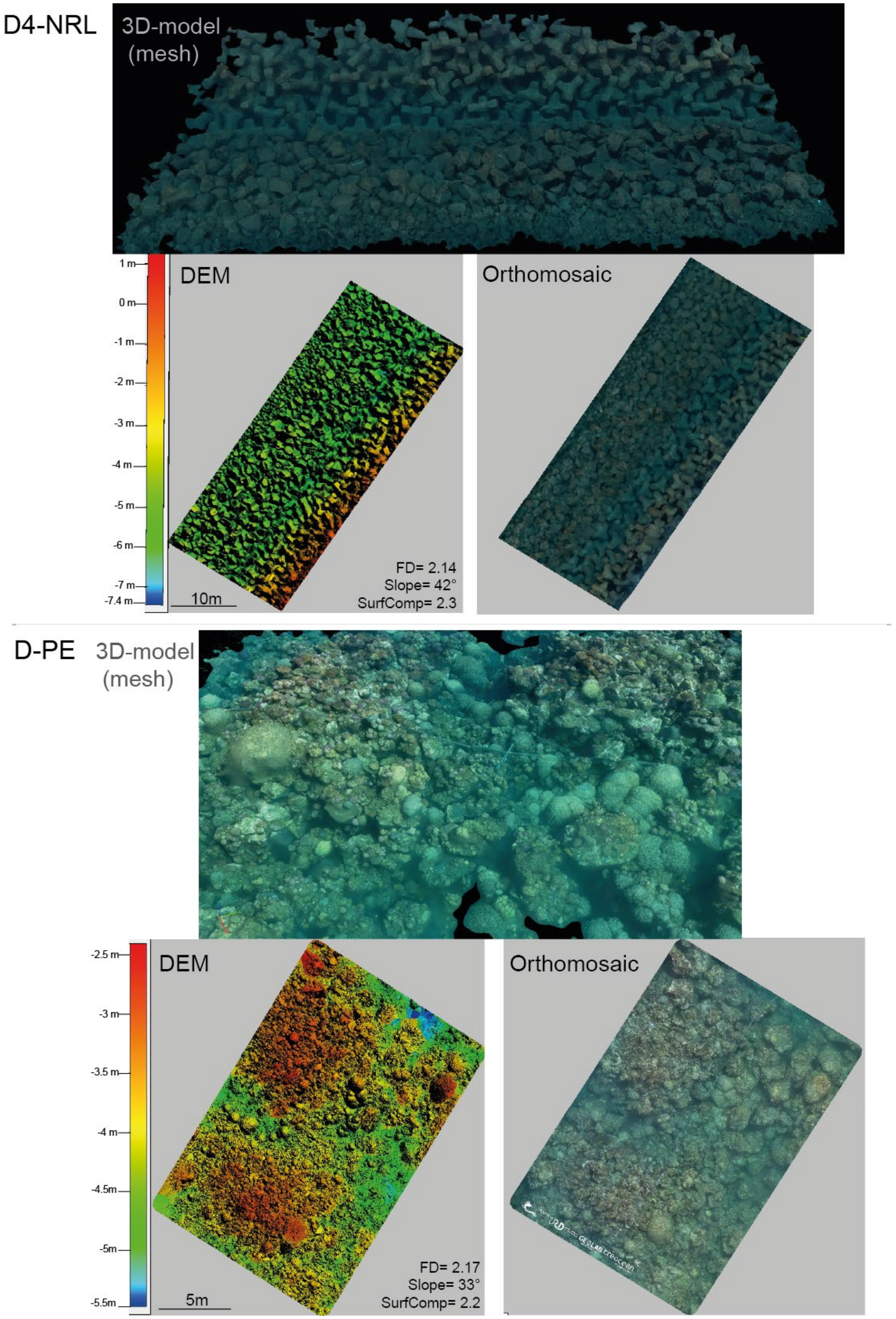
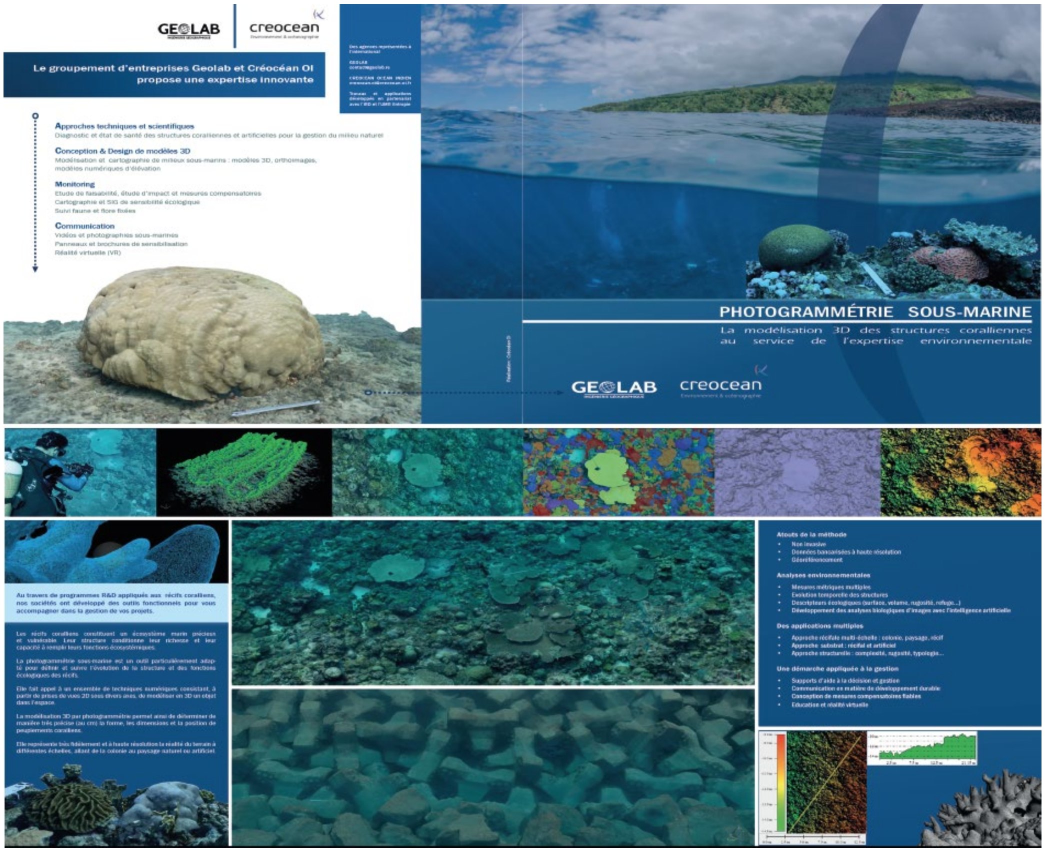


Figure 6.2 3D models, Orthomosaics and digital elevation models of the breakwater sites: D4-NRL tetrapod structures – 650 m² (top); D-PE square blocks structures – 350 m² (bottom). Abbreviations FD= fractal dimension, SurfComp= surface complexity.

6.2 Operability of photogrammetric tools

The photogrammetric protocols allowed accurate 3D reconstructions for the two study scales. Overall, 70.5% of isolated coral colonies were reconstructed into 3D models (120 of 170 colonies sampled), a sufficient amount to conduct 3D measurements and analyses, as well as 100% of reefscapes and breakwater sites. The mean resolution (Ground Sampling Distance – GSD) of the photogrammetric outputs (digital elevation models and orthomosaics) was 0.13 cm pixel^{-1}, suitable for physical and ecological analyses. The operational protocols and ecological analyses developed under this Thesis have enabled a new engineering activity to be used by Creocean OI and Geolab in environmental studies. Today, new offered services apply these photogrammetric tools through both technical and ecological skills (Fig. 6.3). In all, over the last three years, up to ten studies were proposed to clients and calls for projects using photogrammetry expertise in environmental surveys. Notably, the REBIOMA-3D project was selected for the Life4Best grant 2020-2021 (https://www.life4best.org), which supports small-scale field actions for biodiversity conservation and sustainable development in the Outermost Regions of the European Union, funded by the European Commission, OFB (Office Français de la Biodiversité), and AFD (Agence Française de Développement). REBIOMA-3D represents the direct application of the operational methods and tools developed by the Thesis investigations to support coral reef and marine protected area managers. It is also the first commercial achievement of these new operational services (Appendix 6.2, REBIOMA-3D project abstract).



Le groupement d'entreprises Geolab et Créocéan OI propose une expertise innovante

Approches techniques et scientifiques
Diagnostic et état de santé des structures coralliennes et artificielles pour la gestion du milieu naturel

Conception & Design de modèles 3D
Modélisation et cartographie de milieux sous-marins : modèles 3D, orthoimages, modèles numériques d'élévation

Monitoring
Etude de faisabilité, étude d'impact et mesures compensatoires
Cartographie et SIG de sensibilité écologique
Suivi faune et flore fixées

Communication
Vidéos et photographies sous-marines
Panneaux et brochures de sensibilisation
Réalité virtuelle (VR)

PHOTOGRAMMÉTRIE SOUS-MARINE

La modélisation 3D des structures coralliennes au service de l'expertise environnementale

Au travers de programmes R&D appliqués aux récifs coralliens, nos sociétés ont développé des outils fonctionnels pour vous accompagner dans la gestion de vos projets.

Les récifs coralliens constituent un écosystème marin précieux et vulnérable. Leur structure conditionne leur richesse et leur capacité à remplir leurs fonctions écosystémiques.

La photogrammétrie sous-marine est un outil particulièrement adapté pour définir et suivre l'évolution de la structure et des fonctions écologiques des récifs.

Elle fait appel à un ensemble de techniques numériques consistant, à partir de prises de vues 2D sous divers axes, de modéliser en 3D un objet dans l'espace.

La modélisation 3D par photogrammétrie permet ainsi de déterminer de manière très précise (au cm) la forme, les dimensions et la position de peuplements coralliens.

Elle représente très fidèlement et à haute résolution la réalité du terrain à différentes échelles, allant de la colonie au paysage naturel ou artificiel.

Atouts de la méthode
- Non invasive
- Données bancarisées à haute résolution
- Géoréférencement

Analyses environnementales
- Mesures métriques multiples
- Evolution temporelle des structures
- Descripteurs écologiques (surface, volume, rugosité, refuge...)
- Développement des analyses biologiques d'images avec l'intelligence artificielle

Des applications multiples
- Approche récifale multi-échelle : colonie, paysage, récif
- Approche substrat : récifal et artificiel
- Approche structurelle : complexité, rugosité, typologie...

Une démarche appliquée à la gestion
- Supports d'aide à la décision et gestion
- Communication en matière de développement durable
- Conception de mesures compensatoires fiables
- Education et réalité virtuelle

Figure 6.3 Brochure of underwater photogrammetry services of Creocean OI and Geolab firms.

Underwater photogrammetry: expertise and business aspects

The applications of underwater photogrammetry at the national level in France have escalated over the last five years (e.g. Abadie et al., 2018; Marre et al., 2019, this Thesis), with the exception being two institutions that had historically developed this technique, The Computer Science and Systems Laboratory (LIS - UMR 7020) of the Centre National de la Recherche Scientifique (CNRS) and the Compagnie Maritime d'Expertises (Comex), now representing French references in this field. Collaborations between the academic field and international programs have allowed other French research institutes to gain awareness about this new technology and apply it in reef research, including the collaboration between the Service d'Observatoire Corail, created by CRIOBE (Centre de Recherches Insulaires et Observatoire de l'Environnement), and the 100 island challenge (Carlot et al., 2020). French research programs are also led by directors and engineers at the Mixed Research Unit (UMR) Marbec, which collaborated with the Andromede Company to host a Ph.D. program (Marre et al., 2019). The UMR Entropie initiated research in this field in 2017 by hosting this Ph.D. program. All these studies shed light on this technology to public and private domains at national and international levels, and today underwater photogrammetry represents a top interest for French representatives of both fundamental and applied marine sciences. Table 6.2 presents the principal actors of French marine environmental institutions and consultancies, identified from a succinct numerical email survey. The collected information shows that most of this technology's applications are used in research goals; environmental consultancies in mainland France and New Caledonia are still experimenting and do not offer operational or commercial services yet, other than Comex and Adromede. However, this technique and its applications are of high interest, and most of the people contacted (engineers or company directors) wish to develop these skills in the coming years (listed also in Table 6.2). Shifting the attention to the Western Indian Ocean region, there appears to be no company that offers the same type of services that Creocean-OI offers today, giving it a competitive edge.

