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Plongées profondes en Polynésie Française : un nouveau regard sur les écosystèmes coralliens mésophotiques

Gonzalo Perez-Rosales

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THÈSE DE DOCTORAT
DE L'UNIVERSITÉ PSL

Préparée à l'École Pratique des Hautes Études

Plongées profondes en Polynésie Française : un nouveau regard sur les écosystèmes coralliens mésophotiques

Diving deep on the reef slopes in French Polynesia: new insights into mesophotic coral ecosystems

Soutenue par

Gonzalo Pérez-Rosales

Le 13 juillet 2022

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If, while diving, you have ever listened to the call from the depths, this thesis will transfer you into the science of the twilight zone.



Image 1: Makatea at 80 m depth was a “roses” garden of *Leptoseris solida* (Copyright: Julien LEBLOND / UNDER THE POLE / Zeppelin Network).

Humanity’s responsibility to the rest of life and to future generations is clear:
bring with us as much of the environment and biodiversity through
the bottleneck as possible. **E. O. Wilson** preface *Diversity of Life*

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Résumé en français

Le changement climatique, ainsi que d'autres perturbations, sont à l'origine de la perte des récifs coralliens. Les Écosystèmes Coralliens Mésophotiques (ECM) sont situés entre 30 et 150 m de profondeur, et malgré la diminution de la lumière en profondeur, ils sont caractérisés par des coraux photosynthétiques. En dépit de leur rôle potentiel de refuges pour les récifs superficiels, la plupart des ECM restent inexplorés, et des endroits comme la Polynésie Française peu étudiés.

Cette thèse s'inscrit dans DEEPHOPE (une collaboration entre des scientifiques et Under The Pole) pour mettre en lumière les ECM en Polynésie Française avec plus de 800 plongées en recycleur Trimix en dessous de 100 m. L'expédition a permis de tester (1) les patrons de diversité et la couverture corallienne avec la profondeur ; (2) l'acclimatation et l'adaptation des coraux scléactiniaires à la profondeur ; et (3) si les profondeurs mésophotiques sont affectées par le blanchissement thermique des coraux.

Le chapitre 1 présente les récifs coralliens et les ECM dans le monde et le contexte de la Polynésie française pour définir les hypothèses de départ. Il explique également la méthodologie de collecte des données écologiques, physiologiques, environnementales et taxonomiques.

Le chapitre 2 montre que les ECM sont des points chauds de diversité générique des scléactiniaires en Polynésie française, malgré la diminution de la couverture avec la profondeur. Cette diversité est due à un pic de richesse à 40 m et l'augmentation de la diversité spatiale en profondeur. Cela signifie que, alors que les assemblages coralliens superficiels sont similaires, ils sont différents en profondeur.

Le chapitre 3 démontre que bien que la couverture corallienne diminue avec la profondeur, les profondeurs mésophotiques ont une couverture corallienne étonnamment élevée (selon les modèles). Le chapitre met aussi en valeur les fondements de la modélisation environnementale prédictive de la couverture corallienne et de la structure des communautés (avec les morphologies coralliennes) dans les profondeurs mésophotiques.

Le chapitre 4 montre les stratégies de deux espèces scléactiniaires pour faire face à des environnements à faible luminosité : elles augmentent la concentration de chlorophylle, la densité de symbiotes et modifient le squelette morphologique pour suivre la photosynthèse. Les résultats suggèrent aussi l'absence de plasticité nutritionnelle.

Le chapitre 5 dévoile que les communautés coralliennes mésophotiques ont échappé à un événement de blanchissement thermique, avec une mortalité passant de 35 % à 6 m à moins de 5 % à 20 m voire inexistante après 40 m. Cette réduction du blanchissement a été observée chez tous les genres dans leur gamme de distribution de profondeur, ce qui suggère que les ECM pourraient agir comme refuge à court terme contre ces événements.

Le chapitre 6 examine en plus des résultats de DEEPHOPE pour discuter de la structure des communautés, des différences spatiales au sein et en comparaison avec d'autres sites mondiaux, et de certains termes utilisés dans la recherche, compte tenu des abondances quantitatives. Le chapitre aborde aussi l'importance des ECM pour la conservation, leurs limites et les perspectives futures.

Dans l'ensemble, cette thèse augmente la connaissance des ECM en Polynésie Française d'un point de vue quantitatif, démontre le potentiel de cette région, et pose les bases pour de futures études. La thèse montre aussi que les profondeurs mésophotiques pourront être essentielles pour la conservation, avec des récifs très diversifiés, couverts, et moins affectés par le blanchissement thermique. Avec l'avenir incertain des récifs coralliens face au changement climatique, les ECM pourraient jouer un rôle écologique capital dans la résilience des récifs coralliens à l'échelle de l'écosystème. Des études quantitatives similaires seront nécessaires dans d'autres endroits pour étayer le caractère global des résultats de cette thèse.

Summary in English

Climate change and other disturbances are causing the loss of scleractinian coral reefs. Underneath shallow reefs and despite light decreases with depth, Mesophotic Coral Ecosystems (MCEs) are characterised by photosynthetic corals, and associated reef communities, at depths between 30 and 150 m. MCEs interest lies in increasing their knowledge and potential role as shallow reefs refugia, yet most MCEs remain unexplored, with locations like French Polynesia understudied.

This thesis is part of the DEEPHOPE project (a collaboration between scientists and Under The Pole) to shed light on the MCEs in French Polynesia with ~800 Trimix Rebreather dives below 100 m depth. The expedition allowed this thesis to test (1) the diversity patterns and coral cover with depth; (2) the acclimation and adaptation of scleractinian corals to depth; and (3) whether mesophotic depths are impacted by thermal coral bleaching.

Chapter 1 introduces coral reefs and MCEs worldwide and the context for French Polynesia to set the departing hypotheses. It also explains the methodology to collect the ecological, physiological, environmental and taxonomical data.

Chapter 2 shows that MCEs are hotspots of scleractinian generic diversity in French Polynesia despite coral cover decreasing with depth. Hotspots of diversity because the genus richness follows a mid-domain effect with a peak of (alpha) α -diversity between 20 and 60 m and because spatial (beta) β -diversity increases with depth, meaning that while shallow depths are similar across locations, mesophotic depths are different and unique.

Chapter 3 shows that although coral cover decreases with depth generally, mesophotic depths are also home to unexpectedly high (by models) coral cover communities for the depth. These were in some cases more highly coral-covered than shallow reefs and associated with moderate to steep slopes and low sedimentation. It also shows the foundations for predictive environmental modelling of coral cover and community structure (with coral morphologies) in mesophotic depths.

Chapter 4 shows the strategies of two scleractinian species to cope with low-light environments increasing chlorophyll concentration, symbiont density (with no specific shifts in Symbiodiniaceae composition), and modifying morphological skeleton to keep up with photosynthesis. Results suggest no nutritional plasticity (switch to heterotrophy) even if both species reduced the $\delta^{13}\text{C}$ with depth.

Chapter 5 demonstrates that mesophotic coral communities escaped a thermal coral bleaching event in French Polynesia, with subsequent mortality decreasing from 35% at 6 m to less than 5% at 20 m to non-existent after 40 m. This bleaching reduction was observed among all genera from their upper to their lower depth distribution range, suggesting that MCEs might act as short-term refugia from bleaching events.

Chapter 6 also considers some results of DEEPHOPE to discuss the depth zonation and community structure, the spatial differences across islands and with other worldwide locations, and some “terms” used in research, considering quantitative abundances. The importance of MCEs with implications in conservation, the limitations, and future directions to improve MCEs’ research.

Overall, this thesis increases the knowledge of MCEs in French Polynesia from a quantitative perspective, suggesting the potential of this region for MCEs and setting the basis for future studies. Also, to support MCEs’ importance because, in some way or the other, it shows evidence that mesophotic depths are key depths for conservation, with highly diverse and covered communities less affected by thermal bleaching. With the uncertain future of coral reefs with climate change, MCEs could play an ecological role in the ecosystem-wide coral reef resilience. Although our outcomes are at the scale of French Polynesia, similar quantitative studies are necessary for other locations to substantiate the global character of the findings of this thesis.

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List of peer-reviewed articles during my PhD

Published:

- **Pérez-Rosales G**, Brandl SJ, Chancerelle Y, Siu G, Martinez E, Parravicini V, Hédouin L. (2021) Documenting decadal disturbance dynamics reveals archipelago-specific recovery and compositional change on Polynesian reefs. *Marine Pollution Bulletin*. 170:112659.
<https://doi.org/10.1016/j.marpolbul.2021.112659> (**Appendix 3**)
- **Pérez-Rosales G**, Rouzé H, Torda G, Bongaerts P, Pichon M, Parravicini V, Hédouin L. (2021) Mesophotic coral communities escape thermal coral bleaching in French Polynesia. *R. Soc. Open Sci.* 8: 210139.
<https://doi.org/10.1098/rsos.210139> (**Chapter 5**)
- Bongaerts P, **Pérez-Rosales G**, Radice VZ, Eyal G, Gori A, Gress E, Hammerman NM, Hernandez-Agreda A, Laverick J, Muir P, Pinheiro H, Pyle RL, Rocha L, Turner JA, Booker R. (2019) Mesophotic. org: a repository for scientific information on mesophotic ecosystems. *Oxford Database*. baz140
<https://doi.org/10.1093/database/baz140> (**Appendix 1**)
- Rouzé H, Galand PE, Medina M, Bongaerts P, Pichon M, **Pérez-Rosales G**, Torda G, Moya A, Raina JB, Hédouin L. (2021) Symbiotic associations of the deepest recorded photosynthetic scleractinian coral (172 m depth). *The ISME journal*. 15(5):1564-8. <https://doi.org/10.1038/s41396-020-00857-y> (**Appendix 2**)
- Hédouin L, Rouzé H, Berthe C, **Pérez-Rosales G**, Martinez E, Chancerelle Y, Galand PE, Lerouvreur F, Nugues MM, Pochon X, Siu G. (2020) Contrasting patterns of mortality in Polynesian coral reefs following the third global coral bleaching event in 2016. *Coral Reefs*. 39(4):939-52.
<https://doi.org/10.1007/s00338-020-01914-w> (**Appendix 5**)
- Moritz C, Brandl SJ, Rouzé H, Vii J, **Pérez-Rosales G**, Bosserelle P, Chancerelle Y, Galzin R, Liao V, Siu G, Tairui M, Nugues M, Hédouin L. (2021) Long-term monitoring of benthic communities reveals spatial determinants of disturbance and recovery dynamics on coral reefs. *Mar. Ecol. Prog. S* 672:141-152. <https://doi.org/10.3354/meps13807> (**Appendix 4**)
- Carlot J, Rouzé H, Barneche DR, Mercière A, Espiau B, Cardini U, Brandl DJ, Casey JM, **Pérez-Rosales G**, Adjeroud M, Hédouin L, Parravicini V. (2022)

Scaling up calcification, respiration, and photosynthesis rates of six prominent coral taxa. *Ecology and Evolution*. <https://doi.org/10.1002/ece3.8613>

Recently accepted:

- **Pérez-Rosales G**, Pichon M, Rouzé H, Villeger S, Torda G, Bongaerts P, Carlot J, Under The Pole Consortium, Parravicini V, Hédouin L. Mesophotic coral ecosystems of French Polynesia are hotspots of alpha and beta generic diversity for scleractinian assemblages. Submitted to *Diversity & Distribution DDI-2021-0458.R3*. (Article DOI: 10.1111/ddi.13549) (**Chapter 2**)

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- **Pérez-Rosales G**, Hernandez-Agreda A, Rouzé H, Carlot J, Torda G, UTP consortium, Pichon M, Bongaerts P, Parravicini V, Hédouin L. Mesophotic depths hide unexpectedly high coral cover communities in French Polynesia. Submitted to *Science of the Total Environment STOTEN-D-22-08781* (**Chapter 3**)
- Raick X, Di Iorio L, Lecchini D, Gervaise C, Hedouin L, Under The Pole Consortium, **Pérez-Rosales G**, Rouzé H, Bertucci F, Parmentier E. Fish biophony of photic and mesophotic coral reefs: variation with depth and type of island. PNAS-2021-22038

In preparation:

- **Pérez-Rosales G**, Rouzé H, Bongaerts P, Bregere N, Carlot J, Torda G, UTP Consortium, Pichon M, Parravicini V, Hédouin L. Multidisciplinary mechanisms of light-dependent corals to live in the twilight zone. (**Chapter 4**)

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- *Figure 2.2: Depth distribution of the different genera pooled for the 16 study sites of French Polynesia. 'Other Fungiidae' represents genus such as Fungia, Danafungia and Lythophyllon that could not be visually identified. Violin plots show presence-absence and quantiles the mean of the density estimate. The grey background highlights the mesophotic depth range as traditionally delimited (30-150 m). Depth overlaps are higher considering a single presence-absence than considering ≥ 15 observations or ≥ 50 observations (Sup. Fig. S2.6) and pooling all sites together than separating between locations (Sup. Fig. S2.7).*

- *Figure 2.3: Heat map displaying the vertical β -diversity along the depth gradient and the turnover within sites between depths. (Left) Jaccard dissimilarity for the*

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- *Figure 2.4: Spatial β -diversity patterns at different depths. (Left) dissimilarity in composition (Jaccard computed on generic presence-absence). (Right) dissimilarity in dominance in the coral community structure (Bray-Curtis computed on percentage of coral genera). Spatial β -diversity is reflected in the size of the hull polygons. Genus labels are present only for coral genera with a percentage cover higher than 5%. Points indicate the different sites for the given depth. The increase in spatial β -diversity means that while shallow waters between sites are homogeneous (similar in genus composition and genus cover), mesophotic depths are unique (in composition and genus cover including for the dominant genera).*
- *Figure S2.1: Map of French Polynesia with the islands and sampling locations considered in this study. Coordinates are available in supplementary Table S1.*
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I. Chapter 1: General introduction

Coral Reefs and Mesophotic Coral Ecosystems

Scleractinian coral reefs are one of the most spectacular, diverse (Connell, 1978), wealthy (Hoegh-Guldberg, Pendleton and Kaup, 2019) ecosystems but at the same time one of the most threatened (Burke *et al.*, 2011; Hughes *et al.*, 2017) on Earth. Coral reefs are unique ecosystems with a natural heritage that cannot be lost. Despite covering < 0.1% of the ocean surface, coral reefs provide habitat for at least 25% of all already known (we know very little from the depths) marine species (*Census of Marine Life*, n.d.). Present in tropical and subtropical areas, many coastal societies have developed a high reliance on coral reefs for food security (Teh, Teh and Sumaila, 2013), coastal protection (Ferrario *et al.*, 2014) and as means of gaining livelihoods (Spalding *et al.*, 2017). The real number of people highly dependent on the goods and services produced by coral reef ecosystems is difficult to calculate, but estimations suggest more than 500 million worldwide (Burke *et al.*, 2011; Speers *et al.*, 2016). However, coral reefs are under severe threat from local and global disturbances, which risk the future of coral reefs, their associated marine life and the ecosystem services provided to humanity (Hoegh-Guldberg, Pendleton and Kaup, 2019).

The pillars and engineers of coral reefs are Cnidarian animals from the class Anthozoa and the order Scleractinia. The animal ‘polyps’ live in colonies and in symbiosis with single-celled dinoflagellates ‘*Symbiodiniaceae*’ inside their tissues. These symbionts use sunlight to power photosynthesis and transfer > 90% of the necessary energy to the coral host to live and construct their mineral (aragonitic) skeleton (Falkowski *et al.*, 1984; Muscatine, 1990). In return, the coral host provides shelter and access to nutrients (phosphate and ammonium), closing thereby a perfect symbiosis (Blackall, Wilson and Van Oppen, 2015). Under favourable environmental conditions, this symbiosis provides a large amount of energy for scleractinian corals to grow, reproduce and produce their calcium carbonate skeleton that, together with other calcifying organisms, *e.g.*, calcareous green and red algae, invertebrates and protists, construct the three-dimensional framework of coral reefs (Muscatine, 1990; Kennedy *et al.*, 2013).

However, changing environmental conditions can break the mutualistic relationship between the coral host and its endosymbiotic algae (increasing the concentration of toxic by-products, responding to stress) (Brown, 1997; Baird *et al.*, 2009). When it happens, corals start turning white due to the loss of symbionts in a process known as coral bleaching (Hoegh-Guldberg, 1999). Bleached corals are not dead yet, they are under a disease state, but if corals persist without their symbionts for a prolonged time, it results in starvation and death, which is followed by the growth of external turf algae on their white skeleton (Suggett and Smith, 2020). With the death of scleractinian corals, phase shifts to algal dominated reefs may occur (Hughes *et al.*, 2007). Such shifts compromise the persistence of coral reefs through “carbonate imbalance” between reef construction and de-calcification, loss of structural complexity and associated life and ecosystem functions (De’ath, Lough and Fabricius, 2009; Kennedy *et al.*, 2013; Graham, 2014; Darling *et al.*, 2017).

Due to the light-dependency of scleractinian corals (*i.e.*, to make photosynthesis by their symbionts), it was thought that most scleractinian coral reefs occurred close to the surface where light availability is high (down to approximately 30 m). However, studies revealed that photosynthetic scleractinian corals can live in much deeper waters than 30 m. Below the better known shallow coral reefs, we find Mesophotic Coral Ecosystems (MCEs) (Loya, Puglise and Bridge, 2019). MCEs occur in tropical and subtropical waters of the oceans between depths of roughly 30 and 150 m (Ginsburg, 2007; Puglise *et al.*, 2009; Hinderstein *et al.*, 2010). Their denomination comes from the Greek words Μέσος (“*meso*”: middle) and φωτεινός (“*photic*”: light), and therefore we also refer to them as the coral ecosystems of the ‘Twilight zone’. Despite decreasing available light with depth, these ecosystems are largely dominated by the presence of light-dependent scleractinian corals (Pyle and Copus, 2019) and other anthozoans (**Fig. 1.1**).

From now on, when we think about coral ecosystems, we need to consider the shallow coral reefs (< 30 m) but also the deeper MCEs. MCEs are sometimes arbitrarily ‘divided’ into the upper MCEs (30 to 60 m) and lower MCEs (60 to 150 m). The upper imaginary boundary usually corresponds to the limits of traditional scuba diving, while the lower imaginary boundary is supposedly marked by a faunal break around 60 m (Hinderstein *et al.*, 2010; Kahng, Copus and Wagner, 2014). Yet, animals inhabiting in MCEs are not recognising or ignore these human-created “boundaries”, and they are

likely going across (Pyle and Copus, 2019). Due to our lack of knowledge and their suggested potential role as a ‘refugia’ under climate change and other disturbances, these ecosystems have received growing attention from coral scientists in recent years (Bridge *et al.*, 2013; Bongaerts *et al.*, 2019 - **Appendix 1**). However, most MCEs remain largely unexplored.

Coral reefs are presently facing an unprecedented crisis and are disappearing worldwide (Hughes *et al.*, 2017). The main reasons for coral mortality today are mass coral bleaching events triggered by rising sea surface temperatures due to human-induced global warming (Hoegh-Guldberg, Kennedy, *et al.*, 2018; Intergovernmental Panel on Climate Change (IPCC) - AR6, 2021; Magnan *et al.*, 2021). Bleaching events are currently having devastating effects on coral reefs worldwide (Hughes, Anderson, *et al.*, 2018; Hughes, Kerry, *et al.*, 2018; Sakai, Singh and Iguchi, 2019; Sully *et al.*, 2019; Jones *et al.*, 2021; Richards, Juszkiwicz and Hoggett, 2021). Still, coral reefs are also affected by numerous other natural and anthropogenic disturbances such as overfishing, water pollution (including eutrophication caused by nutrients run-off), Crown Of Thorns (COTS) starfish outbreaks, loss of habitat, increasing strength and severity of storms, marine invasions of exotic marine species and ocean acidification (Salvat (ed), 1987; Hoegh-Guldberg *et al.*, 2007; Hughes *et al.*, 2017; Bellwood *et al.*, 2019). Consequently, 14% of shallow coral reefs worldwide have been lost in the last ten years, according to the Global Coral Reef Monitoring Network (GCRMN) report (Souter *et al.*, 2021). Other studies suggested coral cover has declined by around 50% since the early 1980s in multiple locations (Gardner *et al.*, 2003; Bruno and Selig, 2007; De’ath *et al.*, 2012; Hughes, Anderson, *et al.*, 2018). This loss threatens the unmeasurable ecosystem services coral reefs provide to human well-being (Moberg and Folke, 1999; Woodhead *et al.*, 2019). Additionally, the future projections are rather pessimistic (Hoegh-Guldberg, Jacob, *et al.*, 2018; Hoegh-Guldberg, Pendleton and Kaup, 2019). Nevertheless, the presence of deeper scleractinian coral assemblages in MCEs might provide hope because we still do not know whether these disturbances equally affect MCEs or to what level they do.

Importance of MCEs with global changes

The traditional image of shallow coral reefs is just the tip of the iceberg of what is hidden underneath. Indeed, current estimates suggest that 80% of the total area of coral ecosystems worldwide is present in MCEs (Pyle and Copus, 2019). After many years of ignoring their importance (largely due to the sheer ignorance of their existence), MCEs started receiving growing attention from coral scientists during the last 30 years (Bongaerts *et al.*, 2019 - **Appendix 1**). An interest that was driven by the loss of shallow coral reefs (Hughes *et al.*, 2017) and by their potential role as deep refugia (the Deep Reef Refugia Hypothesis, DRRH) for shallow waters species (Glynn, 1996; Bongaerts *et al.*, 2010). The DRRH states that deep reefs may act as ‘refugia’ against major disturbances (*e.g.*, coral bleaching, overfishing) and could provide a source of larvae to reseed decimated shallow reefs (Bongaerts and Smith, 2019). The hypothesis is based on two main assumptions: (1) Mesophotic corals are less affected by local and global perturbations than shallow corals and (2) if mortality occurs on shallow reefs, the mesophotic corals, *a priori* still alive, could potentially replenish the shallows by providing a source of larvae that will recruit on the shallower reefs. Although I provide an example on corals, this hypothesis might also be true for some other taxa. Despite numerous efforts to assess the validity of the DRRH (Smith *et al.*, 2016; Bongaerts *et al.*, 2017; Semmler, Hoot and Reaka, 2017; Montgomery *et al.*, 2021), the current outcomes are still in debate and the ‘refugia’ might be limited to particular locations and species from different types of taxa (Bongaerts and Smith, 2019).

In any case, the interest of MCEs also relies on (a) the discovery of new species; (b) the potential contribution of MCEs as biodiversity hotspots, sanctuaries and bleaching safeguards (Baird *et al.*, 2018; Muir *et al.*, 2018; Montgomery *et al.*, 2021; Hernandez-Agreda *et al.*, 2022); (c) the presence of a vast amount of only thought as shallow species inhabiting these MCEs (Rocha *et al.*, 2018); and (d) the need to understand the functionality and ecological role of MCEs (Turner *et al.*, 2019) to the overall coral reef resilience. The answer to all these hypotheses could prove the importance of considering MCEs in the systematic conservation planning and management of coral reefs (Bridge *et al.*, 2013).

Environmental characteristics of Mesophotic Coral Ecosystems

Most coral reefs and MCEs occur in clear tropical and subtropical oligotrophic waters with high light penetration (Couce, Ridgwell and Hendy, 2012; Pyle and Copus, 2019). These sites are usually situated far from coastal water pollution and upwellings regions (*i.e.*, with high plankton, nutrients and dissolved matter). Although most MCEs remain poorly known, the current knowledge on how the environment and geomorphology influence associated benthic communities are summarised in Kahng *et al.* (2019) and Sherman *et al.* (2019), respectively.

For light-dependent organisms such as scleractinian corals, available light (*i.e.*, Photosynthetic Active Radiation (PAR)) becomes a limiting factor in depth (Kahng *et al.*, 2019). Light attenuates with increasing depth following Beer-Lambert law (Gordon, 1989). The law $PAR_z = PAR_0 \times e^{-Kz}$ says that the light available at depth z (PAR_z) depends on the light at a reference point (PAR_0 ; usually the surface) and a light attenuation coefficient (K) (Fricke and Schuhmacher, 1983; Kirk, 1994; Kahng *et al.*, 2019). There is a correlation between the water clarity by location and the observed lower depth distribution limits of light-dependent corals and other animals (Kahng *et al.*, 2019; Muir and Pichon, 2019; Pyle and Copus, 2019).

Low temperatures might also limit the development of MCEs. Most scleractinian corals require seawater temperatures above 14–18°C for survival (Done, 2011). These temperatures already limit most shallow coral reefs and MCEs to the tropical and subtropical regions (Bellwood *et al.*, 2005). In the ocean, seawater temperatures tend to decrease with depth because the water column is stratified in different density levels, according to temperature and salinity (Talley *et al.*, 2011). However, this decrease is not always noticed because the thermocline can be at deeper than the lower limits of MCEs (approximately 150 m). For instance, far from equatorial regions decreasing temperature show steeper declines with depth than in the tropics because thermoclines are usually shallower at higher latitudes (Fiedler, 2010; Pyle and Copus, 2019). It was believed that temperatures were less variable with increasing depth because of a lower effect of diurnal, seasonal, and climatic variations (Muir and Pichon, 2019). However, several oceanographical processes can cause important water column mixing in deeper depths, such as the internal gravity waves, which result in considerable and rapid temperature

fluctuations (Wolanski and Delesalle, 1995; Harris *et al.*, 2012; Kahng *et al.*, 2019; Wyatt *et al.*, 2020). These variations might expose at depth corals to temperatures beyond their lower tolerance limits (Kahng, Wagner, *et al.*, 2012) or eventually act to release heat during a bleaching event (Wall *et al.*, 2015; Schmidt *et al.*, 2016; Reid *et al.*, 2019; Wyatt *et al.*, 2020). Therefore, temperature regimes can to a variable extent limit the maximum depth of coral growth (Bongaerts, Frade, *et al.*, 2015) and of other benthic communities.

Additionally, geomorphological factors (e.g., a lack of suitable substrate) likely influence MCEs' development. Overall, the substrate type and the seafloor bathymetric slope are defined as the most important variables in determining the distribution of MCEs organisms (Sherman *et al.*, 2010, 2019; Bridge *et al.*, 2011). Most scleractinian corals creating MCEs need hard substrate to settle, and this is most often provided by limestone from ancient coral reefs (Hopley, 1982; Sherman *et al.*, 2019). Conversely, the accumulation of sediments is detrimental to their development (Hubbard, 1986; Liddell and Ohlhorst, 1988; Bridge *et al.*, 2011; Sherman *et al.*, 2016, 2019). These sediments come in part from the erosion of shallow coral reefs because of waves, storms and biological activity (e.g., parrotfishes) and are like a "snowfall" in MCEs, which can eventually end up covering and burying corals (Muir *et al.*, 2015; Sherman *et al.*, 2019).

Community composition of Mesophotic Coral Ecosystems

The upper and lower depth limits MCEs communities are likely influenced by environmental factors (Kahng *et al.*, 2019). Yet, they also respond to biotic interactions e.g., competition for space (Chadwick and Morrow, 2011). For photosynthetic light-dependent benthic taxa such as scleractinian corals and macroalgae diversity and abundance should decrease with depth (Kahng and Kelley, 2007; Bridge, 2016; Kahng *et al.*, 2019; Muir and Pichon, 2019; Spalding, Amado-Filho, *et al.*, 2019). Conversely, diversity and abundance of sessile heterotrophic or less light-dependent taxa, supposed to go deeper than scleractinian corals, should increase with depth to a certain depth of maximum richness and then decrease (Kahng and Kelley, 2007; Bridge *et al.*, 2012; Kahng *et al.*, 2019). Therefore, the typical benthic composition of MCEs should be dominated by: sponges, azooxanthellate octocorallia (gorgonians), hydroids and antipatharia (black corals) (Calder, 2000; Bridge *et al.*, 2012; Reed *et al.*, 2017; Benayahu *et al.*, 2019; Bo *et al.*, 2019; Sanchez *et al.*, 2019). Even macroalgae (some of which

forming occasionally rhodolith beds), can extend deeper than corals (Spalding, Amado-Filho, *et al.*, 2019). According to the number of studied locations, mesophotic ecosystems with high zooxanthellae scleractinian cover remain very low (Pyle and Copus, 2019), yet some MCEs have been described with high (40-90%) coral cover between 60-120 m (Kinzie, 1973; Zlatarski and Estalella, 1982; Zlatarski, 2007; Eyal *et al.*, 2016; Hoeksema, Bongaerts and Baldwin, 2017)



Figure 1.1: Comparison between shallow reefs and Mesophotic Coral Ecosystems in French Polynesia at approximately 80 m. (Copyright top: Lauric THIAULT. Bottom: Gilles SIU).

Regarding the depth distributions, the majority of taxonomic groups or species are not equally abundant along the entire depth range. Many efforts have been invested in defining the particular depth ranges to determine species overlap (Laverick *et al.*, 2018; Montgomery *et al.*, 2021) and relate results to the DRRH (Bongaerts and Smith, 2019). However, most of these limits are influenced by our lack of knowledge. Nevertheless, comparing the community composition between shallow reefs and MCEs (“the 30 m

boundary”) is still one of the most studied topics in mesophotic research, especially for benthic communities such as scleractinian corals (Semmler, Hoot and Reaka, 2017; Laverick *et al.*, 2018; Rocha *et al.*, 2018). For corals, 96% and 82% of known shallow species are also present in MCEs in the Caribbean and the Indo-Pacific, respectively (Muir and Pichon, 2019).

Physiological acclimations and adaptations of scleractinian corals to depth

Light-dependent scleractinian corals living in MCEs have to deal with the decreasing light availability along the reef slope (Muir and Pichon, 2019). Among all zooxanthellae scleractinian corals, there is a vertical structuring where encrusting and laminar specimens, best adapted to inhabit MCEs, replace branching and massive specimens with depth (Fricke and Schuhmacher, 1983; Kramer *et al.*, 2020, 2021; Lesser *et al.*, 2021).

However, individual coral species can also use multiple strategies of traits to acclimate and adapt to different conditions of light availability (Kahng *et al.*, 2019). These eco-physiological capacities allow some coral species to be present in a broad depth range, while restricting some others to much-limited depth ranges (Madin, Anderson, *et al.*, 2016; Muir and Pichon, 2019). Yet, these mechanisms are still unclear because they vary with and within species and regions (Kahng *et al.*, 2019). For example, some species are known to increase zooxanthellae density, chlorophyll concentrations and even switch between symbiotic communities to prioritise photosynthetic pigments more efficient with depth (Wyman *et al.*, 1987; Lesser *et al.*, 2010; Mass *et al.*, 2010; Kahng *et al.*, 2019; Padilla-Gamiño *et al.*, 2019). Additionally, colonies of the same species can modify their skeleton, flattening and growing in more laminar forms, decreasing tissue thickness and modifying polyps size and density with depth to maximise light exposure (Kahng *et al.*, 2020; Kramer *et al.*, 2021; Lesser *et al.*, 2021; Malik *et al.*, 2021). This morphological plasticity explains why individuals of the same species can be branching in the surface and corymbose or encrusting at mesophotic depths (Todd, 2008; Einbinder *et al.*, 2009; Nir *et al.*, 2011). Furthermore, a growing body of literature on results derived from the use of isotopic techniques (especially in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) suggests that corals can modify their trophic strategies by switching to a more active feeding heterotrophy. This trophic plasticity allows corals to rely less on photosynthesis when light is limited (Fricke,

Vareschi and Schlichter, 1987; Farquhar, Ehleringer and Hubick, 2003; Williams *et al.*, 2018; Watanabe *et al.*, 2019) and has also been suggested for bleaching corals (losing symbionts) during thermal stress (Fox *et al.*, 2019; Wall *et al.*, 2019; Conti-Jerpe *et al.*, 2020).

In addition to these acclimation and adaptation strategies, corals might change their physiological priorities when living under minimal light conditions. Some studies suggest that corals minimise their energetic investments to grow, calcify and reproduce (Barnes and Chalker, 1990; Mass *et al.*, 2007; Shlesinger and Loya, 2019) because they need to keep available energy to survive at such depths. The outcomes of transplanting experiments implemented to test these hypotheses are still unclear (Kahng *et al.*, 2019). The physiological acclimations and adaptations of scleractinian corals to depth are still poorly understood because of the intra- and inter-species variability that make them not respond in a uniform manner. In addition, there is a lack of studies conducted deeper than 60 m depth, and the deepest limits for scleractinian corals are still ongoing (Maragos and Jokieli, 1986; Kahng and Maragos, 2006; Rouzé *et al.*, 2021 - **Appendix 2**).

Study of Mesophotic Coral Ecosystems worldwide

Despite the growing interest in recent years (Bongaerts *et al.*, 2019 – **Appendix 1**), most MCEs remain unexplored (Pyle and Copus, 2019). Although there is no argument to justify the lack of knowledge about the ocean depths, the problem with MCEs lies in their extremely difficult direct access (Pyle, 2019). MCEs are too deep for traditional scuba diving and the deployment of small manned submersibles is limited by their availability and high operating costs. Yet, much of the early research on MCEs were carried out by small submersibles, *e.g.*, ‘Yomiyuri-Go’ in Japan, ‘Geo’, and then ‘Iago’ in the Gulf of Eilat (Israel), Bermuda, and Mayotte (France), *SP 350* in Australia, ‘Makali’i’, ‘Pisces *V*’ and several others in Hawaii and Johnston atoll, ‘Nekton beta’ and ‘Nekton gamma’ in the tropical Atlantic, and the more recent ‘Curasub’ in the Dutch West Indies (Pyle, 2019) (**Fig. 1.2**). Other research was carried out by traditional scuba diving beyond the safety limits.

However, recent advances in diving technologies allow easier access to MCEs (Pyle, 2019). Today, most of the research on MCEs is carried out using rebreathers diving (Bongaerts *et al.*, 2019 – **Appendix 1**) with TRIMIX (Helium, Nitrogen and Oxygen) gases (**Fig. 1.2**). This TEK diving allows scientists to go deeper and stay longer (*i.e.* bottom time) than traditional Scuba Diving while decreasing the risks of decompression accidents. Simultaneously, other devices such as Remoted Operated Vehicles (ROV), Autonomous Underwater Vehicles (AUV), manned submersibles, and other technological platforms deployed from the surface are offering the possibility to better explore and study MCEs (Pyle, 2019).

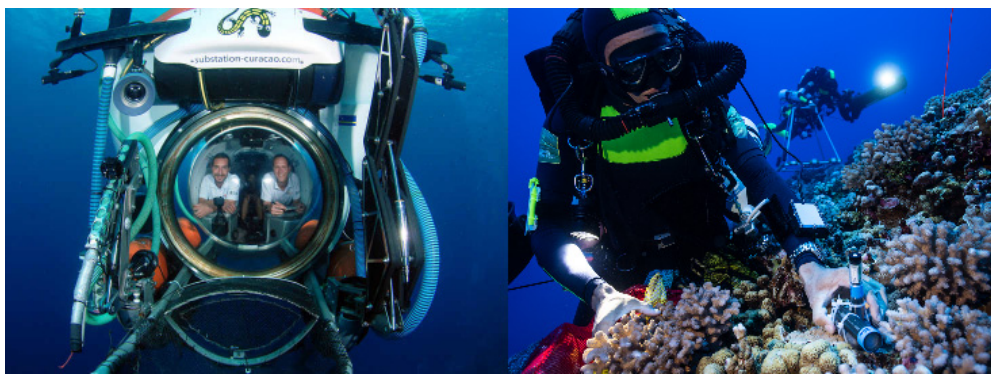


Figure 1.2: Underwater technologies for MCEs research. (Left) Submersible Curaçao (Copyright: Barbara van Bebber - Substation Curaçao). (Right) Closed-circuit-rebreather (Copyright: Franck GAZZOLA / UNDER THE POLE / Zeppelin Network).

This convergence between the potential importance of MCEs and the new technologies led to a sharp increase in their studies in recent years (Bongaerts *et al.*, 2019 – **Appendix 1**). However, this increase occurred specifically in a limited number of locations, such as the Gulf of Eilat (Israel) (Eyal *et al.*, 2019), the Great Barrier Reef (Australia) (Bridge *et al.*, 2019), Curaçao (Dutch West Indies) (Frade *et al.*, 2019), the Ryukyus (Japan) (Sinniger *et al.*, 2019) and some American islands (Puerto Rico (Appeldoorn *et al.*, 2019), US Virgin Islands (Smith *et al.*, 2019) and Hawaii (Spalding, Copus, *et al.*, 2019)). Conversely, several other major reef locations, *e.g.*, Indonesia, The Philippines, Papua New Guinea, The Maldives, and many tropical archipelagos in the Pacific, including *e.g.*, Kiribati, Cook Islands, Tuvalu, Tonga, Fiji, Marianas or Solomon Islands clearly lack studies (Loya, Puglise and Bridge, 2019), except for American Samoa (Montgomery *et al.*, 2019) and Palau (Colin and Lindfield, 2019).

Coral reefs and Mesophotic Coral Ecosystems in French Polynesia

French Polynesia is located between 07°50' S, 27°55' S, 134°28'W, 154°42'W in the South Pacific Ocean. It covers an area of 2,500,000 km², representing a size similar to the European continent and consists of 118 islands from five archipelagos (Society, Tuamotu, Marquesas, Gambier and Austral). The islands present multiple geomorphologies, from high volcanic islands to atolls. Except for the Marquesas Islands, all islands are surrounded by barrier or fringing coral reefs.

The coral reef research in French Polynesia is paradoxical. Although the shallow coral reefs of French Polynesia are well studied (Chevalier, 1980; Kühlmann and Chevalier, 1986; Adjeroud *et al.*, 2012; Collin *et al.*, 2014; Vercelloni *et al.*, 2019; Pérez-Rosales, Brandl, *et al.*, 2021 - **Appendix 3**). This applies in particular to Moorea, which is one of the most studied islands in the world (Galzin, Martin and Salvat, 1993; Adjeroud *et al.*, 2002, 2009; Penin *et al.*, 2007; Edmunds, Leichter and Adjeroud, 2010; Kayal *et al.*, 2012; Holbrook *et al.*, 2018; Moritz *et al.*, 2021 - **Appendix 4**), the knowledge of MCEs is limited (Pichon, 2019). From the high amount of studies conducted in shallow reefs (*i.e.*, most of them restricted to the lagoons or to a maximum depth of 30-40 m on the reef slopes), we know today that French Polynesia is home to ~210 species of zooxanthellae scleractinian corals and ~600 species of fish (Bellwood and Hughes, 2001; Bellwood *et al.*, 2005). These numbers correspond to the global patterns of coral reef species that decrease with distance from the “coral triangle”, where the hot-spot of maximum coral reef biodiversity (> 620 species of corals and > 1,300 species of fish) of the Indo-Pacific occurs (Bellwood and Hughes, 2001; Bellwood *et al.*, 2005).

Although most research was carried out in Moorea (Aires Marines Protégés, [AMP](#) or Long Term Ecological Research, [LTER](#)) or the surrounding islands of the Society and somehow the Tuamotus, there are some on-going monitoring programs across archipelagos ([Polynesia Mana](#)). Long-term data series allowed to study multiple disturbances such as COTs, cyclones and bleaching events (Adjeroud *et al.*, 2009; Kayal *et al.*, 2012; Hédouin *et al.*, 2020 - **Appendix 5**; Pérez-Rosales, Brandl, *et al.*, 2021 - **Appendix 3**). Yet, it also allowed scientists to remark on the extraordinary recovery capacity of corals. After an episode of COTs (2006-2008) followed by a cyclone in 2010 (Kayal *et al.*, 2012b), corals were practically absent (1-5%) at ~12 m in the outer reefs of

some islands from the Society Archipelago in 2012. Then, corals showed an extraordinary recovery capacity, reaching pre-disturbance or even higher cover levels (40-60%) in 2016-2018 (Adjeroud *et al.*, 2018; Pérez-Rosales, Brandl, *et al.*, 2021 - **Appendix 3**). Although corals came back, these reefs were not exempt from significant community shifts questioning resilience (Berumen and Pratchett, 2006). Notably, the rise of *Pocillopora* as the new dominant genus (replacing *Acropora*) due to the high contribution (84%) of the total recovery, which raised questions about the origin of new coral recruits (Tsounis and Edmunds, 2016; Pérez-Rosales, Brandl, *et al.*, 2021 - **Appendix 3**). One of the potential explanations was related to the DRRH (Bongaerts *et al.*, 2010), with new coral larvae coming from deeper reefs. However, this question remains hitherto unanswered.

The state of knowledge of MCEs of French Polynesia before 2019 is somewhat behind that of Eilat or Hawaii but well ahead of neighbouring archipelagos in the Southern Pacific. Until 2018, only a few studies in MCEs had been carried out in Polynesian waters. The state of knowledge was summarised in the chapter *French Polynesia* of the Springer book ‘*Mesophotic Coral Ecosystems*’ (Pichon, 2019) and key results are presented below (Table 1.1). According to Pichon (2019), except for scattered information in the literature, available pictures of Gilles Siu (**Fig. 1.3**) and some unpublished data collections from the French National Museum of Natural History, the deeper zone below 80 m was mostly unknown (except for incidentally dredging data). Yet, from the total number of zooxanthellae scleractinian species, around 45% (96 out of 210 species) were present between 30 and 60 m and just below 6% (14 out of 210 species) deeper than 60 m, with similar results to what is known for other close areas in the Indo-Pacific (Muir *et al.*, 2018). Nevertheless, the author agrees that these results are likely to be slightly (moderately) increased if more research is conducted on the MCEs of French Polynesia.

According to the Springer Chapter (Pichon, 2019) and mesophotic.org (Bongaerts *et al.*, 2019 - **Appendix 1**), **Table 1.1** presents the references, depths, locations, focus groups, platforms and main findings of – to the best of my knowledge –, all available literature from the MCEs (30-150 m) in French Polynesia before the start of this thesis.

Table 1.1: Literature from MCEs (30-150 m) in French Polynesia before 2018-2019. ^a indicates the only missing references in the Springer Chapter French Polynesia (Pichon, 2019) because they were not about benthic community structure. Further information and the depth zonation of the known species are available in (Pichon, 2019 - Table 24).

Reference	Depths (m)	Location (Archipelago)	Focus groups	Platforms	Main findings
(Abbey <i>et al.</i> , 2011) ^a	Variation in deglacial coralgal assemblages and their paleoenvironmental significance: IODP Expedition 310, "Tahiti Sea Level" 45-122	Tahiti (Society)	Scleractinia	Drilling/Paleo	Paleoecology of ecology
(Adjeroud <i>et al.</i> , 2012)	Les coraux scléactiniaux de l'Île de Rapa (Polynésie Française) Rapport IRD 123 p 3-56	Rapa (Austral)	Scleractinia	Scuba diving	Descriptions of species
(Bertucci <i>et al.</i> , 2017) ^a	Snapshot recordings provide a first description of the acoustic signatures of deeper habitats adjacent to coral reefs of Moorea 10-100	Moorea (Society)	General	Acoustics	Sounds decreased with depth
(Bouchon, 1983)	Les peuplements de scléactiniaux de l'atoll de Takapoto (Polynésie française) 1-40	Takapoto (Tuamotu)	Scleractinia	Scuba diving/or unspecified	Agariciidae (<i>Leptoseris</i> and <i>Pachyseris</i>) at 40 m
(Chevalier, 1974)	Aperçu sur les scléactiniaux des Îles Gambier 1-75	(Gambier)	Scleractinia	Scuba diving	Zone of <i>Pachyseris "speciosa" spp.</i> from 25 m
(Chevalier, 1980)	La faune corallienne de l'Île de Tubuai (Archipel des Australes) 1-150	Tubuai (Austral)	Scleractinia	Likely scuba diving and dredging	<i>Leptoseris hawaiiensis</i> at 150 m <i>Echinopora lamellosa</i> , <i>L. hawaiiensis</i> , <i>L. fragilis</i> and <i>Cycloseris wellsi</i> at approximately 100 m
(Chevalier and Kühlmann, 1983)	Les scléactiniaux de Moorea Île de la Société (Polynésie française) 1-45	Moorea (Society)	Scleractinia	Scuba diving	Depth zonation and description of species
(Chevalier <i>et al.</i> , 1986)	Étude géomorphologique et bionomique de l'Atoll de Mururoa (Tuamotu) Unknown	Mururoa (Tuamotu)	Unknown	Unknown	Unknown
(Faure and Laboute, 1984)	L'atoll de Tikehau, Premiers résultats: Formations récifales, 1-Définition des unités récifales et distribution des principaux peuplements de Scléactiniaux. 1-70	Tikehau (Tuamotu)	Scleractinia	Scuba diving	<i>Pachyseris "speciosa" spp.</i> at 45. Below 60-70 m, <i>Leptoseris</i> and <i>Echinophyllia</i> . Confirm <i>Leptoseris</i> deeper than 90 m

Faune corallienne des Iles Rapa et Marotiri Polynésie Française (Iles Australes) in : "Rapa"					
(Faure, 1986)	1-55	Rapa (Austral)	Scleractinia	Scuba diving	Deeper platform corresponds to <i>Leptoseris</i> , <i>Echinophyllia</i> , <i>Scolymia</i> and <i>Pavona</i> . Deeper, the zone of <i>Leptoseris</i>
(Gout, Bablet and Goutière, 1997)	The atolls of Mururoa and Fangataufa (French Polynesia).III The living environment and its evolution. Unknown	Mururoa and Fangataufa (Tuamotu)	Unknown	Unknown	Unknown
(Harmelin-Vivien and Laboute, 1986)	Catastrophic impacts of hurricanes atoll outer reef slopes on in the Tuamotu (French Polynesia). 1-40	Tikehau (Tuamotu)	Disturbances/ Community structure	Scuba diving	Impacts of cyclone on coral reef. Total destruction of <i>Pachyseris</i> laminar colonies by avalanche. High sedimentation also.
(Maritorena <i>et al.</i> , 2002) a	Photoacclimatization in the zooxanthellae of <i>Pocillopora verrucosa</i> and comparison with a pelagic algal community 1-40	Tahiti (Society)	Scleractinia	Scuba diving	Physiological acclimation of <i>P. verrucosa</i>
(Kühlmann and Chevalier, 1986)	The corals (Scleractinians and Hydrocorals) of the Takapoto Atoll, Tuamotu Islands: ecological aspects 1-70	Mururoa and Taiaro (Tuamotu)	Scleractinia and Hydrocorals	Scuba diving	Deep water species are <i>Leptoseris forosa</i> and <i>Fungia cf. granulosa</i>

Indeed, based on available results, French Polynesia might be a potentially key region for MCEs because of the geographical situation with clear waters and remote locations (but see fishing impacts (Roberts, 1995) and “lower” diversity due to global diversity patterns for scleractinian corals (Bellwood and Hughes, 2001; Bellwood *et al.*, 2005)). Nevertheless, prior to 2019, the deepest zooxanthellae scleractinian corals were observed at Johnston Atoll at 165 m (Maragos and Jokiell, 1986; Kahng and Maragos, 2006). Because of the similarities between the Hawaiian and Polynesian conditions remain noteworthy, there is a lot of hope for the potential of French Polynesia for MCEs. However, most MCEs of French Polynesia remain unexplored. The biogeography, maximum depths, diversity, community structure, ecology and physiology are still unclear, and assessments with quantitative data are also missing.

Figure 1.3: Mesophotic Coral Ecosystem landscape with a high presence of laminar scleractinian corals at approximately 70 m depth in French Polynesia (Copyright: Gilles SIU).



Thesis aims and outline

The primary aim of this thesis is to shed light and investigate the diversity, community structure and the potential ecological importance of MCEs to the overall Polynesian coral reefs. With a particular focus on scleractinian corals, I quantitatively studied the MCEs of French Polynesia using photo-quadrats and physiological analyses in an extensive vertical (from 6 to 120 m) and spatial scale (16 locations from up to 2,000 km away).

The overall hypotheses of my thesis were the following:

1. Test if scleractinian diversity decreases with depth along the slope. In other words, testing if the richest depths in terms of alpha (local richness) and beta (spatial comparisons) diversity are in shallow waters as expected for light-dependent corals.
2. Assess where are the depths and locations of the most scleractinian-covered MCEs in French Polynesia. Then, test if environmental variables could predict high scleractinian cover or other benthic communities in MCEs.
3. Test if the photophysiological (*e.g.*, symbiotic communities, photosynthetic pigments, micro-morphology) capacities increase with depth or, otherwise, there is a switch in the nutritional priorities towards heterotrophy to compensate for the low light availability.

4. Test if the prevalence of coral bleaching reduces with depth. Taking advantage of a thermal bleaching episode that impacted French Polynesia in 2019, we assessed coral bleaching impacts along the depth gradient to know if MCEs could act as thermal refugia.

Outline of this thesis

After in **chapter 1**, I introduced the generalities of coral reefs and Mesophotic Coral Ecosystems (MCEs) worldwide and the context for French Polynesia; in **chapter 2**, I examine how alpha and beta coral diversity patterns vary across the depth gradient in French Polynesia. More specifically, I aim to study the depth profiles of coral genus richness (alpha-diversity) and dominance. I estimate the vertical beta-diversity to display overlaps and turnover in communities between depths within sites. Finally, I assess the spatial beta-diversity to display similarity and uniqueness at given depths across locations.

Related to the precedent chapter, in **chapter 3**, I aim to identify and describe potential mesophotic coral communities with a higher coral cover than expected for the depth. Then, I evaluate how environmental factors might promote such high coral cover in mesophotic depths.

In **chapter 4**, I investigate how the endosymbiotic communities, photo-physiology, micro-morphology and nutritional plasticity change along the depth gradient to understand how corals live in such low-light environments.

In **chapter 5**, I test the hypothesis that bleaching impacts decrease with depth to know if MCEs could act as thermal refugia during heat stress events. While doing so, I assessed the bleaching susceptibility among genera over the depth gradient.

In **chapter 6**, I discuss the different outcomes of my research, with some additional preliminary results of the DEEPHOPE expedition (see next section “*The Expedition DEEPHOPE*”), to explain the community structure, ecology and physiology of the scleractinian corals living in MCEs of French Polynesia. Overall, I explain the potential ecological importance of MCEs to the ecosystem-wide coral reef resilience, and I discuss the potential need to consider MCEs for future systematic conservation planning of coral reefs in French Polynesia with climate change.

The expedition DEEPHOPE

To study the Mesophotic Coral Ecosystems of French Polynesia, a collaboration between Under The Pole (UTP) team and researchers from the CRIOBE, and other institutions, led to the DEEPHOPE Research Project funded by the ‘Agence Nationale de Recherche’ (ANR). The present thesis is part of the DEEPHOPE project. This multi-disciplinary program aimed to explore and study the understudied MCEs of French Polynesia on a broad geographical scale. More specifically, the objectives were to: (1) study the biodiversity and community structure of MCEs; (2) understand the physiological functioning of corals with depth, and (3) assess the potential role of MCEs as shallow refugia. Although being a pioneering project, in reality DEEPHOPE included a comprehensive study of the environment, taxonomy, ecology, adaptation, reproduction, nutrition, symbiosis and connectivity to understanding corals from mesophotic depths to the surface.

A 10-month expedition was carried out from August 2018 to July 2019 across 12 islands from the five archipelagos of French Polynesia (**Fig. 1.4**) (**Table 1.2**). During the expedition, over 800 TRIMIX Closed Circuit Rebreather dives to sample across a wide depth range at 6-120 m, with additional dives to 150 m and 175 m were realised. In total, we acquired a comprehensive genetic (~ 6,000 coral specimens [conserved in ethanol]), physiology (~ 250 specimens [conserved in liquid nitrogen at -80°C] – **Chapter 4**), taxonomic (~ 1,800 coral specimens [skeletons bleached]), ecological (~ 3,500 photo-quadrats [taken in high-definition with a Nikon D810 camera in Nautican Housing with 16 mm lens, 37.09-pixel and Keldan strobes] – **Chapters 2, 3, 5**) and environmental (*e.g.*, light [Advantech DEFI 2-L PAR loggers and CTD Midas Valeport 060-6001], temperature [loggers Hobo V2 and the same CTD], bathymetry [Lowrance HDS], nutrients and environmental DNA [Niskin bottle] – **Chapters 3, 4, 5**) repertoire database.

We tried to apply the same protocol to all sites during our data collection. The two sites per island were located on the outer slopes and selected randomly within the constraints imposed by the logistics of technical diving. At each site, we collected the data at the depths of 6, 20, 40, 60, 90 and 120 m, except for the Marquesas islands (stopped between 40-60 m) and Raivavae (Austral Archipelago) (missing 6 m and > 90

m). At each working depth, *in situ* environmental data was collected with loggers deployed for more than 48 hours and CTD profiles (except for Raivavae). The acquisition of photo-quadrats was following four randomly placed line transects of ten quadrats (0.75 x 0.75 m), capturing at least 30 exploitable quadrats, which means that for **chapters 2, 3 and 5**, I analysed a constant sampling effort of 16.8m² of the reef at each depth. The collected samples for the physiology consisted of at least six replicates for each of the two targeted species (*Pocillopora cf. verrucosa* and the complex genetic diversity species of *Pachyseris "speciosa" spp.*) per depth. It means that if, for **chapter 4**, there were no more replicates at particular depths (< 6), it was because specimens could not be found during the diving days. The genetic content for microbiome and connectivity studies was analysed on the same specimens used for the physiology studies and on at least 30 additional specimens (information not available in this thesis).

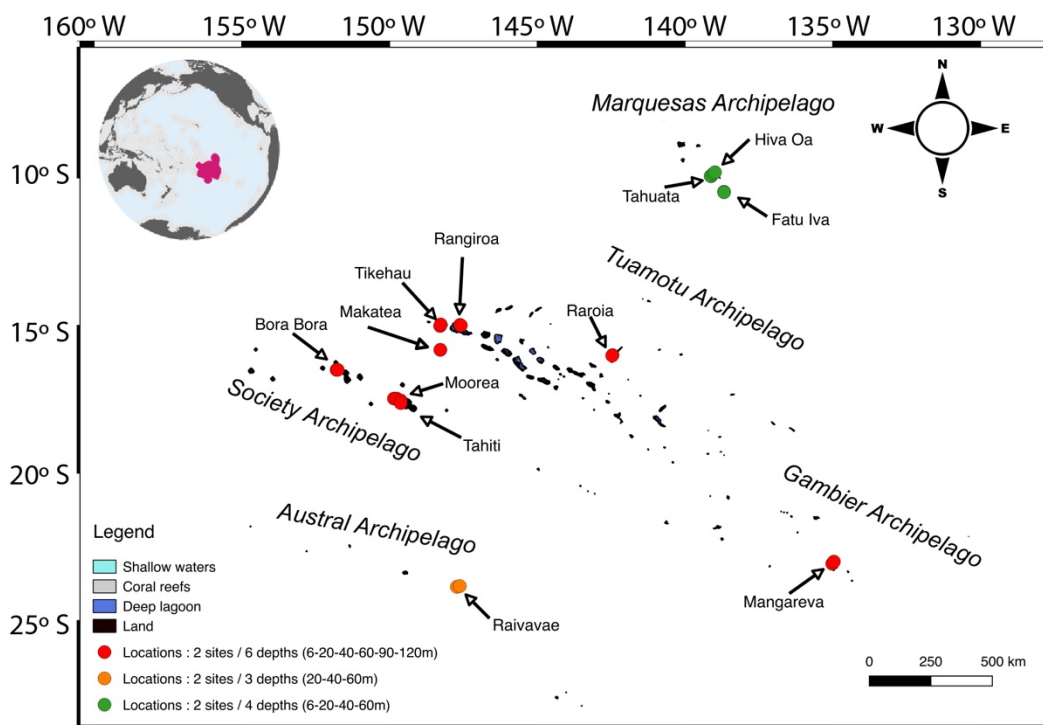


Figure 1.4: Map of French Polynesia with the locations and diving depths of the DEEPHOPE expedition. Exact coordinates for each site are available in Table 1.2.

Table 1.2: Coordinates of the studied locations of the DEEPHOPE expedition.

Survey Dates	Archipelago	Island	Site	Latitude (DDD.DDDD)	Longitude (DDD.DDDD)
Aug 2018	Society	Moorea	1	17.4772° S	149.8511° W
Sep 2018	Society	Moorea	2	17.4773° S	149.7696° W
Sep 2018	Society	Bora Bora	1	16.5031° S	151.7907° W
Sep 2018	Society	Bora Bora	2	16.4367° S	151.7536° W
Oct 2018	Tuamotu	Tikehau	1	15.0173° S	148.2867° W
Oct 2018	Tuamotu	Tikehau	2	14.9641° S	148.2671° W
Oct 2018	Tuamotu	Rangiroa	1	14.9803° S	147.6131° W
Nov 2018	Tuamotu	Rangiroa	2	14.9976° S	147.5843° W
Nov 2018	Tuamotu	Raroia	1	16.0052° S	142.4517° W
Jan 2019	Marquesas	Hiva Oa	1	9.8601° S	139.0443° W
Jan 2019	Marquesas	Hiva Oa	2	9.8085° S	138.9846° W
Jan 2019	Marquesas	Tahuata	1	9.9421° S	139.1195° W
Jan 2019	Marquesas	Tahuata	2	9.9367° S	139.1315° W
Feb 2019	Marquesas	Fatu Hiva	1	10.4717° S	138.6783° W
Feb 2019	Marquesas	Fatu Hiva	2	10.4883° S	138.677° W
Mar 2019	Tuamotu	Raroia	2	16.0231° S	142.4633° W
Mar 2019	Gambier	Gambier	1	23.0731° S	135.0162° W
Apr 2019	Gambier	Gambier	2	23.0010° S	134.9605° W
May 2019	Austral	Raivavae	1	-23.9441° S	-147.7514° W
May 2019	Austral	Raivavae	2	-24.03667° S	-147.6767° W
Jun 2019	Tuamotu	Makatea	1	15.8259° S	148.2797° W
Jun 2019	Tuamotu	Makatea	2	15.8230° S	148.2793° W
Sep 2019	Society	Tahiti	1	17.5422° S	149.6188° W
Sep 2019	Society	Tahiti	2	17.6295° S	149.6210° W

Thanks to the access by Under The Pole divers to mesophotic depths, I could collect the ecological (photo-quadrat and environmental) and physiological data to test my hypotheses and construct the different chapters of my PhD. However, the first necessary point to be commented on is that the Marquesas Islands and Raivavae (Austral Islands) were not further considered in this thesis. The main reason not to consider these

locations in the quantitative results is non-available data at particular depths. We could not collect data at these islands because either a sandy horizontal shelf extended a couple of miles from the coast, making it impossible to access at deeper depths or because meteorological conditions did not guarantee diving safety. Accordingly, I preferred to omit these locations (further reasons to exclude the Marquesas are provided in **chapter 6**) because the strongest characteristic of my data is the constant sampling effort at all depths and sites. Which is rare at mesophotic depths (Bongaerts *et al.*, 2019 - **Appendix 1**; Pyle and Copus, 2019; Roberts, Bridge, *et al.*, 2019) but hugely important for quantitative ecology assessments (Chen *et al.*, 2021).

II. Chapter 2: Coral diversity of MCEs in French Polynesia

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2.1. Abstract

Aim: Revealing how diversity varies across the depth gradient is key for understanding the role of mesophotic coral ecosystems in the functioning of coral reefs. We quantitatively examined how alpha and beta generic diversity of scleractinian coral assemblages vary across a wide depth gradient for coral reefs.

Location: Sixteen sites in eight islands of three archipelagos in French Polynesia.

Methods: We studied generic diversity patterns of scleractinian corals, as derived from the analysis of photo-quadrats, across the seafloor from shallow to lower mesophotic depths (6 to 120 m) and on a wide geographic scale. Our sampling considered quantitative coral cover to explore the patterns of alpha and beta components of diversity across depth and horizontal space.

Results: We show that in French Polynesia, mesophotic coral ecosystems host higher alpha and beta generic diversity than shallow reefs despite decreasing coral cover with depth. The variation of coral genus richness across the depth gradient is mainly driven by a mid-domain-effect with a peak at 40 m depth. At the same time, we found that the differences of coral genera across islands (spatial beta-diversity) increased steadily along the depth gradient.

Main conclusions: Our findings report the first quantitative results of coral cover and diversity from mesophotic coral ecosystems in French Polynesia and also present one of the few existing studies to examine the broad breadth of the mesophotic depth gradient. We demonstrate that mesophotic depths can host unexpectedly high generic richness of scleractinian coral assemblages. At the same time, we showed that increasing depth

increases the differences in generic diversity composition across islands, whereas shallow reefs are similar in between. While a single island could conserve shallow regional biodiversity, mesophotic depths containing the richest diversity require site-specific measures, suggesting that considering these mesophotic depths in conservation is necessary to maintain regional diversity.

Keywords: coral genus biodiversity, coral reefs, diversity patterns, mid-domain-effect, quantitative ecology, regional diversity, scleractinian diversity.

2.2. Introduction

Mesophotic Coral Ecosystems (MCEs) are the deeper counterpart of shallow reef ecosystems. They are characterised by the presence of light-dependent corals from the order Scleractinia and occur in the tropical and subtropical oceans between 30 to 150 m depth, in the twilight ocean's photic zone (Ginsburg, 2007). Our knowledge of the diversity and community composition of coral reefs decreases steadily with increasing depth (Bongaerts et al., 2019; Pyle & Copus, 2019). This decrease is due to the many significant technical and logistical challenges involved in quantitative sampling beyond compressed air SCUBA (self-contained underwater breathing apparatus) diving frontiers at mesophotic depths (Kahng et al., 2014; Sinniger et al., 2016). However, advancements in underwater and diving technologies (including Remoted Operated Vehicles and closed-circuit rebreathers; Pyle, 2019) enabled the discovery that MCEs are more widespread and biodiverse in terms of coral diversity than previously expected (Englebert et al., 2017; Muir et al., 2018; Muir & Pichon, 2019; Rocha et al., 2018). Given the contribution of the mesophotic zone to the total area of reef ecosystems (Bridge et al., 2013; Eyal & Pinheiro, 2020; Laverick et al., 2018; Pyle & Copus, 2019), it is crucial to understand the biological diversity and composition of coral assemblages across the depth gradient, from the upper to the lower limits of photosynthetic Scleractinia. Also, there is a need to comprehend how these gradients vary across locations in this depth zone. The interest in finding such patterns lies on revealing key depths for conservation planning.

A quantitative understanding of the complementary patterns of biodiversity is a major prerequisite for testing ecological predictions and implementing conservation planning (Gaston, 2000; Ferrier, 2002; He' and Legendre, 2002; Parravicini *et al.*,

2013)MacArthur, 1965; MacArthur & Wilson, 2001; Wang & Loreau, 2014). “Alpha (α)-diversity” measures biological diversity within a community (Whittaker, Willis and Field, 2001) and is useful in identifying biodiversity gradients. In contrast, the variation in composition between communities is called “beta (β)-diversity” or dissimilarity (Jost, 2007; Tuomisto, 2010; Meynard *et al.*, 2011). β -diversity measures how many taxa are shared between communities or compositional changes from one reference point to another (Azaele *et al.*, 2015; Harrison *et al.*, 1992; Nekola & White, 1999). These indices allow the study of diversity gradients and assessments of species turnover across horizontal and vertical depth gradients (Fontana *et al.*, 2020; da Silva *et al.*, 2018; Swenson *et al.*, 2011; Wang *et al.*, 2012).

Thus far, the patterns of α - and β -diversity of scleractinian corals across the entire depth gradient, from the upper to the lower limit of the photic zone, are little known and specific to a few locations. Diversity patterns of corals and fish have primarily focused on the spatial variation in shallow communities with less attention to depth gradients (Bellwood *et al.*, 2005; Bellwood & Hughes, 2001; Kusumoto *et al.*, 2020; McDevitt-Irwin *et al.*, 2021). Still, certain studies targeted depth gradients. Among others, some focused on fish (Beaman *et al.*, 2016; Brokovich *et al.*, 2008; Liddell & Ohlhorst, 1997; Rocha *et al.*, 2018), and some on corals (Beaman *et al.*, 2016; Englebert *et al.*, 2017; Laverick *et al.*, 2018; Madin *et al.*, 2016; Muir *et al.*, 2018; Muir & Pichon, 2019; Tamir *et al.*, 2019). However, most studies, especially on corals, were based on qualitative observations, depth distribution ranges and literature. To the best of our knowledge, excluding bibliographic meta-analysis merging observations from studies with different depths and sites, only a few surveys quantitatively assessed coral richness gradients from the shallows to mesophotic depths beyond 30 m. These showed that coral richness increased to a certain depth, between 10 and 40 m across locations, and then decreased. These surveys were between 1-40 m depths (Bouchon, 1983), 1-50 m (Roberts, Bridge, *et al.*, 2019; Roberts, Keith, *et al.*, 2019), 1-60 m (Sheppard, 1980), 5-85 (Laverick, Andradi-Brown and Rogers, 2017), and only two studies beyond 100 m depth, *e.g.*, between 5-100 m (Tamir *et al.*, 2019) and between 1-120 m (Liddell & Ohlhorst, 1988). Consequently, our understanding of reef functioning and conservation decisions are mainly based on data coming only from shallow coral reefs (Cinner *et al.*, 2016; Hedley *et al.*, 2016), with too few exceptions considering MCEs (*e.g.*, lionfish control measures) (Loya, Puglise and Bridge, 2019). This may be seen as a reasonable strategy because, as

a general rule, coral cover decreases with depth (Hoeksema et al., 2017; Kahng et al., 2010; Laverick et al., 2017, 2020). However, if the goal is preserving coral diversity, which correlates with coral reef health and functioning of the whole reef system (Baskett et al., 2010; Benkwitt et al., 2020; Duffy, 2009), the potential contribution of MCEs should be accounted for.

The determination of gradients in α -diversity are fundamental to understanding the ecological contribution of MCEs. At the same time, the assessment of vertical β -diversity along the depth gradient indicates potential taxonomic overlaps (or turnover) among coral assemblages at different depths (Semmler, Hoot and Reaka, 2017; Laverick *et al.*, 2018). For instance, quantifying taxonomic turnover across the depth gradient is essential to test for a potential role of MCEs as a deep reef refuge (Bongaerts et al., 2010, 2019; Bongaerts & Smith, 2019). Finally, the study of spatial β -diversity at given depths will inform the commonness and rarity of compositionally different communities within each site across depths and between different sites also across depths at regional scales. For all these reasons, the delineation of coral diversity patterns along the entire depth gradient seems critical to evaluate the inclusion of MCEs in future conservation planning (He' & Legendre, 2002; Kukkala & Moilanen, 2013; Margules & Pressey, 2000; McIntosh et al., 2017; Socolar et al., 2016).

In the present study, we assessed the diversity patterns of scleractinian corals along the depth gradient (bathymetric slope) and across spatial (geographic) scales in French Polynesia. We used a quantitative database (*i.e.*, 2,880 photo-quadrats from 6 to 120 m depth, from 16 sites of 8 islands with distances from 45 up to 2,000 km apart, covering sites across a total area of $\sim 1,500,000$ km²) at the genus level, where sampling effort was equal (same number of photo-quadrats) all along the depth gradient. Our aims were to (1) map the depth profiles of coral cover, generic richness (α -diversity) and generic dominance; (2) reveal the generic depth distribution; (3) assess the diversity patterns across the depth gradient to display overlaps and turnover in communities between depths (β -diversity within one site across depths); and (4) assess the spatial diversity patterns to display similarity and uniqueness between sites with depth (β -diversity at a given depth across sites).

2.3. Methods

Studying MCEs is challenging because of technical diving constraints (Pyle, 2019). Given our regional objectives, we selected the photo-quadrat technique as the best sampling strategy (Hill & Wilkinson, 2004). This passive high-definition image processing methodology allowed us to (1) keep a systematic sampling effort (Chen et al., 2021; Margules & Pressey, 2000) at any depth, independently of decompression diving limitations and (2) assess the genus diversity patterns of reef-building corals at any depth with the same observational bias. Using photo-quadrats allowed us to quantitatively assess coral communities down to 120 m depth but constrained us to accept collecting data at the genus level. We accepted this loss of taxonomic resolution because visual identification of corals to the species level remains complex in the field even through direct inspection. Additionally, previous studies have used similar generic diversity indexes to quantify β -diversity on coral assemblages (Ateweberhan & McClanahan, 2016) and to successfully inform conservation and management strategies (Hughes, Kerry, *et al.*, 2018; Darling *et al.*, 2019).

Sampling

As part of the DEEPHOPE scientific expedition, we analysed 2,880 photo-quadrats (0.75 x 0.75 m) from eight islands (Bora Bora, Makatea, Gambier, Moorea, Rangiroa, Raroia, Tahiti and Tikehau) from three archipelagos of French Polynesia collected from August 2018 to September 2019 (**Sup. Fig. S2.1, Table S2.1**). All sites were located on outer slopes, and on each island, two sites were selected randomly within the constraints imposed by the logistics of technical diving. We collected these quadrats at the isobaths of 6, 20, 40, 60, 90 and 120 m depths in collaboration with the Under The Pole team using TRIMIX Closed Circuit Rebreather. We randomly placed four line transects of ten meters at each working depth at both sides of a reference point. We photographed ten quadrats on each line (leaving a constant of 25 cm in between quadrats to avoid superposition), resulting in at least 40 photo-quadrats at each depth. We analysed 30 randomly selected quadrats from the available pictures at each depth using the software Photoquad (Version 1.4) (Trygonis & Sini, 2012). Photos were taken with a Nikon D810 camera in Nautican Housing, with a 16mm lens, a 37.09-pixel high-definition resolution and two Keldan strobes. For each photo-quadrat, we quantified (i) the presence-absence of all scleractinian coral genera to account for rare and small genera and (ii) percentage

coverage of scleractinian coral genera, as the proportion of points falling on each coral genus colony in a random stratified sampling point cloud of 75 points in each quadrat. When coral genera could not be identified, for instance, in juvenile corals, we classified them as ‘non-identified’ scleractinian coral, and in cases of lack of visual taxonomic criterion, to the family level (*e.g.*, some Fungiidae genera such as *Fungia*, *Danafungia*, *Lithophyllon* but not *Sandalolitha*, *Herpolitha* or *Pleuractis*). Generic identification was done following coral identification guides (Bosselle *et al.*, 2014; Kelley, 2016) and previous training and supervision from taxonomic experts, who also carried out preliminary on-board identifications. Hereafter, we called the presence-absence data “composition” and the percentage of the coral cover data “coral cover” or “genus cover”. We chose 75 points following recommendations of the available literature on photo-quadrats (Roelfsema *et al.*, 2021; Van Rein *et al.*, 2011) and previous tests to confirm quadrats were thoroughly analysed. Total generic richness at each site and depth was the sum of all unique genera among 30 quadrats (*i.e.*, the presence-absence of all genera for a constant sampling size of 16.8 m² of reef). The total percentage of coral cover at each quadrat was the proportion of points that fell on a scleractinian coral. The total percentage of coral cover at each site and depth was the mean (with standard error) among all 30 quadrats.

Comparing diversity metrics at genus vs species level

To test whether genus level patterns of diversity were representative of species level patterns, we calculated Pearson and Spearman correlations between these two taxonomic levels in three external open-access published databases (Roberts, Bridge, *et al.*, 2019, Roberts, Keith, *et al.*, 2019; Rocha *et al.*, 2018) (**Sup. Fig. S2.2**). For all cases, we found high correlations > 0.95 , demonstrating that the genus level was highly representative of species level. Accordingly, we considered our results at the genus diversity patterns as a proxy for the species diversity patterns (Balmford *et al.*, 1996; Heino & Soininen, 2007).