Table 6.2 French organizations and underwater photogrammetry applications

Organization name	Description and underwater photogrammetry expertise or interests*	Zone of activity
Creocean, Creocean OI (Host company of this Thesis)	Company offering multidisciplinary expertise, in France and abroad, to provide a better understanding of the coastline and offshore marine environments. As a former subsidiary of Ifremer, Creocean is closely linked to scientific institutions (CNRS, Universities, Engineering Schools, etc.) and continues to work on research and technological innovation. The operational applicability of underwater photogrammetry services covers shallow (<40 m depth), tropical, and temperate environments; scuba divers conduct the fieldwork. The surveys are conducted mainly in natural ecosystems or on artificial structures (e.g. artificial reefs, breakwaters). Over the last three years the research and development center works in collaboration with UMR Entropie, which reinforces the	France, Western Indian Ocean, Overseas French territories, International

	scientific rigor of studies and the relevance of ecological analyses and indicators developed for environmental surveys. Websites: https://creocean.fr; http://oceanindien.creocean.fr	
Organization name	**Description and underwater photogrammetry expertise or interests***	**Zone of activity**
Geolab (Technical partner)	Geographic engineering company specialized in topography and geomatic fields. Geolab started exploring underwater photogrammetry in 2016 and continued to develop its expertise throughout this Thesis. It is now specialized in processing and analyzing underwater photogrammetric data. Website: http://www.geolab.re	Western Indian Ocean, France, International
COMEX (Compagnie Maritime d'Expertises)	Company specializing in engineering and deep diving operations. They develop and sell photogrammetry capturing devices, developing an underwater photogrammetric system, Orus 3D, capable of 3D monitoring at sub-millimeter precision in real-time. This system can be operated by divers or mounted on subsea vehicles (ROV, AUV). Algorithms of Orus 3D save time by a factor of 5 to 30 against other photogrammetric systems. For 20 years, they work in close collaboration with CNRS (Centre National de la Recherche Scientifique). Areas of intervention: Offshore oil and gas, archaeology (wrecks), deep ecosystems (coral and canyons). Pers.Com. Julien Seinturier; Antoine Goujard.	France, North sea, West Africa, Russia, Mediterranean sea (Calanques National Park)
Ifremer (Institut français de recherche pour l'exploitation de la mer)	The research institute for marine development and technologies, Ifremer's research supports enacting maritime policies. Photogrammetry applications are mainly led in deep waters (> 50m) using ROV. The "*Récif 3D*" program focuses on high definition camera performances for these samplings, as well as hyperspectral samplings, exploring the potential of combining both technologies to map deep reefs of Reunion Island. Pers. Com.: Magali Duval; Cathy Treguier.	France, Overseas French territories, International
Seaviews	Company created in 2015, which aims to develop and apply new seafloor observation methods, mainly using acoustic systems but also offering underwater photogrammetry services. Col. Info. Website: https://seaviews.fr/fr/	France, Overseas French territories
Septentrion environnement	Non-governmental French association, offering environmental studies for research and management actions. They use the principle of stereophotogrammetry for 3D modeling of marine habitats. Col. Info. Website: https://septentrion-env.com	France

Organization name	Description and underwater photogrammetry expertise or interests*	Zone of activity
Andromede	Company dedicated to the environmental study of Mediterranean marine ecosystems (seagrass and corralligenous reefs). Photogrammetry services are one of their operational activities for environmental surveys. Partnerships with research institutes and universities reinforce their development of photogrammetric tools. Col. Info. Website: https://www.andromede-ocean.com	France, Overseas French territories.
Squale	Marine environment consultancy specializing in monitoring reef communities (impact studies and scientific research) and the management of fishery resources. Very interested in underwater photogrammetry applications for environmental studies or services, though not skilled in this field. Pers. Com.: Bastien Preuss.	New Caledonia
Sopроner	Company specialized in technical studies and management projects. The environmental center led some experiences in research and development applying underwater photogrammetry techniques, but the operational activities are not yet developed. Pers. Com.: Antoine Gilbert.	New Caledonia
Insight	Company specialized in geo-solutions combining GIS and remote sensing tools; services include aerial photogrammetry, but underwater applications are not used. The company is very interested in the applications of this technique for surveys of New Caledonian lagoon ecosystems. Pers. Com.: Sebastien Lagarde.	New Caledonia
CNRS - UMR LIS (Mixed Unity of Research, The Computer Science and Systems Laboratory)	LIS is a research lab (UMR 7020) under the supervision of CNRS, Aix-Marseille University and University of Toulon with the Ecole Centrale de Marseille (ECM) as a partner. For 20 years the laboratory has worked in underwater photogrammetry, mainly for archaeological and biological research. Pers. Com.: Bertrand Chemisky	France
CUFR (Centre Universitaire de Formation et Recherche de Mayotte)	University of Mayotte researchers collect underwater photogrammetry data in shallow reefs (< 25 m); combined with shoreline surveys, they aim to track temporal changes. Their ALLIANCE project (AAP-2019), is the first to apply underwater photogrammetry on Mayotte's reefs. Pers. Com.: Thomas Claverie.	Mayotte

University of Reunion – UMR Entropie (Mixed Unity of Research, Tropical Marine Ecology of the Indian and Pacific Oceans)	University where underwater photogrammetry research is led by the investigations of this Thesis, as well as a collaboration established with Ifremer for the *Récif 3D* project. Website: http://umr-entropie.ird.nc/index.php/portfolio/projets-en-cours/photogrammetrie	Reunion Island, Western Indian Ocean, New Caledonia

** The descriptions are based on information collected from an email survey, personal communications by mail, or meetings with the concerned representatives* (Pers. Com.: *person contacted*). *For the companies that did not answer the email survey, the information was collected* (Col. Info. Website) *from websites, scientific publications or communication actions (e.g. public conferences, TV shows, social media posts). Thus, the present list is not exhaustive.*

Underwater photogrammetry: weaknesses and limits encountered

Few limits and weaknesses of the technique were identified and discussed in Chapters 3, 4 and 5; here I summarize the main points from my personal point of view.

Relating to fieldwork, covered in Chapter 5, environmental factors are more constraining for deploying the photogrammetric method than traditional methods. Mainly, good visibility (low turbidity of water) determines the ability to obtain high-quality images and consequently good photogrammetric reconstructions. It is also important to consider light conditions. For instance, lighting for sampling the outer reef slopes is better after 9 a.m. and before 4 p.m. on a sunny day. In contrast, it's better to work on a cloudy day when sampling in shallows waters (reef flats < 5 m) to avoid the sun's reflection on the sand, which affects the image quality.

Concerning the analyses of the photogrammetric outputs, no particular problems were identified for the mesh or digital elevation models. However, regarding the orthomosaics, Chapters 1 and 5 discuss potential errors in measurements due to the orthographic projection related to the slope and structurally complex sites. In fact, the elements in these specific areas are not correctly represented (being either over or underrepresented). This is one of the main limits of this digital output (whether it is produced from terrestrial, aerial, or underwater photogrammetry). Further investigations about this aspect can propose a possible *correction or adjustment value*. One possibility is to study the mathematical relation between quantitative descriptors of habitat complexity (e.g. the mean slope, the fractal dimension, or the surface complexity) and the orthomosaic measurement (as briefly showed in Chapter 5) at the same given area, for both a low and high habitat complex sites.

A more obvious, but worth noting, constraint is the financial limitations associated with applying underwater photogrammetry; this method requires photographic equipment and computing resources that may not be affordable for all types of organizations (e.g. managers of MPAs or conservation NGOs). Specifically, the photogrammetric software licenses are expensive and often updates imply extra fees, while the open-source software that has been developed is less user-friendly. Also, sufficient computing resources (e.g. processor, video card, RAM, storage) are important to ensure proper software functioning and the efficiency of the 3D modeling processing. However, today a wide range of underwater photographic equipment and cameras (e.g. GoPros, other compact camera models) offer a good compromise between quality and price. Nevertheless, the financial cost can be reduced by adapting underwater equipment to the objectives of the study, using data sharing and processing codes, and working in collaboration with organizations or institutes well equipped in terms of computing resources.

6.3 Adaptation of the conservation programs to changing coral reefs

The 21st century arrived with big challenges for natural ecosystem conservation science and practice. In the Anthropocene, human activities jeopardize the stability of Earth's natural systems, causing the erosion of global biodiversity and the loss of ecosystem goods and services. The reduction in ecosystem functions and the demise of wide areas of natural environments presage a grim future for natural ecosystems and societal well-being. Coral reef ecosystems are not an exception to this crisis. Indeed recent studies report that coral cover has declined over the past century (Bellwood et al., 2019a), with approximately one-third of the world's largest coral reef system already lost (Hughes et al., 2017b), and numerous worldwide reefs critically threatened in the near future (Burke et al., 2011). Exacerbating this, over the past few decades human and natural pressures associated with climate change are increasing in frequency and intensity, bringing these environments to unprecedented crises and functional changes (Bellwood et al., 2004, 2019a,b; Perry and Alvarez-Filip 2019; Williams and Graham 2019).

Scaling up ecological measures to reinforce current reef's management programs

The spatial scale of biophysical processes can be studied measuring two parameters: the resolution of analysis, action, or process, and the extent of the area or time period under consideration or at which a given phenomenon occurs (Turner et al., 2001). Larger spatial scale studies can improve the identification of more resilient and healthier reefs, where management measures should be prioritized (Cinner et al., 2016). This can be particularly useful to avoid the growing spatial mismatch between the increasing scale of threats and the current or planned measures to face them (Bellwood et al. 2019a,b). In this sense, Devillers et al. (2015) propose a four-step framework of questions for planners and policy makers to help emerging residual tendency of MPAs and maximize their effectiveness for conservation.

Scaling up ecological measures, in both space and time, needs new means and tools for monitoring and detecting these areas and their potential changes. Over the last years, a growing body of research showed the useful application of new technologies to extend biological and physical assessments of coral reefs (e.g. Friedman et al., 2012; González-Rivero et al., 2016; Bajjouk et al., 2019; Elise et al., 2019a; Fukunaga et al., 2019; this Thesis). However, some aspects of these new methodologies still need improvement. For instance, in this Thesis the fieldwork was completed by divers and the analyses on orthomosaics were mostly manual, limiting the spatial scale of the mapped reef areas. The same limitations are often discussed in recent research, noting the applicability of new technologies but understanding the limitations of the small spatial or temporal scales for offering perspectives on conservation targets. Yet, these two main limitations can be overcome using automated acquisition (images, video, sound, etc.) as well as automated handling and classification of data (point clouds, meshes, rasters, sound recordings, etc.). These two emerging solutions can support scientists and managers in the efficiency of monitoring programs. The automated acquisition allows obtaining large field data-sets in a broad scale. For instance, the "Catlin Seaview Survey" can map multiple kilometer-scale transects of reef areas (González-Rivero et al., 2014), acoustic records can continuously survey entire reef areas (Elise et al., 2019b), and remotely operated vehicules and autonomous underwater vehicles are increasingly used to explore wide and inaccessible areas (e.g. Ferrari et al., 2016; Price et al., 2019). Complementary to this, the automated handling and classification of data has been deemed essential to analyze the largest amounts of raw data generated by these new data acquisition solutions. Recent studies show the potential of machine or deep learning algorithms or convolutional neuronal network sciences, showing promising results in predicting ecological community attributes (i.e. richness or abundance), classifying reef benthic communities, or identifying reef fishes (e.g. Villon et al., 2018, 2020; Hopkinson et al., 2020; Jaonalison et al., 2020; Mohamed et al., 2020).

On the other hand, some exemplary experiences of local coral reef management success, regional and global scale goals should be reached by scaling up ecological knowledge. The key strategies in this sense are the sharing of field efforts and the standardization and coordination of data workflows and data sharing that could allow scientists and managers to capitalize on data and methods generated by others and avoid redundancy in programs (Devillers et al., 2007; Madin et al., 2019; Obura et al., 2019). These are logical actions that, unfortunately, are often not considered or practiced by scientists, thus playing against the efficiency of coral reef management. In this sense, Chapter 5 presented a comparison study of reef monitoring methods, aiming to share knowledge of new photogrammetric methods to survey coral reefs and guide researchers and managers in the selection of methods considering their resources and program goals.

6.4 Conclusions and perspectives

The main technical contribution of this Thesis is the two underwater photogrammetric protocols developed, which allowed accurate surveys (< 1 cm of resolution) of coral colonies and seascapes. It further demonstrated that the photogrammetric output 3D models, digital elevation models and orthomosaics are useful tools to conduct quantitative ecological analyses at the two study scales and also on different types of substrates: bio-constructed, lava-flows (basaltic), and artificial. Thus, this investigation showed the affordability of this technique to non-specialist ecologists, which is one of the key barriers to overcome for wide application in reef science and conservation programs (Madin et al., 2019; D'Urban et al., 2020).

At the colony scale, the 3D models allowed a non-invasive quantification of their three-dimensional features: surface, volume, shelter, surface complexity, and shelter size factor. For the four major growth forms of Scleractinian corals (branching, columnar, massive, and tabular), the diameter, planar area, and surface of coral colonies were proven to be good proxies to estimate their shelter volume (3D measurements). Also, since the shelter sizes can be inferred from the surface complexity of coral colonies, this shows that more complex colonies represent smaller shelter sizes, with the exception of massive colonies. This was a logical first step to advance the understanding of how the morphology of coral colonies influences specific reef functions and can help in the identification of possible reef degradation or functional recovery of these ecosystems (Kerry and Bellwood 2015; Denis et al., 2017; Zawada et al., 2019a).

At the reefscape scale, the description of its traits can be quantified by the habitat descriptors derived from analyses on digital elevation models and orthomosaics. Among them, the most complementary are shelter capacity, Shannon Shelter Index, coral cover, the abundance of branching colonies, the abundance of massive colonies, the abundance of tabular colonies, and surface complexity. This Thesis demonstrated the links, between these reefscape traits and specific fish groups, that ensure five key reef functions: herbivory-bioerosion, secondary production, plankton assimilation, predation and coral feeding. Quantifying the interconnection between habitat complexity, benthic communities, and fish assemblages contributes to understand the complex dynamics of reefs. Thus, these insights on coral reefs highlight the power of trait-based and functional approaches in understanding and managing high-diversity and rapid change systems today (Pendleton et al., 2016; Bellwood et al., 2019a; Perry and Alvarez-Filip 2019).