Depth variation in coral cover, α -diversity, dominance and distribution

We tested the relationship between coral cover and depth using Bayesian regression models (Table S2.2). In the model, the response variable was coral cover (as the proportion of points falling on a coral according to the total number of points (trials)). The predictor was depth as a numeric variable. The model specified random intercepts

for each site (1|site) and used the Binomial family with the R package ‘brms’ (P. C. Bürkner, 2017). The model converged ($R^2 = 0.542$, $R_{hat} = 1$) with two chains accounting for 4,000 iterations after discarding 1,000 iterations. In the special case of generic richness, we tested for a mid-domain-effect (MDE) to explain the humped relationship with depth. The mid-domain effect is defined as the peak of richness where the increasing overlap of species is found towards the centre (Colwell & Lees, 2000). For the test, we used a simulation (n=10,000) Range Cohesion Model for Ordered Data computed with the R package ‘rangemodelR’ (Colwell, 2008; Gotelli *et al.*, 2009). Finally, we mapped the average relative genus dominance in community structure with depth and the depth distribution of coral genera based on presence-absence within and across locations to help to interpret our results.

Depth variation of communities (vertical β -diversity)

In order to evaluate the vertical β -diversity among depths, we computed complementary indices between all depths in each site (Anderson *et al.*, 2006; Legendre & De Cáceres, 2013). We calculated two dissimilarity indices: Jaccard dissimilarity accounting only for genus presence-absence (*i.e.*, each genus has the same weight; Baselga, 2012; Koleff *et al.*, 2003) and Bray-Curtis dissimilarity accounting for genus cover (*i.e.*, each genus has a different weight according to percentage coverage; Baselga, 2017). If dissimilarity in genera is high, dissimilarity in species can only be higher. Jaccard is close to 0 when communities host the same genera, and it increases when the proportion of unique genera to one of the two communities increases. Bray-Curtis dissimilarity is close to 0 when communities are dominated by the same genera and tends to 1 when the most abundant genera are different. Yet, both indices account for differences in richness (*i.e.* two communities cannot share more genera than the minimum number of genera present in both communities) and genus cover. Thus, we computed for each of these β -diversity indices the contribution of its turnover component (*i.e.*, independent from differences in richness or genus cover; Baselga, 2010, 2013, 2017; Baselga & Orme, 2012) as the ratio between turnover and dissimilarity (Toussaint *et al.*, 2014). A turnover ratio close to 1 means pure turnover, indicating that the dissimilarity is driven only by the replacement of genera along the depth gradient (without changes in richness). Conversely, a turnover ratio close to 0 implies no turnover, indicating that the dissimilarity is driven only by differences in richness (poorest communities hosting a subset of the genera present in the

richest ones). We plotted the average results, for all our sites, with a heat map representing the values between different depths.

Spatial variation of communities (spatial β -diversity)

We measured the values of spatial β -diversity for each depth and the contribution of the turnover component with the same methodology used for the depth dissimilarity gradient. Next, we tested the multivariate homogeneity and dispersion of spatial β -diversity at the different given depths (Anderson, 2006; Anderson, Ellingsen and McArdle, 2006) and the effect of depth using p-values with the R package ‘vegan’ (Oksanen *et al.*, 2013). We then applied linear regressions (Linear Models, LM) to test and quantify the variation of β -diversity with increasing depth. Additionally, we tested if the geographical distance between sites could explain dispersion patterns at the different depths using Mantel tests (Legendre and Legendre, 2012; Oksanen *et al.*, 2013). Finally, we performed a non-metric multidimensional scaling (NMDS) (Kruskal, 1964) with the R package ‘vegan’ (Oksanen *et al.*, 2013) and presented ordination results to visualise spatial generic composition differences between locations for given depths. We created convex hull polygons by depth, the area of which reflected β -diversity. We made all analyses (with statistical significance level of p-values was 0.05) and figures with RStudio (Version 1.3.959). Data and scripts are available in [Data Accessibility](#).

2.4. Results

Depth profiles of coral cover, generic richness and dominance

In general, and considering all locations, the percentage of coral cover decreased on average with depth (Bayesian [Population-Level effect = Depth]: β -slope = -0.02, 1-95% CI = -0.02, u-95% CI = -0.02, Rhat = 1.0, conditional $R^2 = 0.542$ and marginal $R^2 = 0.383$), and the fitted values of the model were similar to the observed ones (**Fig. 2.1a**). However, despite this general trend, a few locations presented higher coral cover at mesophotic depths than shallow waters (e.g., $81 \pm [s.e. = 7.7]$ % of coral cover at 40 m vs 41.2 ± 1.9 % at 6 m in Raroia; 74.5 ± 3.1 % at 60 m vs 55.2 ± 3.4 % at 6 m in Gambier). Also, we sometimes found very high coral cover at lower mesophotic depths such as 68.2 ± 1.7 % in Bora Bora at 60 m; 35.4 ± 6.9 % and 52.8 ± 5.1 % in Makatea and Gambier, respectively, at 90 m; or 42.0 ± 4.2 % in Gambier at 120 m (**Sup. Fig. S2.3**).

Generic richness displayed a humped relationship with depth, peaking at 40 m (between 20-60 m) (**Fig. 2.1b**). This pattern fits with that expected according to the mid-domain effect. Indeed, our simulations show that the generic richness of corals rarely deviates from the null expectation (**Fig. 2.1b**). There were slight deviations between islands in the peak and limits of the Mid-Domain richness (**Sup. Fig. S2.4**), but the observed maximum generic richness was always inside the upper mesophotic zone (40 m depth).

The generic dominance in coral community structure is distributed unequally along the depth gradient. While, on average, *Pocillopora* dominated the relative coral genus assemblages with over 70 % at 6 m depth, other genera such as *Pachyseris* were less dominant with 31 % and 28 % at 40 and 60 m, respectively, or *Leptoseris* with 42 % at 90 m depth. The sum of the top three dominant genera was over 92.2 % at 6 m, 78.4 % at 20 m, 65.1 % at 40 m, 63.2 % at 60 m, 91.5 % at 90 m and 89.7 % at 120 m (**Fig. 2.1c**). The absence of dominant genera at 20, 40 and 60 m promoted more diverse communities. Genus dominance at certain depths was also evident within locations, but showed some spatial variability because the dominance of genera was not equally distributed across sites (**Sup. Fig. S2.5**).

We identified 34 different coral genera across all the study sites. The depth distribution analysis showed that most of these genera were present below 30 m, especially at 40 m inside the mesophotic range (**Fig. 2.2**). For instance, *Leptoseris*, *Porites* and *Montipora* were present in the entire depth range studied, qualifying as depth generalist genera. *Pocillopora*, a dominant genus of shallow reefs, was generally present down to 60 m depth and *Pachyseris*, a typical genus of mesophotic assemblages (Bongaerts et al., 2021), was present from 20 to 90 m. However, if we consider a threshold of multiple occurrences (≥ 15 or 50), some rare genera had a slightly reduced depth distribution range (**Sup. Fig. S2.6**). Finally, the depth zonation within sites showed less overlap but still showed that generalist coral genera can be present at all depths at particular locations (**Sup. Fig. S2.7**).

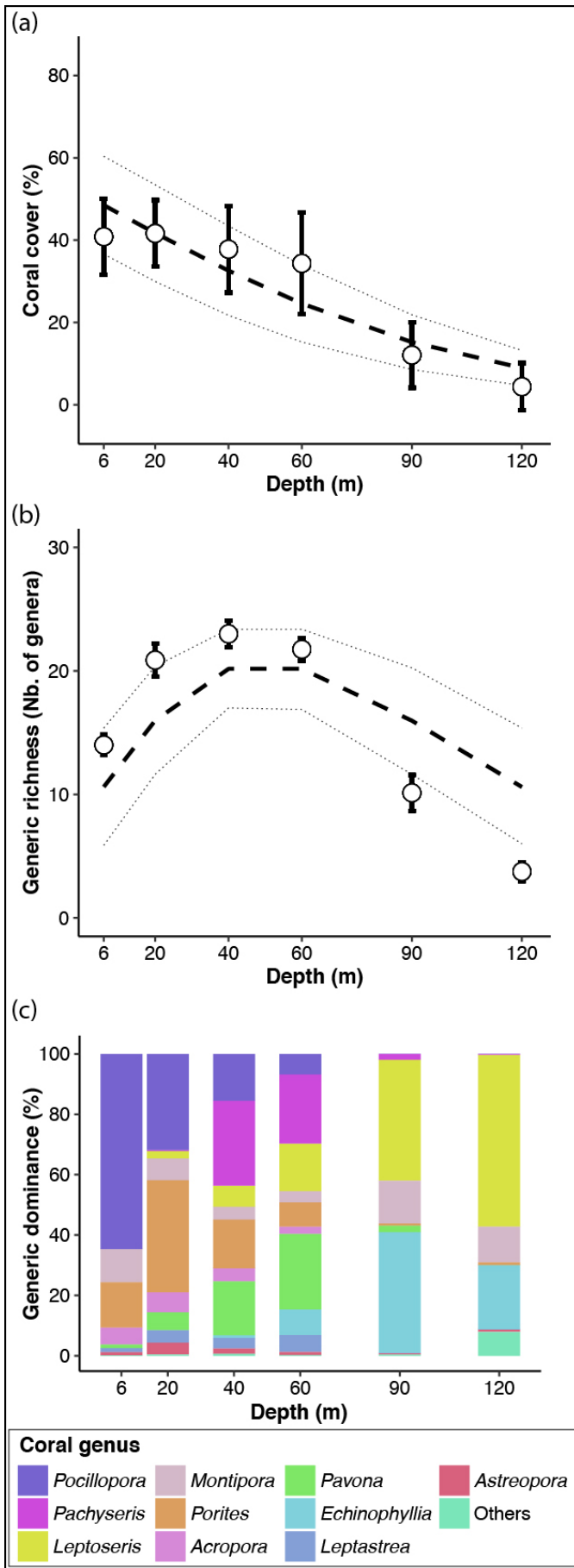


Figure 2.1: Coral vertical profiles. (a) Coral cover with depth. White dots indicate the mean values for all islands with 95% confidence intervals. Dashed lines indicate predicted values for the Bayesian regression model and dotted lines the standard deviations from the posterior distribution. Spatial variability of coral cover with depths across islands and sites is available in Sup. Fig. S2.3 (b) Generic richness with depth. White dots indicate the mean values for all islands with standard errors. Dashed lines indicate predicted values for the Mid-Domain-Effect model and dotted lines are interquartile values of $Q_{2.5}$ and $Q_{97.5}$. Spatial variability of generic richness with depth across islands and sites is available in Sup. Fig. S2.4. (c) Generic dominance of the main genera in community structure with depth. Main genera are considered if relative genus cover was above 5% at the site and depth. Relative percentages are the average within locations for each depth. Standard errors are not displayed but spatial variability across locations is available in Sup. Fig. S2.5. It displays that while particular genera largely dominate at some depths, other depths show a more balanced generic distribution.

Dissimilarity along the depth gradient

Both Jaccard (*i.e.*, composition) and Bray-Curtis (*i.e.*, coral cover) dissimilarity indices increased with differences in depth (**Fig. 2.3**). The high dissimilarity between distant depths was explained mainly by turnover, meaning very few genera were shared between shallowest and deepest depths. The lower dissimilarity within shallow waters (6 and 20 m) and within deep waters (90 and 120 m) was paired with a lower contribution of the turnover, meaning that beyond differences in richness, both depths contained shared genera with the richest depths. Intermediate depths with the highest generic richness (20, 40 and 60 m) had lower dissimilarities (Jaccard < 0.6) with shallow (6 m) assemblages than with deep mesophotic (90 and 120 m) assemblages (Jaccard > 0.8). The contribution of turnover to the dissimilarity between shallow and mid-depth and between mid-depth and deep assemblages was moderate (0.4-0.6). Hence, distant depths had lower generic richness and hosted, unique genera in between, but genera also present in the intermediate depths. Thus, intermediate depths shared genera with both shallow (6 m) and deep (90 and 120 m) assemblages (**Fig. 2.3** and Sup. Fig. S2.5).

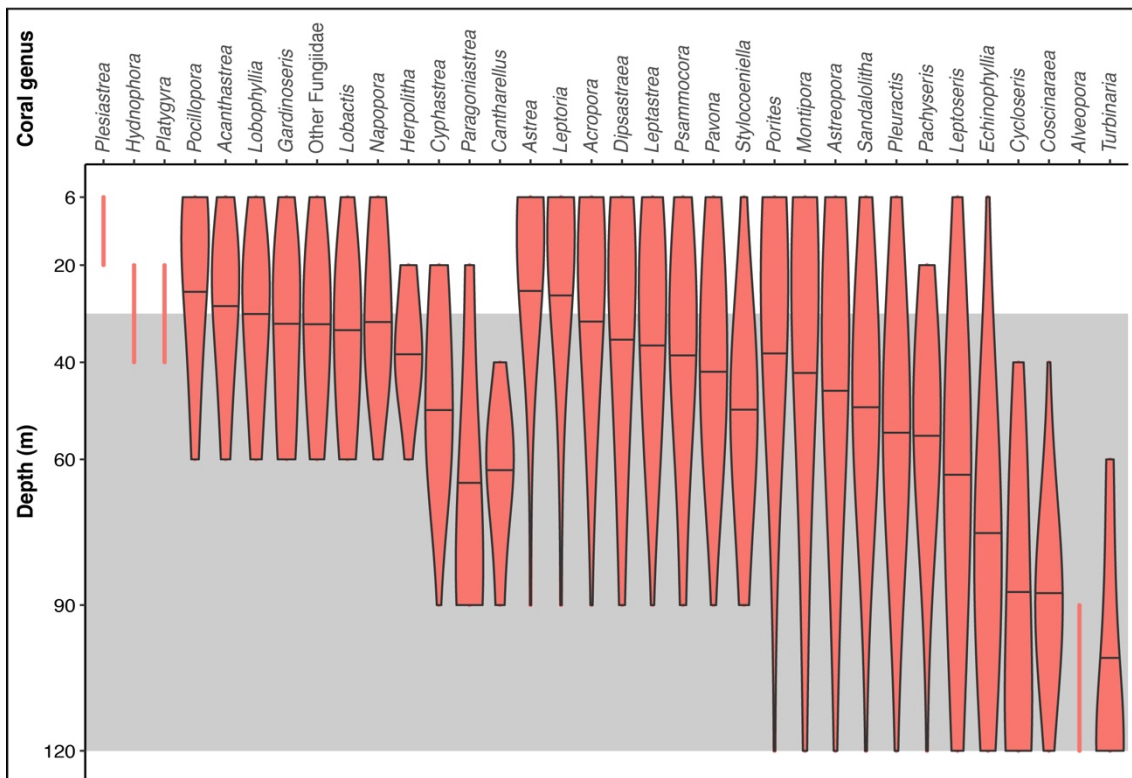


Figure 2.2: Depth distribution of the different genera pooled for the 16 study sites of French Polynesia. 'Other Fungiidae' represents genus such as *Fungia*, *Danafungia* and *Lythophyllon* that could not be visually identified. Violin plots show presence-absence and quantiles the mean of the density estimate. The grey background highlights the mesophotic depth range as traditionally delimited (30-150 m). Depth overlaps are higher considering a single presence-absence than considering ≥ 15 observations or ≥ 50 observations (Sup. Fig. S2.6) and pooling all sites together than separating between locations (Sup. Fig. S2.7).

Spatial diversity patterns at different depths

We found an increase of β -diversity with depth in both the Jaccard (i.e., composition) and Bray-Curtis (i.e., coral cover) dissimilarity. This increase is represented by the sequentially larger area of the convex hull polygons in the NMDS plot along the depth gradient (**Fig. 2.4**). While shallow-water communities were relatively similar between sites (small β -diversity), mesophotic assemblages were relatively unique at each site (high β -diversity). The visual impression in the increase of β -diversity with depth was statistically significant for Bray-Curtis (LM regressions: Jaccard = $0.0022 \times \text{Depth} + 0.336$, $R^2 = 0.58$, Sig. = 0.1; and Bray-Curtis = $0.0027 \times \text{Depth} + 0.5192$, Sig. = 0.001, $R^2 = 0.75$), but somehow consistent for composition and coral cover data. Geographical distance explained the high β -diversity with depth because we found significant correlations for mesophotic reefs (Jaccard at 60 m, Mantel.stat.r (Mantel) = 0.393, Sig. = 0.026 and at 120 m, Mantel = 0.466, Sig. = 0.01; and Bray-Curtis at 60 m, Mantel = 0.324, Sig. = 0.006, at 90 m, Mantel = 0.375, Sig. = 0.01 and at 120 m, Mantel = 0.359, Sig. = 0.022) but not in shallow waters (Sig. > 0.05; except for Bray-Curtis at 6 m, Mantel = 0.629, Sig. = 0.001; **Sup. Fig. S2.8**).

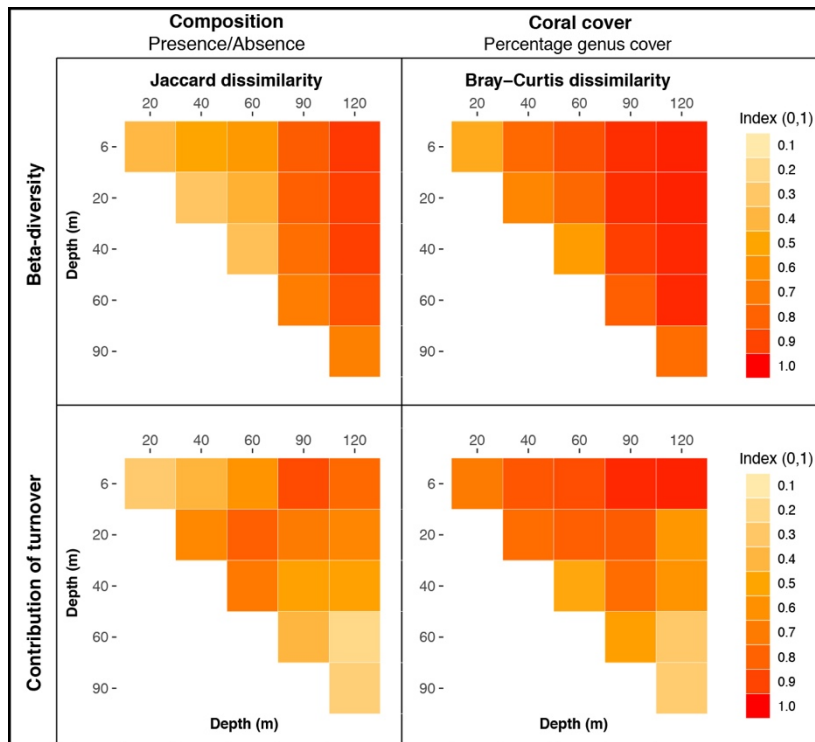


Figure 2.3: Heat map displaying the vertical β -diversity along the depth gradient and the turnover within sites between depths. (Left) Jaccard dissimilarity for the presence-absence (i.e., composition) and the ratio of turnover. (Right) Bray-Curtis dissimilarity for the coral cover (i.e., percentage genus cover) and turnover ratio. β -diversity ($0 \rightarrow 1$) near 1 means coral assemblages have different genera (or different dominant genera for Bray-Curtis) between the compared depths, while 0 means having the same genera. The contribution of turnover to dissimilarity ($0 \rightarrow 1$) close to 1 means the dissimilarity is driven only by the replacement of genera along the depth gradient (i.e., without changes in richness). Conversely, close to 0 means the dissimilarity is driven only by differences in richness (i.e., poorest communities hosting a subset of the genera present in the richest one). Individual genus depth distributions are available for all and separate islands in Fig. 2.2 and Sup. Fig. S2.6 and Fig. S2.7.

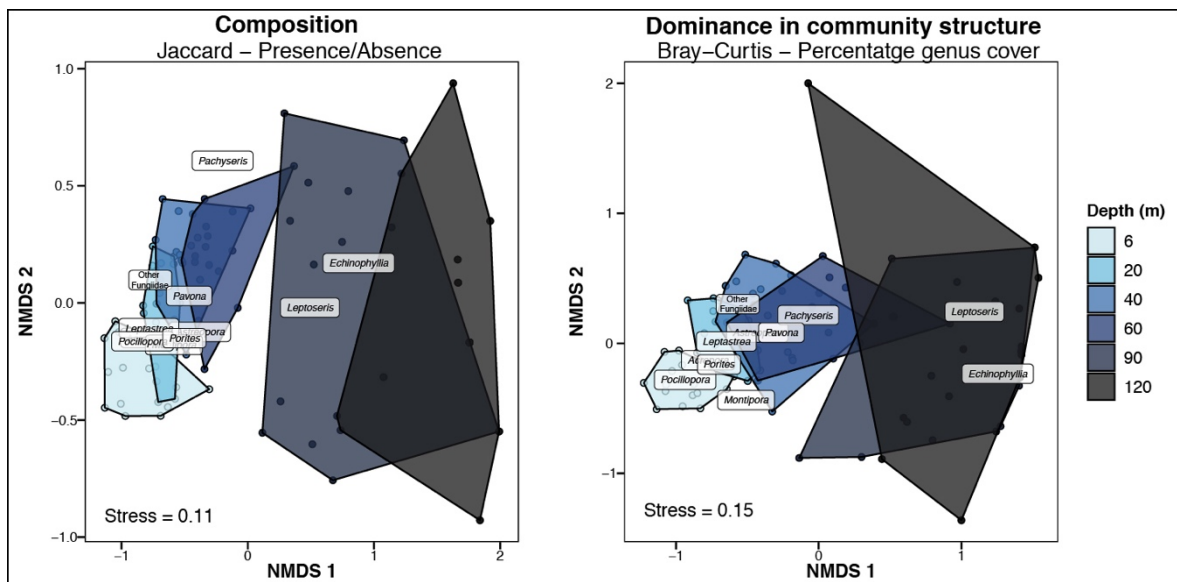


Figure 2.4: Spatial β -diversity patterns at different depths. (Left) dissimilarity in composition (Jaccard computed on generic presence-absence). (Right) dissimilarity in dominance in the coral community structure (Bray-Curtis computed on percentage of coral genera). Spatial β -diversity is reflected in the size of the hull polygons. Genus labels are present only for coral genera with a percentage cover higher than 5%. Points indicate the different sites for the given depth. The increase in spatial β -diversity means that while shallow waters between sites are homogeneous (similar in genus composition and genus cover), mesophotic depths are unique (in composition and genus cover including for the dominant genera).

2.5. Discussion

The present study suggests that the depths between 20 and 60 m host a high (α -diversity) and unique (β -diversity) generic diversity for scleractinian corals in French Polynesia. Our findings raise the importance of these depths for conservation based on the patterns of coral genus diversity obtained by the quantitative analysis of standardised photo-quadrats. Quantitative coral assemblage studies with identical sampling effort at each depth, which is an essential prerequisite for studying diversity patterns (Chen *et al.*, 2021) and over such a wide depth range (6-120 m), are rare worldwide in MCE literature (Bongaerts *et al.*, 2019; Roberts, Bridge, *et al.*, 2019; but see: Liddell & Ohlhorst, 1988; Tamir *et al.*, 2019), and novel for French Polynesia (Pichon, 2019).

Overall, our patterns revealed that the depths around 40 m host the highest richness (α -diversity) of coral genera. According to our analysis, this is mainly due to a mid-domain effect (MDE) along the depth gradient, where the richness and overlap converge towards the centre (Colwell & Less, 2000), similarly to available studies on fish communities (Brockovich *et al.*, 2008). More precisely, the peak in the richness of coral genera seems to be generated by the range overlap of assemblages typical of shallow and deep communities. This high richness mid-domain is present despite the fact that, in general, coral cover decreased with depth as previously expected for light-dependent scleractinian corals (Kahng *et al.*, 2010; Kahng & Kelley, 2007; Laverick *et al.*, 2020). Also, our results showed that coral cover generally decreased with depth, but at some sites, it was as high or even higher in the 40 and 60 m zone than on the shallows (e.g., 81% at 40 m or 70% at 60 m) (**Sup. Fig. S2.3**). These high cover values are unexpected for the light dependency of scleractinian corals (Kahng *et al.*, 2019) but similar to other locations in the Indo-Pacific at such depths (Hopley, Smithers, & Parnell, 2007; Kahng & Kelley, 2007). In any case, the importance here is that the role of the communities between 20 and 60 m may be a zone of transition between shallow and mesophotic coral genus communities as supported by the β -diversity pattern across the depth gradient, which highlights a moderate overlap of this mid-zone with communities at both 6 and 120 m depth.

A hypothesis to explain the humped relationship between genus richness and depth could be that the sum of disturbances seems to be relatively more intense and

frequent (chronic) at shallow depths than in MCEs (Smith, Holstein and Ennis, 2019), especially for global disturbances such as thermal bleaching events (Baird *et al.*, 2018; Pérez-Rosales, Rouzé, *et al.*, 2021). However, our patterns are similar across multiple locations (**Sup. Fig. S3**) and comparable with previous studies conducted elsewhere with quantitative techniques but on narrower depth gradients (Loya, 1972; Bouchon, 1978; Sheppard, 1980; Liddell and Ohlhorst, 1988; Laverick, Andradi-Brown and Rogers, 2017; Roberts, Bridge, *et al.*, 2019; Roberts, Keith, *et al.*, 2019; Tamir *et al.*, 2019). For instance, our findings at 40 m are similar to Tamir (2019) in surveys down to 100 m in the Red Sea. Slightly deeper than 30 m, found by Loya (1972) in the Red Sea, where sampling stopped, Bouchon (1978) in La Reunion Islands, in surveys down to 40 m, and Liddell & Ohlhorst (1988) in Jamaica, in surveys down to 120 m. On the other hand, our findings are deeper than Roberts, Bridge *et al.* (2019) and Roberts, Keith, *et al.* (2019) at 20 m in Papua New Guinea, in surveys down to 50 m depth, Sheppard (1980) also at 20 m in the Chagos Archipelago, in surveys down to 60, and finally, Laverick *et al.* (2017) at 10 m in Honduras, in surveys down to 85 m depth. Moreover, the analyses of available time series in French Polynesia (SO CORAIL, Polynesia Mana) reveals that generic coral richness in shallow waters did not decline substantially in the last 15 years, despite important changes in the composition of coral assemblages (**Sup. Fig. S2.9**) (Tsounis and Edmunds, 2016; Moritz *et al.*, 2021; Pérez-Rosales, Brandl, *et al.*, 2021). Similar to the time series with *Pocillopora* emerging as the new dominant genus (from < 50% in 2005 to > 70% in 2018 of coral composition), we also found this particular dominance in shallow waters (between 30 and 90% at 6 m) (**Fig. 2.1c**). However, we did not find this dominance in mesophotic depths, with *Pocillopora* contributing between 0-50% of composition at 40 m and 60 m), potentially allowing extra space for a higher richness. Therefore, we suggest that the deeper peak of genus richness found in this study compared to that reported in the literature for other locations might be attributed to (i) the optimal conditions for light-dependent corals in the crystal clear waters of French Polynesia (Pichon, 2019; Pichon *et al.*, 2021); (ii) a slight bias between genus and species level analyses (but see Methods - *Comparing diversity metrics at genus vs species level*); (iii) the wide depth range considered in our study, or (iv) the higher diversity allowed because of the lack of more highly competitive genus.

The spatial analysis along the reef slope reveals an increase of β -diversity with depth. This increase suggests that when comparing sites, shallow water assemblages are

similar in composition but deeper assemblages, at mesophotic depths, differ from site to site. This mismatch in β -diversity patterns between shallow and mesophotic depths challenges our perception of conservation needs. The low β -diversity in shallow waters suggests that the protection of a single location, if large enough, may be effective in protecting regional diversity. In contrast, for the high β -diversity of mesophotic coral ecosystems, we may need the protection of multiple sites because each site at these depths seems unique. Such a mismatch adds complexity to the Single Large Or Several Small (SLOSS) debate about establishing Marine Protected Areas (Diamond, 1975; Fahrig, 2017, 2020), with the same ecosystems requiring different protection strategies at different depths. This finding also suggests that we could protect all coral genera present along the depth gradient by deciding the protected locations according to the condition of these transition zone.

Our approach based on photo-quadrats has intrinsic limitations, the most evident being the relatively coarse taxonomic resolution. However, diving constraints limit our capacity to perform sampling techniques that require extended time at mesophotic depths (Pyle, 2019). The method of photo-quadrats represents one of the best compromises to obtain standardised sampling effort and adequate replication across the depth gradient (Hill & Wilkinson, 2004). In addition, we showed that genus and species levels are highly correlated (**Sup. Fig. S2.2**; Heino & Soininen, 2007; Jimenez et al., 2010), and we carefully considered results only when correct for both taxonomic levels. We emphasise the need for caution with the interpretation of similarity patterns at the genus level because whether these also hold at the species or genetic level is unclear (Bongaerts et al., 2017, 2021). In any case, potential misidentifications, regardless of the taxonomic level, were systematic because all quadrats were analysed by a single observer, and therefore, they should not modify the general patterns we found. Even at the genus level and specific to the fore reefs of French Polynesia, our results are pioneering and increase the knowledge of understudied MCEs (Turner *et al.*, 2019), setting the starting point for future studies in this little-known region of the Southern Central Pacific. Lastly and most importantly, our photo-quadrats strategy corrected the associated problems of uneven sampling design studies (*i.e.*, built from depth distributions of observations and scientific literature) with significant differences in sampling effort between well-studied shallow depths and poorly-studied mesophotic depths (Bongaerts et al., 2019; Pyle & Copus, 2019). Additionally, all our interpretations came from the complementarity of α and β -

diversity (with composition and coral cover) patterns that highlight the robustness of our results.

In this study, we provide new perspectives that if we seek to preserve the regional coral genus biodiversity of shallow and mesophotic reefs in French Polynesia, the depths between 20-60 m are an important area from a systematic conservation perspective (Kukkala & Moilanen, 2013; Margules & Pressey, 2000; McIntosh et al., 2017; Myers et al., 2000). Indeed, this zone hosts the highest coral generic richness and the coral genus assemblages typical of both ranges, the shallow and deep; thus, it could act as a safeguard of biodiversity. In conclusion, we suggest that conservation planning for coral reefs cannot ignore and should account for MCEs (Bridge *et al.*, 2013; Kahng, Copus and Wagner, 2016; Pyle *et al.*, 2016; Pyle and Copus, 2019; Soares *et al.*, 2020) and consider multiple locations because each is spatially unique in their coral composition. The high α and β -diversity of mesophotic coral ecosystems highlight how they may be crucial for preserving coral biodiversity and coral reef ecosystems as a whole. This is particularly relevant in the light of ever-increasing human pressures and climate change effects, which seem to be less severe with increasing depth.

2.6. Extra information

2.6.1. Acknowledgements

We thank all the Under The Pole Expedition III team for making the collection of data on deep mesophotic coral ecosystems possible. This research was funded by the ANR DEEPHOPE (ANRAAPG 2017 #168722), the Délégation à la Recherche DEEPCORAL, the CNRS DEEPRÉEF, the EPHE, the IFRECOR and the OFB POLYAFB. We also thank Paul Muir for sharing his ideas while discussing the first results. The present work consists of photo-quadrats (pictures) and no export permits apply on French Polynesia for these data.

Under The Pole Consortium⁶ G. Bardout, J. Fauchet, A. Ferucci, F. Gazzola, G. Lagarrigue, J. Leblond, E. Marivint, A. Mittau, N. Mollon, N. Paulme, E. Périé-Bardout, R. Pete, S. Pujolle, G. Siu.

2.6.2. Data availability

All analyses, scripts and data necessary to replicate this study are at Github:

https://github.com/gonzalopr/Cover_with_Depth

2.6.3. Supplementary information

Supplementary figures

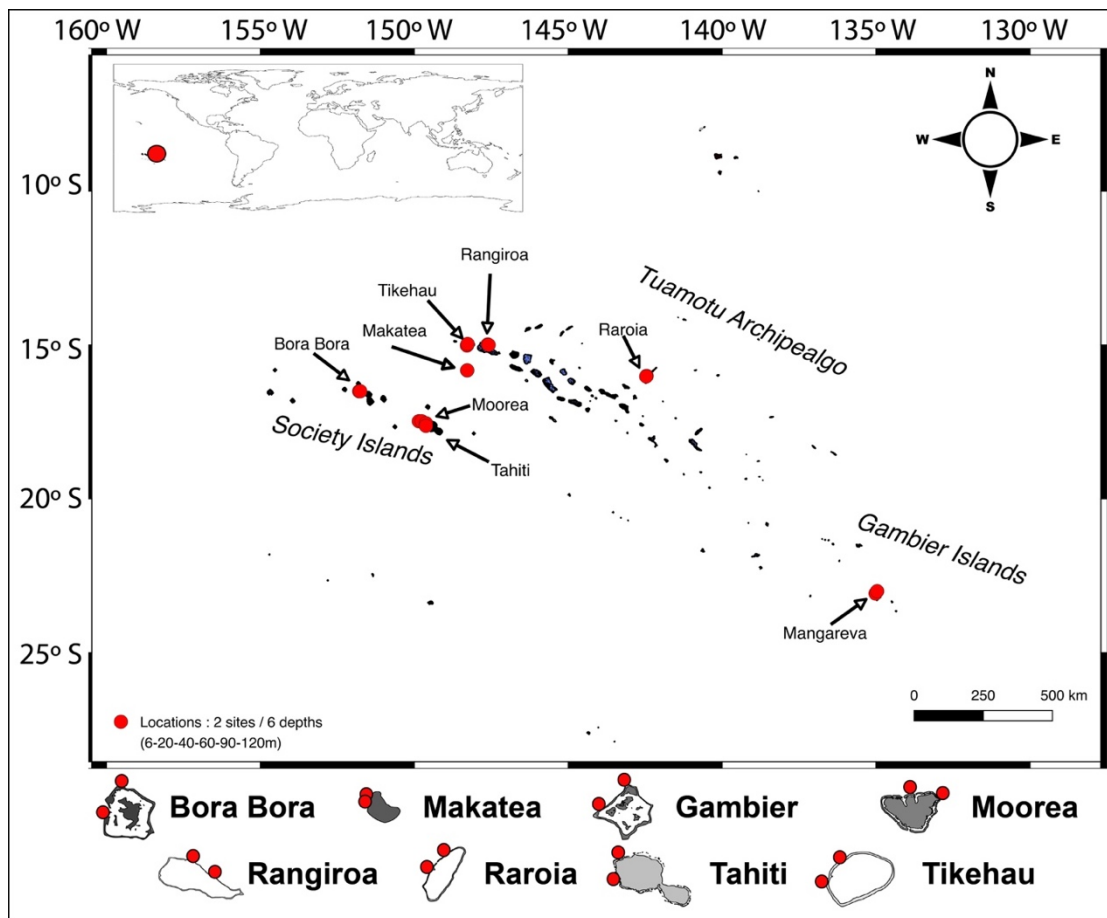


Figure S2.1: Map of French Polynesia with the islands and sampling locations considered in this study. Coordinates are available in supplementary Table S1.

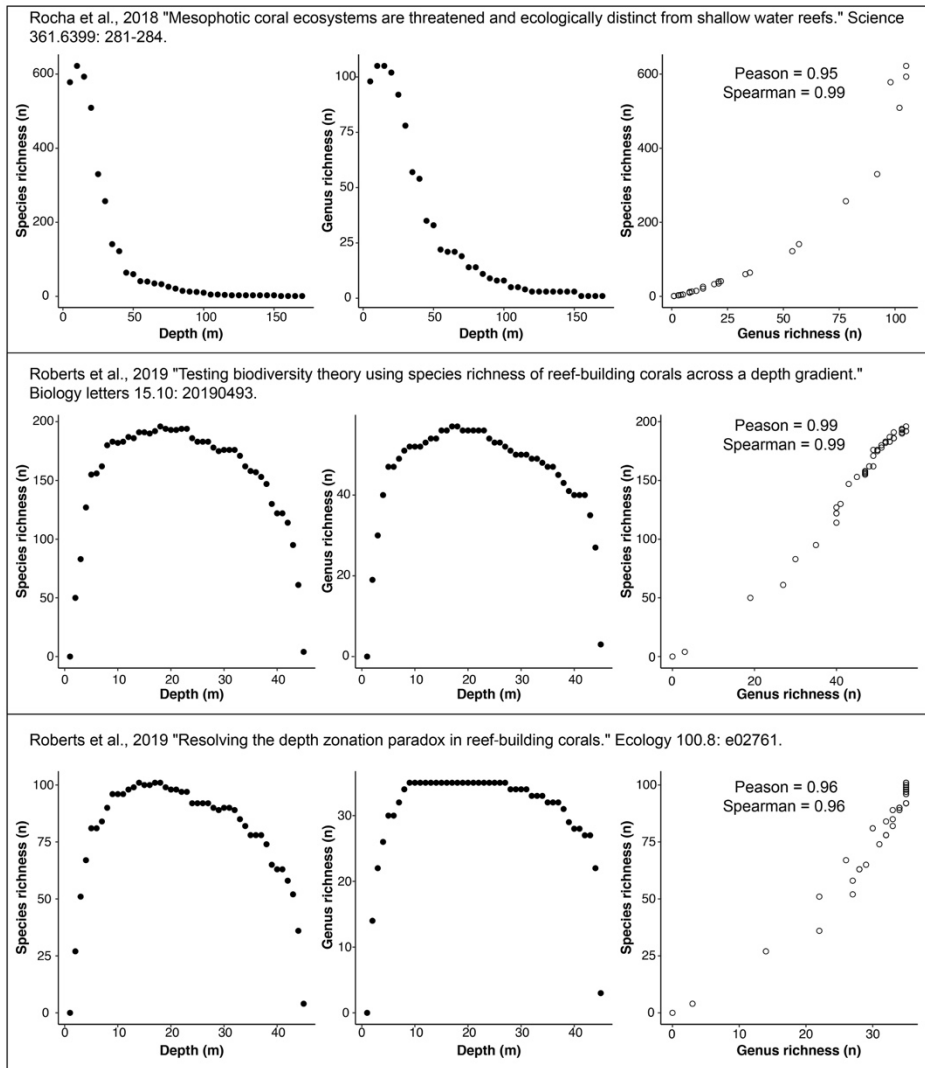


Figure S2.2: Pearson and Spearman's correlations between diversity metrics at species and genus levels for external databases were above 0.9. High correlations show that genus level patterns are representative of species level patterns.

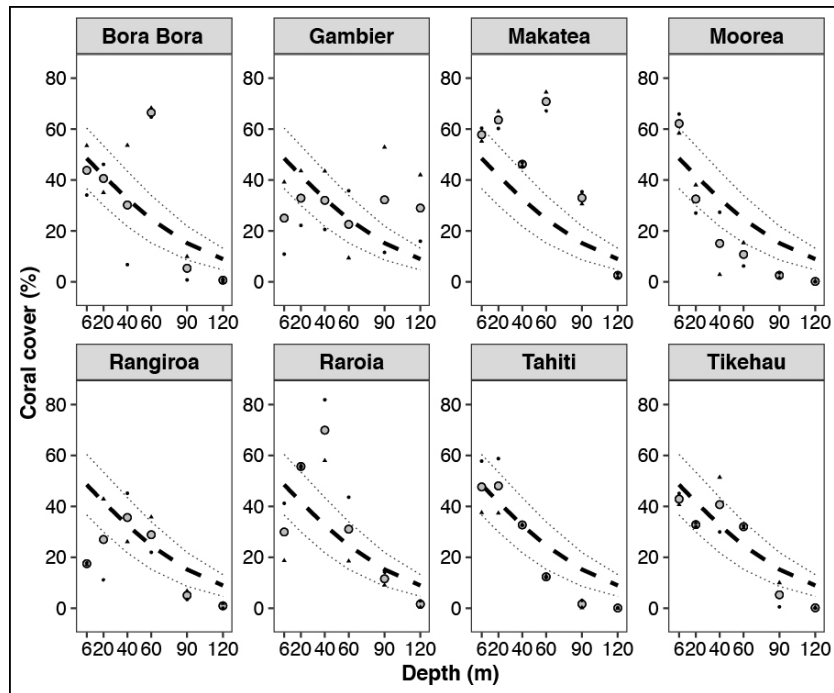


Figure S2.3: Coral cover decreases with increasing depth for the different islands. Grey dots indicate the mean coral cover at each depth per island, considering the two sites of the island. Small black shapes indicate coral cover at island sites, triangles Site 1 and points Site 2 of each island. Dashed lines indicate the predicted values of the Bayesian regression model. Dotted lines are \pm standard deviations from the posterior distribution of the model. There were positive and negative spatial deviations in several islands from the general Bayesian model that overall decreased the posterior distribution of coral cover with depth ([Population-Level effect = Depth]: β -slope = -0.02, l-95% CI = -0.02, u-95% CI = -0.02, Rhat = 1.0, conditional R^2 = 0.542 and marginal R^2 = 0.383).

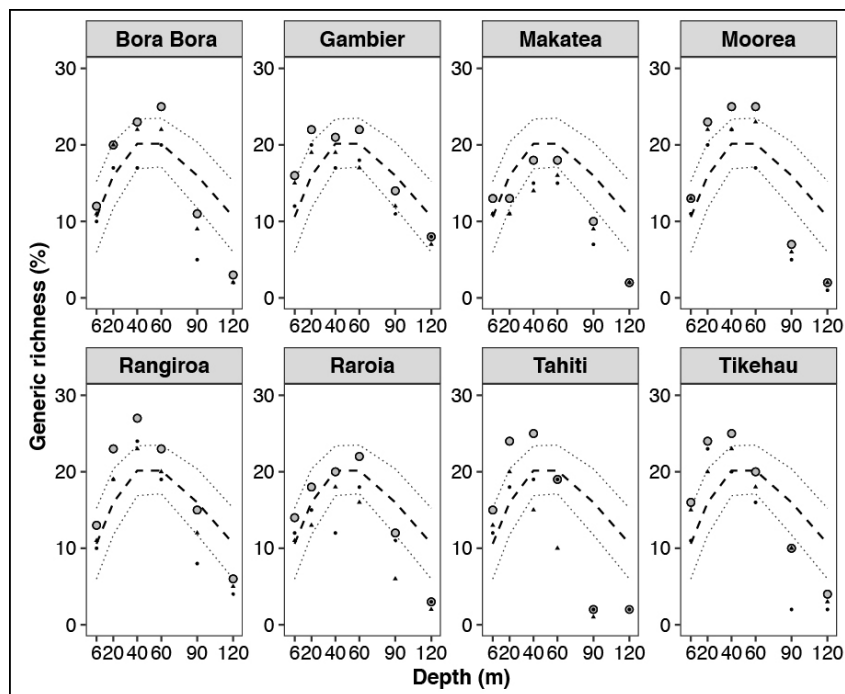


Figure S2.4: Generic richness and Mid-Domain-Effect with depth for the different islands. Grey dots indicate the unique generic richness at each depth per island. Small black shapes indicate unique richness at island sites, triangles for Site 1 and circles for Site 2 of each island. Dashed lines indicate the predicted values of the Mid-Domain-Effect model. Dotted lines are interquartile values of Q2.5 and Q97.5. The few deviations represent that sometimes surface waters harbour more richness than profound mesophotic depths.

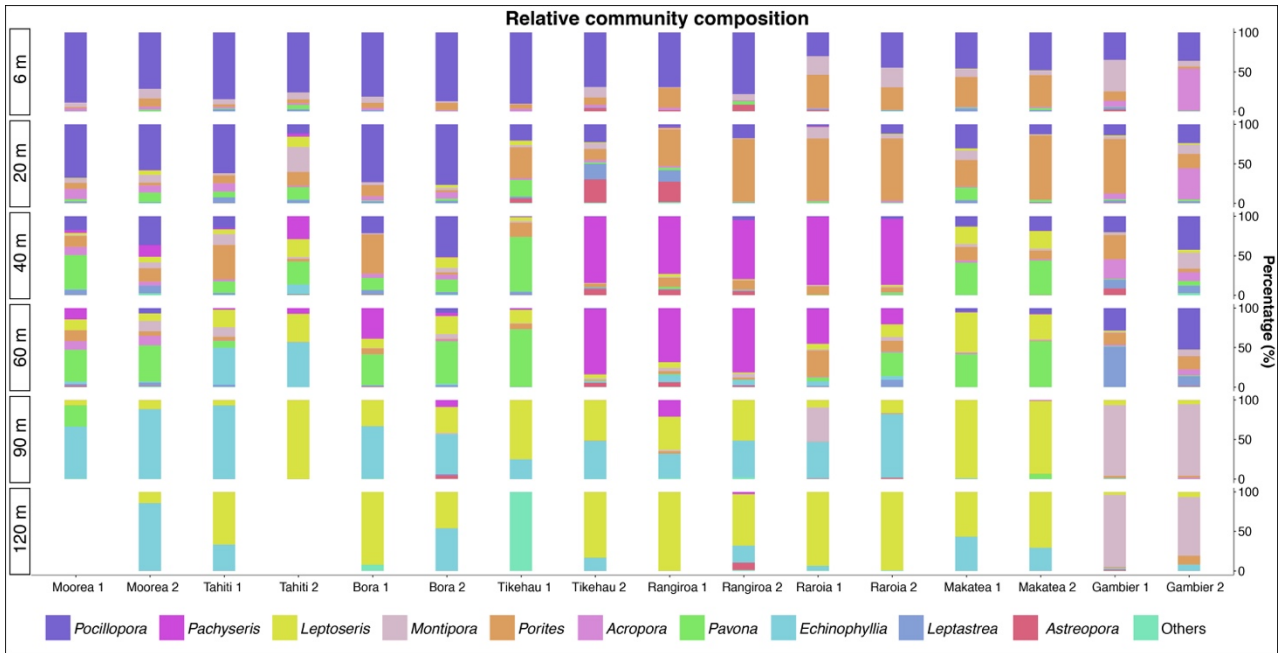


Figure S2.5: Stacked barplots of the vertical relative abundances of the main genera composition for the different depths (left) and locations (bottom). Main genera are considered if relative genus cover was higher than 5% at the site and depth.

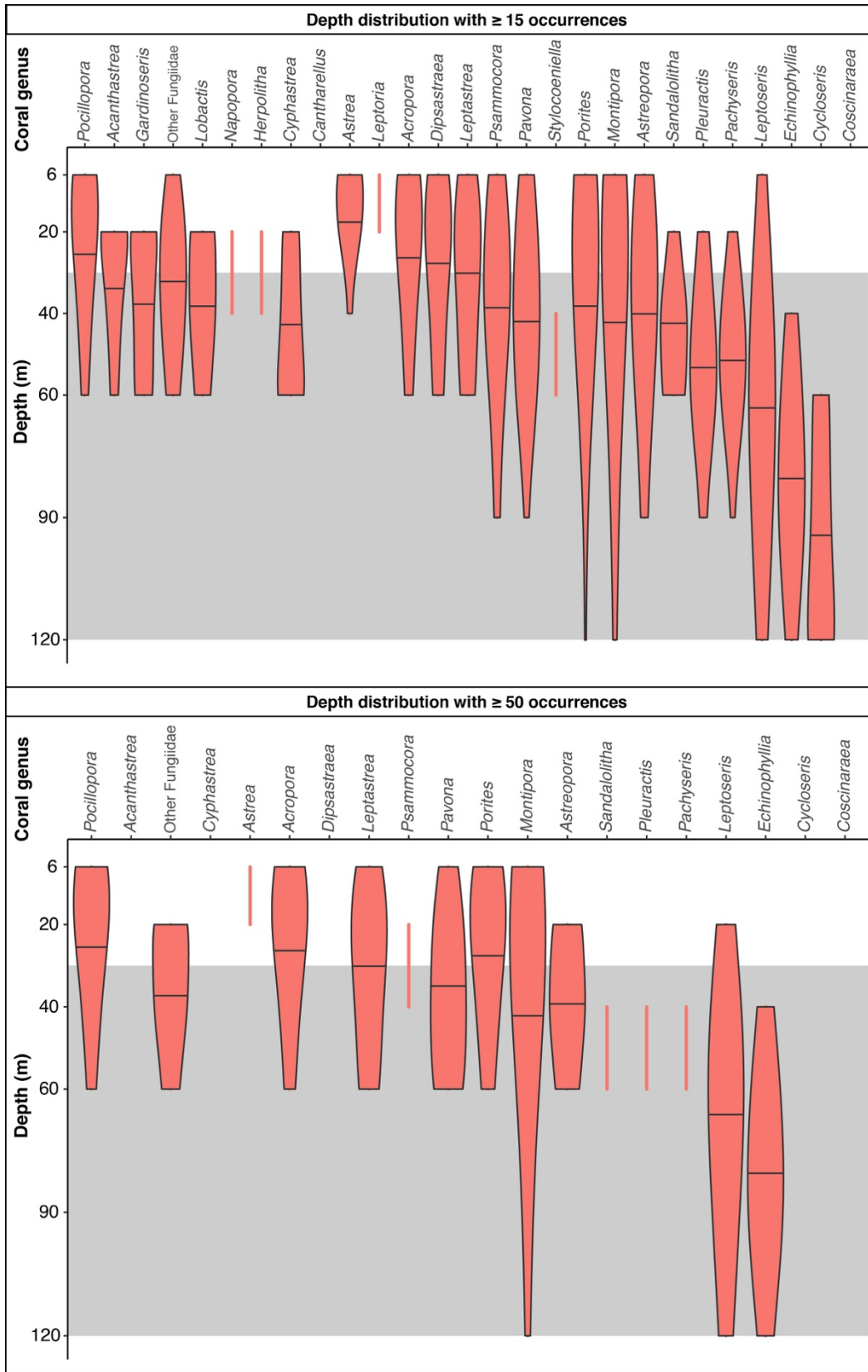


Figure S2.6: Depth distribution of the different genera considering a threshold of ≥ 15 (top) and ≥ 50 (bottom) occurrences. 'Other Fungiidae' represents genera such as *Fungia*, *Danafungia* and *Lythophyllon* that could not be visually identified. The overlap was lower than with a single presence-absence. Genera appearing without lines were present at a single depth.

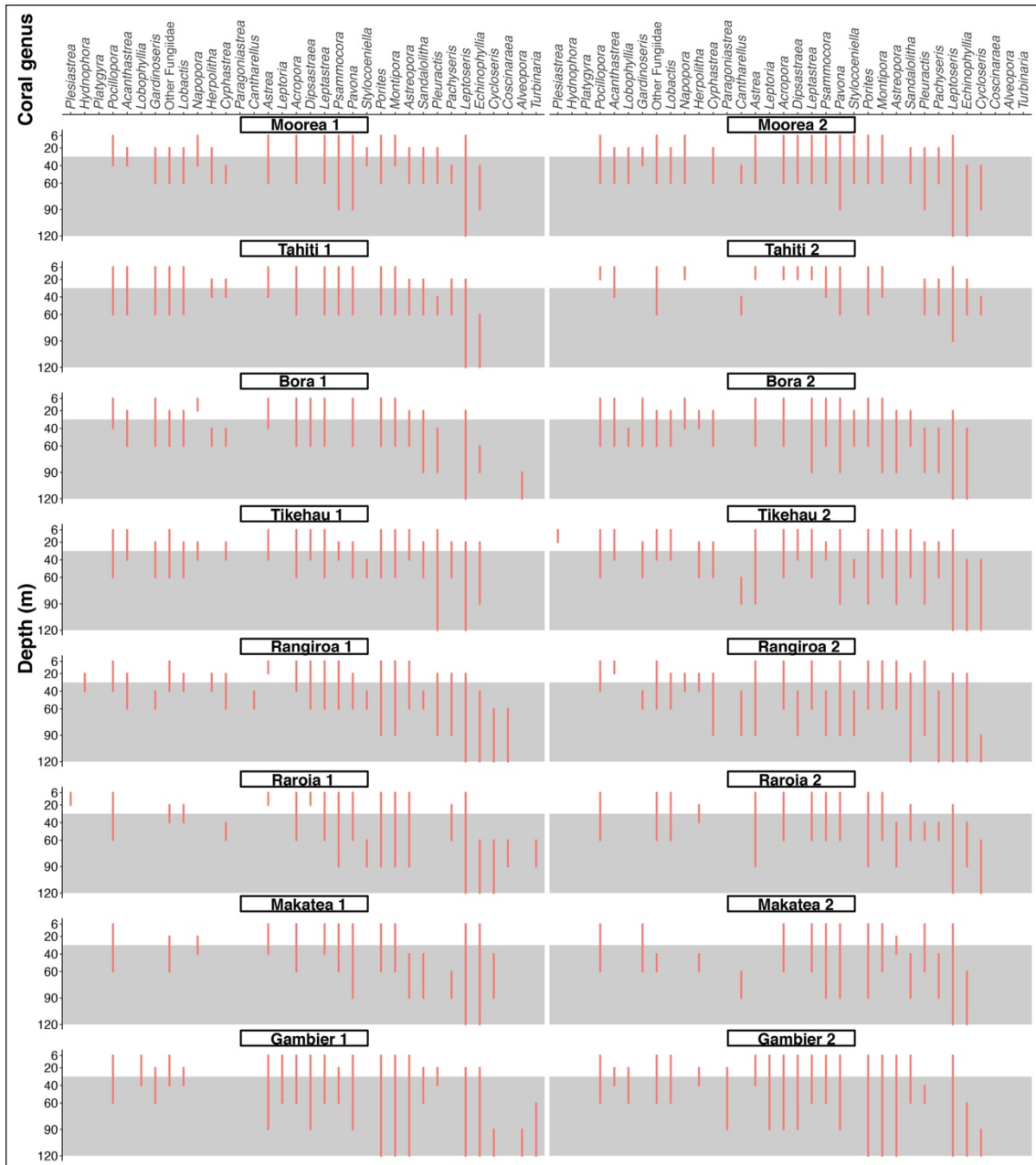


Figure S2.7: Depth distribution considering the presence-absence of the different genera for each separate site. 'Other Fungiidae' represents genera such as *Fungia*, *Danafungia* and *Lythophyllon* that could not be visually identified. When separating between sites, the overlap was lower than pooling all sites together.

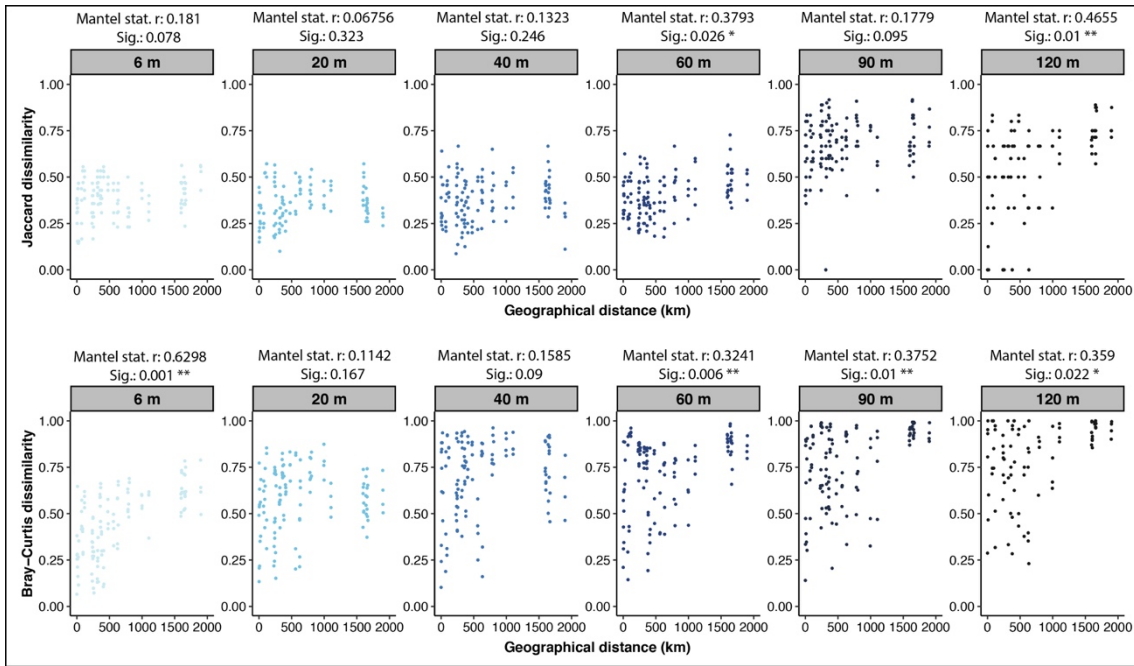


Figure S2.8: Spatial β -diversity at different depths vs geographical distance. Mantel tests correlations and significance are displayed on top of the graphs. Significant correlations of spatial β -diversity with geographical distances were mostly found at deep mesophotic depths.

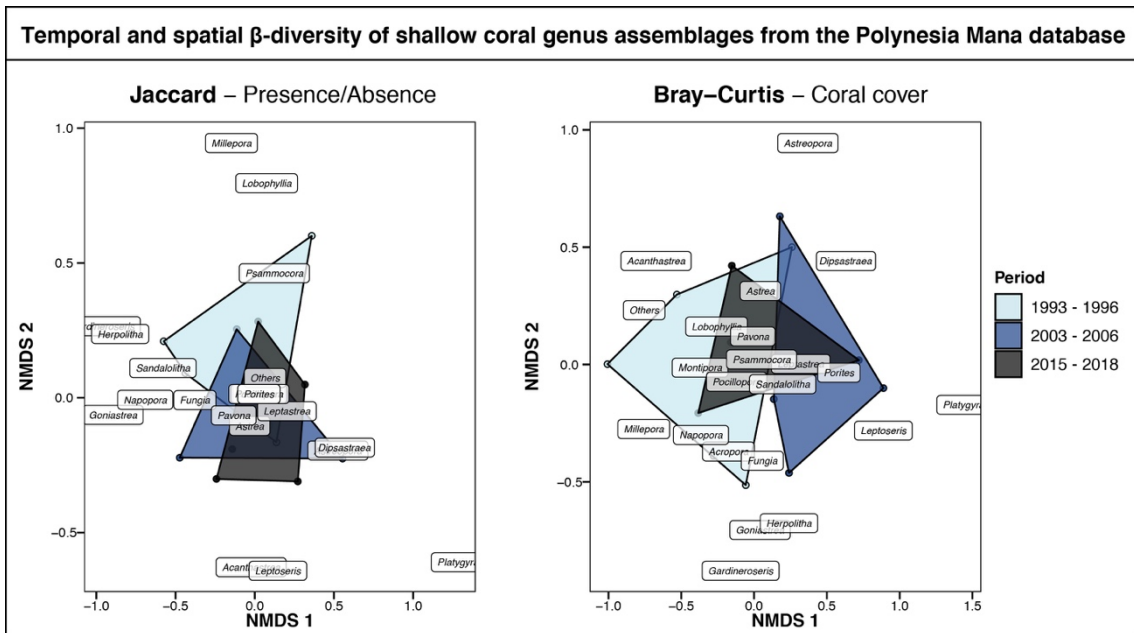


Figure S2.9: Temporal and spatial β -diversity patterns from shallow waters (10 m) in French Polynesia from the Polynesia Mana dataset. (Left) Jaccard dissimilarity for the presence-absence (i.e., composition). (Right) Bray-Curtis dissimilarity for the percentage genus cover (i.e., dominance in coral community structure). Spatial β -diversity is reflected in the size of the hull polygons. Genus labels consider all coral genera from the dataset. Dots indicate the different islands ($n = 5$) for the three given periods of time (i.e., 1993-1996, 2003-2006 and 2015-2018). The decrease in the size of spatial β -diversity means that shallow depths are losing spatial coral genus diversity with time. However, the α -diversity or genus richness is stable for the three period of time (e.g., Moorea: 1st period = 10, 2nd period = 15, 3rd period = 9; Raiatea: 7, 10, 14; Tahiti: 13, 14, 11; Tetiaroa: 12, 10, 11; Tikehau: 12, 11, 12).

Supplementary tables

Table S2.1: Dates and locations of the study. Each site was studied at 6, 20, 40, 60, 90 and 120 m depth.

Survey Dates	Archipelago	Island	Site	Latitude (DM.m)	Longitude (DM.m)
Aug 2018	Society	Moorea	1	17° 28. 631 S	149° 51. 067 W
Sep 2018	Society	Moorea	2	17° 28. 638 S	149° 51. 083 W
Sep 2018	Society	Bora	1	16° 30. 510 S	150° 47. 441 W
Sep 2018	Society	Bora	2	16° 26. 205 S	151° 45. 217 W
Oct 2018	Tuamotu	Tikehau	1	15° 01. 040 S	148° 17. 205 W
Oct 2018	Tuamotu	Tikehau	2	14° 57. 845 S	148° 16. 027 W
Oct 2018	Tuamotu	Rangiroa	1	14° 58. 818 S	147° 36. 789 W
Nov 2018	Tuamotu	Rangiroa	2	14° 59. 858 S	147° 35. 059 W
Nov 2018	Tuamotu	Raroia	1	16° 00.310 S	142° 27. 102 W
Mar 2019	Tuamotu	Raroia	2	16° 01.386 S	142° 27. 796 W
Mar 2019	Gambier	Gambier	1	23° 04. 383 S	135° 00. 973 W
Apr 2019	Gambier	Gambier	2	23° 00. 061 S	134° 57. 631 W
Jun 2019	Tuamotu	Makatea	1	15° 49. 556 S	148° 16. 780 W
Jun 2019	Tuamotu	Makatea	2	15° 49.383 S	148° 16. 758 W
Sep 2019	Society	Tahiti	1	17° 32.531 S	149° 37.125 W
Sep 2019	Society	Tahiti	2	17° 37.171 S	149° 37.261 W

Table S2.2: Relationship between coral cover and depth. First, we used traditional generalised linear mixed-models with the package ‘lme4’. The null models have only the random effects (Sites). The full models have the fixed effect (Depth) and the random effects (Sites). We selected the model with the lowest Akaike Information Criterion (AIC) for the formula. Since the normality of the percentages of the model could not be validated entirely, with Shapiro’s, Levene’s test and ‘DHARMA’ package on the residuals, we only used the “lmer” model to confirm that the site effect is better than a nested effect with Site / Island and to obtain the formula of the model. Second, we used Bayesian regression models with the package ‘brms’ with different families, and we conserved the model with the highest R². All models displayed here converged (Rhat = 1). More information is available in the GitHub repository: see Data Accessibility Statement.

Inferential models with Gaussian family			
Relationship of coral cover with depth	Parameters (Estimate intercept & β-slope)	AIC	R² (Marginal = Marg. & Conditional = Cond.)
Cover ~ (1 Site)	Est. = 29.1 & β = NA	874.3	Cond = 0.02
Cover ~ Depth + (1 Site)	Est. = 48.4 & β = -0.35	823.9	Marg = 0.39 & Cond = 0.490
Cover ~ Depth + (Depth Site)	Est. = 48.4 & β = -0.35	827.8	Marg = 0.39 & Cond = 0.498
Cover ~ 1 + Depth + (1 + Depth Site)	Est. = 48,32 & β = -0.35	827.8	Marg = 0.39 & Cond = 0.498
Cover ~ 1 + Depth + (1 + Depth Site) + (1 Site)	Est. = 48,44 & β = -0.35	829.3	Marg = 0.39 & Cond = 0.498
Cover ~ (1 Site / Island)	Est. = 29.1 & β = NA	876.4	Cond = 0.02
Cover ~ Depth + (1 Site / Island)	Est. = 48.4 & β = -0.35	825.9	Marg = 0.39 & Cond = 0.490
Bayesian models with different families			
Relationship of coral cover with depth	Parameters (Estimate intercept & β-slope)	Family	R² (Marginal = Marg. & Conditional = Cond.)
Coral points trials (Total Points) ~ Depth + (1 Site)	Est. = 0.08 & β = -0.02 CI: 1-95% = -0.02 & u-95% = -0.02	Binomial	Marg = 0.39 & Cond = 0.542

Cover Beta [0-1] ~ Depth + (1 Site)	Est. = 0.11 & β = -0.02 CI: 1-95% = -0.03 & u-95% = -0.02	Beta	Marg = 0.39 & Cond = 0.463
Cover Beta [0-1] ~ Depth + (1 Site)	Est. = 0.11 & β = -0.02 CI: 1-95% = -0.03 & u-95% = -0.02	Zero inflated beta	Marg = 0.39 & Cond = 0.456
Cover (%) ~ Depth + (1 Site)	Est. = 48.7 & β = -0.37 CI: 1-95% = -0.45 & u-95% = -0.29	Student	Marg = 0.41 & Cond = 0.49

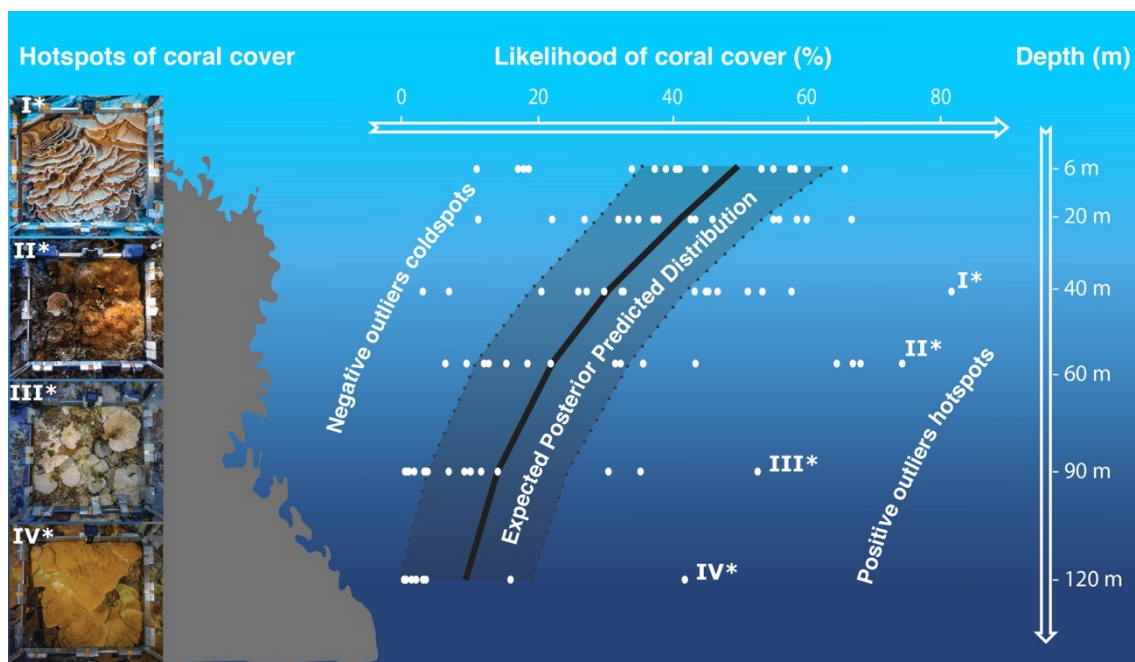
III. Chapter 3: Coral cover of MCEs in French Polynesia

This chapter is published in *Science of the Total Environment* as:

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<https://doi.org/10.1016/j.scitotenv.2022.157049>

3.1. Graphical abstract and highlights



- Quantitative studies along wide depth ranges identify high coral cover communities
- Scleractinian cover reached 81% at 40 m, 74.5% at 60 m, 53% at 90 m or 42% at 120 m
- Hard benthos and steep to moderate slopes increase the likelihood of coral hotspots
- French Polynesia raises as a potential region for Mesophotic Coral Ecosystems

3.2. Abstract

The rapid decline of shallow coral reefs has increased the interest in the long-understudied mesophotic coral ecosystems (MCEs). However, MCEs are usually characterised by rather low to moderate scleractinian coral cover, with only a few descriptions of high coral cover at depth. Here, we explored eight islands across French Polynesia and over a wide depth range (6 to 120 m) to identify coral cover hotspots at mesophotic depths and the co-occurrent biotic groups and abiotic factors that determine such high scleractinian cover. Using Bayesian modelling, we found that 31% of studied deep sites in the mesophotic range exhibited a coral cover higher than expected when considering the depth (e.g. as high as 81.8% at 40 m, 74.5% at 60 m, 53% at 90 m and 42% at 120 m). Omitting the collinear factors light-irradiance and depth, these ‘hotspots’ of coral cover corresponded to mesophotic sites and depths characterised by hard substrate, a steep to moderate slope and the dominance of laminar corals. Our work unveils the presence of unexpectedly and unique high coral cover communities in mesophotic depths in French Polynesia, highlighting the importance of expanding the research on deeper depths for the potential relevance in the conservation management of tropical coral reefs.

Keywords: Mesophotic Coral Ecosystems; high coral cover; scleractinian, Bayesian, predictive modelling, French Polynesia

3.3. Introduction

The unprecedented coral loss due to climate change (Hoegh-Guldberg *et al.*, 2007; Hughes *et al.*, 2017) triggered global efforts to find and conserve the most preeminent coral-dominated reefs (Cinner *et al.*, 2016; Beyer *et al.*, 2018). With the advance of new technologies (Pyle, 2019), new research emerged in extreme and marginal coral reef environments to identify resistant and resilient coral species, high coral cover communities for conservation (Camp *et al.*, 2018), and explore the mesophotic zone (Loya, Puglise and Bridge, 2019). As a continuation of shallow coral reefs counterparts, Mesophotic Coral Ecosystems (MCEs) occur between 30 - 150 m depths, characterised by benthic communities of low to medium coverage of light-dependent scleractinian corals (Ginsburg, 2007; Puglise *et al.*, 2009). However, exceptionally high coral cover at mesophotic depths (from 40 to more than 90% between 60 - 120 m) has been described

in a few reef locations since the early 70s (Kinzie, 1973; Zlatarski and Estalella, 1982; Sánchez, 1999; Zlatarski, 2018; Hopley, Smithers and Parnell, 2007; Zlatarski, 2007; Kahng *et al.*, 2010; Bridge *et al.*, 2012; Kahng, Hochberg, *et al.*, 2012; Kahng, Copus and Wagner, 2014; Eyal *et al.*, 2016; Hoeksema, Bongaerts and Baldwin, 2017), triggering questions about the potential environmental conditions (other than light, *e.g.*, temperature, geomorphology) and benthic interactions (*i.e.*, competing for space) promoting such reefs communities (Chadwick and Morrow, 2011; Done, 2011; Kahng *et al.*, 2019; Sherman *et al.*, 2019).

Despite increasing interest in MCEs (Bongaerts *et al.*, 2019; Pyle and Copus, 2019), little is known about the regional variability of the cover and composition of MCEs, and the biotic and abiotic factors driving the vertical distribution of mesophotic organisms (Kahng *et al.*, 2019; Sherman *et al.*, 2019). Scleractinian corals and other photosynthetic taxa like macroalgae are predicted to decrease in diversity and abundance over depth following light-irradiance attenuation (Gordon, 1989; Kahng and Kelley, 2007; Muir and Pichon, 2019; Spalding, Amado-Filho, *et al.*, 2019). In contrast, heterotrophic or non-photosynthetic taxa such as sponges, azooxanthellate octocorals (particularly gorgonian) and antipatharians are expected to increase their abundance with depth (Bridge *et al.*, 2012; Beaman *et al.*, 2016; Benayahu *et al.*, 2019; Bo *et al.*, 2019; Sanchez *et al.*, 2019). A trade-off between the levels of light-irradiance, the slope of the seafloor, and the transport and accumulation of sediments has been hypothesised to provide suitable conditions for thriving scleractinian corals in MCEs (Liddell and Ohlhorst, 1988; Liddell, Avery and Ohlhorst, 1997; Sherman *et al.*, 2010, 2019; Bridge *et al.*, 2011; Appeldoorn *et al.*, 2016; Englebert *et al.*, 2017). However, the nature of this environmental trade-off and the hierarchy and ranges of these variables to generate such suitable conditions for high coral coverage remain unexplored.

Despite MCEs are considered biodiversity hotspots (Muir *et al.*, 2018; Pérez-Rosales *et al.*, in prep.) with a potential role in short-term thermal refuge (Muir *et al.*, 2017; Baird *et al.*, 2018; Frade *et al.*, 2018; Giraldo-Ospina, Kendrick and Hovey, 2020; Pérez-Rosales, Rouzé, *et al.*, 2021) and larval sources for damaged shallow reef areas (Bongaerts and Smith, 2019; Montgomery *et al.*, 2021), they have been traditionally overlooked in conservation management efforts as these are mainly focused on shallow reefs (Cinner *et al.*, 2016; Beyer *et al.*, 2018; Kuempel *et al.*, 2021; Souter *et al.*, 2021).