Methodological advances reached in this Thesis demonstrated that traditional methods for coral reef surveys, the Line Intercept Transect (LIT) and photoquadrats, can be well reproduced on orthomosaics. The evaluation of their effectiveness showed that LIT is less time-consuming and more effective for specific taxonomic identifications but is the most limited in terms of descriptors and representativeness of the ecosystem. The surface analysis on the orthomosaics is the most efficient method studied considering the quantity and quality of data that can be gathered and the time expenditure. However, limitations related to the measurements on orthomosaics should be investigated to improve the accuracy of this method. Nowadays, the transition of traditional to innovative methods for coral reefs surveys and the need for standardization of data are key factors to improve reef conservation programs. Studies in this sense would help correctly launch this progress to the new era of reef ecological monitoring (Obura et al., 2019; Hernández-Landa et al., 2020).

Overall, my investigation showed the great potential in the application of a relatively new technology, underwater photogrammetry, for reef studies, conservation sciences, and environmental impact assessments. The studies led here contribute to better understanding the different aspects that compose the habitat complexity of coral reefs. The works directly respond to the increasing need in management and conservation sciences to complement traditional methods of reef monitoring, developing operable and affordable tools and expanding ecological knowledge of these ecosystems.

Perspectives

The main perspectives that arise from this Thesis relate to enhancing predictive models, sharing data to promote collaborations at regional and international levels, using 3D models for new experiences to raise awareness, and working on new solutions to support this new technology for the automated classification of benthic data.

The improvement of shelter predictive models is possible through new measurements of 3D models, adding new parameters such as new morphologies, or varying the orientations of colonies. Also, for highly structurally complex or steep mapped areas, developing a *correction factor or adjustment value* for surface measures can improve the orthomosaics method. Another possibility to overcome this limit is to work directly on the 3D models (point clouds or meshes) to extract metrics of interest.

Sharing the data of this Thesis and conducting new studies with larger data sets are both important aspects that I aim to address in future work. These two propositions will be led using open platforms and establishing new collaborations to contribute in worldwide reef photogrammetric surveys.

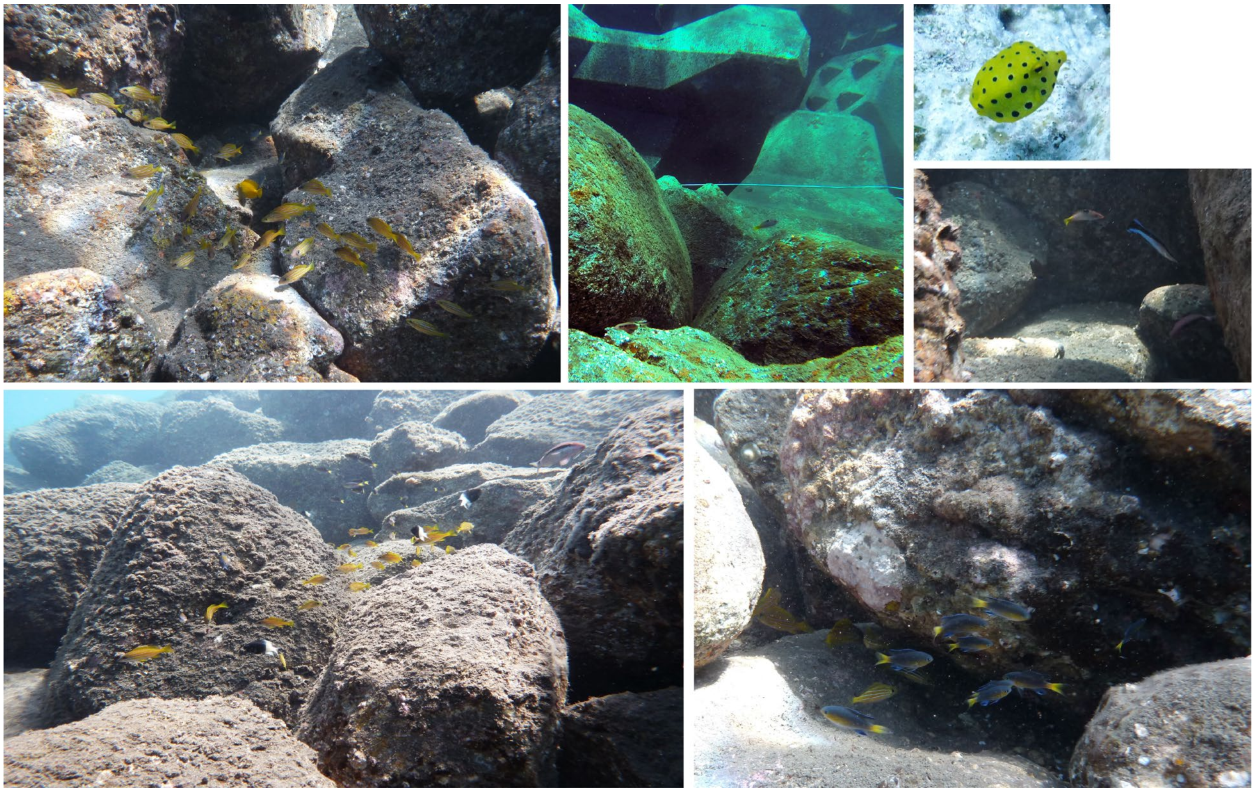
Regarding the direct applications, the photogrammetric methods and scientific knowledge developed will be used in future environmental studies (e.g. REBIOMA 3D project). In the case of coastal installations, it could be worthwhile to continue a temporal survey of the breakwaters sites to support and guide seascape planners in environmental measures, such as designing avoidance, reduction, or compensation actions.

Innovative tools to experience coral reefs, like immersive virtual reality using 3D models generated for this Thesis, is a very exciting possibility for education and awareness on stewardship of these environments.

Finally, the one of most interesting perspective unlocked from my Thesis is the possibility to develop an automated classification of reef benthic communities on orthomosaics by applying artificial intelligence. In fact, the manual classification of colonies on orthomosaics is already being used as the *'training data'* for computer algorithms in machine and deep learning. This is a key factor for photogrammetry becoming a standard in reefs surveys.

Appendices - Chapter 6

Appendix 6.1

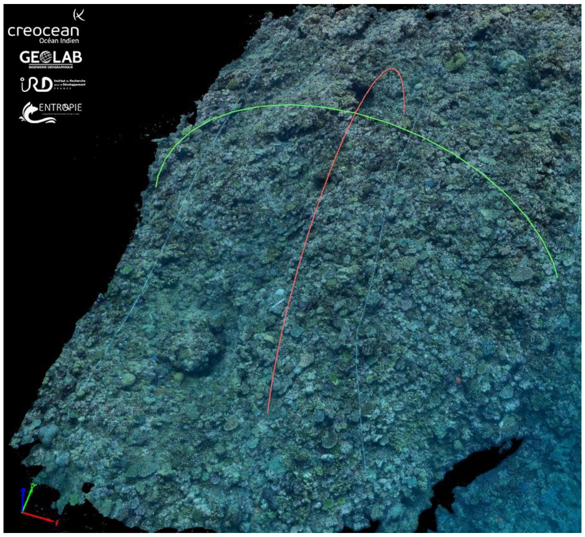


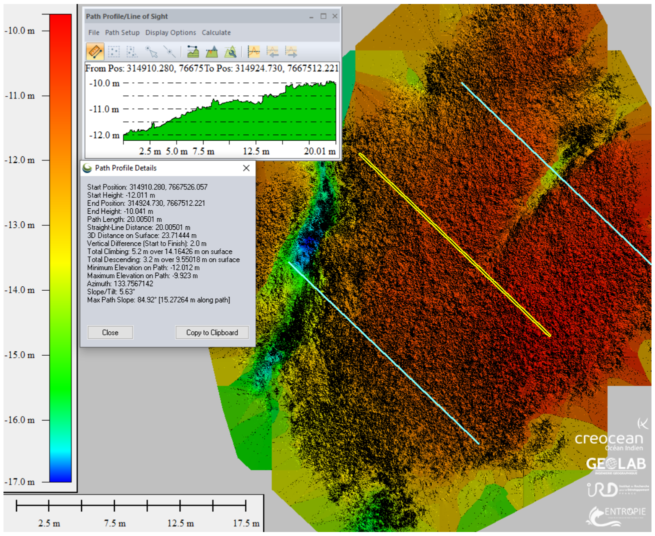
Juvenile fish - breakwaters structures.

Appendix 6.2

Structure 3D des RÉcifs, étude pilote pour l'amélioration de gestion de la BIOdiversité récifale de MAyotte

- REBIOMA 3D -





From Pos: 314910.280, 76675To Pos: 314924.730, 7667512.221

Start Position: 314910.280, 7667526.057
Start Height: -12.011 m
End Position: 314924.730, 7667512.221
End Height: -10.041 m
Path Length: 20.00501 m
Straight-Line Distance: 20.00501 m
3D Distance on Surface: 23.71444 m
Vertical Difference (Start to Finish): 2.0 m
Total Climbing: 5.2 m over 14.16426 m on surface
Total Descending: 3.2 m over 9.55018 m on surface
Minimum Elevation on Path: -12.012 m
Maximum Elevation on Path: -9.923 m
Azimuth: 133.7567142
Slope/Tilt: 5.63°
Max Path Slope: 84.92° [15.27264 m along path]

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Résumé

Selon l'UNESCO, 50% des récifs coralliens pourraient disparaître d'ici 2030. Outre leur rôle majeur pour la biodiversité, ils fournissent de nombreux services écosystémiques à plus de 500 millions de personnes (tourisme, pêche, protection de la côte). La complexité structurelle des récifs coralliens ainsi qu'autres caractéristiques 3D (i.e. capacité en refuge, dimension fractale, pente) représentent des aspects fondamentaux du fonctionnement des récifs. Malgré leur importance, peu de programmes de suivi en tiennent compte pour déterminer l'état de santé des récifs. La photogrammétrie sous-marine permet de créer des modèles tridimensionnels des récifs à différentes échelles spatiales, allant de la colonie corallienne aux paysages récifaux. La reconstitution 3D par photogrammétrie sous-marine permet également un suivi temporel précis des communautés récifales. Outre le calcul des descripteurs classiquement utilisés (pourcentages de recouvrement, diversité, etc.), les analyses photogrammétriques permettent de définir de nouveaux descripteurs des caractéristiques physiques 3D du récif tel que la complexité structurelle, les volumes des colonies coralliennes, la capacité de refuge, la rugosité, la pente des composantes benthiques et du paysage.

Les récifs coralliens représentent des écosystèmes emblématiques du patrimoine naturel Mahorais et sont exceptionnels dans toute la région de l'Océan Indien. Les forçages naturels et diverses pressions anthropiques (e.g. fréquentation touristique, piétinement, aménagements littoraux) mettent en péril le maintien de la fonctionnalité de ces écosystèmes, leur biodiversité et les biens et services qu'ils procurent à la population locale. Le programme de suivi récifal le plus précis à Mayotte (GCRMN) utilise des descripteurs standards mais ne prend pas en compte l'aspect tridimensionnel des récifs. L'application de la photogrammétrie sous-marine et le calcul de descripteurs 3D permettront ainsi de compléter l'évaluation de l'état de santé de ces récifs. Du fait de la haute précision des modèles et de l'analyse 3D, cette technique est la plus adaptée pour quantifier d'éventuels impacts de la structure récifale et s'avère la plus pertinente pour le suivi des zones qui auront des perturbations du au projets d'aménagements littoraux mais également du à la fréquentation touristique.

REBIOMA-3D propose, à travers une étude pilote par photogrammétrie sous-marine, une analyse morpho-biologique et physique de six zones récifales de Mayotte : 3 en réserve et 3 soumis à des possibles impacts du au développement urbain. L'objectif est de faire un « Po » et de déterminer des éventuelles dégradations liées aux impacts anthropiques ainsi que préconiser des mesures de gestion dans le but de conservation de leur biodiversité de ses services écosystémiques. Les objectifs spécifiques du projet :

Objectif 1. Appliquer la technique de photogrammétrie sous-marine sur les zones récifales de Mayotte pour étudier leurs caractéristiques 3D, calculer les nouveaux descripteurs de l'habitat.

Objectif 2. Identifier des impacts anthropiques sur la structure récifale (i.e. destruction physique, perte de la complexité structurelle, macro-déchets).

Objectif 3. Proposer des mesures de conservation et préconiser de mesures de gestion, en concertation étroite avec les gestionnaires.

Objectif 4. Sensibiliser la population locale à l'importance de la préservation des récifs coralliens.

Le projet propose, in fine, un «Point 0» de suivi morpho-écologique des récifs coralliens étudiés par photogrammétrie.