To advance coral reefs' conservation strategies that allow consideration of MCEs and their functional roles, it is essential to decipher the environmental trade-off promoting suitable habitats for thriving mesophotic scleractinian reefs. Here, we identify high coral cover 'hotspots' across MCEs in French Polynesia and evaluate the role of environmental factors in determining coral cover and major benthic communities over a wide depth range.

3.4. Materials and Methods

Wide-depth-range benthic surveys were conducted on the fore reefs of three archipelagos and eight islands of French Polynesia between August 2018 and September 2019 (**Fig. 3.1a**). Considering navigation and technical diving safety, two random sites were selected at each island to collect 30 random photo-quadrats (0.75×0.75 m) from line transects at 6, 20, 40, 60, 90 and 120 m depth, resulting in 2,880 quadrats and a total area of 1,620 m². Photo-quadrats were taken using mixed-gas closed-circuit rebreathers and a Nikon D810 camera in Nautican Housing, with 16 mm lens, 37.09-pixel high-definition resolution and Keldan strobes. The relative cover of each benthic group was quantified and identified to the maximum taxonomic resolution possible in 75 stratified random points per quadrat (Van Rein *et al.*, 2011; Roelfsema *et al.*, 2021) using the software "Photoquad" (Trygonis and Sini, 2012). Taxonomic identifications were grouped in the following biotic categories: (a) branching coral, (b) massive coral, (c) encrusting coral, (d) solitary and free-living colonial coral, (e) laminar coral, (f) *Halimeda spp.*, (g) fleshy macroalgae, (h) crustose algae, (i) crustose coralline algae (CCA), (j) gorgonians, (k) sponges, (h) hydroids, and (i) antipatharians. Light-dependent organisms from the order Scleractinia (Sup. Table S3.1) were considered as 'coral', except for massive and encrusting *Millepora*, which were assigned to "massive coral" or "encrusting coral", respectively, due to their similar ecological role. Soft corals and other sessile invertebrates were not separated into higher taxonomic groups for the current analysis (Sup. Table S3.2). Points falling on abiotic categories (except for turf) were classified into hard-fixed, soft sediment and rubble. Coral cover was calculated as the proportion of points falling in all scleractinian-coral categories.

Only environmental parameters measured *in situ* and varying over the depth gradient were considered in the analysis (*i.e.*, constant variables such as coordinates, coast

orientation, island geomorphology, annual sea surface temperatures and bleaching history were excluded). At each depth, Photosynthetically Active Radiation (PAR) light and temperature were recorded with DEFI2-L JFE Advantech light-irradiance loggers and HOBO Water Temperature Pro v2 Data loggers, respectively. Conductivity-Temperature-Depth (CTD) profiles (Valeport Midas) were used to validate and fill missing temperature gaps. To account for different deployment times, we normalised light and temperature data to their respective 6 m value (“surface value,” *i.e.*, shallowest sampling depth) (Kahng *et al.*, 2019), obtaining light relative index and temperature relative index. Temperature variability at each site and depth was estimated as the difference between the highest and lowest temperatures during the registered time. Bathymetric reef slope profiles were reconstructed from divers’ visual estimates at each site and depth and were complemented with visual assessment in photo-quadrats and reef scape panoramic photographs. Following Englebort *et al.* (2017) and Sherman *et al.* (2019), reef slopes were categorised as (a) ‘Gentle’, from subhorizontal shelves to up to 30°; (b) ‘Moderate’ ~ 45°; (c) ‘Steep’, ~ from 50 to 70°; and (d) ‘Wall’, > 75° slope. Dominant substrate type (‘hard-fixed’, ‘soft-sediment’ and ‘rubble’) was determined from quadrats’ analysis.

Two Bayesian Regression Models (package *brms*, Bürkner, 2017, 2018) were tested to explore the relationship between coral cover and depth. The first model was used to identify outliers of high coral cover, *i.e.*, values outside the expected distribution by the model. The second model was used to estimate the likelihood of coral cover according to the variability of environmental variables across the depth gradient. For both models, we used a binomial regression family considering an intercept for the fixed factor and a random intercept for “site”, and we estimated coral cover as the proportion of identified points falling on a scleractinian coral out of the total number of points (*i.e.*, number of successes for each trial, standardised by the total number of points). The first model was a null model exploring coral cover over depth and converged ($R^2 = 0.48$) with two chains of 4,000 iterations after 1,000 iterations warm-up for each chain. The posterior samples were used to define the sites and depths on which coral cover was above or below the Expected Values of the Posterior Predictive Distribution (*i.e.* positive and negative outliers, respectively; **Sup. Fig. S3.1**). Based on similar studies applying this approach (Parravicini *et al.*, 2014; Cinner *et al.*, 2016; Edmunds, 2021), positive outliers were

named as ‘hotspots’ of coral cover in the mesophotic zone (Sup. Box1 Page 1 and 2), whereas negative outliers as ‘coldspots’ (Sup. Box 2).

The second model explored the relationship between coral cover and the environmental variables, including their interaction with depth. This model converged ($R^2 = 0.62$) with two chains of 4,000 iterations after a 1,000 iterations warm-up for each chain. To evaluate the effects of the environment at each depth, the conditional effects were used to measure the posterior likelihood of scleractinian coral as the proportion of successes for each trial standardised by the total number of points (*i.e.*, equivalent to coral cover), considering the interaction of the environmental predictors at each depth. The data was standardised, and to compare the numerical environmental predictors across depth, these were also scaled using conditional effects. The relative index light (correlated with depth) and the relative temperature (almost invariant along the depth gradient) were excluded from the model to avoid collinearity and increase the sensibility of other environmental variables.

Joint species distribution models were used to explore how environmental variables determined the cover of individual benthic categories across the depth gradient. This approach allows identifying the environmental variables correlated with the cover of individual species while accounting for potential biotic interactions between species (Warton *et al.*, 2015). Generalised joint attribute modelling was run with the package *GJAM* (Clark *et al.*, 2017) to study the co-occurrence between multiple species by building a network of correlations between benthic groups and in response to environmental parameters. This approach uses a hierarchical probit regression to combine habitat modelling with community ecology providing inference on sensitivity to input variables and the interactions between species. For this analysis, the cover of the 13 above-described benthic groups (*i.e.*, breaking down coral cover into the different morphology forms) was modelled by ‘depth’ and the most important environmental factorial predictors, ‘bathymetry slope’ and ‘dominant substrate’ (q matrix). We displayed the positive, neutral and negative correlations of our benthic groups by similarities in their responses to each benthic group (s) (co-existence) and the environmental predictors (q). The overall sensitivity of coral cover to depth changes (*i.e.* grouping scleractinian coral morphologies) was also evaluated with the same approach.

Spatial (across sites) and across depths differences in the structure of benthic communities, scleractinian coral cover, coral morphologies were evaluated using a permutational analysis of variance (*PERMANOVA*, blocked by quadrat), pairwise analyses (*PERMUTEST*), and homogeneity of variances (*BETADISPER*) with 999 permutations using the package *vegan* (Oksanen *et al.*, 2019). We ran principal component analyses with the packages *Ade4* and *FactoMineR* (Dray and Dufour, 2007; Lê, Josse and Husson, 2008). The necessary data and scripts to replicate our analyses are available at: https://github.com/gonzalopr/Cover_with_Depth.

3.5. Results

Thirty-two percent of the studied sites (20 out of 64) within the mesophotic range (40 – 120 m) harboured a higher scleractinian coral cover than the expected posterior predictive distribution of the null model at each depth (**Fig. 3.1b** and **Sup. Fig. S3.1**), with some of these ‘hotspots’ showing higher coral cover at mesophotic depths than their shallow counterparts, e.g. Raroia Site 1 (S1) at 40 m (coral cover, $81 \pm 7.7\%$, s.e.), Bora Bora sites at 60 m (64.7 to 68%), Makatea S2 at 60 m ($74.5 \pm 3.1\%$) and Gambier S2 at 90 and 120 m ($52.8 \pm 5.1\%$ and $42 \pm 4.2\%$, respectively) (**Fig. 3.1** and **Sup. Fig. S3.1**). While Moorea and Tahiti presented a sharp decrease in the coral cover below 40 m (from $\sim 30\%$ to $\sim 10\%$ at 60 m to $< 3\%$ at 90 m), other islands, such as Tikehau, Rangiroa and Raroia, exhibited a very high coral cover (18 to 43%) from 6 m and 20 m to 60 m. The highest coral cover at the deepest depths was observed in Makatea and Gambier islands (**Fig. 3.1b**; **Sup. Fig. S3.2**; *i.e.*, top-right of the graph), with Makatea exhibiting over 30% of coral cover from 6 m to 90 m, and only decreasing to $\sim 2\%$ at 120 m; and Gambier Islands (particularly in site 2), with $> 40\%$ coral cover across the depth range from 6 to 120 m (except at 60 m).

The overall structure of the benthic communities significantly changed across the depth gradient despite the high variability across sites (PERMANOVA, $p < 0.001$ for both benthos and scleractinian coral cover). Across sites, the highest variability in benthic community structure was observed at 40 m (BETADISPER: distance to centroids 0.36 at 40 m vs 0.29 – 0.31 at other depths) despite 40 m showing similar scleractinian coral cover across sites (20-50% coverage, **Fig. 3.1b**). In general, we found that coral cover tended to decrease along the depth gradient (**Sup. Fig. S3.1**), despite the spatial variability across locations (pairwise tests, $p < 0.001$). However, we found no correlation between individual depths on scleractinian coral cover, except for the communities between 90 and 120 m ($p < 0.05$), where the cover was generally lower ($< 25\%$, **Fig. 3.1b** and **Sup. Fig. S3.1** and **S3.2**). Thus, within sites, the coral cover at a particular depth seems to be independent of the rest along the depth gradient (**Fig. 3.2b** and **3.3**, and **Sup. Fig. S3.2**).

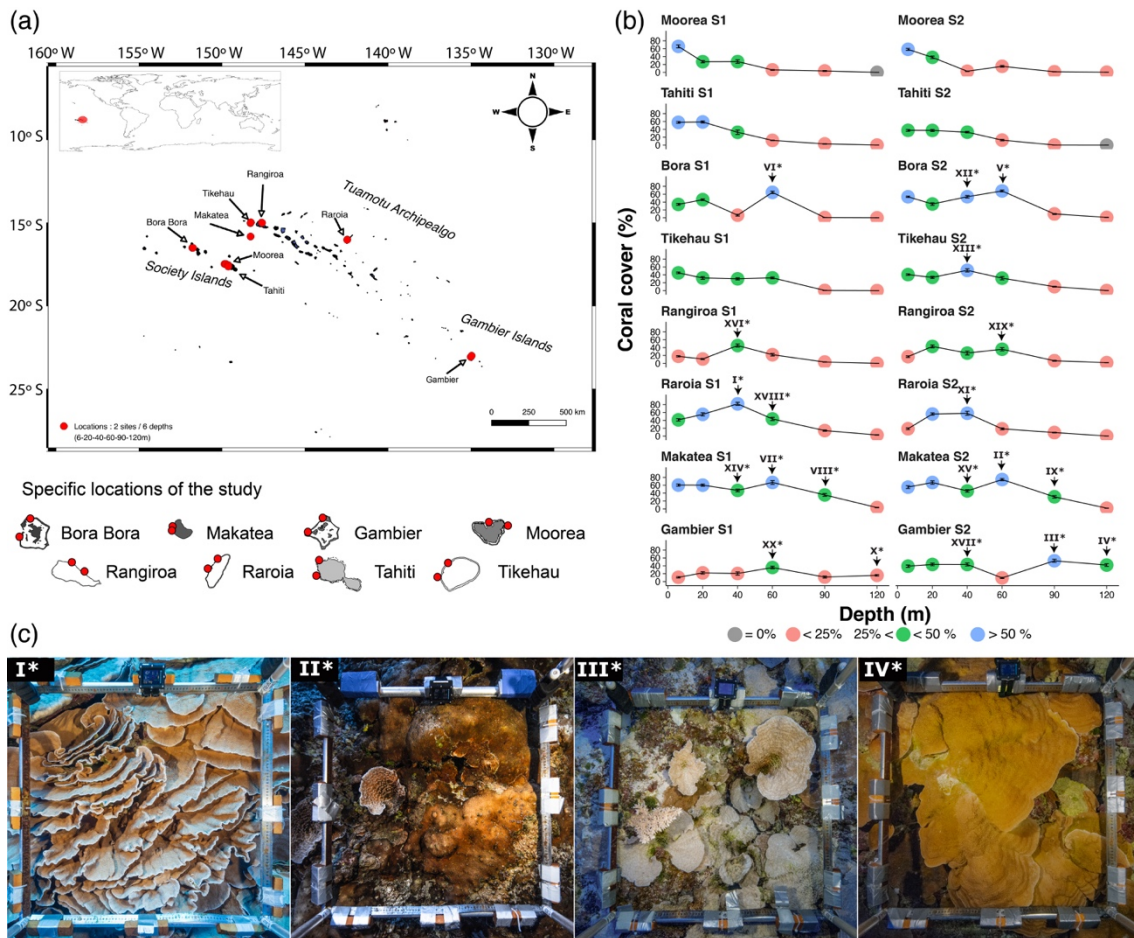


Figure 3.1: High scleractinian coral cover ‘hotspots’ (positive outliers). (a) Map of French Polynesia detailing the study locations by islands. (b) Scleractinian coral cover profiles over depth across locations. ‘Hotspots’ outliers from the null expected distribution are indicated with arrowheads, roman numerals and asterisks (see model in **Sup. Fig. S3.1** and correlations over depth in **Sup. Fig. S3.2**). (c) Example of ‘hotspots’ positive outliers [I*. Raroia S1 at 40 m. II*. Makatea S2 at 60 m. III*. Gambier S2 at 90 m. IV*. Gambier S2 at 120 m]. Top 10 outliers and their descriptions are displayed in **SBox3.1 Page 1** and **Page 2**.

The light relative index (negatively correlated with depth, Cor. test, -0.85 , $p < 0.05$) followed by the type of substrate and the gradient slope were the most influencing predictors for the likelihood of high coral coverage while increasing depth (**Fig. 3.2**). Based on the second (full) model ($R^2 = 0.62$), the likelihood of coral cover is lower at deeper depths (negative β slope, upper Confidence Interval (CI) 0.003), displaying some depths at sites as exceptions, the ‘hotspots’. Hard-fixed substrates with steep-to-moderate slopes are more likely to harbour scleractinian coral cover at deeper depths than other substrates and slopes. Moderate and steep slopes maintained the likelihood of coral cover along the depth gradient. In contrast, the high likelihood of coral cover in gentle slopes became lower than the observed for moderate slopes from 40 m and deeper, and even lower than walls below 90 m depth. Compared to hard substrates, sediment and rubble benthic substrates had a lower likelihood of harbouring coral cover at deeper depths (negative slope and negative 95% CI). Below 60 m depth, the likelihood of coral cover on soft and rubble dominant substrates was nearly inexistent. The coral cover was poorly predicted by other environmental variables. For example, the high-temperature variability (*i.e.*, increasing over depth) had a negative effect on the likelihood of coral cover (negative slope with a negative 95% CI), whereas the low-temperature variability (*i.e.*, frequently observed in shallow waters) maintained the likelihood of coral cover along the depth gradient. The relative temperature was constant along the depth gradient and had no effect over depth, with differences of less than 1°C in most locations of the Society and Tuamotu, and the highest difference (4°C) between 6 and 120 m in the Gambier Islands (**Sup. Fig. 3**).

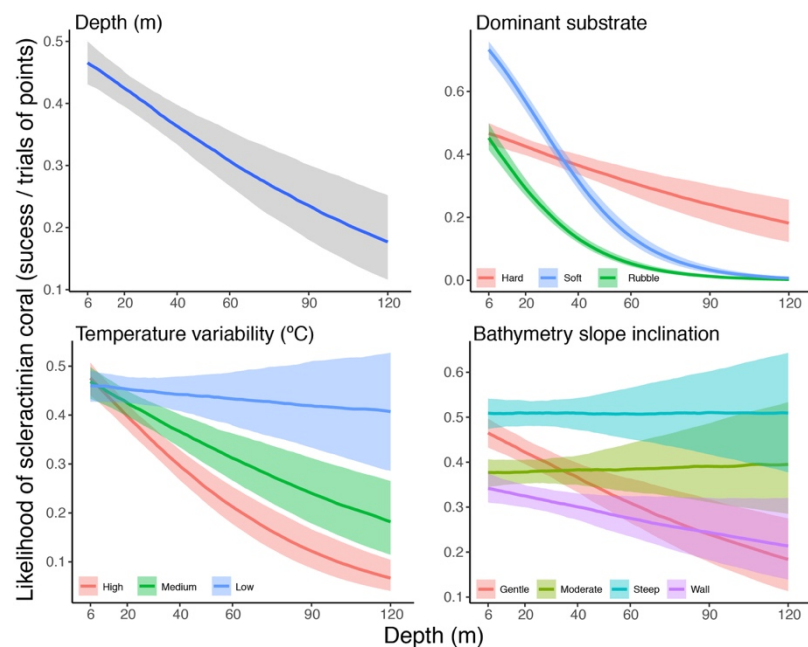


Figure 3.2: Bayesian prediction probability of the likelihood of scleractinian corals (success / trials of total number of points) according to environmental variables covarying with increasing depth. Depth and the light relative index are collinear (negatively correlated; cor. test, -0.85 , $p < 0.05$) and equally determined the likelihood of scleractinian coral cover.

Breaking down the scleractinian cover into coral morphologies, we found a general dominance trend over depth, with branching corals showing higher cover at shallow reefs, laminar corals dominating at deeper depths, and the highest diversity of coral morphologies at 40 m (**Fig. 3.3** and **Sup. Fig. S3.4**, BETADISPER: distance to centroids 21.76 at 40 m vs 4.47 – 19.2 at other depths). The high coral-cover ‘hotspots’ at MCEs were either dominated by monotypic stands of laminar corals (*i.e.*, mainly *Agariciidae* family, but also *Acroporidae*) or by multiple coral forms (Sup. Box 1 and 2). Monotypic stands at 40 m mainly consisted of *Pachyseris “speciosa” spp.*; deeper at 60 – 90 m, of *Leptoseris solida* showing diverse sizes across locations (*e.g.* in Makatea, sizes could reach up to 2,000 cm²); and at 90 and 120 m, of large thin plates of *Montipora spp.* (*e.g.* in Gambier, sizes could reach 2,500 cm²). When mesophotic reefs were not monotypic stands, encrusting corals were the most common coral form (*e.g.*, *Pavona varians*, *Leptoseris incrustans*, *Leptoseris myscetoseroides*, *Leptastrea spp.*), although other coral morphologies, such as massive *Porites spp.* and branching *Pocillopora spp.*, were occasionally present with covers varying between 1-26% in upper mesophotic depths (40-60 m). At the deepest depths (>100 m), only small and thin laminar coral colonies (≤ 20 cm²) of *Leptoseris hawaiiensis*, *Leptoseris scabra*, *Leptoseris fragilis*, *Echinophyllia aspera* and *Oxypora echinata* were found. Contrary to the ‘hotspots’ of coral cover, ‘coldspots’ reefs were mainly dominated by CCA and sponges (average cover across sites of $7.23 \pm 1.8\%$ and $9.09 \pm 1.7\%$ at 90 m and $3.83 \pm 0.9\%$ and $11.8 \pm 2.1\%$ at 120 m, respectively), and when characterised by negative slopes, high sediment and bare fixed substrate, ‘coldspots’ presented coverage of gorgonians, hydroids and antipatharians of up to $3.64 \pm 1.3\%$, $3.51 \pm 0.6\%$, and $0.76 \pm 0.5\%$ at 90 m and $7.02 \pm 1.6\%$, $5.6 \pm 1.3\%$ and $2.44 \pm 0.7\%$ at 120 m, respectively (maximum cover across sites, see **Sup. Fig. S3.5**, **Sup. Table S3.1**, **S3.2**).

Based on the benthic groups co-occurrence over depth, shallow depths were characterised by branching and massive corals and macroalgae *Halimeda spp.* (positive correlations within the shallow group, **Fig. 3.4** and **Sup. Fig. S3.6** and **S3.7**), whereas at deeper depths by laminar corals co-occurring with gorgonians, antipatharians, and sponges (positive correlations within the deep group). Co-occurrence of deep laminar corals and other coral morphologies at shallow depths had a negative correlation. CCA and crustose algae showed mostly a neutral correlation across depth, although the last one showed a higher sensitivity towards the deep group. On the other hand, CCA, and

encrusting and solitary corals, were grouped in a third cluster with intermediate sensitivity, although these two coral morphologies had a slightly higher correlation with the shallow group (**Sup. Fig. S3.6b**). Overall, we found that each coral form benefited from different environmental conditions and laminar corals dominated at lower mesophotic depths (**Sup. Fig. S3.7**). Regarding the correlations between distinct benthic groups and environmental predictors, we found that soft sediment sandy substrate was negatively correlated with scleractinian corals but favoured the occurrence of gorgonians and hydroids (**Fig. 3.4b**). On the contrary, rubble favoured encrusting and solitary corals (fungiids) while negatively correlated to gorgonians and hydroids. Steep or vertical slopes favoured laminar corals, whereas a gentle slope the presence of branching corals.

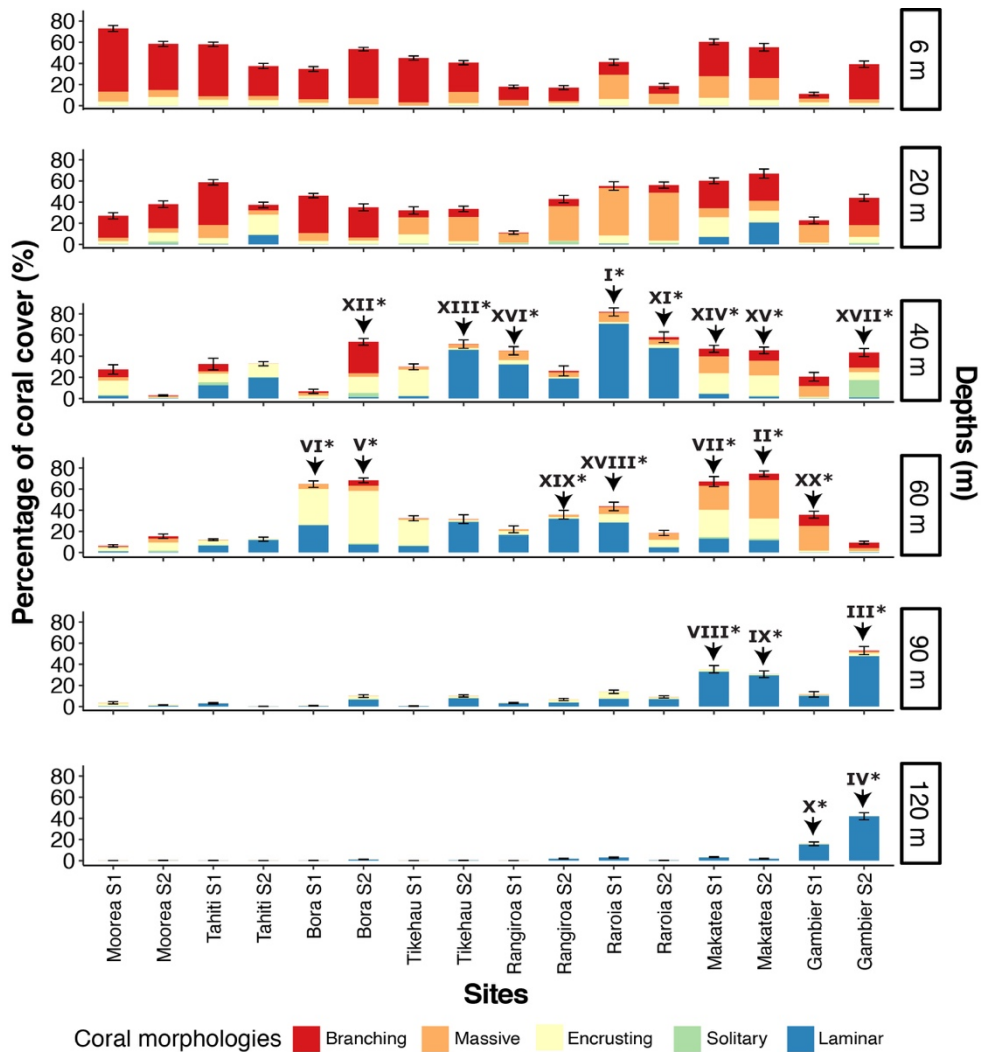


Figure 3.3: Scleractinian coral cover composition by morphologies. 'Hotspots' outliers of coral cover are indicated with arrowheads, roman numbers and asterisks (see model in S3.1).

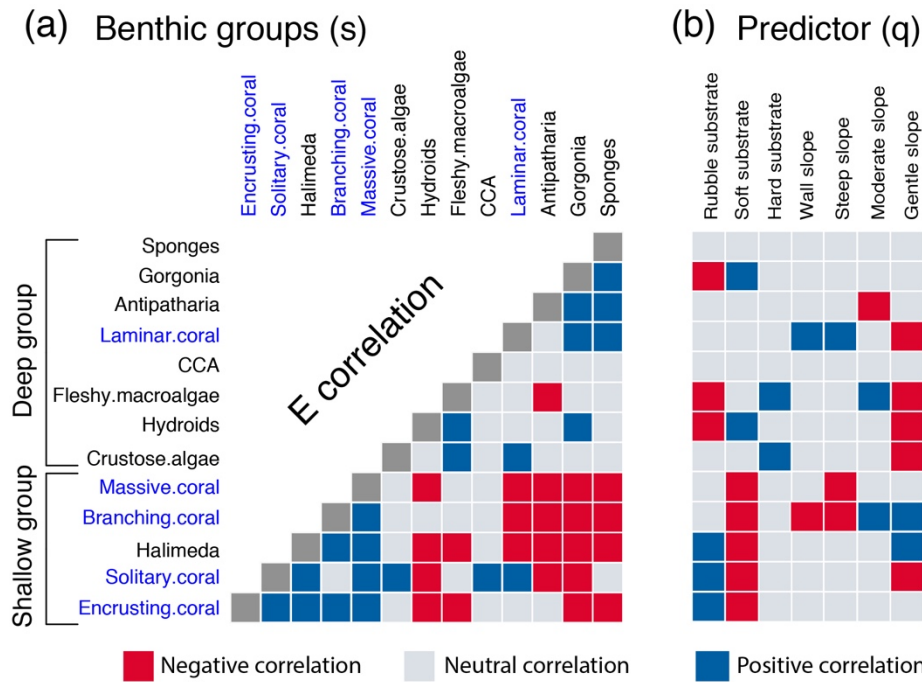


Figure 3.4: Correlation between the different benthic groups (s) and the most important environmental predictors (q). Correlations were simplified into negative (< -0.4), neutral ($-0.4 < 0.4$) and positive (> 0.4). Neutral correlations are interpreted as neither positive nor negative influence, or the absence of supporting data. Shallow and deep groups were clustered based on E correlation (S3.6 and S3.7).

3.6. Discussion

We identified 20 ‘hotspots’ with a higher scleractinian cover than expected for the depth across the French Polynesia MCEs. Light and depth (co-variables) mainly explained the differences in community structure, benthic and environmental co-occurrence, and the dominance of certain scleractinian morphologies over depth. Following the influence of light-depth covariance (also previously reported by (Kahng *et al.*, 2019; Laverick *et al.*, 2020), the substrate type and the slope inclination were key variables on the environmental trade-off for the likelihood of high scleractinian cover, being hard substrate and moderate/steep slopes (30 to 70°) the most common substrate for positive outliers (13 out of 20 ‘hotspots’). Our results expand on previous observations of the positive correlation between the scleractinian cover and hard-fixed substrates (e.g., limestone; Hopley, 1982; Liddell and Ohlhorst, 1988; Englebert *et al.*, 2017; Pyle and Copus, 2019) and the negative correlations with sediment and rubble (Hubbard, 1986; Perry, 2007; Bridge *et al.*, 2011; Appeldoorn *et al.*, 2016; Sherman *et al.*, 2016, 2019), suggesting the slope inclination as a potential compensatory variable for the light decay over depth and sediments in the water column. Given the geomorphology and water clarity in fore reefs, our results indicate that this mid-region of the South Pacific

represents a promising bioregion for the identification and research of high scleractinian cover in MCEs (as in Pichon *et al.*, 2021; Rouzé *et al.*, 2021).

The positive outliers reflected the morphologic dominance observed in the overall coral community composition over depth, with laminar morphologies almost exclusively covering outlier assemblages at 90 and 120 m and at least six ‘hotspots’ at 40 m and 60 m. Although at first could appear as monotypic stands, laminar-dominated outliers were diverse, comprising between 8 and 22 scleractinian species (**Sup. Box S3.1 and S3.2**). Some of the most common scleractinian species at steep slopes or near-vertical walls were laminar *Leptoseris solida*, *L. hawaiiensis*, *Echinophyllia aspera*, *Oxypora echinata* and *Cycloseris wellsi*, whereas *P. “speciosa” spp.* and *Porites rus* were associated with more moderate slopes at 40 and 60 m. The dominance of large laminar/plating corals at mesophotic depths has been previously reported in the Caribbean and the Indo-Pacific (Zlatarski and Estalella, 1982; Bouchon, 1983; Faure and Laboute, 1984; Kühlmann and Chevalier, 1986; Hopley, Smithers and Parnell, 2007; Kahng and Kelley, 2007; Kahng *et al.*, 2010; Rooney *et al.*, 2010; Kahng, Copus and Wagner, 2014; Pyle *et al.*, 2016; Hoeksema, Bongaerts and Baldwin, 2017), and hypothesised to be related to potential physiological adaptations inherent to the host (Kahng *et al.*, 2020), or acquired through symbiosis (Gonzalez-Zapata, Gómez-Osorio and Sánchez, 2018). For example, the observed skeletal geometry in laminar *Leptoseris* and *Montipora* species confers a higher efficiency in light harvesting (Kahng, Hochberg, *et al.*, 2012), promoting moderate growth rates of these genera (Kahng *et al.*, 2020), which could result in advantage while colonising mesophotic depths. Further, potential symbiosis with the endolithic green algae *Ostreobium*, observed as part of the benthonic community in some of the positive outliers (*e.g.*, outliers III, IV, VII, VIII, IX; Sup. Box 1), could benefit the success of these species at mesophotic depth by providing fixed carbon (Fine and Loya, 2002; Iha *et al.*, 2021; Rouzé *et al.*, 2021). Additional research is necessary on potential coral ecological interactions with other benthic groups.

Our identification and characterisation of positive outliers highlight the unique characteristics of MCEs, but only scratched the surface on elucidating the factors that determine unexpected high coral cover at mesophotic depths. Analysing positive outliers considering biological processes that could contribute to the observed high scleractinian cover (*i.e.*, connectivity, competition, susceptibility to bleaching and diseases, suitable

geomorphology, photophysiology performance) will importantly advance the understanding of MCEs ecology, but also contribute to deciphering its potential role for overall coral reef resilience. Improving our predicting capacity to identify high coral cover MCEs requires a worldwide effort to capture the high spatial variability among sites (shown across outliers in this study), regions (Rocha *et al.*, 2018) and the diverse life histories across coral species. While coral reefs continue to be threatened by climate change (Hughes, Anderson, *et al.*, 2018; Bellwood *et al.*, 2019; Souter *et al.*, 2021), MCEs remain not considered in the conservation planning of tropical coral reefs (Bridge *et al.*, 2013; Rocha *et al.*, 2018). By establishing a baseline for the geographical and temporal monitoring of MCEs in French Polynesia, we expect to advance in understanding the ecology and functioning of MCEs to ultimately inform on ecosystem-wide decisions that warrant the conservation of coral reefs.

3.7. Extra information

3.7.1. Acknowledgements

We thank all the Under The Pole Expedition III team for making the collection of benthic and environmental data on deep mesophotic coral ecosystems possible. We also thank Charlène Guillaumot (Marine Biology Lab, Université Libre de Bruxelles) for providing advice on species distribution modelling. The present work is based on photo-quadrats (pictures) and environmental data, and no export permits are required for these data in French Polynesia.

Under The Pole Consortium⁶ G. Bardout, J. Fauchet, A. Ferucci, F. Gazzola, G. Lagarrigue, J. Leblond, E. Marivint, A. Mittau, N. Mollon, N. Paulme, E. Périé-Bardout, R. Pete, S. Pujolle, G. Siu.

3.7.2. Data availability


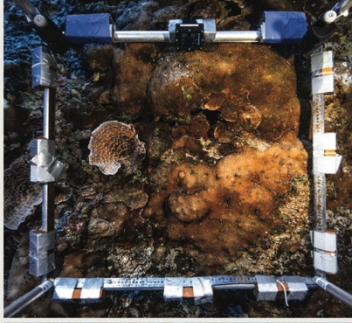
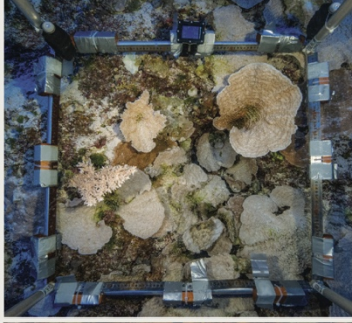
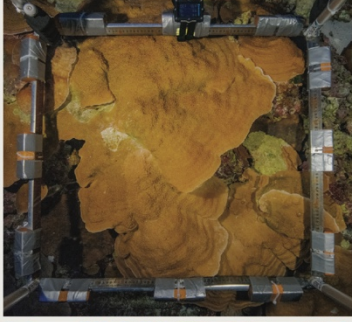
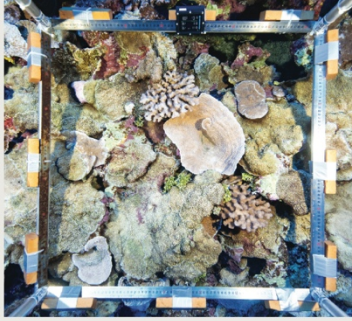
All scripts and data necessary to replicate the analysis of this study are at: https://github.com/gonzalopr/Cover_with_Depth.

3.7.3. Funding

This research was funded by the ANR DEEPHOPE (ANRAAPG 2017, grant no. 168722), the Délégation à la Recherche DEEPCORAL, the CNRS DEEPRÉEF, the EPHE and the IFRECOR.

3.7.4. Supplementary information

Box S3.1: Top 10 'hotspots'/positive outliers with high scleractinian coral cover. Sites were defined as outliers if the scleractinian coral cover was above the expected posterior distribution of the null Bayesian model (S3.1).