References

Abadie, A., Boissery, P., and Viala, C. (2018). Georeferenced underwater photogrammetry to map marine habitats and submerged artificial structures. *The Photogrammetric Record*, 33(164), 448–469. doi:10.1111/phor.12263

Abdo, D.A., Seager, J.W., Harvey, E.S., McDonald, J.I., Kendrick, G.A., and Shortis, M.R. (2006). Efficiently measuring complex sessile epibenthic organisms using a novel photogrammetric technique. *Journal of Experimental Marine Biology and Ecology*, 339(1), 120–133. doi:10.1016/j.jembe.2006.07.015

Adjeroud, M., Kayal, M., and Penin, L. (2016). Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages. *Marine Animal Forests*, 549-569. doi:10.1007/978-3-319-21012-4

Agudo-Adriani, E.A., Cappelletto, J., Cavada-Blanco, F., and Croquer, A. (2019). Structural complexity and benthic cover explain reef-scale variability of fish assemblages in Los Roques National Park, Venezuela. *Frontiers in Marine Science*, 6:690. doi:10.3389/fmars.2019.00690

Airoldi, L., Balata, D., and Beck, M.W. (2008). The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology*, 366, 8–15. https://doi.org/10.1016/j.jembe.2008.07.034

Albertz, J. (2001). Albrecth Meydenbauer - Pioneer of Photogrammetric Documentation of the Cultural Heritage. In: *Proceedings 18th International Symposium CIPA 2001*. Retrieved from http://www.theulegium.de/fileadmin/user_upload/Texte/Meydenb.pdf

Alvarez-Filip, L., Dulvy, N.K., Gill, J., and Watkinson, A.R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, 276(1669), 3019–3025. http://doi.org/10.1098/rspb.2009.0339

Alvarez-Filip, L., Dulvy, N.K., Côté, I.M., Watkinson, A.R., and Gill, J.A. (2011). Coral identity underpins architectural complexity on Caribbean reefs. *Ecological Applications*, *21*(6), 2223–2231. doi:10.1890/10-1563.1

Alvarez-Filip, L., Carricart-Ganivet, J.P., Horta-Puga, G., and Iglesias-Prieto, R. (2013). Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific Reports*, 3, 1–5. doi:10.1038/srep03486

Baine, M. (2001). Artificial reefs: a review of their design, application, management and performance. *Ocean and Coastal Management*, 44, 241–259. https://doi.org/10.1016/S0964-5691(01)00048-5

Bajjouk, T., Mouquet, P., Ropert, M., Quod, J.P., Hoarau, L., Bigot, L., Le Dantec, N., Delacourt, C., and Populus, J. (2019). Detection of changes in shallow coral reefs status: Towards a spatial approach using hyperspectral and multispectral data. *Ecological Indicators*, 96, 174–191. doi:10.1016/j.ecolind.2018.08.052

Barde, J., Bonhommeau, S., Chassot, E., and Motah, B. (2018). Coastal mapping and kitesurfing. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 42, 3–10. doi:10.5194/isprs-archives-XLII-4-W8-3-2018

Bastidas, C., Bone, D., Croquer, A., Debrot, D., Garcia, E., Humanes, A., Ramos, R., and Rodríguez, S. (2012). Massive hard coral loss after a severe bleaching event in 2010 at Los Roques, Venezuela. *Revista de Biologia Tropical*, 60, 29–37.

Beenaerts, N. and Berghe, E.V. (2007). Comparative Study of Three Transect Methods to Assess Coral Cover, Richness and Diversity. *Western Indian Ocean Journal of Marine Science*, 4(1). doi:10.4314/wiojms.v4i1.28471

Bell, J., and Galzin, R. (1984). Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series*, *15*, 265–274. doi:10.3354/meps015265

Bellwood, D.R., Hoey, A.S., and Choat, J.H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function of coral reefs. *Ecology Letters*, *6*(4), 281–285. doi:10.1046/j.1461-0248.2003.00432.x

Bellwood, D.R., Hughes, T.P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, 429, 827–833. doi:10.1038/nature02691

Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G., Day, J.C., Grantham, R., Grech, A., Hoey, A.S., Jones, G.P., Pandolfi, J.M., Tebbett, S.B., Techera, E., Weeks, R., and Cumming, G.S. (2019a). Coral reef conservation in the Anthropocene: Confronting spatial mismatches and prioritizing functions. *Biological Conservation*, 236, 604–615. doi:10.1016/j.biocon.2019.05.056

Bellwood, D.R., Streit, R.P., Brandl, S.J., and Tebbett, S.B. (2019b). The meaning of the term 'function' in ecology: A coral reef perspective. *Functional Ecology*, 33(6), 948–961. doi:10.1111/1365-2435.13265

Beukers, J.S., and Jones, G.P. (1997). Habitat complexity modifes the impact of piscivores on a coral reef fish population. *Oecologia*, 114, 50–59. http://doi.org/10.1007/s004420050419

Bigot, L., Bruggemann, J.H., Cadet, C., Chabanet, P., Durville, P., Mulochau, T., Cauvin, B., Guillaume, M., Penin, L., and Urbina-Barreto, I. (2016). Point 1 du suivi de «l'effet réserve» sur les communautés ichtyologiques et benthiques récifales de La Réserve Naturelle Nationale Marine de La Réunion. Rapport Réserve Naturelle Nationale Marine de La Réunion.

Blue Marble Geographics (2019). Global Mapper: Release 19. Hallowell, ME.

Bozec, Y.M., Dolédec, S., and Kulbicki, M. (2005). An analysis of fish-habitat associations on disturbed coral reefs: Chaetodontid fishes in New Caledonia. *Journal of Fish Biology*, *66*(4), 966–982. doi:10.1111/j.0022-1112.2005.00652.x

Bozec, Y.M., Alvarez-Filip, L., and Mumby, P.J. (2015). The dynamics of architectural complexity on coral reefs under climate change. *Global Change Biology*, 21(1), 223–235. http://doi.org/10.1111/gcb.12698

Bradbury, R.H., and Reichelt, E. (1983). Fractal Dimension of a Coral Reef. *Marine Ecology Progress Series*, 10, 169–171.

Brandl, S.J., Rasher, D.B., Côté, I.M., Casey, J.M., Darling, E.S., Lefcheck, J.S., and Duffy, J.E. (2019). Coral reef ecosystem functioning: eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment*, 17(8), 445–454. doi:10.1002/fee.2088

Bryson, M., Ferrari, R., Figueira, W., Pizarro, O., Madin, J., Williams, S., and Byrne, M. (2017). Characterization of measurement errors using structure-from-motion and photogrammetry to measure marine habitat structural complexity. *Ecology and Evolution*, 7(15), 5669–5681. doi:10.1002/ece3.3127

Burke, L., Reytar, K., Splading, M., and Perry, A. (2011). *Reefs at risk*. World Resources Institute.

Burkepile, D.E., and Hay, M.E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences of the United States of America*, 105(42), 16201–16206. doi:10.1073/pnas.0801946105

Burns, J.H.R., Delparte, D., Gates, R.D., and Takabayashi, M. (2015a). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ*, 3, e1077. doi:10.7717/peerj.1077

Burns, J.H.R., Delparte, D., Gates, R.D., and Takabayashi, M. (2015b). Utilizing underwater three-dimensional modeling to enhance ecological and biological studies of coral reefs. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 40, 61–66. doi:10.5194/isprsarchives-XL-5-W5-61-2015

Burns, J.H.R., Delparte, D., Kapono, L., Belt, M., Gates, R.D., and Takabayashi, M. (2016a). Assessing the impact of acute disturbances on the structure and composition of a coral community using innovative 3D reconstruction techniques. *Methods in Oceanography*, 15, 49-59. doi:10.1016/j.mio.2016.04.001

Burns, J.H.R., Alexandrov, T., Ovchinnikova, E., Gates, R.D., and Takabayashi, M. (2016b). Investigating the spatial distribution of growth anomalies affecting Montipora capitata corals in a 3-dimensional framework. *Journal of Invertebrate Pathology*, 140, 51–57. doi:10.1016/j.jip.2016.08.007

Burns, J.H.R., and Delparte, D. (2017). Comparison of commercial structure-from-motion photogrammety software used for underwater three-dimensional modeling of coral reef environments. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 42, 127–131. https://doi.org/10.5194/isprs-archives-XLII-2-W3-127-2017

Burns, J.H.R., Fukunaga, A., Pascoe, K.H., Runyan, A., Craig, B.K., Talbot, J., Pugh, A., and Kosaki, R.K. (2019). 3D Habitat Complexity of Coral Reefs in the Northwestern Hawaiian Islands Is Driven By Coral Assemblage Structure. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, XLII-2/W10, 61–67. doi:10.5194/isprs-archives-XLII-2-W10-61-2019

Bythell, J., Pan, P., and Lee, J. (2001). Three-dimensional morphometric measurements of reef corals using underwater photogrammetry techniques. *Coral Reefs*, 20(3), 193–199. doi:10.1007/s003380100157

Caldwell, Z.R., Zgliczynski, B.J., Williams, G.J., and Sandin, S.A. (2016). Reef fish survey techniques: Assessing the potential for standardizing methodologies. *PLoS ONE*, 11(4), e0153066. https://doi.org/10.1371/journal.pone.0153066

Cappelletto, J., and Agudo-Adriani, E.A. (2017). Reconstrucciones tridimensionales generadas a partir de vídeos e imágenes para aplicaciones morfométricas . *Acta Biologica Venezuelica*, 37, 2.

Carlot, J., Rovere, A., Casella, E., Harris, D., Grellet-Muñoz, C., Chancerelle, Y., Dormy, E., Hedouin, L., and Parravicini, V. (2020). Community composition predicts photogrammetry-based structural complexity on coral reefs. *Coral Reefs*. doi:10.1007/s00338-020-01916-8

Casella, E., Collin, A., Harris, D., Ferse, S., Bejarano, S., Parravicini, V., Hench, J.L., and Rovere, A. (2016). Mapping coral reefs using consumer-grade drones and structure from motion photogrammetry techniques. *Coral Reefs*, 36(1), 1–7. doi:10.1007/s00338-016-1522-0

Chabanet, P., Ralambondrainy, H., Amanieu, M., Faure, G., and Galzin, R. (1997). Relationships between coral reef substrata and fish. *Coral Reefs*, 16(2), 93–102. doi:10.1007/s003380050063

Chabanet, P., Bigot, L., Naim, O., Garnier, R., and Tessier, E. (2001). Coral reef monitoring at Reunion island (Western Indian Ocean) using the GCRMN method. In: *Proceedings 9th International Coral Reef Symposium*, Bali, Indonesia 23-27 October 2000, Vol. 2. pp. 1–6.

Cinner, J.E., Huchery, C., MacNeil, M.A., Graham, N.A.J., McClanahan, T.R., Maina, J., Maire, E., Kittinger, J.N., Hicks, C.C., Mora, C., Allison, E.H., D'Agata, S., Hoey, A., Feary, D.A., Crowder, L., Williams, I.D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G., Stuart-Smith, R.D., Sandin, S.A., Green, A.L., Hardt, M.J., Beger, M., Friedlander, A., Campbell, S.J., Holmes, K.E., Wilson, S.K., Brokovich, E., Brooks, A.J., Cruz-Motta, J.J., Booth, D.J., Chabanet, P., Gough, C., Tupper, M., Ferse, S.C., Sumaila, U.R., and Mouillot, D. (2016). Bright spots among the world's coral reefs. *Nature*, 535(7612), 416–419. doi:10.1038/nature18607

Cinner, J.E., Zamborain-mason, J., Gurney, G.G., Graham, N.A.J., Macneil, M.A., Hoey, A.S., Mora, C., Villéger, S., Maire, E., McClanahan, T.R., Maina, J.M., Kittinger, J.N., Hicks, C.C., D'agata, S., Huchery, C., Barnes, M.L., Feary, D.A., Williams, I.D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G.J., Stuart-Smith, R.D., Sandin, S.A., Green, A.L., Beger, M., Friedlander, A.M., Wilson, S.K., Brokovich, E., Brooks, A.J., Cruz-Motta, J.J., Booth, D.J., Chabanet, P., Tupper, M., Ferse, S.C.A., Sumaila, U.R., Hardt, M.J., and Mouillot, D. (2020). Meeting fisheries, ecosystem function, and biodiversity goals in a human-dominated world. *Science*, 368, 307–311.

Cocito, S., Sgorbini, S., Peirano, A., and Valle, M. (2003). 3-D reconstruction of biological objects using underwater video technique and image processing. *Journal of Experimental Marine Biology and Ecology*, 297(1), 57–70. doi:10.1016/S0022-0981(03)00369-1

Collin, A., Ramambason, C., Pastol, Y., Casella, E., Rovere, A., Thiault, L., Espiau, B., Siu, G., Lerouvreur, F., Nakamura, N., Hench, J.L., Schmitt, R.J., Holbrook, S.J., Troyer, M., and Davies, N. (2018). Very high resolution mapping of coral reef state using airborne bathymetric LiDAR surface-intensity and drone imagery. *International Journal of Remote Sensing*, 39(17), 5676-5688. doi:10.1080/01431161.2018.1500072

Cornwall, W. (2019). The reef builders. *Science*, 363(6433), 1264–1269. doi:10.1126/science.363.6433.1264

Costanza, R., Arge, R., de Groot, R., Farberk, S., Grasso, M., Hannon, B., and Van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253–260. http://doi.org/10.1038/387253a0

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., and Turner, R.K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26(1), 152–158. http://doi.org/10.1016/j.gloenvcha.2014.04.002

Creocean-OI. (2016). Suivi environnemental lié au dragage au droit du quai d'accostage du Port Est VINCI – MT3 NRL.

Crowder, L.B., and Cooper, W.E. (1982). Habitat Structural Complexity and the Interaction Between Bluegills and Their Prey. *Ecological Society of America*, 63(6), 1802–1813.

Cullen, N.D., Kumar Verma, A., and Clare Bourke, M. (2018). A comparison of structure from motion photogrammetry and the traversing micro-erosion meter for measuring erosion on shore platforms. *Earth Surface Dynamics*, 6(4), 1023–1039. doi:10.5194/esurf-6-1023-2018

D'Urban Jackson, T., Williams, G.J., Walker-Springett, G., and Davies, A.J. (2020). Three-dimensional digital mapping of ecosystems: A new era in spatial ecology. *Proceedings of the Royal Society B: Biological Sciences*, 287(1920), 1–10. doi:10.1098/rspb.2019.2383

Dahl, A.L. (1981). *Coral Reef Monitoring Handbook*. South Pacific Comission 1981. Bridge Printery Sidney, Autralia

Darling, E.S., Alvarez-Filip, L., Oliver, T.A., McClanahan, T.R., and Côté, I.M. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, 15(12), 1378–1386. doi:10.1111/j.1461-0248.2012.01861.x

Darling, E.S., Graham, N.A.J., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S., and Wilson, S.K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, 36(2), 561–575. doi:10.1007/s00338-017-1539-z

Darling, E.S., McClanahan, T.R., Maina, J., Gurney, G.G., Graham, N.A.J., Januchowski-Hartley, F., Cinner, J.E., Mora, C., Hicks, C.C., Maire, E., Puotinen, M., Skirving, W.J., Adjeroud, M., Ahmadia, G., Arthur, R., Bauman, A.G., Beger, M., Berumen, M.L., Bigot, L., Bouwmeester, J., Brenier, A., Bridge, T.C.L., Brown, E., Campbell, S.J., Cannon, S., Cauvin, B., Chen, C.A., Claudet, J., Denis, V., Donner, S., Estradivari, Fadli, N., Feary, D.A., Fenner, D., Fox, H., Franklin, E.C., Friedlander, A., Gilmour, J., Goiran, C., Guest, J., Hobbs, J.P.A., Hoey, A.S., Houk, P., Johnson, S., Jupiter, S.D., Kayal, M., Kuo, C. yang, Lamb, J., Lee, M.A.C., Low, J., Muthiga, N., Muttaqin, E., Nand, Y., Nash, K.L., Nedlic, O., Pandolfi, J.M., Pardede, S., Patankar, V., Penin, L., Ribas-Deulofeu, L., Richards, Z., Roberts, T.E., Rodgers, K.S., Safuan, C.D.M., Sala, E., Shedrawi, G., Sin, T.M., Smallhorn-West, P., Smith, J.E., Sommer, B., Steinberg, P.D., Sutthacheep, M., Tan, C.H.J., Williams, G.J., Wilson, S., Yeemin, T., Bruno, J.F., Fortin, M.J., Krkosek, M., and Mouillot, D. (2019). Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. *Nature Ecology and Evolution*, 3, 1341–1350. https://doi.org/10.1038/s41559-019-0953-8

Denis, V., Ribas-Deulofeu, L., Sturaro, N., Kuo, C.Y., and Chen, C.A. (2017). A functional approach to the structural complexity of coral assemblages based on colony morphological features. *Scientific Reports*, 7(1), 1–11. doi:10.1038/s41598-017-10334-w

Devillers, R., Bédard, Y., Jeansoulin, R., and Moulin, B. (2007). Towards spatial data quality information analysis tools for experts assessing the fitness for use of spatial data. *International Journal of Geographical Information Science*, 21, 261–282. https://doi.org/10.1080/13658810600911879

Devillers, R., Pressey, R.L., Grech, A., Kittinger, J.N., Edgar, G.J., Ward, T., and Watson, R. (2015). Reinventing residual reserves in the sea: Are we favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems*, 25, 480–504. https://doi.org/10.1002/aqc.2445

Dornelas, M., Madin, J.S., Baird, A.H., and Connolly, S.R. (2017). Allometric growth in reef-building corals. *Proceedings of the Royal Society B: Biological Sciences*, 284(1851). doi:10.1098/rspb.2017.0053

Drap, P., Merad, D., Seinturier, J., Peloso, D., Boï, J., and Chemisky, B. (2013). Underwater photogrammetry for archaeology and marine biology. In: *2013 Digital Heritage International Congress* (pp. 97–104).

Duarte, C.M., Agusti, S., Barbier, E., Britten, G.L., Castilla, J.C., Gattuso, J.-P., Fulweiler, R.W., Hughes, T.P., Knowlton, N., Lovelock, C.E., Lotze, H.K., Predragovic, M., Poloczanska, E., Roberts, C., and Worm, B. (2020). Rebuilding marine life. *Nature*, 580(7801), 39–51. doi:10.1038/s41586-020-2146-7

Dumas, P., Bertaud, A., Peignon, C., Léopold, M., and Pelletier, D. (2009). A 'quick and clean' photographic method for the description of coral reef habitats. *Journal of Experimental Marine Biology and Ecology*, 368(2), 161–168. doi:10.1016/j.jembe.2008.10.002

Dustan, P., Doherty, O., and Pardede, S. (2013). Digital Reef Rugosity Estimates Coral Reef Habitat Complexity. *PLoS ONE*, 8(2). doi:10.1371/journal.pone.0057386

Eakin, C.M., Sweatman, H.P.A., and Brainard, R.E. (2019). The 2014–2017 global-scale coral bleaching event: insights and impacts. *Coral Reefs*, 38(4), 539–545. doi:10.1007/s00338-019-01844-2

Ehrenfeucht, S. (2014). Artificial Coral Reefs as a Method of Coral Reef Fish Conservation. Undergraduate Honors Theses. Paper 83.

Elise, S., Bailly, A., Urbina-Barreto, I., Mou-Tham, G., Chiroleu, F., Vigliola, L., Robbins, W.D., and Bruggemann, J.H. (2019a). An optimised passive acoustic sampling scheme to discriminate among coral reefs' ecological states. *Ecological Indicators*, 107, 105627. doi:10.1016/j.ecolind.2019.105627

Elise, S., Urbina-Barreto, I., Pinel, R., Mahamadaly, V., Bureau, S., Penin, L., Adjeroud, M., Kulbicki, M., and Bruggemann, J.H. (2019b). Assessing key ecosystem functions through soundscapes: A new perspective from coral reefs. *Ecological Indicators*, 107, 105623. doi:10.1016/j.ecolind.2019.105623

Emslie, M.J., Pratchett, M.S., Cheal, A.J., and Osborne, K. (2010). Great Barrier Reef butterflyfish community structure: the role of shelf position and benthic community type. *Coral reefs*, 29(3), 705-715. doi: 10.1007/s00338-010-0619-0

English, S., Wilkinson, C., and Baker, V. (1997) *Survey manual for tropical marine resources*. Australian Institute of Marine Science, second edition.

ESRI (2019). ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Facon, M., Pinault, M., Obura, D., Pioch, S., Pothin, K., Bigot, L., and Quod, J.P. (2015). A comparative study of the accuracy and effectiveness of Line and Point Intercept Transect methods for coral reef monitoring in the southwestern Indian Ocean islands. *Ecological Indicators*, 60, 1045–1055. http://doi.org/10.1016/j.ecolind.2015.09.005

Ferrari, R., Bryson, M., Bridge, T., Hustache, J., Williams, S.B., Byrne, M., and Figueira, W. (2016). Quantifying the response of structural complexity and community composition to environmental change in marine communities. *Global Change Biology*, 22(5), 1965–1975. doi:10.1111/gcb.13197

Ferrari, R., Malcolm, H.A., Byrne, M., Friedman, A., Williams, S.B., Schultz, A., Jordan, A.R., and Figueira, W.F. (2017a). Habitat structural complexity metrics improve predictions of fish abundance and distribution. *Ecography*, 40, 1–14. doi:10.1111/ecog.02580

Ferrari, R., Figueira, W., Pratchett, M.S., Boube, T., Adam, A., Kobelkowsky-vidrio, T., Doo, S.S., Atwood, T.B., and Byrne, M. (2017b). 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. *Scientific Reports*, 1637, 1–9. doi:10.1038/s41598-017-16408-z

Figueira, W., Ferrari, R., Weatherby, E., Porter, A., Hawes, S., and Byrne, M. (2015). Accuracy and Precision of Habitat Structural Complexity Metrics Derived from Underwater Photogrammetry. *Remote Sensing*, 7(7), 16883–16900. doi:10.3390/rs71215859

FishBase (2019). http://www.fishbase.in/ [15 January 2020].

Fleury, P., Cadet, C., Turban, S., and Le Bonniec, S. (2012). Suivi des pêches à pied traditionnelles et de la chasse sous-marine de 2008 à 2011 dans la Réserve Naturelle Marine de La Réunion - Rapport Ifremer RST-DOI-2012-03.

Floeter, S.R., Krohling, W., Gasparini, J.L., Ferreira, C.E.L., and Zalmon, I.R. (2007). Reef fish community structure on coastal islands of the southeastern Brazil: The influence of exposure and benthic cover. *Environmental Biology of Fishes*, 78(2), 147–160. doi:10.1007/s10641-006-9084-6

Flower, J., Ortiz, J.C., Chollett, I., Abdullah, S., Castro-Sanguino, C., Hock, K., Lam, V., and Mumby, P.J. (2017). Interpreting coral reef monitoring data: A guide for improved management decisions. *Ecological Indicators*, 72, 848–869. doi:10.1016/j.ecolind.2016.09.003

Fonstad, M.A., Dietrich, J.T., Courville, B.C., Jensen, J.L., and Carbonneau, P.E. (2013). Topographic structure from motion: A new development in photogrammetric measurement. *Earth surface processes and Landforms*, 38(4), 421-430.

Fox, J., and Weisberg, S. (2019). *A R Companion to Applied Regression* (third). Thousand Oaks (CA): Sage. Retrieved from https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Friedlander, A.M., and Parrish, J.D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology*, 224, 1–30. doi:10.1016/S0022-0981(97)00164-0

Friedlander, A.M., Brown, E.K., Jokiel, P.L., Smith, W.R., and Rodgers, K.S. (2003). Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs*, 22(3), 291–305. doi:10.1007/s00338-003-0317-2

Friedman, A., Pizarro, O., Williams, S.B., and Johnson-Roberson, M. (2012). Multi-Scale Measures of Rugosity, Slope and Aspect from Benthic Stereo Image Reconstructions. *PLoS ONE*, 7(12), 1–14. doi:10.1371/journal.pone.0050440

Fukunaga, A., Burns, J., Craig, B., and Kosaki, R. (2019). Integrating Three-Dimensional Benthic Habitat Characterization Techniques into Ecological Monitoring of Coral Reefs. *Journal of Marine Science and Engineering*, 7(2), 27. doi:10.3390/jmse7020027

Fulton, C.J., Abesamis, R.A., Berkström, C., Depczynski, M., Graham, N.A.J., Holmes, T.H., Kulbicki, M., Noble, M.M., Radford, B.T., Tano, S., Tinkler, P., Wernberg, T., and Wilson, S.K. (2019). Form and function of tropical macroalgal reefs in the Anthropocene. *Functional Ecology*, 33, 989–999. https://doi.org/10.1111/1365-2435.13282

Gautier-Debernardi, J., Riera, E., Dini, E., Hubas, C., Lamy, D., Lescinski, J., and Tazelaar, J. (2017). The 3D printed artificials reefs, a modern tool to restore habitats in marine protected areas. Larvotto-Monaco context. In: *International Marine Protected Areas Congress*, Chile, 2017.

Gee, J.M., and Warwick, R.M. (1994). Body-size distribution in a marine metazoan community and the fractal dimensions of macroalgae. *Journal of Experimental Marine Biology and Ecology*, 178(2), 247–259. doi:10.1016/0022-0981(94)90039-6

Gilbert, D., and Quod, J.P. (2018) Coral Reef Monotoring Coping with Climate Change, Toward a Social-ecological System Perspective. *Communicating Climate Change Information Decision-Making*. Springer Climate. Springer, Cham.

González-Barrios, F.J., and Álvarez-Filip, L. (2018). A framework for measuring coral species-specific contribution to reef functioning in the Caribbean. *Ecological Indicators*, 95, 877–886. doi:10.1016/j.ecolind.2018.08.038

González-Rivero, M., Bongaerts, P., Beijbom, O., Pizarro, O., Friedman, A., Rodriguez-Ramirez, A., Upcroft, B., Laffoley, D., Kline, D., Bailhache, C., Vevers, R., and Hoegh-Guldberg, O. (2014). The Catlin Seaview Survey - kilometre-scale seascape assessment, and monitoring of coral reef ecosystems. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(S2), 184–198. doi:10.1002/aqc.2505

González-Rivero, M., Beijbom, O., Rodriguez-Ramirez, A., Holtrop, T., González-Marrero, Y., Ganase, A., Roelfsema, C., Phinn, S., and Hoegh-Guldberg, O. (2016). Scaling up ecological measurements of coral reefs using semi-automated field image collection and analysis. *Remote Sensing*, 8(1). doi:10.3390/rs8010030

González-Rivero, M., Harborne, A.R., Herrera-Reveles, A., Bozec, Y.M., Rogers, A., Friedman, A., and Hoegh-Guldberg, O. (2017). Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Scientific Reports*, 7(1),1-15. http://doi.org/10.1038/s41598-017-14272-5

Goreau, T. (1959). The ecology of Jamaican coral reefs. I. species composition and zonation. *Ecology*, 40(1), 67–90.

Graham, N.A.J, Wilson, S.K., Jennings, S., Polunin, N.V., Bijoux, J.P., and Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences*, 103(22), 8425-8429. doi: 10.1073/pnas.0600693103

Graham, N.A.J, Chabanet, P., Evans, R.D., Jennings, S., Letourneur, Y., Macneil, M.A., McClanahan, T.R., Ohman, M.C., Polunin, N.V.C., and Wilson, S.K. (2011a). Extinction vulnerability of coral reef fishes. *Ecology Letters*, 14(4), 341–348. doi:10.1111/j.1461-0248.2011.01592.x

Graham, N.A.J., Nash, K.L., and Kool, J.T. (2011b). Coral reef recovery dynamics in a changing world. *Coral Reefs*, 30(2), 283–294. http://doi.org/10.1007/s00338-010-0717-z

Graham, N.A.J., and Nash, K.L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, 32(2), 315–326. doi:10.1007/s00338-012-0984-y

Graham, N.A.J, Bellwood, D.R., Cinner, J.E., Hughes, T.P., Norström, A.V., and Nyström, M. (2013). Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment*, 11(10), 541–548. doi:10.1890/120305

Graham, N.A.J. (2014). Habitat complexity: Coral structural loss leads to fisheries declines. *Current Biology*. doi:10.1016/j.cub.2014.03.069

Gratwicke, B., and Speight, M.R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, 66, 650–667. doi:10.1111/j.1095-8649.2005.00629.x

Green, A.L., and Bellwood, D.R. (2009). *Monitoring Functional Groups of Herbivorous Reef Fishes as Indicators of Coral Reef Resilience: A practical guide for coral reef managers in the Asia Pacific Region*. (IUCN, Ed.).