'Hotspots'/positive outliers description	
<p>I*</p> <p>Depth = 40 m Location = Tuamotu Archip. Raroia - Site 1 Coordinates = 16.01°S / 142.45°W --- Coral cover = 81.8 (se=7.7) % Monoculture of <i>Pachyseris "speciosa" spp.</i> roses. Slope = Steep. Hard substrate. Coral dominated followed by macroalgae Generic richness P/A quadrat = 12 (Tax=13)</p>	
<p>II*</p> <p>Depth = 60 m Location = Tuamotu Archip. Makatea - Site 2 Coordinates = 23.00°S / 134.96°W --- Coral cover = 74.5 (3.1) % Encrusting <i>Leptoseris mycetoseroides</i> and <i>Pavona varians</i>. Laminar <i>Leptoseris solida</i>. Slope = Wall. Fixed hard substrate. Coral dominated followed by crustose macroalgae Generic richness P/A quadrat = 16 (Tax=20)</p>	
<p>III*</p> <p>Depth = 90 m Location = Gambier Islands. Gambier - Site 2 Coordinates = 15.82°S / 148.28°W --- Coral cover = 52.9 (5.1) % Laminar <i>Montipora spp.</i> Slope = Moderate. Fixed hard substrate. Minimal presence of green algae Generic richness P/A quadrat = 12 (Tax=11)</p>	
<p>IV*</p> <p>Depth = 120 m Location = Gambier Islands. Gambier - Site 2 Coordinates = 15.82°S / 148.28°W --- Coral cover = 42 (4.2) % Laminar <i>Leptoseris spp.</i> and <i>Montipora spp.</i> (colonies up to ~2,500 cm²) Slope = Moderate. Fixed hard substrate. Coral dominated landscape with minimal presence of CCA Generic richness P/A quadrat = 7 (Tax=8)</p>	
<p>V*</p> <p>Depth = 60 m Location = Society Archip. Bora Bora - Site 2 Coordinates = 16.43°S / 151.75°W --- Coral cover = 68.3 (1.8) % High diversity. Laminar <i>Pachyseris "speciosa" spp.</i> and encrusting <i>Pavona spp.</i> Slope = Moderate. Fixed hard substrate. Coral dominated with high presence of CCA Generic richness P/A quadrat = 22 (Tax=18)</p>	

'Hotspots'/positive outliers description

VI*

Depth = **60 m**
 Location = Society Archip. **Bora Bora** - Site 1
 Coordinates = 16.52°S / 150.78°W

 Coral cover = **64.7 (se=2.2) %**
 Mostly *Pachyseris speciosa* spp. roses, but also encrusting *Pavona* spp. and massive *Porites* spp.
 Slope = Steep. Fixed hard substrate.
 Coral dominated with high presence of CCA.
 Generic richness P/A quadrat = 20 (Tax=11)



VII*

Depth = **60 m**
 Location = Tuamotu Archip. **Makatea** - Site 1
 Coordinates = 15.82°S / 148.28°W

 Coral cover = **67.1 (3.1) %**
 Laminar and encrusting *Leptoseris* spp.
 Slope = Moderate. Fixed hard substrate.
 Low/minimal presence of green algae.
 Generic richness P/A quadrat = 15 (Tax=19)



VIII*

Depth = **90 m**
 Location = Tuamotu Archip. **Makatea** - Site 1
 Coordinates = 15.82°S / 148.28°W

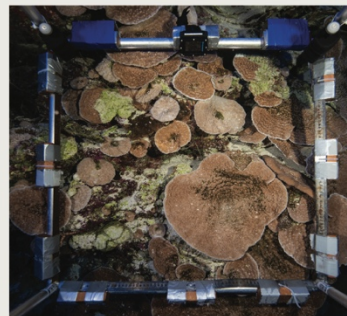
 Coral cover = **35.4 (6.9) %**
 Monoculture of *Leptoseris solida* roses.
 Slope = Wall. Sediment substrate.
 High abundance/cover of green crustose macroalgae.
 Generic richness P/A quadrat = 7 (Tax=16)



IX*

Depth = **90 m**
 Location = Tuamotu Archip. **Makatea** - Site 2
 Coordinates = 15.82°S / 148.28°W

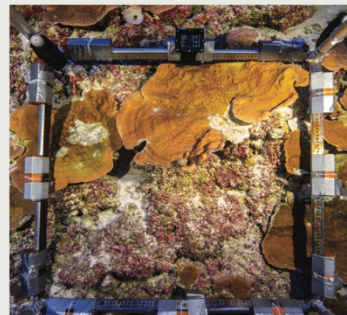
 Coral cover = **30.6 (5.5) %**
 Monoculture of *Leptoseris solida* roses.
 Slope = Wall. Fixed hard substrate.
 High abundance/cover of green crustose macroalgae.
 Generic richness P/A quadrat = 9 (Tax=10)



X*

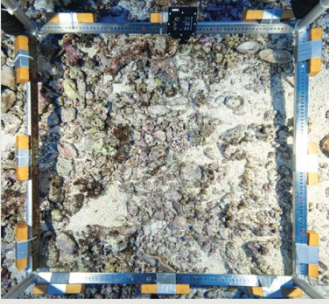
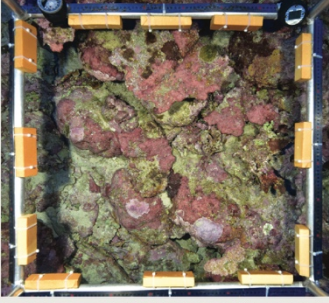
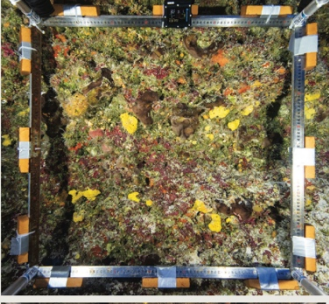

Depth = **120 m**
 Location = Gambier Islands. **Gambier** - Site 1
 Coordinates = 23.07°S / 135.01°W

 Coral cover = **15.9 (1.5) %**
 Laminar *Montipora* spp. and *Leptoseris* spp.
 Slope = Moderate. Sediment soft substrate.
 Coral dominated landscape with high CCA cover and patches of sand.
 Generic richness P/A quadrat = 7 (Tax=8)



Box S3.2: 'Coldspots'/negative outliers with the lowest scleractinian coral cover at each depth. Sites were identified as cold/negative outliers if the scleractinian coral cover was below the expected posterior distribution of the null Bayesian model (S3.1).

'Coldspots'/negative outliers description

I^{CS}	<p>Depth = 40 m Location = Society Archip. Moorea - Site 2 Coordinates = 17.47°S / 149.76°W --- Coral cover = 2.8 (se=0.04) % Slope = Moderate. Sediment substrate. Sand, rubble and uncolonized CCA. Generic richness P/A quadrat = 22 (Tax=13)</p>	
II^{CS}	<p>Depth = 60 m Location = Society Islands. Moorea - Site 1 Coordinates = 17.47°S / 149.85°W --- Coral cover = 6.2 (0.19) % Slope = Moderate. Fixed hard substrate. Sediment and uncolonized CCA. Generic richness P/A quadrat = 17 (Tax=4)</p>	
III^{CS}	<p>Depth = 90 m Location = Tuamotu Archip. Tikehau - Site 1 Coordinates = 15.01°S / 148.28°W --- Coral cover = 0.5(0.13) % Slope = Wall. Fixed hard substrate. Sponges, turf and caves. Generic richness P/A quadrat = 2 (Tax=4)</p>	
IV^{CS}	<p>Depth = 120 m Location = Society Islands. Tahiti - Site 2 Coordinates = 17.63°S / 149.62°W --- Coral cover = 0 % Slope = Wall. Sediment substrate. Black sediment, sponges and gorgonias. Generic richness P/A quadrat = 0 (Tax=0)</p>	

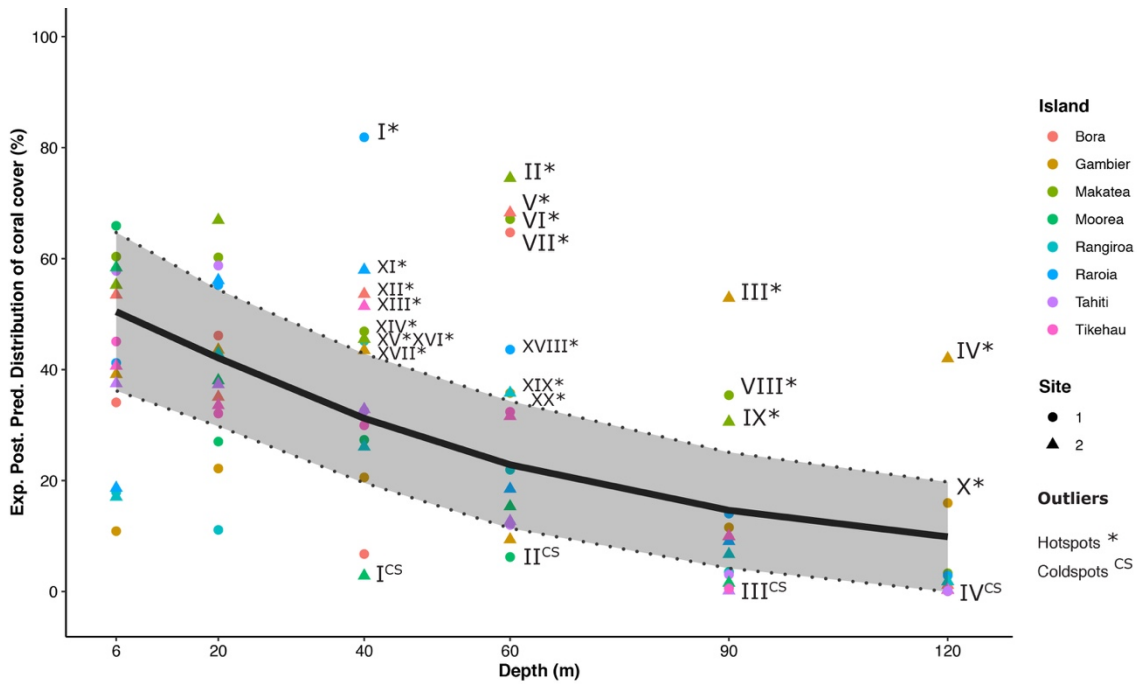


Figure S3.1: Bayesian model of scleractinian coral cover over depth. Sites outside the shaded grey area (i.e., expected posterior distribution) are considered as 'hotspots'/positive outliers of coral cover (with the extreme cover values displayed in Box S3.1 Page 1 and 2 as top 10 outliers) or 'coldspots'/negative outliers (Box S3.2). Positive outliers are indicated with roman numbers and asterisks, and negative outliers with roman numbers and ^{CS}. X* and IV^{CS} (within the expected distribution) were included in Box S3.1 and Box S3.2 to allow comparisons. All hotspots are displayed in Sup. Table S3.3.

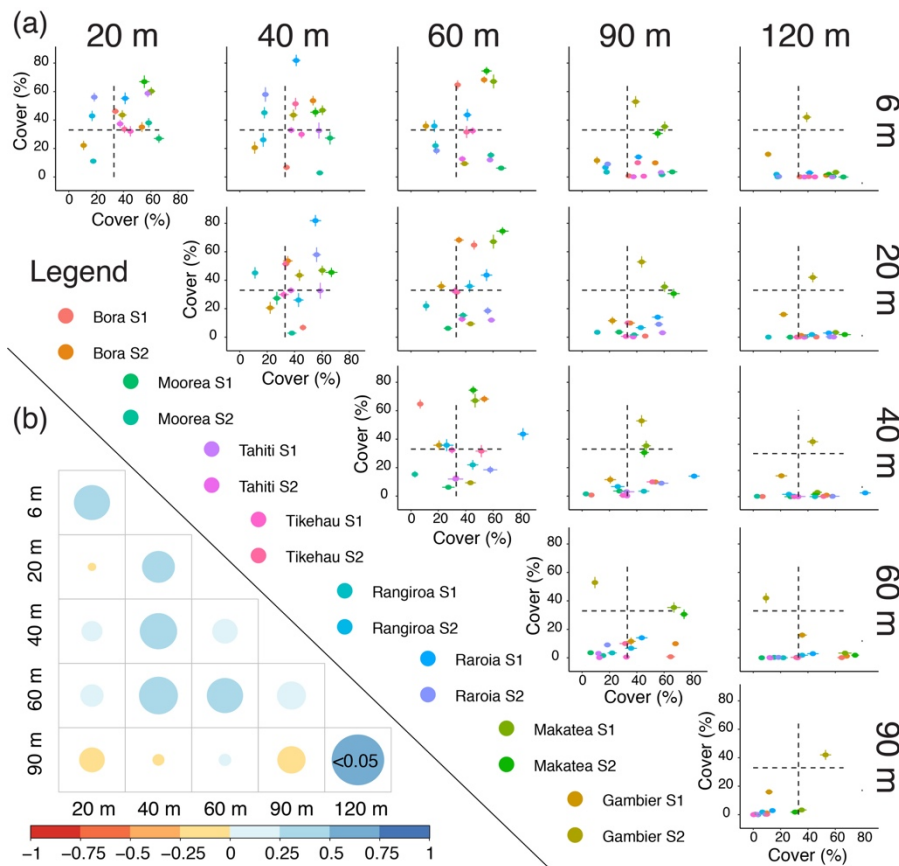


Figure S3.2: Scleractinian coral correlations over depth. (a) Matrix of correlations of scleractinian coral cover across different depths (6, 20, 40, 60, 90 and 120 m). Each of the four sections of the dashed line shows correlations between the compared depths. (b) Correlations (0.95 CI) across the different depths (6, 20, 40, 60, 90 and 120 m). Numbers inside circles show significant p-values < 0.05.

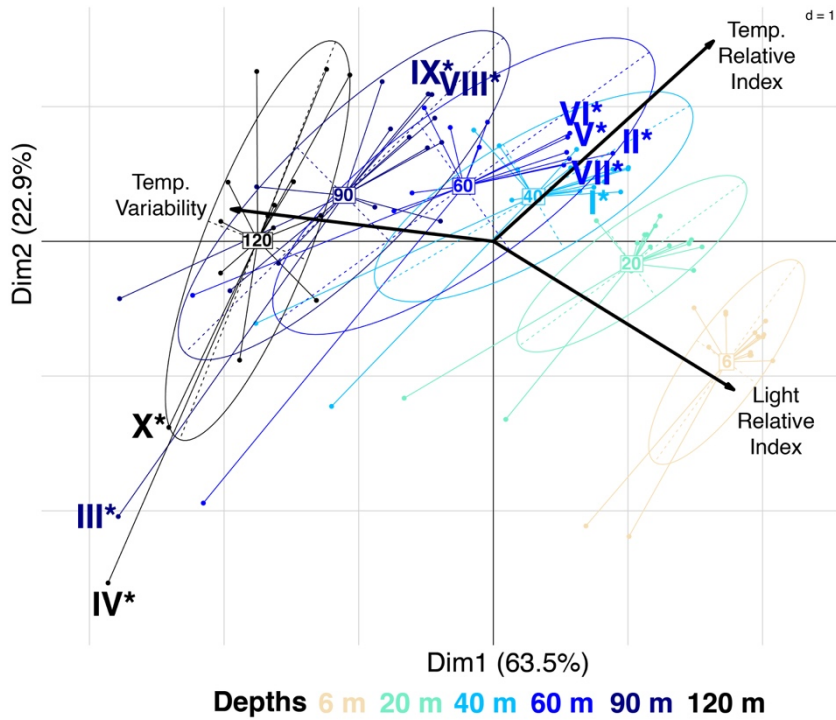


Figure S3.3: Principal component analysis (PCA) on the main three abiotic/numeric environmental (light relative index, temperature relative index and temperature variability) coloured by depths displayed with ellipses. The first axis explained 63.5% of the ordination and the second axis 22.9%. Each ordination point represents individual depths sites. Top 10 'hotspots' /positive outliers are indicated with roman numbers and asterisks.

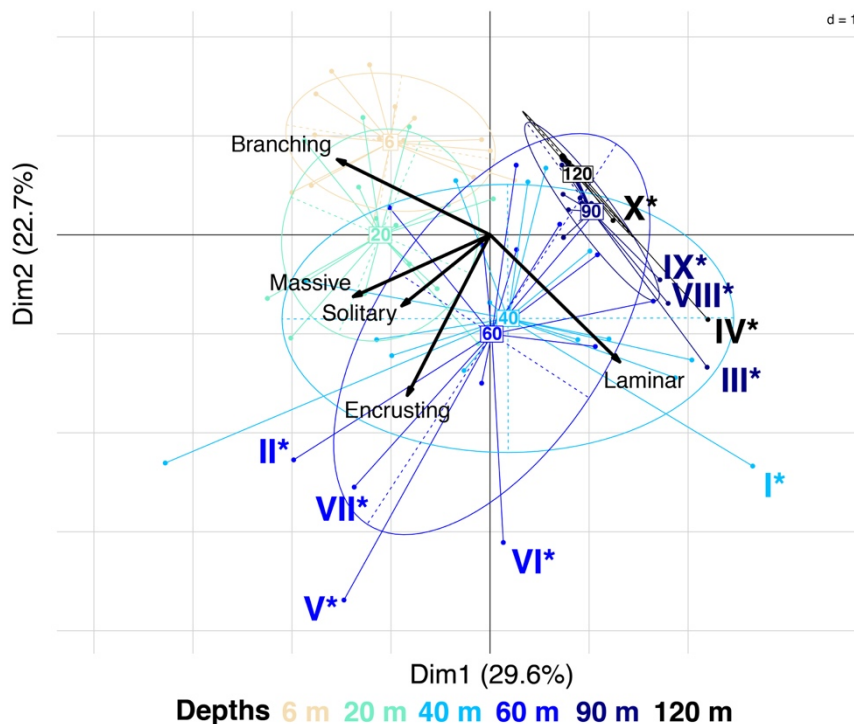


Figure S3.4: (a) Principal component analysis (PCA) on the different biotic/coral morphologies (branching, massive, solitary, encrusting and laminar) coloured by depths displayed with ellipses. The first axis explained 29.6% of the ordination and the second axis 22.7%. Each ordination point represents individual depth sites. Top 10 'hotspots' /positive outliers are indicated with roman numbers and asterisks.

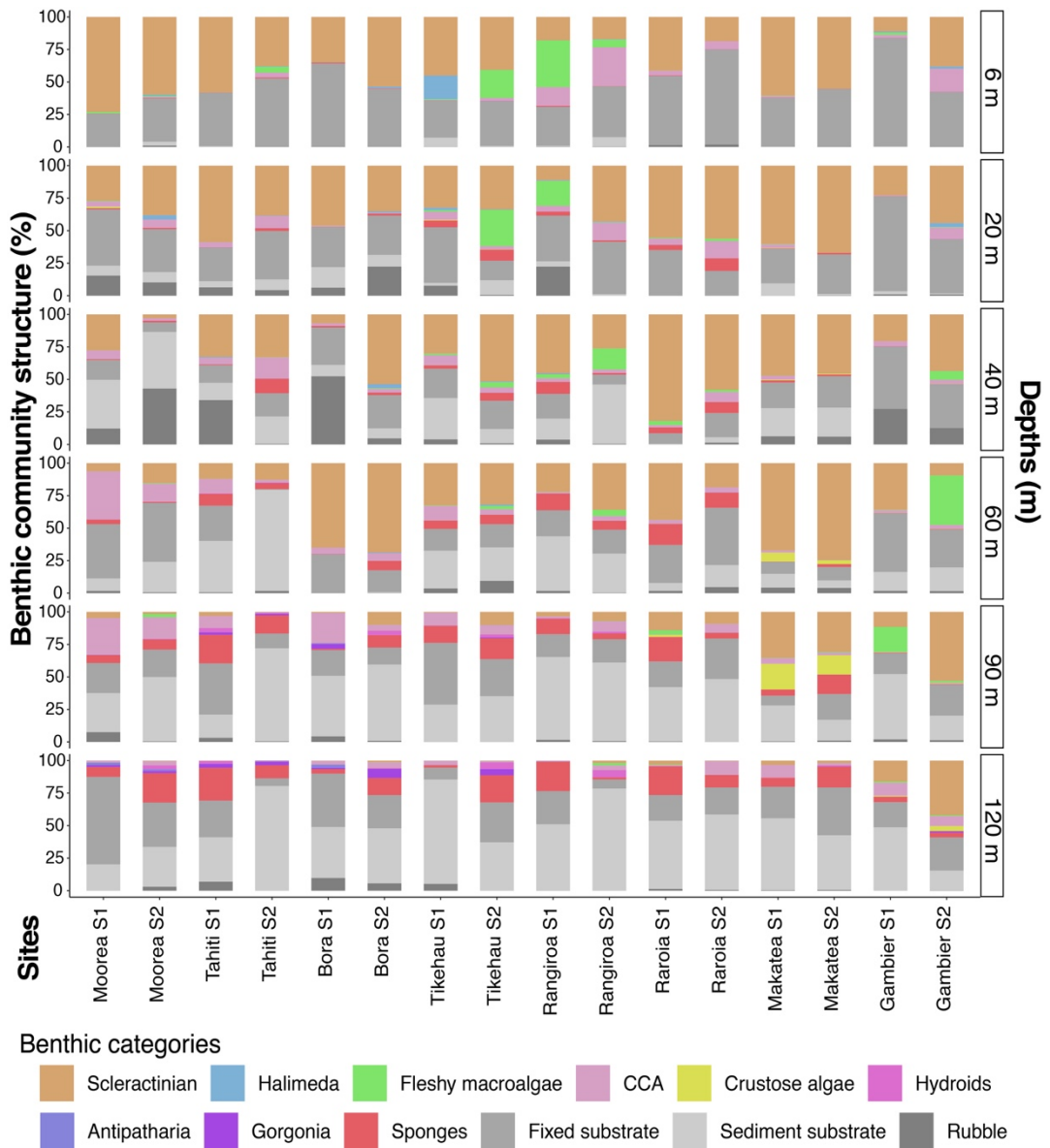


Figure S3.5: Benthic community structure across depths and sites.

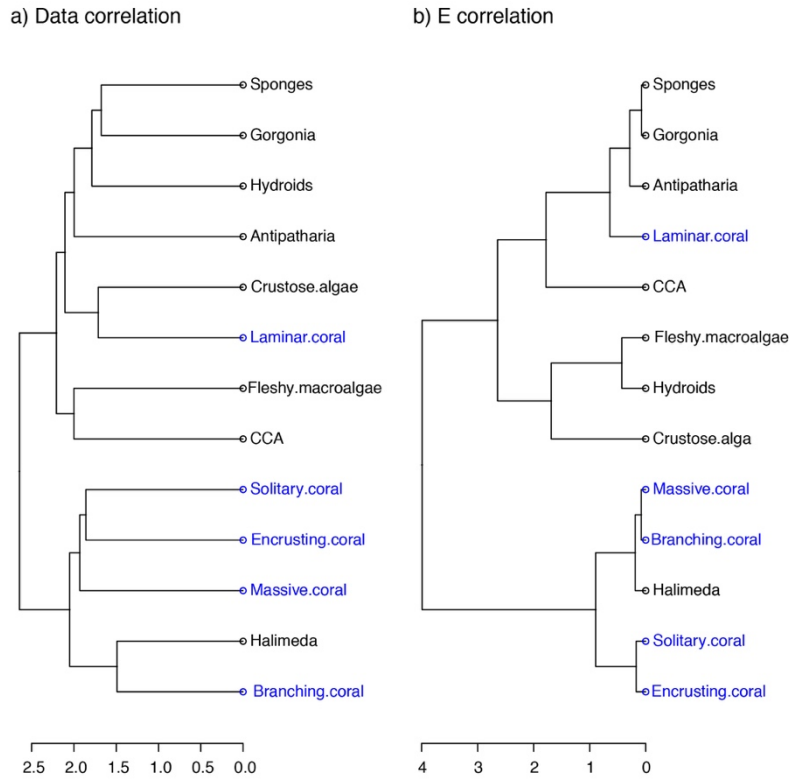


Figure S3.6: Clustering of benthic groups in response to benthic interactions and environmental variables. Generalised joint attribute modelling (GJAM) highlights similarities among benthic groups based on (a) data correlation as a proxy of co-occurrence; and (b) their response to environmental variables (E correlation). Based on this clustering shallow and deep reefscapes are identified, with the dominance of particular taxa. Scleractinian coral morphologies are displayed in blue.

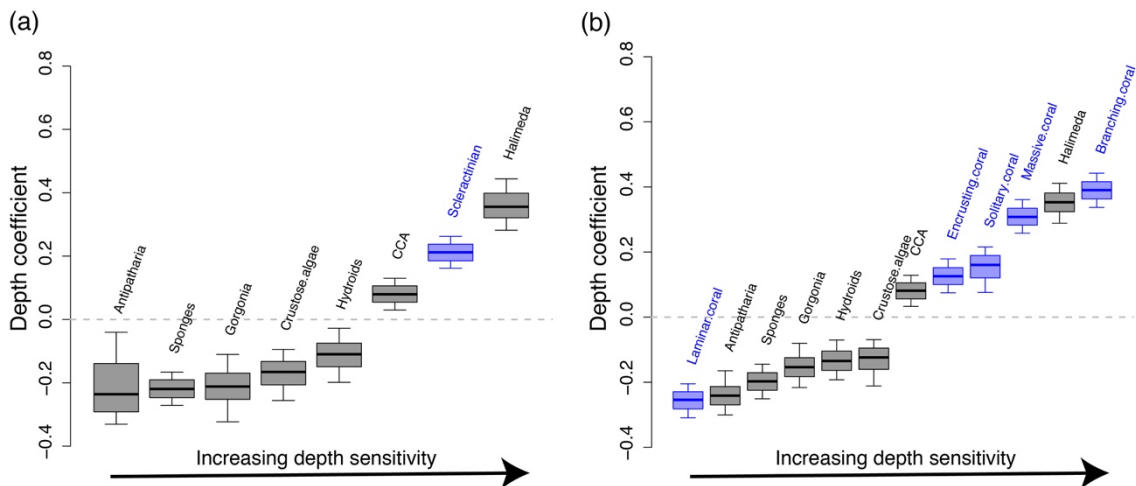


Figure S3.7: Posterior summary of beta coefficients from the Generalised joint attribute modelling (GJAM) of species distribution to show depth sensitivity among the different benthic groups. While overall scleractinian is very sensitive to depth, grouping with other shallow groups (a), when breaking down into the different coral morphologies, laminar corals raise as depth specialist, grouping with other deep benthic groups (such as antipatharians, sponges, gorgonians and hydroids), having a low sensitivity to depth (b). Branching and massive corals showed high sensitivity to increasing depth and grouped with shallow benthic groups such as Halimeda spp. Scleractinian coral morphologies are displayed in blue.

Table S3.1: Coral morphology groups. Only dominant genera and species at mesophotic depths (below 30 m depth) collected and taxonomically identified during the expedition are presented.

Coral morphology group	Main genera	Main species
● Laminar coral	<i>Leptoseris</i>	<i>L. solida</i> , <i>L. hawaiiensis</i> , <i>L. scabra</i> , <i>L. fragilis</i> , <i>L. foliosa</i> , <i>L. spp.</i>
	<i>Echinophyllia</i>	<i>E. aspera</i> , <i>E. tarae</i>
	<i>Oxypora</i>	<i>O. echinata</i>
	<i>Pachyseris</i>	<i>P. "speciosa" spp.</i> (see Bongaerts <i>et al.</i> , 2021)
	<i>Montipora</i>	<i>M. spp.</i>
	<i>Cycloseris</i>	<i>C. wellsi</i> , <i>C. explanulata</i> ,
	<i>Astreopora</i>	<i>A. myriophthalma</i> , <i>A. spp.</i>
	<i>Psammocora</i>	<i>P. columna</i>
	<i>Turbinaria</i>	<i>T. spp.</i>
	<i>Pavona</i>	<i>P. varians</i> , <i>P. minuta</i> , <i>P. explanulata</i> <i>P. spp.</i>
	<i>Porites</i>	<i>P. rus</i> , <i>P. vauhani</i> , <i>P. spp.</i>
	<i>Gardineroseris</i>	<i>G. planulata</i>
	<i>Non Identified</i>	-
● Encrusting coral	<i>Leptoseris</i>	<i>L. incrustans</i> , <i>L. mycetoseroides</i> , <i>L. spp.</i>
	<i>Pavona</i>	<i>P. varians</i> , <i>P. chiriquiensis</i> , <i>P. duerdeni</i> , <i>P. minuta</i> , <i>P. spp.</i>
	<i>Echinophyllia</i>	<i>E. aspera</i> , <i>E. tarae</i>
	<i>Oxypora</i>	<i>O. echinata</i>
	<i>Porites</i>	<i>P. rus</i> , <i>P. vauhani</i> , <i>P. lichen</i> , <i>P. spp.</i>
	<i>Montipora</i>	<i>M. verrucosa</i> , <i>M. spp.</i>
	<i>Astreopora</i>	<i>A. myriophthalma</i>
	<i>Psammocora</i>	<i>P. profundacella</i> , <i>P. nierstraszi</i> , <i>P. columna</i>
	<i>Leptastrea</i>	<i>L. pruinosa</i> , <i>L. transversa</i> , <i>L. purpurea</i> , <i>L. spp.</i>
	<i>Cyphastrea</i>	<i>C. serailia</i> , <i>C. spp.</i>
	<i>Acanthastrea</i>	<i>A. echinata</i>
	<i>Gardineroseris</i>	<i>G. planulata</i>
	<i>Stylocoeniella</i>	<i>S. guentheri</i>
	<i>Turbinaria</i>	<i>T. spp.</i>
	<i>Cycloseris</i>	<i>C. explanulata</i> , <i>C. wellsi</i>
	<i>Alveopora</i>	<i>A. tizardii</i> , <i>A. ocellata</i> , <i>A. fenestrata</i>
<i>Non Identified</i>	-	
● Solitary and free-living colonial corals	<i>Danafungia</i>	<i>D. horrida</i>
	<i>Lithophyllon</i>	<i>L. concinna</i>
	<i>Lobactis</i>	<i>L. scutaria</i>
	<i>Pleuractis</i>	<i>P. paumotensis</i> , <i>P. granulosa</i> , <i>P. spp.</i>
	<i>Sandalolitha</i>	<i>S. dentata</i> , <i>S. robusta</i>

	<i>Herpolitha</i>	<i>H. limax</i>
	<i>Cantharellus</i>	<i>C. sp.</i>
	<i>Cycloseris</i>	<i>C. spp.</i>
	<i>Homophyllia</i>	<i>H. australis</i>
	<i>Non Identified</i>	-
● Massive coral	<i>Porites</i>	<i>P. lobata, P. vaughani, P. australiensis, P. lichen, P. spp.</i>
	<i>Dipsastraea</i>	<i>D. amicorum, D. favus, D. spp.</i>
	<i>Astrea</i>	<i>A. curta, A. annuligera</i>
	<i>Pavona</i>	<i>P. varians, P. duerdeni, P. spp.</i>
	<i>Montipora</i>	<i>M. spp.</i>
	<i>Astreopora</i>	<i>A. myriophthalma, A. spp.</i>
	<i>Leptastrea</i>	<i>L. pruinosa, L. transversa, L. purpurea</i>
	<i>Cyphastrea</i>	<i>C. serailia, C. spp.</i>
	<i>Gardineroseris</i>	<i>G. planulata</i>
	<i>Alveopora</i>	<i>A. tizardii, A. ocellata, A. fenestrata</i>
	<i>Lobophyllia</i>	<i>L. vitiensis, L. hemprichii, L. corymbosa</i>
	<i>Leptoria</i>	<i>L. phrygia</i>
	<i>Plesiastrea</i>	<i>P. versipora</i>
	<i>Paragoniastrea</i>	<i>P. australensis</i>
	<i>Acanthastrea</i>	<i>A. echinata</i>
	<i>Non Identified</i>	-
	<i>Millepora</i>	<i>M. platyphylla</i>
● Branching coral	<i>Pocillopora</i>	<i>P. verrucosa, P. damicornis, P. eydouxi</i>
	<i>Acropora</i>	<i>A. hyacinthus, A. speciosa, A. spp.</i>
	<i>Porites</i>	<i>P. rus</i>
	<i>Pavona</i>	<i>P. maldivensis</i>
	<i>Psammocora</i>	<i>P. stellata</i>
	<i>Napopora</i>	<i>N. irregularis</i>
		<i>Non Identified</i>

Table S3.2: Other benthic groups. Only dominant taxa at mesophotic depths (below 30 m depth) are presented.

Benthic group	Composition and genus
● Fleshy macroalgae	Green: <i>Caulerpa, Palmogloea</i> Brown: <i>Spathoglossum</i> Red: <i>Platoma, Titanophora, Cryptonemia, Galaxaura</i> (segmented algae mostly erect) Green_Algae fleshy Brown algae fleshy Red algae fleshy
● Crustose algae	Red: <i>Peyssonnelia, Pneophyllum</i> Red algae encrusting Green algae encrusting Brown algae encrusting Green filamentous encrusting to sediment algae
● Halimeda	<i>H. spp.</i>

• CCA	Crustose coralline algae on hard substrate, rubble, dead coral, etc.
• Sponges	Clionidae, encrusting and massive sponges (from the genus <i>Astrosclera</i>)
• Gorgonians	Mostly family Plexauridae but also Ellisellidae, Nidalidae, etc.
• Antipatharians	<i>Antipathes</i> , <i>Cirripathes</i>
• Hydroids	<i>Macrorhynchia</i> , <i>Lytocarpia</i>

Table S3.3: Coral cover and standard errors for each island, site and depth. All “hotspots” with higher coral cover than expected for the depth are indicated in bold.

Depth	Archi pelago	Society Islands						Tuamotu Archipelago						Gambier Archip.				
	Island	Moorea		Tahiti		Bora		Tikehau		Rangiroa		Raroia		Makatea		Gambier		
	Site	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	
Shallow Waters	6	CC % (se)	65.91 (5.66)	58.39 (3.6)	57.78 (4.27)	37.51 (2.93)	34.08 (3.35)	53.46 (7.38)	45.06 (5.68)	40.66 (2.15)	17.91 (1.49)	17.06 (1.50)	41.20 (1.88)	18.66 (0.91)	60.35 (3.19)	55.24 (3.45)	10.89 (0.44)	39.15 (2.01)
	20	CC % (se)	27.01 (1.06)	38.04 (0.93)	58.75 (2.11)	37.33 (0.63)	46.13 (2.32)	35.06 (1.57)	31.09 (0.65)	33.55 (0.55)	11.11 (0.23)	42.88 (1.90)	55.24 (2.72)	56.09 (3.31)	60.22 (2.10)	66.93 (5.34)	22.17 (0.85)	43.55 (1.04)
Upper mesophotic	40	CC % (se)	27.33 (0.51)	2.84 (0.04)	32.58 (0.79)	32.84 (0.88)	6.75 (0.19)	53.59 (1.13)	29.95 (1.24)	51.42 (2.09)	45.15 (1.86)	26.09 (0.96)	81.86 (7.71)	57.96 (3.13)	46.89 (1.55)	45.51 (1.61)	20.58 (0.58)	43.46 (0.75)
	60	CC % (se)	6.22 (0.19)	15.33 (0.34)	11.99 (0.36)	12.66 (0.94)	64.71 (2.19)	68.26 (1.76)	31.40 (1.64)	31.60 (1.48)	21.95 (0.86)	35.77 (1.63)	43.60 (1.48)	18.49 (0.45)	67.11 (3.11)	74.49 (3.05)	35.77 (1.22)	9.37 (0.32)
Lower mesophotic	90	CC % (se)	3.55 (0.32)	1.55 (0.41)	3.07 (1.31)	0.17 (0.0)	0.75 (0.09)	9.91 (0.51)	0.53 (0.13)	9.99 (1.19)	3.42 (0.17)	6.71 (0.30)	14.04 (0.77)	9.06 (0.99)	35.38 (6.94)	30.58 (5.54)	11.55 (1.04)	52.88 (5.12)
	120	CC % (se)	0.0	0.31 (0.11)	0.13 (0.02)	0.0	0.13 (0.0)	1.15 (0.04)	0.04 (0.0)	0.27 (0.09)	0.04 (0.0)	1.82 (0.15)	2.89 (0.66)	0.31 (0.11)	3.29 (0.22)	1.82 (0.38)	15.95 (1.54)	42.00 (4.20)

Table S3.4: Dates of sampling and coordinates of locations.

Survey Dates	Archi pelago	Island	Site	Latitude (DM.m)	Longitude (DM.m)
Aug 2018	Society	Moorea	1	17° 28. 631 S	149° 51. 067 W
Sep 2018	Society	Moorea	2	17° 28. 638 S	149° 51. 083 W
Sep 2018	Society	Bora	1	16° 30. 510 S	150° 47. 441 W
Sep 2018	Society	Bora	2	16° 26. 205 S	151° 45. 217 W
Oct 2018	Tuamotu	Tikehau	1	15° 01. 040 S	148° 17. 205 W

Oct 2018	Tuamotu	Tikehau	2	14° 57. 845 S	148° 16. 027 W
Oct 2018	Tuamotu	Rangiroa	1	14° 58. 818 S	147° 36. 789 W
Nov 2018	Tuamotu	Rangiroa	2	14° 59. 858 S	147° 35. 059 W
Nov 2018	Tuamotu	Raroia	1	16° 00.310 S	142° 27. 102 W
Mar 2019	Tuamotu	Raroia	2	16° 01.386 S	142° 27. 796 W
Mar 2019	Gambier	Gambier	1	23° 04. 383 S	135° 00. 973 W
Apr 2019	Gambier	Gambier	2	23° 00. 061 S	134° 57. 631 W
Jun 2019	Tuamotu	Makatea	1	15° 49. 556 S	148° 16. 780 W
Jun 2019	Tuamotu	Makatea	2	15° 49.383 S	148° 16. 758 W
Sep 2019	Society	Tahiti	1	17° 32.531 S	149° 37.125 W
Sep 2019	Society	Tahiti	2	17° 37.171 S	149° 37.261 W

IV. Chapter 4: Coral physiology with increasing depth

This chapter is in preparation for *Coral reefs* as:

Gonzalo Pérez-Rosales, Héloïse Rouzé, Pim Bongaerts, Nelly Bregere, Michel Pichon, Jeremy Carlot, Gergely Torda, UTP consortium, Valeriano Parravicini, Laetitia Hédouin. Multiple strategies of two light-dependent scleractinian corals to live in the twilight zone.