Grutter, A.S., Rumney, J.G., Sinclair-Taylor, T., Waldie, P., and Franklin, C.E. (2011). Fish mucous cocoons: The 'mosquito nets' of the sea. *Biology Letters*, 7(2), 292–294. doi:10.1098/rsbl.2010.0916

Guillemot, N., Kulbicki, M., Chabanet, P., and Vigliola, L. (2011). Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. *PLoS ONE*, 6(10). doi:10.1371/journal.pone.0026735

Guo, T., Capra, A., Troyer, M., Gruen, A., Brooks, A.J., Hench, J.L., Schmitt, R.J., Holbrook, S.J., and Dubbini, M. (2016). Accuracy assessment of underwater photogrammetric three dimensional modelling for coral reefs. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 41, 821–828. doi:10.5194/isprsarchives-XLI-B5-821-2016

Gutiérrez-Heredia, L., D'Helft, C., and Reynaud, E.G. (2015). Simple methods for interactive 3D modeling, measurements, and digital databases of coral skeletons. *Limnology and Oceanography: Methods*, 178–193. doi:10.1002/lom3.10017

Gutiérrez-Heredia, L., Benzoni, F., Murphy, E., and Reynaud, E.G. (2016). End to End Digitisation and Analysis of Three-Dimensional Coral Models, from Communities to Corallites. *PLoS ONE*, 11, 1–24. https://doi.org/10.1371/journal.pone.0149641

Harborne, A.R., Rogers, A., Bozec, Y.-M., and Mumby, P.J. (2017). Multiple Stressors and the Functioning of Coral Reefs. *Annual Review of Marine Science*, 9(1), 445–468. doi:10.1146/annurev-marine-010816-060551

Harris, D.L., Rovere, A., Casella, E., Power, H., Canavesio, R., Collin, A., Pomeroy, A., Webster, J.M., and Parravicini, V. (2018). Coral reef structural complexity provides important coastal protection from waves under rising sea levels. *Science Advances*. 1–8. doi:10.1126/sciadv.aao4350

Hatcher, G.A., Warrick, J.A., Ritchie, A.C., Dailey, E.T., Zawada, D.G., Kranenburg, C., and Yates, K.K. (2020). Accurate Bathymetric Maps From Underwater Digital Imagery Without Ground Control. *Frontiers in Marine Science*, 7, 1–20. https://doi.org/10.3389/fmars.2020.00525

Hedley, J., Roelfsema, C., Chollett, I., Harborne, A., Heron, S., Weeks, S., Skirving W., Strong, A., Mark C., Christensen T., Ticzon Victor., Bejarano S., and Mumby, P. (2016). Remote Sensing of Coral Reefs for Monitoring and Management: A Review. *Remote Sensing*, 8(2). doi:10.3390/rs8020118

Heenan, A., Williams, G.J., and Williams, I.D. (2020). Natural variation in coral reef trophic structure across environmental gradients. *Frontiers in Ecology and the Environment*, 18(2), 69-75.

Hein, A.M., and Gillooly, J.F. (2011). Predators, prey, and transient states in the assembly of spatially structured communities. *Ecology*, 92, 549–555.

Hernández-Landa, R.C., Barrera-falcon, E., and Rioja-nieto, R. (2020). Size-frequency distribution of coral assemblages in insular shallow reefs of the Mexican Caribbean using underwater photogrammetry. *PeerJ*, 1–30. doi:10.7717/peerj.8957

Herzfeld, U.C., and Overbeck, C. (1999). Analysis and simulation of scale-dependent fractal surfaces with application to seafloor morphology. *Computers and Geosciences*, 25(9), 979–1007. doi:10.1016/S0098-3004(99)00062-X

Hill, J., and Wilkinson, C. (2004). *Methods for ecological monitoring of coral reefs*. Australian Institute of Marine Science (1), Townsville. doi:10.1017/CBO9781107415324.004

Hixon, M.A., and Beets, J.P. (1993). Predation , Prey Refuges , and the Structure of Coral-Reef Fish Assemblages. *Ecological Monographs*, 63(1), 77–101.

Hoegh-Guldberg, O., Kennedy, E.V., Beyer, H.L., McClennen, C., and Possingham, H.P. (2018). Securing a long-term future for coral reefs. *Trends in Ecology and Evolution*, 33(12), 936-944.

Hoey, A.S., and Bellwood, D.R. (2011). Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecology letters*, 14(3), 267-273. doi:10.1111/j.14610248.2010.01581.x

Hopkinson, B.M., King, A.C., Owen, D.P., Johnson-Roberson, M., Long, M.H., and Bhandarkar, S.M. (2020). Automated classification of three-dimensional reconstructions of coral reefs using convolutional neural networks. *PLoS ONE*, 15(3), 1–20.

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50(3), 346–363.

House, J.E., Brambilla, V., Bidaut, L.M., Christie, A.P., Pizarro, O., Madin, J.S., and Dornelas, M. (2018). Moving to 3D: relationships between coral planar area, surface area and volume. *PeerJ*, 6, e4280. doi:10.7717/peerj.4280

Hu, H., Ferrari, R., Mckinnon, D., Roff, G.A, Smith, R., Mumby, P.J., and Upcroft, B. (2012). Measuring reef complexity and rugosity from monocular video bathymetric reconstruction. *International Coral Reef Symposium*, 12, 9–13.

Hughes, T.P., Barnes, M.L., Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B., Kleypas, J., van de Leemput, I.A., Lough, J.M., Morrison, T.H., Palumbi, S.R., van Nes, E.H., and Scheffer, M. (2017a). Coral reefs in the Anthropocene. *Nature*, 546(7656), 82-90.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M., Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M., Figueira, W.F., Gilmour, J.P., Harrison, H.B., Heron, S.F., Hoey, A.S., Hobbs, J.P.A., Hoogenboom, M.O., Kennedy, E. V., Kuo, C.Y., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm, H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T., Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L., and Wilson, S.K. (2017b). Global warming and recurrent mass bleaching of corals. *Nature,* 543, 373–377. https://doi.org/10.1038/nature21707

Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Liu, G., McWilliam, M.J., Pears, R.J., Pratchett, M.S., Skirving, W.J., Stella, J.S., and Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature*, 556(7702), 492–496. doi:10.1038/s41586-018-0041-2

Jaonalison, H., Durand, J., Mahafina, J., Demarcq, H., Teichert, N., and Ponton, D. (2020). Predicting species richness and abundance of tropical post-larval fish using machine learning. *Marine Ecology Progress Series*, 645, 125–139. doi:10.3354/meps13385

Johansen, J.L., Bellwood, D.R., and Fulton, C.J. (2008). Coral reef fishes exploit flow refuges in high-flow habitats. *Marine Ecology Progress Series*, 360, 219–226. http://doi.org/10.3354/meps07482

Jones, C.G., Lawton, J.H., and Shachak, M. (1994). Organisms as Ecosystem Engineers. *Oikos*, 69. doi:10.2307/3545850

Jones, G.P., and Syms, C. (1998). Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology*, 23(3), 287–297. doi:10.1111/j.1442-9993.1998.tb00733.x

Jouval, F., Latreille, A.C., Bureau, S., Adjeroud, M., and Penin, L. (2019). Multiscale variability in coral recruitment in the Mascarene Islands: From centimetric to geographical scale. *PLoS ONE*, 14(3), e0214163. doi:10.1371/journal.pone.0214163

Kalacska, M., Lucanus, O., Sousa, L., Vieira, T., and Arroyo-Mora, J.P. (2018). Freshwater fish habitat complexity mapping using above and underwater structure-from-motion photogrammetry. *Remote Sensing*, 10(12). doi:10.3390/rs10121912

Kassambara, A. (2019). ggpubr:'ggplot2' Based Publiaction Ready Plots. R package version 0.2.2. Retrieved from https://cran.r-project.org/package=ggpubr

Kenchington, R. (2018). Science and the management of coral reefs. *Marine Pollution Bulletin*, 136, 508–515. doi:10.1016/j.marpolbul.2018.09.046

Kerry, J.T., and Bellwood, D.R. (2012). The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs*, 31(2), 415–424. doi:10.1007/s00338-011-0859-7

Kerry, J.T., and Bellwood, D.R. (2015). Do tabular corals constitute keystone structures for fishes on coral reefs? *Coral Reefs*, 34(1), 41–50. doi:10.1007/s00338-014-1232-4

Knudby, A., and LeDrew, E. (2007). Measuring Structural Complexity on Coral Reefs. *Proceedings of the American Acadamy of Underwater Sciences 26th Symposium*, 181–188. Retrieved from http://dspace.rubicon-foundation.org:8080/xmlui/handle/123456789/7005

Kohler, K.E., and Gill, S.M. (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences*, 32(9), 1259–1269. doi:10.1016/j.cageo.2005.11.009

Kovalenko, K.E., Thomaz, S.M., and Warfe, D.M. (2012). Habitat complexity: Approaches and future directions. *Hydrobiologia*, 685(1), 1–17. doi:10.1007/s10750-011-0974-z

Kulbicki M., Mouillot D., and Parravicini V. (2015) Patterns and processes linked to body size. C.Mora ed. In: *Ecology of fishes on coral reefs*. Oxford Univ. Press. pp. 104-115

Labrosse, P., Kulbicki, M., and Ferraris, J. (2002). Underwater visual fish census surveys: proper use and implementation, in: *REAT- Reef Resources Assessment Tools*. 54 pp. https://doi.org/10.1051/alr:2004020

Lam, K., Shin, P.K.S., Bradbeer, R., Randall, D., Ku, K.K.K., Hodgson, P., and Cheung, S.G. (2006). A comparison of video and point intercept transect methods for monitoring subtropical coral communities. *Journal of Experimental Marine Biology and Ecology*, 333(1), 115–128. doi:10.1016/j.jembe.2005.12.009

Lam, V.Y.Y., Doropoulos, C., and Mumby, P.J. (2017). The influence of resilience-based management on coral reef monitoring: A systematic review. *PLoS ONE*, 12(2), 1–15. doi:10.1371/journal.pone.0172064

Lavy, A., Eyal, G., Neal, B., Keren, R., Loya, Y., and Ilan, M. (2015). A quick, easy and non-intrusive method for underwater volume and surface area evaluation of benthic organisms by 3D computer modelling. *Methods in Ecology and Evolution*, 6, 521–531. https://doi.org/10.1111/2041-210X.12331

Leatherdale, J.D., and Turner, D.J. (1983). Underwater Photogrammetry in the North Sea. *Technical Meeting of the Society*, 167, 151–167.

Lecours, V., Dolan, M.F.J., Micallef, A., and Lucieer, V.L. (2016). A review of marine geomorphometry, the quantitative study of the seafloor. *Hydrology and Earth System Sciences*, 20(8), 3207–3244. doi:10.5194/hess-20-3207-2016

Leon, J.X., Roelfsema, C.M., Saunders, M.I., and Phinn, S.R. (2014). Measuring coral reef terrain roughness using 'Structure-from-Motion' close-range photogrammetry. *Geomorphology*, 242. doi:10.1016/j.geomorph.2015.01.030

Leujak, W., and Ormond, R.F.G. (2007). Comparative accuracy and efficiency of six coral community survey methods. *Journal of Experimental Marine Biology and Ecology*, 351(1–2), 168–187. http://doi.org/10.1016/j.jembe.2007.06.028

Levoy, M., and Whitted, T. (1985). *The Use of Points as a Display Primitive Marc Levoy Turner Whitted*. Computer science departement. University of North Carolina.

Li, J., Schill, S.R., Knapp, D.E., and Asner, G.P. (2019). Object-based mapping of coral reef habitats using planet dove satellites. *Remote Sensing*, 11(12). doi:10.3390/rs11121445

Longo, G.O., Morais, R.A., Martins, C.D.L., Mendes, T.C., Aued, A.W., Cândido, D.V., de Oliveira, J.C., Nunes, L.T., Fontoura, L., Sissini, M.N., Teschima, M.M., Silva, M.B., Ramlov, F., Gouvea, L.P., Ferreira, C.E.L., Segal, B., Horta, P.A., and Floeter, S.R. (2015). Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in South Atlantic: Rocas atoll, NE Brazil. *PLoS ONE*, 10(6), 1–29. doi:10.1371/journal.pone.0127176

Lowe, D.G. (2004). Distinctive Image features from Scale-Invariant Keypoints. *International Journal of Computer Vision*, 60, 91–110.

Lowe, M.K., Adnan, F.A.F., Hamylton, S.M., Carvalho, R.C., and Woodroffe, C.D. (2019). Assessing Reef-Island Shoreline Change Using UAV-Derived Orthomosaics and Digital Surface Models. *Drones*, 3, 44. https://doi.org/10.3390/drones3020044

Loya, Y. (1972). Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine Biology*, 13(2), 100–123. doi:10.1007/BF00366561

Loya, Y. (1978). Plotless and transect methods. In D.R.S. and R.E. Johannes (Ed.), *Monographs on Oceanic Methodology. Coral Reefs : Research Methods* (Vol. 5, pp. 197–218). UNESCO Press.

Luckhurst, B.E., and Luckhurst, K. (1978). Analysis of the Influence of Substrate Variables on Coral Reef Fish Communities. *Marine Biology*, 49(4), 317–324.

MacNeil, M.A., Graham, N.A., Cinner, J.E., Wilson, S.K., Williams, I.D., Maina, J., Newman, S., Friedlander, A.M., Jupiter, S., Polunin, N.V.C., and McClanahan, T.R. (2015). Recovery potential of the world's coral reef fishes. *Nature*, 520(7547), 341-344.

Madin, J.S., Hoogenboom, M.O., Connolly, S.R., Darling, E.S., Falster, D.S., Huang, D., Keith, S.A., Mizerek, T., Pandolfi, J.M., Putnam, H.M., and Baird, A.H. (2016a). A Trait-Based Approach to Advance Coral Reef Science. *Trends in Ecology and Evolution*, 31(6), 419–428. doi:10.1016/j.tree.2016.02.012

Madin, J.S., Anderson, K.D., Andreasen, M.H., Bridge, T.C.L., Cairns, S.D., Connolly, S.R., Darling, E.S., Diaz, M., Falster, D.S., Franklin, E.C., Gates, R.D., Harmer, A.M.T., Hoogenboom, M.O., Huang, D., Keith, S.A., Kosnik, M.A., Kuo, C.-Y., Lough, J.M., Lovelock, C.E., Luiz, O., Martinelli, J., Mizerek, T., Pandolfi, J.M., Pochon, X., Pratchett, M.S., Putnam, H.M., Roberts, T.E., Stat, M., Wallace, C.C., Widman, E., and Baird, A.H. (2016b). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data*, 3, 160017. doi:10.1038/sdata.2016.17

Madin, E.M.P., Darling, E.S., and Hardt, M.J. (2019). Emerging Technologies and Coral Reef Conservation: Opportunities, Challenges, and Moving Forward. *Frontiers in Marine Science*, 6, 1–7. doi:10.3389/fmars.2019.00727

Magel, J.M.T., Burns, J.H.R., Gates, R.D., and Baum, J.K. (2019). Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. *Scientific Reports*, 9(1), 1–12. doi:10.1038/s41598-018-37713-1

Mandelbrot, B. (1967). How Long Is the Coast of Britain? Statistical Self-Similarity and Fractional Dimension. *Science*, 156, 636–638. doi:10.1017/CBO9781107415324.004

Margalef, R. (1963). On Certain Uniying Principles in Ecology. *The American Naturalist*, 97(897), 357–374. Retrieved from https://doi.org/10.1086/282286

Mark, D. (1984). Fractal dimension of a coral reef at ecological scales: a discussion. *Marine Ecology Progress Series*, 14, 293–294. doi:10.3354/meps014293

Marre, G., Holon, F., Luque, S., Boissery, P., and Deter, J. (2019). Monitoring marine habitats with photogrammetry: a cost-effective, accurate, precise and high-resolution reconstruction method. *Frontiers in Marine Science*, 6, 276. doi:10.3389/FMARS.2019.00276

Martin-Smith, K.M. (1993). Abundance of mobile epifauna: The role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology*, 174(2), 243–260. doi:10.1016/0022-0981(93)90020-O

McClanahan, T.R., Graham, N.A.J., MacNeil, M.A., Muthiga, N.A., Cinner, J.E., Bruggemann, J.H., and Wilson, S.K. (2011). Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, 108(41), 17230–17233. doi:10.1073/pnas.1106861108

McClanahan, T.R., Donner, S.D., Maynard, J.A., MacNeil, M.A., Graham, N.A.J., Maina, J., Baker, A.C., Alemu I., J.B., Beger, M., Campbell, S.J., Darling, E.S., Eakin, C.M., Heron, S.F., Jupiter, S.D., Lundquist, C.J., McLeod, E., Mumby, P.J., Paddack, M.J., Selig, E.R., and van Woesik, R. (2012). Prioritizing Key Resilience Indicators to Support Coral Reef Management in a Changing Climate. *PLoS ONE*, 7. https://doi.org/10.1371/journal.pone.0042884

McClanahan, T.R. (2014). Recovery of functional groups and trophic relationships in tropical fisheries closures. *Marine Ecology Progress Series*, 497, 13–23. doi:10.3354/meps10605

McCarthy, J., and Benjamin, J. (2014). Multi-image Photogrammetry for Underwater Archaeological Site Recording: An Accessible, Diver-Based Approach. *Journal of Maritime Archaeology*, 9(1), 95–114. http://doi.org/10.1007/s11457-014-9127-7

Mcleod, E., Anthony, K.R.N., Mumby, P.J., Maynard, J., Beeden, R., Graham, N.A.J., Heron, S.F., Hoegh-Guldberg, O., Jupiter, S., MacGowan, P., Mangubhai, S., Marshall, N., Marshall, P.A., McClanahan, T.R., Mcleod, K., Nyrström, M., Obura, D., Parker, B., Possingham, H.P., Salm, R.V., and Tamelander, J. (2019). The future of resilience-based management in coral reef ecosystems. *Journal of Environmental Management*, 233, 291–301. doi:10.1016/j.jenvman.2018.11.034

McWilliam, M., Hoogenboom, M.O., Baird, A.H., Kuo, C.Y., Madin, J.S., and Hughes, T.P. (2018). Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences of the United States of America*, 115(12), 3084–3089. doi:10.1073/pnas.1716643115

Ménard, A., Turgeon, K., Roche, D.G., Binning, S.A., and Kramer, D.L. (2012). Shelters and their use by fishes on fringing coral reefs. *PLoS ONE*, 7. doi.org/10.1371/journal.pone.0038450

Micheletti, N., Chandler, J., and Lane, S.N. (2015). *Structure-from-motion photogrammetry. Geomorphological Techniques (Online Edition)*. London: British Society for Geomorphology. ISSN: 2047-0371, Chap. 2, Sec. 2.2, pp 36–39.

Moberg, F., and Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, 29(2), 215–233. doi:10.1016/S0921-8009(99)00009-9

Mohamed, H., Nadaoka, K., and Nakamura, T. (2020). Towards Benthic Habitat 3D Mapping Using Machine Learning Algorithms and Structures from Motion Photogrammetry. *Remote Sensing.* doi:10.3390/rs12010127

Morais, R.A., and Bellwood, D.R. (2019). Pelagic Subsidies Underpin Fish Productivity on a Degraded Coral Reef. *Current Biology*, 29. doi:/10.1016/j.cub.2019.03.044

Mouillot, D., Villeger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J.E., Bender, M., and Bellwood, D.R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences*, 111(38), 13757–13762. http://doi.org/10.1073/pnas.1317625111

Mumby, P.J. and Hastings, A. (2008) The impact of ecosystem connectivity on coral reef resilience. *Journal of Applied Ecology*, 45, 854–862. 10.1111/j.1365-2664.2008.01459.x

Mumby, P.J., Broad, K., Brumbaugh, D.R., Dahlgren, C.P., Harborne, A.R., Hastings, A., Holmes, K.E., Kappel, C. V., Micheli, F., and Sanchirico, J.N. (2008). Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. *Conservation Biology*, 22, 941–951. https://doi.org/10.1111/j.1523-1739.2008.00933.x

Naeem, S., Duffy, J.E., and Zavaleta, E. (2012). The Functions of Biological Diversity in an Age of Extinction. *Science*, 336(6087), 1401–1406. http://doi.org/10.1126/science.1215855

Newman, S.P., Meesters, E.H., Dryden, C.S., Williams, S.M., Sanchez, C., Mumby, P.J., and Polunin, N.V.C. (2015). Reef flattening effects on total richness and species responses in the Caribbean. *Journal of Animal Ecology*, 84, 1678–1689. https://doi.org/10.1111/1365-2656.12429

NOAA Office for Coastal Management (2020). September 3. Coral Reefs. Retrieved from: https://coast.noaa.gov/states/fast-facts/coral-reefs.html

Noonan, S.H.C., Jones, G.P., and Pratchett, M.S. (2012). Coral size, health and structural complexity: Effects on the ecology of a coral reef damselfish. *Marine Ecology Progress Series*, 456, 127–137. doi:10.3354/meps09687

Nyström, M., Graham, N.A.J., Lokrantz, J., and Norström, A.V. (2008). Capturing the cornerstones of coral reef resilience: Linking theory to practice. *Coral Reefs*, 27(4), 795–809. http://doi.org/10.1007/s00338-008-0426-z

Obura, D., and Grimsditch, G. (2009) Resilience Assessment of Coral Reefs bleaching and thermal stress. *IUCN Resilience Science Group Working Paper Series*, 5, pp 70.

Obura, D. (2014). Coral Reef Monitoring Manual South-West Indian Ocean islands. *Indian Ocean Communications*, 68.

Obura, D.O., Aeby, G., Amornthammarong, N., Appeltans, W., Bax, N., Bishop, J., Brainard, R.E., Chan, S., Fletcher, P., Gordon, T.A.C., Gramer, L., Gudka, M., Halas, J., Hendee, J., Hodgson, G., Huang, D., Jankulak, M., Jones, A., Kimura, T., Levy, J., Miloslavich, P., Chou, L.M., Muller-Karger, F., Osuka, K., Samoilys, M., Simpson, S.D., Tun, K., and Wongbusarakum, S., (2019). Coral Reef Monitoring, Reef Assessment Technologies, and Ecosystem-Based Management. *Frontiers in Marine Science*, 6. https://doi.org/10.3389/fmars.2019.00580

Ohlhorst, S.L., Liddell, W.D., Taylor, R.J., and Taylor, J.M. (1988). Evaluation of reef census techniques. *Proceedings of the 6th International Coral Reef Symposium*, Australia, 2, 319–324.

Olds, A.D., Connolly, R.M., Pitt, K.A. and Maxwell, P.S. (2012) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. *Marine Ecology Progress Series*, 462, 191–203. https://doi.org/10.3354/meps09849

Olinger, L.K., Scott, A.R., McMurray, S.E., and Pawlik, J.R. (2019). Growth estimates of Caribbean reef sponges on a shipwreck using 3D photogrammetry. *Scientific Reports*, 9, 1–12. https://doi.org/10.1038/s41598-019-54681-2

Palma, M., Casado, M.R., Pantaleo, U., and Cerrano, C. (2017). High resolution orthomosaics of African coral reefs: A tool for wide-scale benthic monitoring. *Remote Sensing*, 9, 1–26. https://doi.org/10.3390/rs9070705

Parsons, M., Bratanov, D., Gaston, K.J., and Gonzalez, F. (2018). UAVs, hyperspectral remote sensing, and machine learning revolutionizing reef monitoring. *Sensors (Switzerland)*, 18(7), 1–20. doi:10.3390/s18072026

Pendleton, L.H., Hoegh-Guldberg, O., Langdon, C., and Comte, A. (2016). Multiple stressors and ecological complexity require a new approach to coral reef research. *Frontiers in Marine Science*, 3. doi:10.3389/fmars.2016.00036

Pereira, P.H.C., and Munday, P.L. (2016). Coral colony size and structure as determinants of habitat use and fitness of coral-dwelling fishes. *Marine Ecology Progress Series*, 553, 163–172. https://doi.org/10.3354/meps11745

Perry, C.T., and Alvarez-Filip, L. (2019). Changing geo-ecological functions of coral reefs in the Anthropocene. *Functional Ecology*, 33, 976–988. https://doi.org/10.1111/1365-2435.13247

Peterson, G., Allen, C.R., and Holling, C.S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, 1(1), 6–18.

Pinault, M., Bollard, S., Bissier, Y.-C.L., Quod, J.P., and Galzin, R. (2010). Artificial reefs as tool to supply artisanal fishery in Réunion Island: scientific evaluation and statistic incrementation, in: *French-Japanese Symposium*, Ifremer Sète France. pp. 140–144.

Pinault, M. (2013). Evaluation de la fonctionnalité des récifs artificiels à vocation non extractive, dans un contexte d'habitats naturels fragmentés - cote nord-ouest de l'île de la Réunion. École Doctorale de l'École Pratique des Hautes Études. 314p.

Pinault, M., Bissery, C., Gassiole, G., Magalon, H., Quod, J.P., and Galzin, R. (2014). Fish community structure in relation to environmental variation in coastal volcanic habitats. *Journal of Experimental Marine Biology and Ecology*, 460, 62–71. doi:10.1016/j.jembe.2014.06.005

Pinca, S., Kronen, M., Magron, F., Mcardle, B., Vigliola, L., Kulbicki, M., and Andréfouët, S. (2012). Relative importance of habitat and fishing in influencing reef fish communities across seventeen Pacific Island Countries and Territories. *Fish and Fisheries*, 13(4), 361–379. doi:10.1111/j.1467-2979.2011.00425.x

Pittman, S.J., Costa, B.M., and Battista, T.A. (2009). Using Lidar Bathymetry and Boosted Regression Trees to Predict the Diversity and Abundance of Fish and Corals. *Journal of Coastal Research*, 10053, 27–38. doi:10.2112/SI53-004.1

Pizarro, O., Friedman, A., Bryson, M., Williams, S.B., and Madin, J. (2017). A simple, fast, and repeatable survey method for underwater visual 3D benthic mapping and monitoring. *Ecology and Evolution*, 7(6), 1770–1782. doi:10.1002/ece3.2701

Pratchett, M.S. (2005). Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology*, 148, 373-382.

Pratchett, M.S., Munday, P.L., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., and McClanahan, T.R. (2008). Effects of climate-induced coral bleaching on coral-reef fishes - ecological and economic consequences. *Oceanography and Marine Biology: an annual review*, 46, 251–296. https://doi.org/10.1201/9781420065756.ch6.