4.1. Abstract

Light-dependent scleractinian corals live in mesophotic coral ecosystems even if light becomes less available with increasing depth. In the present study, we analyse the physiological changes of *Pocillopora cf. verrucosa* from 6 to 60 m and *Pachyseris "speciosa" spp.* from 10 to 90 m depth across four different islands of French Polynesia to understand acclimations and adaptations to live at such depths with low light environments. Particularly, we studied the associated symbiotic communities, the photophysiology (*e.g.*, Symbiodiniaceae density, chlorophyll concentrations, isotopic signatures and micromorphology) and the nutritional plasticity individually for each mechanism and together. Our results indicate diverse symbiotic ITS2 profiles mainly represented by Symbiodiniaceae belonging to *Cladocopium* for the two species. However, these were not specialised in community composition along the depth gradient. At the same time, both corals increase their chlorophyll pigment concentration and make changes in their skeleton morphology. While *P. cf. verrucosa* increases the inter-distance in between and the size of corallites, *P. "speciosa" spp.* decreases the height of septa with depth. In contrast, we found no evidence of switching to heterotrophy as their primary energy source, although both corals reduce the $\delta^{13}\text{C}$ with increasing depth. Overall, our findings show common and specific strategies, with natural and spatial variability to evidence the extraordinary multi capacities of scleractinian corals to live and colonise low-light environments.

4.2. Introduction

Commonly known as “reef-building corals”, scleractinian corals are light-dependent animals because their symbiotic algae Symbiodiniaceae (*i.e.*, called zooxanthellae) rely on the sunlight to photosynthesise and provide the coral host up to 95% of the necessary energy for vital roles (Falkowski *et al.*, 1984; Blackall, Wilson and Van Oppen, 2015). The energy provided by the photosynthetic activity fuels their metabolic activities, such as growth, reproduction, and bio-calcification of the mineral skeleton that constructs and sustains coral reefs (Muscatine, 1990; Allemand *et al.*, 2011). More specifically, the energetic contribution of the coral host metabolism will vary according to the composition of coral-associated Symbiodiniaceae communities, driven by the host species, but also according to the biogeography and environmental conditions (*e.g.*, Rowan and Knowlton, 1995; Rowan *et al.*, 1997; Stat, Morris and Gates, 2008; Eckert *et al.*, 2020). Several studies demonstrated that physiological attributes and distinct responses (*i.e.*, contrasted tolerances) to environmental conditions and stressors could depend on the associated coral holobiont phenotypes in Symbiodiniaceae species and/or lineages (Baker *et al.*, 2004; Rouzé *et al.*, 2016; Wham, Ning and LaJeunesse, 2017; Hume *et al.*, 2020). However, the responses within coral holobiont from species having wide colonisation depth ranges remain scarce, restricted to specific locations and very rare considering the whole depth gradient of species (Bongaerts, Muir, *et al.*, 2015; Ziegler *et al.*, 2015; Eckert *et al.*, 2020).

Although scleractinian corals are usually associated with shallow animals, the exploration of Mesophotic Coral Ecosystems (MCEs; from 30 to 150 m depth (Puglise *et al.*, 2009)) shed light on the capacity of these photosynthetic scleractinian corals to colonise light-limited/low-light environments (Pyle and Copus, 2019). Indeed, the environmental conditions change along the depth gradient slope, especially the amount and composition of light or Photosynthetically Active Radiation (PAR) (Kahng *et al.*, 2019; Laverick *et al.*, 2020). As expected for light-dependent animals, the main limiting factor for coral development is the exponential decrease in light irradiance with depth (Fricke and Schuhmacher, 1983; Gordon, 1989). Additionally, the spectral composition at such depths is altered because only the smaller visible waves (*e.g.*, blue, violet) can penetrate into the ocean depths (Kahng *et al.*, 2019). Other environmental conditions likely influence coral development, *e.g.*, potential drops in seawater temperatures, low

nutrient enrichment and low hydrodynamic flow (Huston, 1985; Kahng *et al.*, 2010, 2019; Rooney *et al.*, 2010). Yet, most literature agrees that it is essentially light that drives the vertical distributions for scleractinian corals (Kahng *et al.*, 2019; Tamir *et al.*, 2019). Today, the deepest scleractinian coral ever found is at 172 m, towards the depth limit of the photic zone (<1% of the light received at 6 m depth) (Rouzé *et al.*, 2021). However, not all corals are equally distributed along the depth gradient, and their vertical zonation suggests particular acclimation and or adaptation strategies to environmental changes with depth.

Several physiological mechanisms might allow corals to thrive in contrasted low or high light environments. On the one hand, some coral species present specific adaptations to a narrow vertical range. These are known as ‘depth-specialists’, either to shallow or deep depths, because they are rare outside these ranges. On the other hand, some coral species are more plastic in their eco-physiological properties and, therefore, can colonise a wider depth range distribution. Known as ‘depth-generalists’ (*e.g.*, *Leptoseris hawaiiensis* (3 - 172) or *Leptoseris scabra* (5 - 127); Muir and Pichon, 2019; Rouzé *et al.*, 2021), these present high plasticity in their eco-physiological properties and can colonise shallower or deeper depths via their dispersive reproduction strategies (Shlesinger and Loya, 2019). Despite numerous efforts to understand them, the physiological performances with acclimation and adaptation strategies to different light conditions are still not completely understood due to the high variability among species or within regions (Ziegler *et al.*, 2015; Kahng *et al.*, 2019). It is still unclear if these generalist corals keep the metabolic and physiological rates of the surface at such lower depths (Cooper *et al.*, 2011; Shlesinger and Loya, 2019). While some studies suggest they reduce their energetic needs in-depth (Barnes and Chalker, 1990; Grigg, 2006; Mass *et al.*, 2007; Bongaerts, Frade, *et al.*, 2015), there is a lack of knowledge to know if corals might optimise their performance to live as in the shallows (with similar energetic needs) but with much lower light availability (Kahng *et al.*, 2019).

Previous studies reported several different mechanisms to acclimate to low light environments (Kahng *et al.*, 2019). For example, (i) increase the symbionts’ density or the photosynthetic pigments for photosynthesis (Wyman *et al.*, 1987; Maritorena *et al.*, 2002; Stambler, Levy and Vaki, 2008; Mass *et al.*, 2010; Smith *et al.*, 2017; Padilla-Gamiño *et al.*, 2019); (ii) Flat the skeleton to increase light exposure (Muir *et al.*, 2015;

Malik *et al.*, 2021); (iii) Reduce the number of polyps per surface area to limit energy needs (Soto *et al.*, 2018); (iv) Decrease tissue thickness to reduce the energy required for calcification (Kaniewska *et al.*, 2011); (v) Shift endosymbiotic (Symbiodiniaceae) composition to more low-light adapted communities (Bongaerts, Frade, *et al.*, 2015); (vi) Increase active feeding (heterotrophy) (Williams *et al.*, 2018; Watanabe *et al.*, 2019) with a change in nutrition acquisition to rely less on photosynthesis; or even (vii) decrease growth and reproductive efforts to conserve the energy for vital requirements (Mass *et al.*, 2007; Shlesinger and Loya, 2019).

Most studies investigating coral depth acclimations and adaptations to low light environments generally focused on particular mechanisms separately (Kahng *et al.*, 2019). Nonetheless, as corals are meta-organisms living in symbiosis with a myriad of organisms, there is a need to understand biological mechanisms together to decipher the combination of strategies acting in response to light as an environmental constraint. So far, the literature studying multiple mechanisms at the same time is scarce (Lesser *et al.*, 2010; Padilla-Gamiño *et al.*, 2019). Additionally, from the available studies focusing on particular species, there is a significant inter and even intra-specific variability, with studies on the same species differing in results across locations showing a big spatial variability (Soto *et al.*, 2018; Padilla-Gamiño *et al.*, 2019). Finally, very few studies consider the entire depth distribution for the targeted species (Kahng *et al.*, 2019). For all these reasons, the knowledge today of how corals acclimate or adapt to low light environments in lower depths is still unclear.

Using two widely spread and abundant corals (*Pocillopora cf. verrucosa* and *Pachyseris "speciosa" spp.*) in French Polynesia as a model, we tested eco-physiological changes along the depth gradient slope. Considering their wide depth ranges, we aimed to study distinct mechanisms involved in depth-acclimation in collected specimens from 6 to 60 m and from 20 to 90 m, respectively, in four islands of two archipelagos of French Polynesia. In particular, we investigate individually and through a multi-disciplinary approach the qualitative composition of coral-associated Symbiodiniaceae communities, the biological traits involved in the coral holobiont photophysiology (including morphology), and the nutritional pathways to better apprehend the importance of each mechanism to the overall response.

4.3. Materials and Methods

Coral species model

We selected two widely present species or complex of species based on their large vertical range distribution: *Pocillopora cf. verrucosa* (Ellis and Solander, 1786) and the complex of species *Pachyseris “speciosa” spp.* (Dana and Wilkes, 1846). These are ideal model species for studying physiological responses to depth because of their (a) broad depth range zonation (Muir and Pichon, 2019); (b) different families and contrasted morphologies (Schmidt-Roach *et al.*, 2014; Soto *et al.*, 2018; Bongaerts *et al.*, 2021); and (c) wide presence in the Indo-Pacific (DeVantier and Turak, 2017; Bongaerts *et al.*, 2021).

Pocillopora cf. verrucosa (Ellis and Solander, 1786) is a common branching coral in the Indo-Pacific, living in lagoons and fore reefs. Its depth distribution is primarily in shallow waters in the outer reef, but it is also usually found down to 60 m depth in French Polynesia.

The complex of species *Pachyseris “speciosa” spp.*, previously known as *Pachyseris “speciosa”* (Dana and Wilkes, 1846), are ubiquitous laminar corals from the 40-60 m zone of the Indo-Pacific. The species has been recently described as a complex of at least 3 distinct genetic clades (Bongaerts *et al.*, 2021). Colonies are highly present at mesophotic depths in the outer slope. Their depth distribution in French Polynesia ranges from approximately 20 m to 90 m.

According to collected data as part of the present study, these two species had an exclusive depth (6 m for *P. cf. verrucosa* and 90 m for *P. “speciosa” spp.*) and a shared depth zone (20 to 60 m), allowing for a better deciphering of the acclimation and/or adaptive strategies. The two species are widespread and play a significant role in the overall structure of coral reefs in French Polynesia from 6 to 60 m (Pérez-Rosales, Brandl, *et al.*, 2021; Pichon *et al.*, 2021; Pérez-Rosales *et al.*, in prep. *Diversity and Distributions* Article DOI: 10.1111/ddi.13549). We identified both species with morphological taxonomic expertise (Veron and Pichon, 1979; Bosserelle *et al.*, 2014; Schmidt-Roach *et al.*, 2014). Although we applied the same approach and performed the same analysis for each of the two species, we studied each species separately.

Study locations and sampling

Between September and November of 2018, we sampled four islands of two archipelagos of French Polynesia: Moorea (17°28.64'S, 149°51.08'W) and Bora Bora (16°26.19'S, 151°45') in the Society Islands, and Tikehau (14°57.84'S, 148°16.03'W) and Rangiroa (14°59.85'S, 147°35.06'W) in the Tuamotu during the *DEEPHOPE* project. We used technical Trimix Closed Circuit Rebreather diving to collect fragments of the two selected scleractinian corals, "*Pocillopora cf. verrucosa*" and "*Pachyseris "speciosa" spp.*", from their shallower to the deeper presence of their distribution range. In total, we collected 118 replicates of *P. cf. verrucosa* from 6 to 60 m depths, and 116 replicates of *P. "speciosa" speciosa* from 10 or 20 to 90 m depths were collected to provide a minimum number of replicates (**Fig 4.1 - table**). During the collection of each coral sample, we immediately sampled 3-5 micro-fragment that we conserved into 96% ethanol for further genetic analyses and one fragment of ~ 5 cm that we quickly flash-frozen in liquid Nitrogen (-80°C) for further physiological and morphometric analyses. At the same time, we measured *in situ* light - Photosynthetically Active Radiation (PAR) at our study depth and sampling sites (DEFI2-L JFE Advantech) (**Sup. Fig. S4.1**). We estimated the little missing data using the Beer-Lambert equation (Gordon, 1989). We normalised depth relative values according to the shallowest depth available at 6 m to avoid seasonality differences and variation across locations.

(a) *Pocillopora cf. verrucosa*

Depth (m)	Moorea (n)	Bora Bora(n)	Rangiroa (n)	Tikehau (n)
6	5	6	10	9
20	9	8	9	9
40	6	9	10	10
60	10	7	NA	NA



(b) *Pachyseris "speciosa" spp.*

Depth (m)	Moorea (n)	Bora Bora(n)	Rangiroa (n)	Tikehau (n)
10	NA	NA	NA	7
20	1	NA	6 (25m*)	7
40	8	6	8	7
60	7	7	8	7
90	2	10	10	7



Figure 4.1: Coral species model and number of replicates used in this study (a) *Pocillopora cf. verrucosa*. (b) the complex of species from *Pachyseris "speciosa" spp.* (Copyright images: Franck GAZZOLA / UNDER THE POLE / Zeppelin Network).

Genetic identification of Symbiodiniaceae communities

We extracted the total genomic DNA of the coral samples (averaging 1 cm²) from both the tissue and skeleton. We used the MOBIO PowerSoil DNA Isolation Kit (Qiagen, Hilden, Germany) for the DNA extraction following standard published protocols (Sunagawa, Woodley and Medina, 2010) but with slight modifications (Rouzé *et al.*, 2021). Specifically, we added a pre-lysis step of 3 cryo-shock cycles (5 min in liquid nitrogen followed by 5 min at 65°C and 2 min of vortex). Then, we followed mechanical treatments using lysing matrix A (MP Biomedicals, Strasbourg, France) and the FastPrep Cell Disruptor system (3 cycles: speed 6 m/s during 30 sec with pause time of 60 sec) (MP Biomedicals). We retrieved Symbiodiniaceae communities amplifying the ITS2 gene with the following specific primers SYM_VAR_5.8S and SYM_VAR_REV (Hume *et al.*, 2015). We sequenced the PCR products using the MiSeq Illumina platform under previously described conditions (Comeau *et al.* 2017). All amplification and sequencing were carried out at the Integrated Microbiome Resource (www.imr.bio, Canada). We submitted the demultiplexed forward and reverse fastq.gz Illumina sequencing files to SymPortal.org to predict ITS2 type profiles from specific sets of defined intragenomic ITS2 sequence variants (access date of the SymPortal database: 2020-12-03_DBV) (Hume *et al.*, 2019). Finally, we used the predicted profiles derived from SymPortal to

compare different depths following Kenkel's script (Eckert *et al.*, 2020). The raw ITS2 sequencing datasets have been deposited in the SymPortal database (pending).

Symbiodiniaceae density and chlorophyll pigments

We removed the tissue from the frozen (conserved at -80°C) coral fragment from each sample using the air-pick technique with filtered seawater (FSW obtained with glass microfiber filters GF-F 47mm - Whatman). We mixed and homogenised the tissue in falcon tubes with the used FSW and then centrifuged (20 minutes, 12.000 rpm and 4°C) as many times as necessary to completely separate the two fractions: the pellet (*i.e.*, Symbiodiniaceae fraction), and the supernatant (*i.e.*, polyps fraction). With the Symbiodiniaceae fraction, we resuspended with 5ml FSW and subsampled 0.5 ml of the solution for estimating Symbiodiniaceae density (i) and 1.5 ml for chlorophyll pigment analyses (ii) that we centrifuged (20 minutes, 12.000 rpm and 4°C), dried, and dissolved with 1 ml acetone to break the cell walls and liberate the photosynthetic pigments during 24 hours. At this stage, we stored the remaining volume of both Symbiodiniaceae and polyp fractions for further isotopic analyses and the coral fragment (without tissue) to measure the surface (iii) and morpho-acclimation analysis.

We estimated the Symbiodiniaceae density (i) manually counting (≥ 6 times) the cells present in the resuspended Symbiodiniaceae fraction using a hemocytometer and a molecular microscope, considering the mean of the counts normalised by the volume and divided by the surface of the coral fragment (iii, see below). We measured the chlorophyll pigments concentrations (ii) from the remaining 1.5 mL resuspended Symbiodiniaceae fraction after 24 hours of chlorophyll extraction. We centrifuged (5 minutes, 12.000 rpm, and 4°C) for decantation of the pellet, and we measured pigments concentration with a spectrometer at 663, 630, 660, and 750 wavelengths (Thermo Scientific Evolution 60 S UV-Visible). We dried, dissolved again with 1 ml acetone, and repeated this process 24 hours later to ensure we completely extracted fluorescing pigments. We repeated this until finding reading values equal to the blank. With the spectrometer readings, we used Jeffrey & Humphrey (1975) equations (eq 1-2) to obtain chlorophyll *a*, *c*₂ and its *c*₂/*a* ratio. We computed concentrations of chlorophyll *a* and *c*₂ according to the surface of the coral fragment. Also, according to the number of Symbiodiniaceae cells and the ratios of chlorophyll *c*₂:*a* and *a*:*c*₂. At all stages, we kept samples at 4°C and in dark conditions.

$$\text{eq 1: Chl a } [\mu\text{g/mL}] = 11.43 \times (A_{663\text{nm}} - A_{750\text{nm}}) - 0.64 \times (A_{630\text{nm}} - A_{750\text{nm}})$$

$$\text{eq2: Chl c}_2 [\mu\text{g/mL}] = 27.09 \times (A_{630\text{nm}} - A_{750\text{nm}}) - 3.63 \times (A_{663\text{nm}} - A_{750\text{nm}})$$

Finally, we measured the surface of the coral fragment (iii) using Einscan Sp Software to reconstruct the coral fragment in 3D. This photogrammetry technique allowed us to measure the geometric surfaces of the corals that we used to normalise Symbiodiniaceae density and chlorophyll concentration per unit of surface. We applied the same protocol to all coral samples. We stored the same coral fragments for further morphometric analyses.

Coral holobiont (host and symbionts) isotopic signatures in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

To measure the isotopic content in both the polyps (coral-host) and the Symbiodiniaceae (coral-symbionts) fraction, we previously burned (4 hours, 460°C) filters (XGF-F 47 mm of diameter) with a vacuum system. Then, we filtered between 1.5 and 2 ml of each of the two fraction solutions. For the Symbiodiniaceae fraction, we briefly used 0.5 mL of 1N HCl (1N) to remove any remaining carbonated skeleton fragments and then rinsed them with Milli-Q water. We constantly sterilised material with an autoclave and cleaned between samples with HCl, acetone, Milli-Q water and FSW. We stored the filters at 60°C and dried conditions before sending them for isotopic analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at Cornell University Stable Isotope Laboratory (COIL). With the available $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data for symbionts (later called *symbionts*) and host (later called *polyps*) fraction, we kept and measured the following variables: the $\delta^{13}\text{C}$ for polyps, the $\delta^{13}\text{C}$ for symbionts, the $\delta^{15}\text{N}$ for polyps, the $\delta^{15}\text{N}$ for symbionts, the ratio of $\delta^{13}\text{C} / \delta^{15}\text{N}$ for the polyps, the ratio of $\delta^{13}\text{C} / \delta^{15}\text{N}$ for the symbionts, the delta $\delta^{13}\text{C}$ (polyps – symbionts), the delta of $\delta^{15}\text{N}$ (polyps – symbionts).

Micro-morphological traits

We measured multiple morphological features according to classic morphological traits used in taxonomy (pers. comm. Michel Pichon; Veron and Pichon, 1979; Schmidt-Roach *et al.*, 2014; Soto *et al.*, 2018; Bongaerts *et al.*, 2021). Readings were done using a

binocular microscope and software Leica Application Suite EZ. For *P. cf. verrucosa*, we measured the corallite size (CS) and the inter-corallite distance (CD). We performed the measures in two zones of the colony because of the formation of different micro-environments of light exposure due to the branching morphology (Soto *et al.*, 2018). We realised the measures in the apical (*i.e.*, which was the top axial part of the branch); and the basal (*i.e.*, which was the bottom part of the branch next to the main body) zones of the colony (**Sup. Fig. S4.2**). Finally, we decided to keep them separately as measures from the apical and basal zones because they were significantly different ($p < 0.001$). For *P. "speciosa" spp.*, we measured the septa height (HS) from the valley floor to the top of the ridge, septa distance (DS) and valley width (VW) (**Sup. Fig. S4.3**).

Relative index loss of light, depth and spatial variability analysis

We considered depth rather than light for the final analysis because for all islands, light decreased with depth and both variables were highly correlated (Pearson correlation = 0.85; p -value < 0.001; **Sup. Fig. S4.1**). With this assumption and running our tests according to depth independently for each location, we omitted the potential site variability that could bias our outcomes (*i.e.*, potential seasonal differences because the light loggers registered measures at different periods). Another reason to support our decision of using depth instead of relative light and test separately for each separate location (4 islands) is to consider site variability while reducing inter-site data deviations and increasing the robustness of our results. Like this, the model results will be calculated for each location separately to answer the same question of how it changes in depth. This strategy means we considered spatial variability but omitted spatial comparisons because the paper aimed to study coral physiology along the depth gradient. Despite not considering each location separately would have meant a higher number of replicates, we preferred to compensate for the few replicates running Bayesian models with higher interactions because considering each site is statistically more correct.

Finally, we considered each sample as individual entries of our analyses and models for most analyses. However, we had to analyse the *Associated Symbiodiniaceae ITS2 type profiles* and the *Nutritional plasticity along the depth gradient* as separate analyses because of the minimum number of replicates required. These two sections were then studied separately with increasing depth.

Associated Symbiodiniaceae ITS2 type profiles analysis

Subsequent statistical analyses were carried out on ITS2 type profile sequencing reads, which are representative of putative Symbiodiniaceae taxa. The *betadisper* function from the *vegan* packages was used to calculate multivariate homogeneity of dispersion (PERMDISP) using Bray-Curtis distances (Oksanen *et al.*, 2019). Permutational multivariate analysis of variance (PERMANOVA) was used to test for differences in Symbiodiniaceae ITS2 type profiles due to the balance of sampling design and the demonstrated lack of sensitivity to the heterogeneity of dispersion compared to other multivariate statistical tests (e.g., ANOSIM; Anderson and Walsh, 2013). Depths and sampling sites were used as fixed factors in the *adonis* function in *vegan* with 9,999 permutations of residuals from Bray-Curtis dissimilarities. After significant PERMANOVA results, pairwise PERMANOVA tests were conducted with the package *pairwiseAdonis* (Martinez Arbizu, 2017) using false discovery rate (FDR) corrected p-values. Finally, similarity percentage (SIMPER) analyses were performed to determine ITS2 type profiles that contributed the most between depths and sites.

Biological traits of coral-symbiont analysis (Photophysiology) analysis

Considering the photophysiology “*Symbiodiniaceae density and chlorophyll pigments analyses*”, “*Micro-morphology*”, and the “*Coral holobiont (host and symbionts) isotopic signatures in $\delta^{13}C$ and $\delta^{15}N$* ”, we tested the variables from an individual analysis with increasing depth to a global analysis to see the differences between depths. First, we standardised the data by subtracting the mean and dividing by the standard deviation to allow comparisons between measures of different levels. Second, we measured a matrix of correlations between all variables and depth using the package *ggcorrplot* (Kassambara and Kassambara, 2019). We omitted variables for which correlations were above (> 0.75) for statistical and modelling purposes to avoid collinearity, yet these were commented on in the results (**Sup. Fig. S4.4** and **S4.5**). Third, we presented a Principal Component Analysis (PCA) using the package *FactoMinerR* and *Factoshiny* (Lê, Josse and Husson, 2008; Vaissie, Monge and Husson, 2021) for the distribution of all quantitative variables (excluding depth as the unique environmental variable). These results gave a visual impression of variables correlated with depth that aligned more or less with the principal component axes of the analysis. Depth was not among these computed variables of the PCA as it was considered the quantitative supplementary variable. Indeed, we only used the categorical depth to group with ellipses by similarities with a significance level of 0.5.

We displayed different symbols according to locations. Fourth, we ran a multivariate Bayesian model using the package *brms* (P.-C. Bürkner, 2017) to test how the different measures responded to increasing depth. The model used a student family distribution and kept a random intercept and slope for each site to consider spatial variability. We compensated for the few replicates increasing the number of interactions to 4,000. We considered the slopes with (Confidence Intervals (CI) of 95%) from the converged model to see the effect of increasing depth with each measured variable. Fifth, we computed a dissimilarity matrix and tested a permutational multivariate analysis of variance (PERMANOVA) using the package *vegan* (Oksanen *et al.*, 2019). In this stage, we also tested whether depth significantly separated these variables by different groups and ran pairwise comparisons (Pairwise PERMANOVA) between depths. All individual values and comparisons between sites and depths are available in supplementary data.

Nutritional plasticity analysis

We ran additional analyses for the nutritional plasticity. To do so, we used *HOTELLING* tests from the package *Hotelling* to measure the distances between the polyps and symbionts fractions of both isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to study the trophic niches at different depths. Suppose the distances of centroids are distinct between the two fractions and the p-values significant; it means the coral switches to heterotrophy. Additionally, we tested how these distances interacted with increasing depth. Then, we used the *SIBER* command from the package *Siber* (Jackson *et al.*, 2011) to study the dispersions (area of the convex hull, standard ellipse and distance to the centroid means) of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the two fractions, the polyps and the symbionts. Finally, we measured the relative degree of heterotrophy (RDH) that corresponded with the delta $\delta^{13}\text{C}$ (RDH, $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{Host}} - \delta^{13}\text{C}_{\text{Symbiont}}$) (Williams *et al.*, 2018) as an indicator of potential heterotrophy shifts.

All analyses were performed using the software R (version 3.6.1) (R Development Core Team). All data and codes to replicate the present study are available in the Data Availability statement.

4.4. Results

4.1. *Pocillopora cf. verrucosa*

4.1.1. Associated Symbiodiniaceae ITS2 type profiles along the depth gradient

The ITS2 sequences revealed that the associations of *P. cf. verrucosa* with Symbiodiniaceae were mainly from the genus *Cladocopium* (formerly clade C) and in less prevalence with *Durusdinium* (formerly clade D) and *Gerakladium* (formerly clade G) (**Fig. 4.2a**). In total, we identified 12 ITS2 profiles across all samples, seven of which were from the genus *Cladocopium*. More particularly, the community composition of Symbiodiniaceae varied significantly by depth (ANOVA $F = 5.57$, $p < 0.005$) with and without interaction of site (PERMANOVA Pseudo- $F = 1.74$, $p < 0.05$, Table 4.1). Pairwise analyses revealed significant differences in Symbiodiniaceae communities between corals from 6 m and all other depths (PERMANOVA; 6 vs. 20: Pseudo- $F = 10.6$, $p < 0.05$; 6 vs. 40: Pseudo- $F = 13.8$, $p < 0.05$; and 6 vs. 60: Pseudo- $F = 26.7$, $p < 0.05$) (Table 4.1) and between corals from 20 m and 60 m depth (PERMANOVA: Pseudo- $F = 3.4$, $p = 0.03$). While non-exclusive to 6 m depth, the ITS2 type profiles dominated with C42 lineages (see **Fig. 4.2**) profiles *P2* and *P4* were largely predominant in that shallowest depth and accounted for over respectively 38-42% and 9-12% of the dissimilarity with deeper depths (SIMPER tests). However, from 20 m to mesophotic depths, we observe two different patterns showing no significant depth effect. In the Society Islands, most of the associated Symbiodiniaceae community compositions were characterised with predicted ITS2 type profiles dominated with C1 and C42-related at 85% (**Fig. 4.2**): mostly profile *P1* (85%) or profile *P2* (21%). In the Tuamotu Archipelago, associated Symbiodiniaceae communities were more diverse and overlapped with ITS2 type profiles dominated by C1 and C42-related (74%) and rarely composed of D1-related (26%).

4.1.2. Biological coral-symbiont traits along the depth gradient

For *P. cf. verrucosa*, the ensemble of measured variables clustered by depths and not by locations (**Fig. 4.3a**). These differentiations were because some variables had clear patterns with increasing depth, which at the same time aligned with PC1 (23.7% of data). In order of importance, the most changing variables that increased with depth were: the distance between corallites in the basal part ($\beta > 0$ and 95 % CI > 0); the total chlorophyll concentration per unit of surface [$(a+c_2)/\text{surface}$]; and the size of corallites in the apical

part ($\beta > 0$ with 95 % CI > 0) (**Fig. 4.3a**). For example, the inter-corallite distance in the basal part increased from *ca.* 0.67 cm at 6 m to *ca.* 0.85 cm at 60 m. The total chlorophyll concentration increased from *ca.* 13 $\mu\text{g}/\text{mL}/\text{cm}^2$ at 6 m to *ca.* 25 $\mu\text{g}/\text{mL}/\text{cm}^2$ at 60 m. Finally, the size of corallites in the apical part increased from *ca.* 0.79 cm at 6 m to 0.87 cm at 60 m (Sup. Table S4.1). These findings were also reflected in the positive correlations with depth (SF3 a). Conversely, the most aligned variables that had a decreasing pattern with increasing depth were the $\delta^{13}\text{C}$ in its polyps and symbionts fraction ($\beta < 0$ with 95 % CI < 0) (**Fig. 4.3b**). For example, the signature of $\delta^{13}\text{C}$ decreased from -15 ‰ $\delta^{13}\text{C}$ at 6 m to -19 ‰ $\delta^{13}\text{C}$ at 60 m depth (**Sup. Table S4.2**). These variables were negatively correlated with depth (**Sup. Fig. S3a**).

On the other hand, the rest of the variables were less affected by depth and aligned with PC2 (12.43 % of data). For example, these were the ratio of chlorophylls types [Chl c_2 / Chl a], the $\delta^{15}\text{N}$ in its symbionts and polyps fraction, the ratio of $\delta^{13}\text{C}$ / $\delta^{15}\text{N}$ in its polyps and symbionts fraction and the Delta $\delta^{13}\text{C}$ polyps – symbionts. These variables were neutrality correlated with depth ($< [\text{abs } 0.5]$) (SF3) and, therefore, had positive and negative slopes in its 95 % CI with increasing depth. These variables did not significantly affect the separation of the different depth groups.

However, because of the individual variables that had clear patterns with depth, the specimens with quantitative measures were clustered by depth groups when considering a significance level for the ellipses of 0.5 (**Fig. 4.3a (left)**). The effect of depth in this differentiation was statistically significant (PERMANOVA $F = 18.8$, $p = 0.001$), notably between the 6 m and the rest of depths (PERMANOVA-pairwise comparisons; $p < 0.05$), 20 and 60 m (PERMANOVA-pairwise comparisons; $F = 110.44$; $R^2 = 0.73$; $p < 0.05$), while they were not significant between 20 and 40 m and 40 and 60 m (PERMANOVA-pairwise comparisons; $p > 0.01$). Finally, the remaining variables described in the methods but missing in these graphs were omitted because they were correlated (> 0.7) to at least one of the presented ones (**Sup. Fig. S4.3**). For example, the symbionts density [symbionts/surface], or the concentrations of chlorophyll a and c_2 , also increased with depth because they followed the same patterns with increasing depth as chlorophyll.

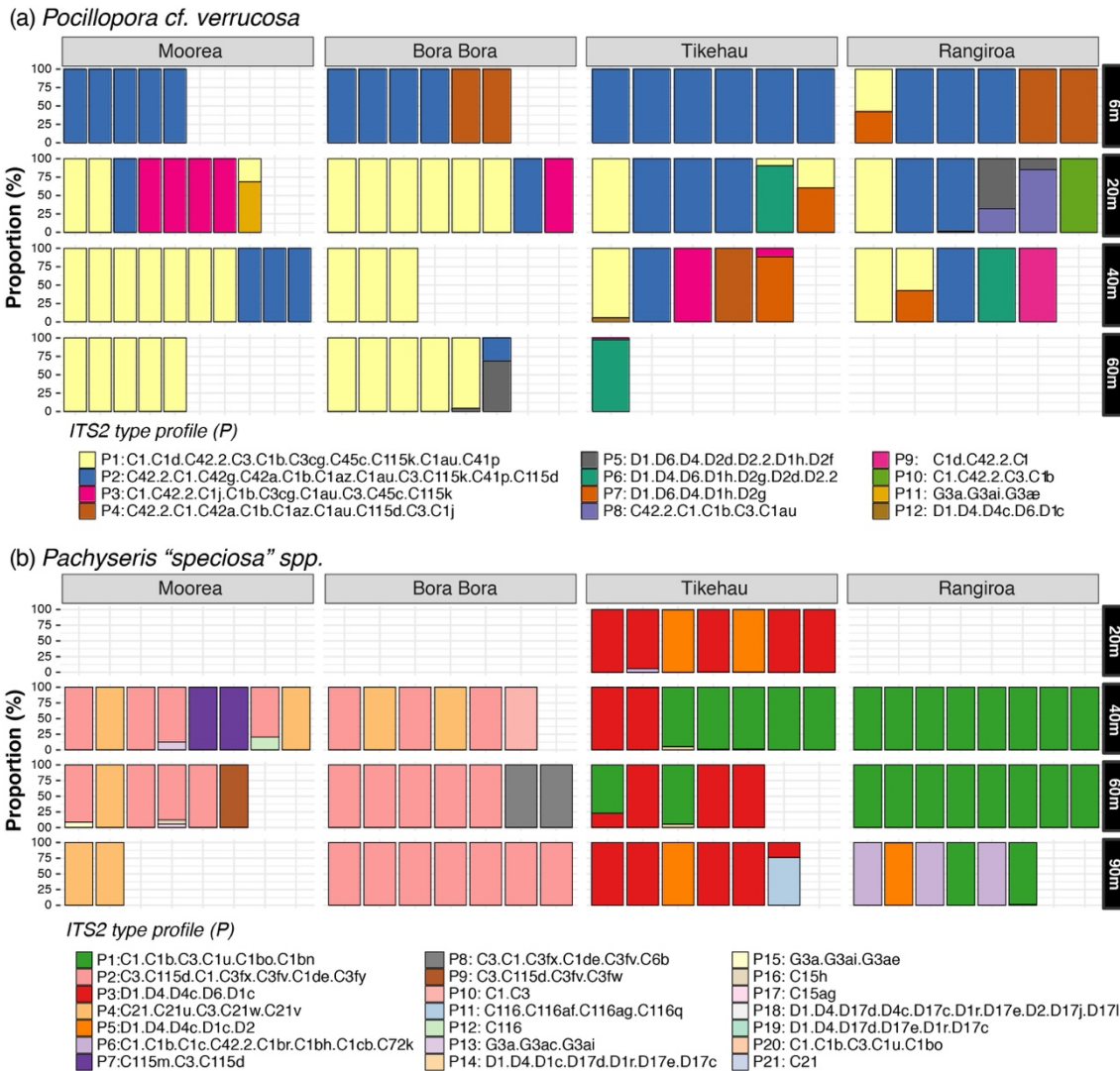


Figure 4.2: Normalised relative proportion of ITS2 type profiles from (a) *Pocillopora cf. verrucosa* and (b) *Pachyseris "speciosa" spp.* ITS2 type profiles are listed in order of overall abundance.