Pratchett, M.S., Hoey, A.S., and Wilson, S.K. (2014). Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Current Opinion in Environmental Sustainability*, 7, 37–43. http://doi.org/10.1016/j.cosust.2013.11.022

Price, D.M., Robert, K., Callaway, A., Lo lacono, C., Hall, R.A., and Huvenne, V.A.I. (2019). Using 3D photogrammetry from ROV video to quantify cold-water coral reef structural complexity and investigate its influence on biodiversity and community assemblage. *Coral Reefs*, 38(5), 1007–1021. doi:10.1007/s00338-019-01827-3

Proudfoot, B., Devillers, R., and Brown, C.J. (2020). Integrating fine-scale seafloor mapping and spatial pattern metrics into marine conservation prioritization. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30, 1613–1625. https://doi.org/10.1002/aqc.3360

Pu, J.H., Hussain, A., Guo, Y. kun, Vardakastanis, N., Hanmaiahgari, P.R., and Lam, D. (2019). Submerged flexible vegetation impact on open channel flow velocity distribution: An analytical modelling study on drag and friction. *Water Science and Engineering*, 12(2), 121–128. doi:10.1016/j.wse.2019.06.003

QGIS Development Team (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project.

Raoult, V., Reid-Anderson, S., Ferri, A., and Williamson, J. (2017). How Reliable Is Structure from Motion (SfM) over Time and between Observers? A Case Study Using Coral Reef Bommies. *Remote Sensing*, 9(7), 740. doi:10.3390/rs9070740

R Core Team. (2019). R : A language and Statistical, statistical computing. R Foundation for Computing, Vienna, Austria. URL https://www.R-project.org/.

Rees, M.J., Knott, N.A., Neilson, J., Linklater, M., Osterloh, I., Jordan, A., and Davis, A.R. (2018). Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves. *Biological Conservation*, 224, 100–110. doi:10.1016/j.biocon.2018.04.040

Reguero, B.G., Beck, M.W., Agostini, V.N., Kramer, P., and Hancock, B. (2018). Coral reefs for coastal protection: A new methodological approach and engineering case study in Grenada. *Journal of Environmental Management*, 210, 146–161. doi:10.1016/j.jenvman.2018.01.024

Reichert, J., Schellenberg, J., Schubert, P., and Wilke, T. (2016). 3D scanning as a highly precise, reproducible, and minimally invasive method for surface area and volume measurements of scleractinian corals. *Limnology and Oceanography: Methods*. doi:10.1002/lom3.10109

Richardson, L.E., Graham, N.A.J., and Hoey, A.S. (2017a). Cross-scale habitat structure driven by coral species composition on tropical reefs. *Scientific Reports*, 7(1), 1–11. doi:10.1038/s41598-017-08109-4

Richardson, L.E., Graham, N.A.J., Pratchett, M.S., and Hoey, A.S. (2017b). Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environmental Biology of Fishes*, 100(3), 193–207. doi:10.1007/s10641-016-0571-0

Riedl, R. (1980). Marine Ecology - a century of changes - P.S.Z.N.1. *Marine Ecology*, *1*, 3–46.

Risk, M. (1972). Fish diversity on a Coral Reef in the Virgin Island. *Atoll Research Bulletin*.

Rogers, A., Blanchard, J.L., and Mumby, P.J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, 24(9), 1000–1005. http://doi.org/10.1016/j.cub.2014.03.026

Rossi, P., Castagnetti, C., Capra, A., Brooks, A.J., and Mancini, F. (2019). Detecting change in coral reef 3D structure using underwater photogrammetry : critical issues and performance metrics. *Applied Geomatics*, 12, 3-17.

Sandström, A., and Karas, P. (2002). Tests of artificial substrata as nursery habitat for young fish. *Journal of Applied Ichthyology*, 18, 102–105.

Sano, M., Shimizu, M., and Nose, Y. (1984). Changes in Structure of Coral Reef Fish Communities by Destruction of Hermatypic Corals : Observational and Experimental Views ! *Pacific Science*, 38, 51–79.

Santos, L., Araújo, F., and Brotto, D. (2008). Artificial structures as tools for fish habitat rehabilitation in a neotropical reservoir. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 656, 636–656. doi:10.1002/aqc

Schleyer, M.H., Benayahu, Y., Parker-Nance, S., van Soest, R.W.M., and Quod, J.P. (2016). Benthos on submerged lava beds of varying age off the coast of Reunion, western Indian Ocean: sponges, octocorals and ascidians. *Biodiversity*, 8386, 1–8. https://doi.org/10.1080/14888386.2016.1190669

Shao, Z., Yang, N., Xiao, X., Zhang, L., and Peng, Z. (2016). A multi-view dense point cloud generation algorithm based on low-altitude remote sensing images. *Remote Sensing*, 8(5). doi:10.3390/rs8050381

Shewchuck, J.R. (2002). Delaunay refinement algorithms for triangular mesh generation. *Computational Geometry*, 22, 21–74.

Silver, A. (2019). Drone takes to the skies to image offshore reefs. *Nature*, 570(7762), 545-546.

Storlazzi, C.D., Dartnell, P., Hatcher, G.A., and Gibbs, A.E. (2016). End of the chain? Rugosity and fine-scale bathymetry from existing underwater digital imagery using structure-from-motion (SfM) technology. *Coral Reefs*, 35(3), 889-894. doi:10.1007/s00338-016-1462-8

Sugihara, G., and May, M.R. (1990). Applications of fractals in ecology. *Trends in Ecology and Evolution*, 5(3), 79–86. doi:10.1016/0169-5347(90)90235-6

Tavera, L.D., Páez, A., Rocha, L.A., Dallos, L.A., Gonzales, J.D., and Upegui, E. (2019). SFM photogrammetry as a tool for the conservation of the cultural heritage of Bogotá (Colombia), within the framework of the Adopt a monument program. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 42(2/W17), 363–370. doi:10.5194/isprs-archives-XLII-2-W17-363-2019

Tebbett, S.B., Streit, R.P., and Bellwood, D.R. (2020). A 3D perspective on sediment accumulation in algal turfs: Implications of coral reef flattening. *Journal of Ecology*, 108(1), 70–80. doi:10.1111/1365-2745.13235

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., and Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1), 79–92. doi:10.1046/j.0305-0270.2003.00994.x

Triggs, B., Mclauchlan, P., Hartley, R., Fitzgibbon, A. (2000). Bundle Adjustment – A Modern Synthesis. In: *International workshop on vision algorithms* (pp. 298-372). Springer, Berlin, Heidelberg.

Troisi, S., Del Pizzo, S., Gaglione, S., Miccio, A., and Testa, R.L. (2015). 3D models comparison of complex shell in underwater and dry environments. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 40(5W5), 215–222. https://doi.org/10.5194/isprsarchives-XL-5-W5-215-2015

Turner, M.G., Gardner, R.H., and O'Neill, R.V. (2001). *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer-Verlag, New York.

Tyler, C. (2000). Artificial reefs. *New Scientist*, 168(2266), 59.

Vallès, H., Oxenford, H.A., and Henderson, A. (2019). Switching between standard coral reef benthic monitoring protocols is complicated: Proof of concept. *PeerJ*, 2019(12), 1–24. doi:10.7717/peerj.8167

Veron, J.E.N. (2000). *Corals of the world Vols 1-3*. Australian Institute of Marine Science.

Villon, S., Mouillot, D., Chaumont, M., Darling, E.S., Subsol, G., Claverie, T., and Villéger, S. (2018). A Deep learning method for accurate and fast identification of coral reef fishes in underwater images. *Ecological Informatics*, 48, 238–244. doi.org/10.1016/j.ecoinf.2018.09.007

Villon, S., Mouillot, D., Chaumont, M., Subsol, G., Claverie, T., and Villéger, S. (2020). A new method to control error rates in automated species identification with deep learning algorithms. *Scientific Reports*, 10, 10972. doi.org/10.1038/s41598-020-67573-7

Walters, D.A., Lynch, W.E., and Johnson, D.L. (1991). How depth and interstice size of artificial structures influence fish attraction. *North American Journal of Fisheries Management,* 11, 319–329

Wedding, L.M., and Friedlander, A.M. (2008). Determining the influence of seascape structure on coral reef fishes in Hawaii using a geospatial approach. *Marine Geodesy*, 31, 246–266. https://doi.org/10.1080/01490410802466504

Wedding, L.M., Jorgensen, S., Lepczyk, C.A., and Friedlander, A.M. (2019). Remote sensing of three-dimensional coral reef structure enhances predictive modeling of fish assemblages. *Remote Sensing in Ecology and Conservation*, 5(2), 150–159. doi:10.1002/rse2.115

Weinberg, S. (1981). A comparison of coral reef survey methods. *Bijdragen Tot de Dierkunde*, 51(2), 199–218.

West, G.B., Woodruff, W.H., and Brown, J.H. (2002). Allometric scaling of metabolic rate from molecules and mitochondria to cells and mammals. *Proceedings of the National Academy of Sciences of the United States of America,* 99, 2473–2478. doi:10.1073/pnas.012579799

Westoby, M.J., Brasington, J., Glasser, N.F., Hambrey, M.J., and Reynolds, J.M. (2012). 'Structure-from-Motion' photogrammetry: A low-cost, effective tool for geoscience applications. *Geomorphology*, 179, 300–314. doi:10.1016/j.geomorph.2012.08.02

Wickham D.A., Watson J.W., Jr and Ogren L.H. (1973) The efficacy of midwater artificial structures for attracting pelagic sport fish. *Transactions of American Fisheries Society*, 3, 563–572.

Wickman, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York.

Wild, C., Hoegh-Guldberg, O., Naumann, M.S., Colombo-Pallotta, M.F., Ateweberhan, M., Fitt, W.K., Iglesias-Prieto, R., Palmer, C., Bythell, J.C., Ortiz, J.-C., Loya, Y., and van Woesik, R. (2011). Climate change impedes scleractinian corals as primary reef ecosystem engineers. *Marine and Freshwater Research*, 62(2), 205–215. doi:10.1071/MF10254

Wilkinson, C., Green, A., Almany, J., and Dionne, S. (2003). *Monitoring coral reef marine protected areas. A practical guide on how monitoring can support effective management of MPAs.* Australian Institute of Marine Science, 1, 72 pp.

Williams, G.J., and Graham, N.A.J. (2019). Rethinking coral reef functional futures. *Functional Ecology*, 33(6), 942–947. doi:10.1111/1365-2435.13374

Williams, G.J., Graham, N.A.J., Jouffray, J.B., Norström, A. V., Nyström, M., Gove, J.M., Heenan, A., and Wedding, L.M. (2019). Coral reef ecology in the Anthropocene. *Functional Ecology*, 33, 1014–1022. https://doi.org/10.1111/1365-2435.13290

Wilson, S.K., Graham, N.A.J., and Polunin, N.V.C. (2007). Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, 151, 1069–1076. https://doi.org/10.1007/s00227-006-0538-3

Wilson, S.K., Burgess, S.C., Cheal, A.J., Emslie, M., Fisher, R., Miller, I., Polunin, N.V.C., and Sweatman, H.P.A. (2008). Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology*, 77, 220–228. doi:10.1111/j.1365-2656.2007.0

Wilson, S.K., Depczynski, M., Fulton, C.J., Holmes, T.H., Radford, B.T., and Tinkler, P. (2016). Influence of nursery microhabitats on the future abundance of a coral reef fish. *Proceedings of the Royal Society B: Biological Sciences*, 283(1836). doi:10.1098/rspb.2016.0903

Wilson, S.K., Robinson, J.P.W., Chong-Seng, K., Robinson, J., and Graham, N.A.J. (2019). Boom and bust of keystone structure on coral reefs. *Coral Reefs*, 38(4), 625–635. doi:10.1007/s00338-019-01818-4

Yanovski, R., Nelson, P.A., and Abelson, A. (2017). Structural Complexity in Coral Reefs: Examination of a Novel Evaluation Tool on Different Spatial Scales. *Frontiers in Ecology and Evolution*, 5, 1–9. https://doi.org/10.3389/fevo.2017.00027

Yanovski, R., and Abelson, A. (2019). Structural complexity enhancement as a potential coral-reef restoration tool. *Ecological Engineering*, 132, 87–93. doi:10.1016/j.ecoleng.2019.04.007

Young, G.C., Dey, S., Rogers, A.D., and Exton, D. (2017). Cost and time-effective method for multi-scale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D models. *PLoS ONE*, 12(4), e0175341. doi:10.1371/journal.pone.0175341

Zawada, D.G., and Brock, J.C. (2009). A Multiscale Analysis of Coral Reef Topographic Complexity Using Lidar-Derived Bathymetry. *Journal of Coastal Research*, 53, 6–15. doi:10.2112/si53-002.1

Zawada, D.G., Piniak, G.A., and Hearn, C.J. (2010). Topographic complexity and roughness of a tropical benthic seascape. *Geophysical Research Letters*, 37(14), 1–6. doi:10.1029/2010GL043789

Zawada, K.J.A., Dornelas, M., and Madin, J.S. (2019a). Quantifying coral morphology. *Coral Reefs*, 38(6), 1281-1292. doi:10.1007/s00338-019-01842-4

Zawada, K.J.A., Madin, J.S., Baird, A.H., Bridge, T.C.L., and Dornelas, M. (2019b). Morphological traits can track coral reef responses to the Anthropocene. *Functional Ecology*, 33(6), 962–975. doi:10.1111/1365-2435.13358

Zurk, L., Lotz, J., Ellis, T., and McNames, J. (2006). Sonar mapping for coral reef conservation. *The Journal of the Acoustical Society of America,* 120(5), 3060-3060. doi: 10.1121/1.4787314


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