4.1.2.1. Morphological analysis of the branching zones

Besides the increasing inter-corallite distance in the basal zone and increasing corallites size in the apical zone with depth, we found (*i.e.*, comparing the two zones of the branch) that the distance between the corallites was significantly smaller in the apical than the basal zone of the colony (ANOVA $F = 99.53$, $p < 0.001$ for the zone; and ANOVA $F = 20.84$, $p < 0.001$ for the interaction of zone and depth). There are more corallites in the more light-exposed zones of the colony. However, the sizes of the corallites were bigger in the apical part than in the basal part (ANOVA $F = 20.98$, $p < 0.001$ for the zone and ANOVA $F = 0.46$, $p > 0.05$ for the interaction of zone and depth). This result means that

in the more light-exposed areas of the colony “apical zone”, the corallites have a bigger size, and therefore, it decreases the distance between corallites.

4.1.3. Nutritional plasticity along the depth gradient

Testing the trophic niche priority, the hotelling test for each depth revealed no significant switch to heterotrophy because it did not find significant differences (HOTELLING p-value > 0.05) of trophic niches between the polyps (host) and the symbionts (Symbiodiniaceae) for any island. The distances between the polyps and the symbionts communities (Hotelling test stat values were independent of depth) did not follow a particular pattern with increasing depth because they changed across locations with considerable variability between depths. We also found that increasing depth did not significantly affect dispersion (ANOVA linear model on the distance to the centroids; p-value > 0.05) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in neither the polyps (host) nor the symbionts fraction validating Hotelling Tests. Although the dispersions of the polyps (host) fraction looked more dispersed than the symbionts fraction, both fractions were not significantly different in SEAc (ANOVA linear model p-value = 0.056). Although depth significantly decreased individual fractions of $\delta^{13}\text{C}$ in both fractions (host and symbionts), the relative degree of heterotrophy or delta (Host – Symbionts) for $\delta^{13}\text{C}$ did not increase nor decrease significantly with depth. All these results suggest that corals conserved an autotrophic strategy along the depth gradients.

4.2. *Pachyseris “speciosa” spp.*

4.2.1. Associated Symbiodiniaceae ITS2 type profiles along the depth gradient

The ITS2 sequences revealed that the associations of *P. “speciosa” spp.* with Symbiodiniaceae from 20 to 90 m depth were mainly from the genus *Cladocopium* (formerly clade C) and in less prevalence with *Durusdinium* (formerly clade D) and *Gerakladium* (formerly clade G) like for *P. cf. verrucosa* (Fig. 4.2b). In total, we identified 21 ITS2 profiles across all *P. “speciosa” spp.* samples, including 14 from the genus *Cladocopium*. Although the shallowest samples studied were at 10 and 20 m depth, these were specific to one site (Tikehau). For statistical reasons, we performed the

analyses of dissimilarity from 40 to 90 m depth, excluding extreme superficial depths. The pairwise PERMANOVA revealed non-significant differences in community composition of Symbiodiniaceae across depth with all sites included between corals from 40 m and 90 m depth (PERMANOVA results **table 4.1**, p values non-significant). However, it varied across sites (PERMANOVA $p < 0.001$, Table 4.1) with and without interaction with depth (results of PERMANOVA, $p < 0.005$). Reducing the spatial variation by looking within the distinct populations, the Symbiodiniaceae ITS2 profiles along the depth gradient did not differ for the Society (Moorea and Bora Bora). Populations from the Society were mainly represented by two ITS2 profiles: *P2* dominated with c3/c1-like at 63.9% and *P4* dominated with c21-like at 16.7%. Conversely, the pairwise PERMANOVA revealed that the Symbiodiniaceae ITS2 profiles along the depth gradient differed in the Tuamotus between 90 m and upper depths (Tikehau and Rangiroa; **Table 4.1**). This difference was due to: (i) different proportions of common ITS2 profiles such as *P3* dominated with D1-related at Tikehau (28% at 40 m, 60% at 40 m and 66% at 90 m) or *P1* dominated C1-related at Rangiroa (100% at 40 and 60m vs. 33% at 90 m); and/or (ii) rare exclusive ITS2 type profiles such as *P11* dominated with C116-related at Tikehau and profile *P6* dominate with C1-related at Rangiroa.

Table 4.1: Test results from permutational multivariate analysis of variance (PERMANOVA; 9,999 permutations) of Symbiodiniaceae ITS2 type profiles from *P. cf. verrucosa* and *P. "speciosa" spp.* colonies and pairwise comparisons between all depth zones (FDR corrected).

Species	Test	Comparison	Pseudo-F	P adjusted	
<i>P. cf. verrucosa</i>	Overall	Depth	8.59	<0.001	***
		Site	2.27	0.03	*
		Depth:Site	1.74	0.02	*
	Depth	6 vs. 20	10.60	<0.001	***
		6 vs. 40	13.79	<0.001	***
		6 vs. 60	26.74	<0.001	***
		20 vs. 40	0.93	0.41	
		20 vs. 60	3.44	0.03	*
		40 vs. 60	1.70	0.15	
	<i>P. "speciosa" spp.</i> (20m excluded)	Overall	Depth	3.6421	<0.005
Site			20.6661	<0.001	***
Depth:Site			2.8504	<0.001	***
Depth		40 vs. 60	0.802	0.5009	
		40 vs. 90	2.972	0.0567	
		60 vs. 90	1.881	0.1527	
Overall Society		Depth	1.2935	0.2520	
		Site	2.1144	0.1018	
		Depth:Site	2.9604	0.0209	*
Overall Tuamotus		Depth	7.7891	<0.001	***
	Site	16.6986	<0.001	***	
	Depth:Site	2.1567	0.08		
Depth	40 vs. 60	0.6530	0.41730		
	40 vs. 90	8.5196	<0.005	**	
	60 vs. 90	4.8657	0.05	*	

4.2.2. Biological traits of coral-symbiont measures along the depth gradient

For *P. "speciosa" spp.*, the measured quantitative variables clustered by depths, especially between the 90 m and the rest of the depths, and not by locations (**Fig. 4.3b**). This differentiation was because some variables aligned with PC1 (32.7 % of data) that had clear increasing or decreasing patterns with increasing depth. The total chlorophyll concentration per unit of surface $[(a+c_2)/\text{surface}]$ had a clear increasing pattern with depth ($\beta > 0$ and 95 % CI > CI) (**Fig. 4.3b**). This increase was from *ca.* 30 $\mu\text{g/mL/cm}^2$ at 20 m to *ca.* 80 $\mu\text{g/mL/cm}^2$ at 90 m (**Sup. Table S4.3**). This increase of chlorophyll per surface also means the increase of Symbiodiniaceae density per unit of surface and chlorophyll *a* and *c*₂ alone because the variables were highly correlated (> 0.9 , SF3 b). Conversely, the height of septa had a clear decreasing pattern with increasing depth ($\beta < 0$ with 95 % CI < 0), from heights of 2.7 cm at 20 m to heights of 1 cm at 90 m (**Fig. 4.3b** (right) and **Sup. Table S4.3**). This pattern was supported by the negative correlation with depth (**Sup. Fig. S3b**).

On the other hand, the rest of the variables were less affected by depth and aligned more with PC2 (13.8 % of data). For example, the delta (Polyps - Symbionts) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the septa distance or the ratio $\delta^{13}\text{C} / \delta^{15}\text{N}$ did not vary or correlate with increasing depth (**Fig. 4.3b** (right) and **Sup. Fig. S4.3b**). These last variables did not contribute to separating the different depth groups.

However, due to the contribution of the individual variables with clear patterns with increasing depth, specimens clustered by different depth groups (**Fig. 4.3a**). Indeed, we found that depth significantly affected the differentiation of similarity between groups (PERMANOVA $F = 4.28$, $p = 0.001$). However, these differences were not significant between any particular depths, not even between the 90 m and the rest of the depths (PERMANOVA-pairwise comparisons; $p > 0.05$). As for *P. cf. verrucosa*, the remaining variables described in the methods but missing in these graphs were omitted because they were correlated (> 0.7) to the presented ones (**Sup. Fig. S3**).

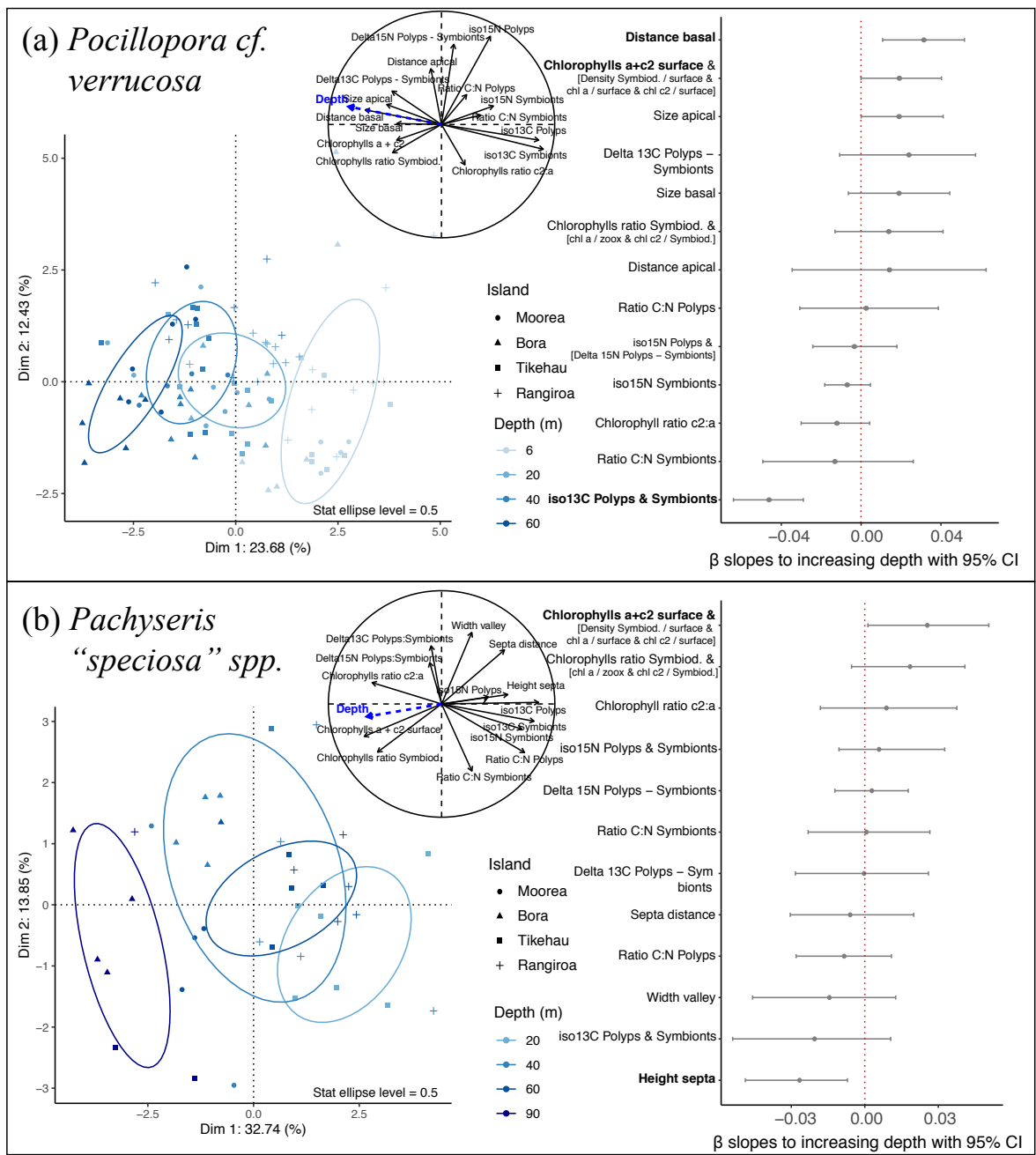


Figure 4.3: (a) *Pocillopora cf. verrucosa* and (b) *Pachyseris "speciosa" spp.* (Left) Principal component analysis grouping by depths. Ellipses represent significance level = 0.5. (Right) Slopes of all variables responding to increasing depth from the multivariate Bayesian model. The model considered spatial variability with a random intercept and slope for each location. The variables (in bold) are the ones whose interval confidence 95% (IQ 2.5 and IQ 07.5) does not go across 0.0. Between brackets and lower size show variables correlated to the represented variable Sup. Fig. 4.4 and 4.5.

4.2.3. Nutritional plasticity along the depth gradient

The Hotelling test for *P. "speciosa" spp.* revealed no significant switch to heterotrophy along the depth gradient in any islands (HOTELLING p-value > 0.05 between the Polyps

(host) and symbionts for all depths), except for 90 m at Tikehau (Hotelling p-value = 0.03). In this particular island, the distance between polyps and symbionts communities seems to increase with depth (HOTELLING stat at 10 m = 0.31, 40 m = 1.1, and 90 m = 9.5), although in the other islands did not (HOTELLING stat for Bora Bora at 40 m = 4.5, 60 m = 1.8, and 90 m = 0.2). These values changed across locations with important spatial and depth variability. We also found that increasing depth did not affect the dispersion of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in neither the polyps fraction (ANOVA linear model on the distance to the centroids, p-value = 0.5) nor the symbionts fraction (p-value = 0.09) validating the Hotelling tests. The dispersions of the symbionts and polyps (host) were not significantly different with the depth interaction (ANOVA linear model p-value = 0.79), suggesting that corals conserved an autotrophic strategy along the depth gradient.

Finally, the amount of $\delta^{13}\text{C}$ with increasing depth decreased in both fractions showing an apparent gradient effect (**Fig. 4.4b**). However, the decrease was not confirmed with the 95 % CI of the model (**Fig. 4.3b**). The relative degree of heterotrophy (delta Host - Symbionts for $\delta^{13}\text{C}$) was stable with depth in all locations, even in Tikehau, suggesting that specimens conserved an autotrophic strategy along the depth slope.

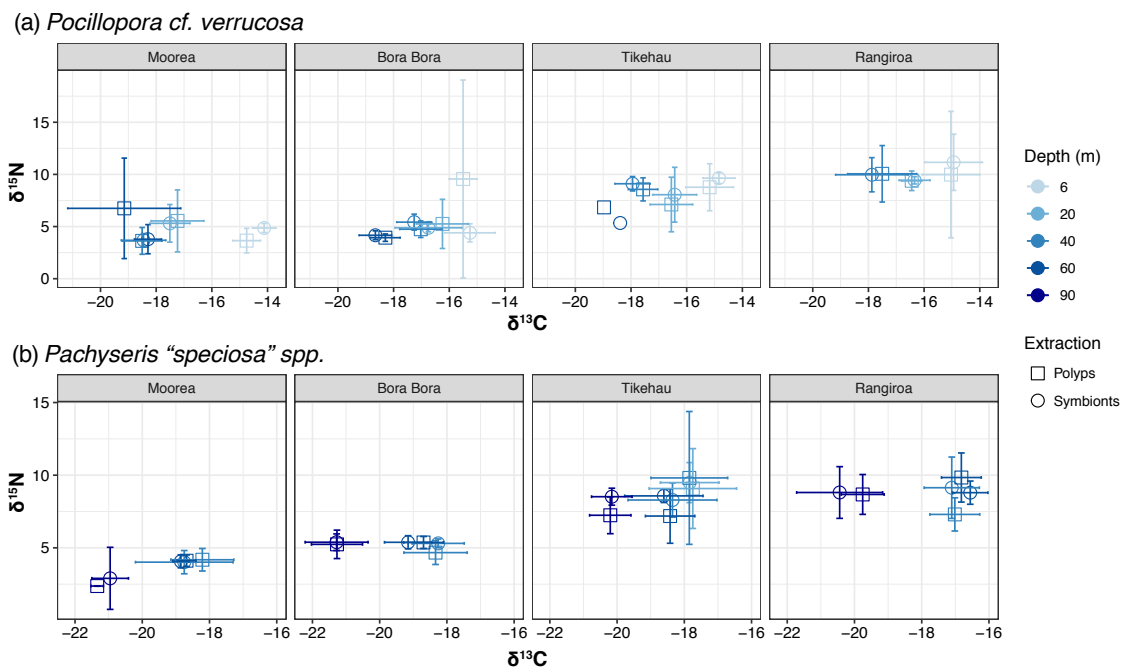


Figure 4.4: Coral host and algal symbiont stable isotope $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios for the different depths across locations. Nutritional plasticity was assessed with Hotelling tests measuring the distance between the host and the symbionts.

4.5. Discussion

To assess the adaptation and acclimation mechanisms of scleractinian corals to live in low light environments, we studied the coral holobiont response of two widely spread species along their depth gradients in French Polynesia (*Pocillopora cf. verrucosa* from 6 to 60 m and *Pachyseris “speciosa” spp.* from ~ 40 to 90 m; **Fig. 4.1 - Table**). Both drive the coral community structure of the outer reef at such depths (Pérez-Rosales et al., in prep. *Diversity and Distributions* Article DOI: 10.1111/ddi.13549), *P. cf. verrucosa* being more a shallow species but able to colonise reefs at 40-60 m, while *P. “speciosa” spp.* more a common mesophotic species but able to inhabit reefs at 15-20 m depth. Despite different depth zonation, the capacity of both species to live in lower light environments (below 50 m depth) remain to be explored. Our data revealed that both species increased chlorophyll pigments concentrations and the symbionts’ density with depth likely to keep up with photosynthesis despite decreasing light availability (Wyman et al., 1987; Lesser et al., 2010; Mass et al., 2010; Kahng et al., 2019; Padilla-Gamiño et al., 2019). Simultaneously, they modified the skeleton morphology, increasing corallite size and height of septa, likely to increase the light-harvesting capacity (Kramer et al., 2021). However, we found no evidence of a switch in Symbiodiniaceae communities or nutritional plasticity as previously suggested for some scleractinian corals (Bongaerts, Muir, et al., 2015; Williams et al., 2018). Our multidisciplinary approach to studying the coral holobiont suggests that corals’ acclimation/adaptation to depth involves multiple strategies rather than a single unique mechanism (Kahng et al., 2019). These strategies are sometimes shared among scleractinian species and other times specific yet, not exempt from considerable variability with and within species and locations (Apprill, Bidigare and Gates, 2007; Nir et al., 2011), thus highlighting the need for future studies but also the high plasticity of corals to multiple depths (Kahng et al., 2019; Padilla-Gamiño et al., 2019).

The photoacclimation mechanism through the specialisation of algal symbiont assemblages has been observed (Bongaerts, Muir, et al., 2015; Ziegler et al., 2015) and non-observed (Polinski and Voss, 2018; Eckert et al., 2020) depending on regions, habitats, scales and or targeted species. Here, we demonstrate that both *P. cf. verrucosa* and *P. “speciosa” spp.* live at different depths without specific shifts in their

Symbiodiniaceae community profiles, which are characterised by similar ITS2 sequencing along the depth gradient. As previously reported in different coral species or spatial contexts, including shallow vs deep environments (Bongaerts *et al.*, 2011; Ziegler *et al.*, 2015), we also found that *Cladocopium* was the dominant genus involved in associated Symbiodiniaceae communities to both studied species. *P. cf. verrucosa* was mostly represented by lineages belonging to C1 and C42 ITS2 types across different depths (6-60 m), corroborating with congeners previously described in shallow reefs from French Polynesia (*e.g.*; Putnam *et al.*, 2012) or other regions (De Palmas *et al.*, 2021). Similarly, *P. "speciosa" spp.* displayed no differences in its community composition driven by the depth. However, we observe contrasted Symbiodiniaceae communities between the Society Islands dominated with ITS2 type profiles having lineages C3 and the Tuamotu Archipelago dominated with C1 lineages or with D1 lineages belonging to *Durusdinium* exclusively in Tikehau. Interestingly, the genus *Durusdinium* is known for its higher tolerance to thermal stress or stressors in general (Stat and Gates, 2011; Rouzé *et al.*, 2016; Silverstein, Cunning and Baker, 2017). Hence, this genus is associated continuously along the depth gradient suggesting higher thermal regimes or specific environmental conditions on the reefs studied in Tikehau. Rather than a genetic shift in the Symbiodiniaceae communities to cope with the decreasing light, we believe that the two coral species studied use other photoacclimation strategies.

We found multiple strategies of corals, from macro skeletal morphological changes to cell scale changes inside the coral tissue, to cope with low light environments as previously described in the synthesis of Kahng *et al.* (2019). The morphological plasticity of corals in-depth with a tendency to flatten morphologies is well reported (Kramer *et al.*, 2021; Lesser *et al.*, 2021). We also found that laminar *P. "speciosa" spp.* had a deeper zonation (very common at 40 to 60 m and rarer at 10-20 m and 90 m) than the branching *P. cf. verrucosa* (very common at 6-40 m and rarer at 60 m). Likewise, we noticed changes at the level of its micro-morphology skeletons with traits acclimations to increase the harvesting of light towards the coral polyps (Kramer *et al.*, 2021). These differed because of the contrasted morphologies (branching vs laminar). Specifically, *P. cf. verrucosa* increased the size and distance of corallites similar to other branching corals (Nir *et al.*, 2011; Soto *et al.*, 2018). These findings were also observed between different colony zones exposed to higher (axial zone) or lower (basal zone) light levels. In the basal zone, corallites are more distant from each other, contrasting to the axial zone, where

corallites are closer and bigger (*i.e.*, suggesting that corallites disperse with low light while aggregate with high light; **Sup. Fig. S4.2**). *P. "speciosa" spp.* also changed its micromorphology with depth by decreasing the height of septa, which is likely a way to reduce shading at a polyp scale. However, morphological changes seem trait and species-specific and even highly variable within species according to individuals and local environmental conditions (Todd, 2008; Soto *et al.*, 2018), which might explain the spatial variability of our results. Still, other strategies seem shared across species (*e.g.* decreasing tissue thickness) (Wangpraseurt *et al.*, 2012). Our results suggest that, once light penetrates inside the coral polyps, corals might increase photosynthetic efficiency with a higher concentration of chlorophyll pigments and Symbiodiniaceae density with depth, a strategy shared among most scleractinian corals (**Fig. 4.3**) (Wyman *et al.*, 1987; Maritorena *et al.*, 2002; Apprill, Bidigare and Gates, 2007; Mass *et al.*, 2007, 2010; Stambler, Levy and Vaki, 2008; Lesser *et al.*, 2010; Smith *et al.*, 2017; Kahng *et al.*, 2019; Kramer *et al.*, 2021). Although some studies suggest that different proportions of chlorophyll ratio a/c_2 might be more depth specific (Nir *et al.*, 2011), we did not find this pattern with depth. Still, we found high spatial and specific inter and intra-variability, making the understanding of corals' photophysiological capacities more complex (Kahng *et al.*, 2019). Overall, our acclimation findings suggest that our two species could compensate for the lack of light even at their deepest depths, where only 10-12% of the surface light was available at 60 m and 3-4% at 90 m. However, whether corals change their growth, calcification and reproduction along the depth gradient remains poorly known, raising necessary future studies.

Our results suggest that corals kept up with photophysiology acclimations with depth because we did not find evidence of nutritional plasticity towards heterotrophy. Some studies have suggested such corals' strategy to compensate for the lack of light with depth (Lesser *et al.*, 2010; Williams *et al.*, 2018; Radice *et al.*, 2019). We did not find such a change in the nutrition acquisition towards heterotrophy in any of the two species, even if we observed a reduction of $\delta^{13}\text{C}$ in both the symbionts and polyps with increasing depth for the two species (Muscatine, Porter and Kaplan, 1989; Williams *et al.*, 2018; Padilla-Gamiño *et al.*, 2019; Radice *et al.*, 2019). Although some studies defined a decrease of $\delta^{13}\text{C}$ in symbionts as an indication of heterotrophy (Farquhar, Ehleringer and Hubick, 1989; Muscatine, Porter and Kaplan, 1989; Padilla-Gamiño *et al.*, 2019;

Watanabe *et al.*, 2019), our Hotelling tests did not find such a switch (Turner *et al.*, 2010). However, the relative degree of heterotrophy (*i.e.*, or the delta $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{Host}} - \delta^{13}\text{C}_{\text{Symbiont}}$; Williams *et al.*, 2018) neither increased enough with depth to support this higher reliance on active feeding (*i.e.*, with $\delta^{13}\text{C}$ more similar to zooplankton as a food source) (Muscatine *et al.*, 1989; Palardy, Rodrigues and Grotoli, 2008). We believe it might be because photophysiological changes were sufficient to compensate for the lack of light for the metabolic demand of the host, and no significant switch to heterotrophy was required. Nevertheless, the interpretation of stable isotopes remains very complex and, accordingly, still very discussed in the literature, with different interpretations implying different conclusions (Kahng *et al.*, 2019). These changes in trophic plasticity seem to be very variable, specific to particular species and conditions with significant spatial differences (Fox *et al.*, 2019; Watanabe *et al.*, 2019). These changes in trophic strategy also depend on environmental conditions, for instance, a switch to heterotrophy for certain species during bleaching (Wall *et al.*, 2019; Conti-Jerpe *et al.*, 2020; Radice *et al.*, 2020). Therefore, heterotrophy may help corals compensate for the lack of light during certain conditions. Comparing our two species, it seems that *P. cf. verrucosa* might augment heterotrophy more than *P. "speciosa" spp.*, which could also be explained by the increase of the corallites size (polyps mouth) in *P. cf. verrucosa*. In contrast, *P. "speciosa" spp.* prefers to decrease the height of septa to facilitate a good light-harvesting in lower depths. Nevertheless, no significant difference was documented, and our data still suggest that both species depend on their photophysiology at their deepest distributions.

Future studies on other coral species and locations are still needed to draw robust conclusions about the overall scleractinian strategies to colonise MCEs (Muir and Pichon, 2019). The considerable variability of our results (within individuals and across species and locations), and the divergent literature outcomes in this field, highlight how little we still know about coral's capacity to deal with low-light environments with depth (Kahng *et al.*, 2019). Although the outcomes of this study derive from rigorous statistical analysis (Bayesian) (Bürkner, 2018), considering spatial variability albeit reducing the number of replicates, we are confident that our findings are valid for four different study locations answering the same question. Nevertheless, we acknowledge the need to understand the variability, which is likely influenced by the coral physiology and environment (*e.g.*, temperature, nutrients), with a better understanding of coral biology and the local

oceanographic and atmospheric conditions (Padilla-Gamiño *et al.*, 2019). Since we cannot replicate ‘mesophotic’ conditions in aquariums to control these external factors, we call for more transplantation and long-term experiment studies (Kahng *et al.*, 2019). We need standardised protocols with more accurate techniques (notably in analysing stable isotopes). Applying the same protocols, we will better understand the reasons for this high variability and decipher whether corals use plastic acclimations or specific long-term adaptation strategies to live with low light. Also, future investigations are necessary on corals’ interactions with other microorganisms (*e.g.*, microbiome, endolithic green algae *Ostreobium*) likely contributing to the adaptation of low-light conditions (Halldal, 1968; Peixoto *et al.*, 2017; Rouzé *et al.*, 2021). Finally, our findings suggest that the two corals we studied can compensate for the lack of light thanks to photophysiology strategies, *e.g.* increase of symbionts, chlorophyll concentration and morpho skeleton modifications, suggesting no necessity of switching to active feeding (*i.e.*, heterotrophy). However, we do not know if they still have enough energy to grow, calcify and reproduce. Therefore, we recommend future studies on average colonial size, photosynthesis, reactive oxygen species, respiration, calcification and histology along the depth slope.

In conclusion, thanks to physiological assessments along the entire wide depth gradient of two of the main species in the community structure of French Polynesia, the findings of this study, together with the variability, highlight the extraordinary and multidisciplinary strategies capacity of light-dependent corals to live in low light conditions. This capacity is mainly due to the coral’s ability to combine multiple mechanisms rather than rely on a single mechanism, increasing the potential for vertical range zonation. The study suggests that scleractinian corals likely live deeper than expected and could eventually be only present at deeper depths if shallow waters become hostile due to climate change.

4.6. Extra information

4.6.1. Acknowledgements

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Under The Pole Consortium⁶ G. Bardout, J. Fauchet, A. Ferucci, F. Gazzola, G. Lagarrigue, J. Leblond, E. Marivint, A. Mittau, N. Mollon, N. Paulme, E. Périé-Bardout, R. Pete, S. Pujolle, G. Siu.

4.6.2. Supplementary information

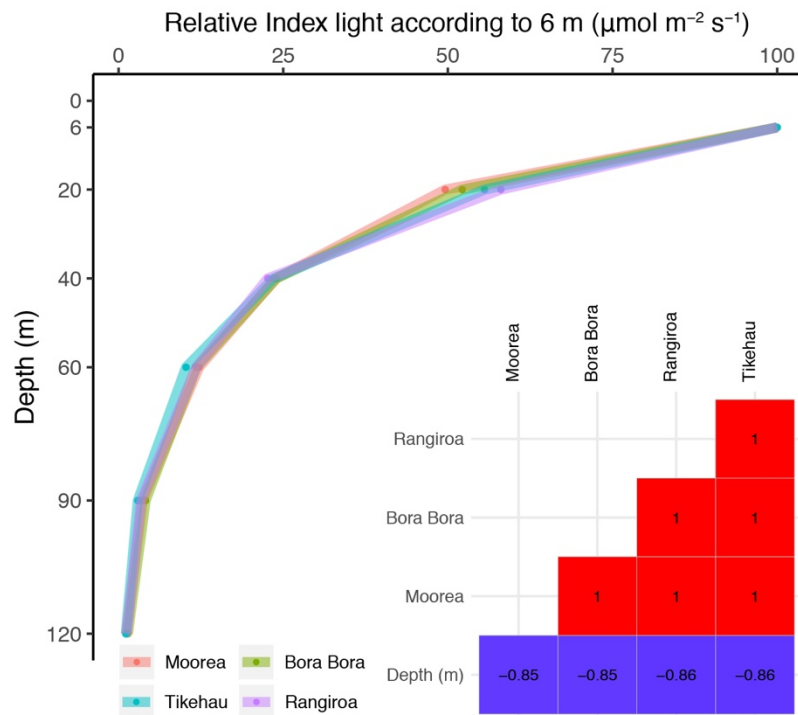


Figure S4.1: Relative index loss of light (%) with depth. Light decreased with depth following the Lambert Equation. All sites were very correlated with depth. The correlations between the different sites were very close to 1. The index relative light and depth for all sites were negatively correlated (Pearson -0.85; p -value < 0.0005). See Sup. Table 1 for exact values of light. Spatial comparisons between islands are subject to seasonality because light loggers were not deployed at the exact time.

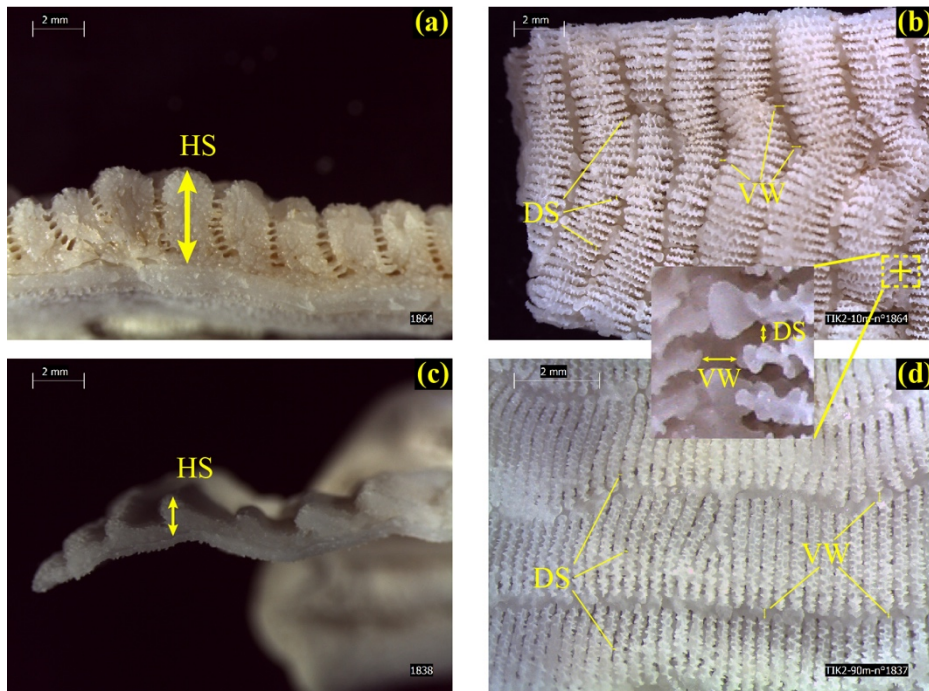


Figure S4.2: Morphological traits measured in the skeleton of *Pachyseris "speciosa" spp.* (a) and (b) colony from 10 m. (c) and (d) colony from 90 m. **HS**: height of septa (mm); **DS**: distance between septa (mm); and **VW**: valley width (mm). The dashed square and the + symbol show a magnification zoom.

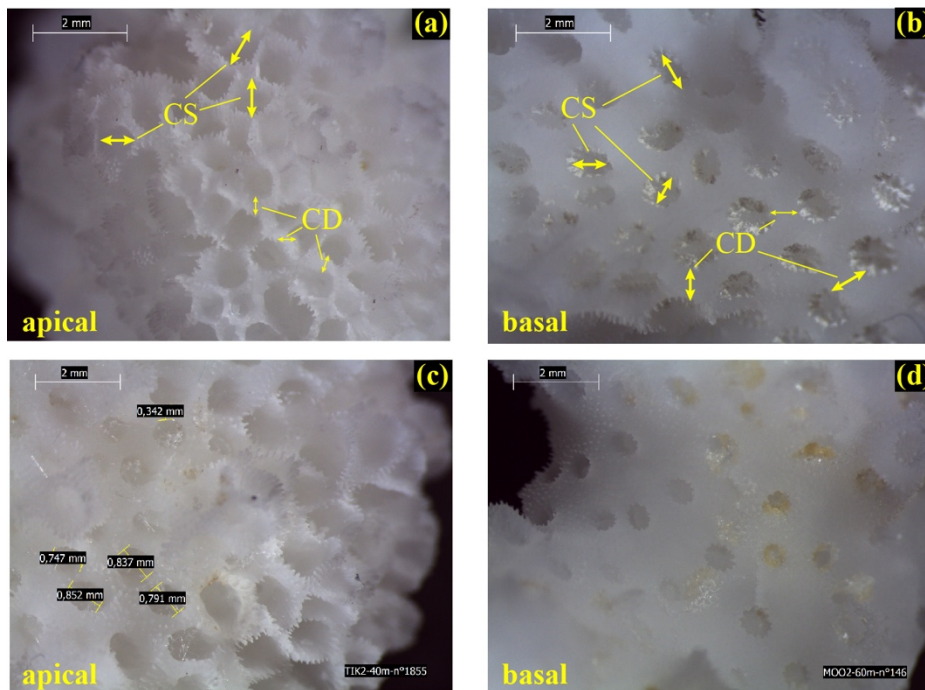


Figure S4.3: Morphological traits measured in the skeleton of *Pocillopora cf. verrucosa*. (a) and (b) colony from 6 m in the apical (left) and basal (right) zones of the branching colony. (c) and (d) colony from 60 m. **CS**: corallites size (mm); **CD**: corallites distance (mm).

Table S4.1: Additional tests for *Pocillopora cf. verrucosa* to compare the basal and apical zones of the colony in the branching morphological measures.

<i>Pocillopora cf. verrucosa</i>	Test	Comparison	Sum sq	F value	Pr (>F)	
Distance	Anova type 3	Intercept	1.854	210.022	< 2.2e-16	***
		Depth	0.00594	0.673	0.4129	
		Zone	0.878	99.539	< 2.2e-16	***
		Depth:Zone	0.1842	20.842	8.332e-06	***
		Residuals	1.924			
Size	Anova type 3	Intercept	1.8.013	1716.4847	< 2.2e-16	***
		Depth	0.1197	11.4076	0.00086	***
		Zone	0.878	99.539	< 2.2e-16	***
		Depth:Zone	0.0048	0.4558	0.50003	
		Residuals	2.2877			

Table S4.2: Quantitative measures of *Pocillopora cf. verrucosa*. Mean values for each site and depth among the different replicates. The variables (in bold) are the ones whose slope of the Bayesian model, interval confidence 95% (IQ 2.5 and IQ 07.5), does not go across zero.

Archipelago	Society Islands								Tuamotu Archipelago					
Island	Moorea				Bora Bora				Rangiroa			Tikehau		
Depth / Parameter	6 m	20 m	40 m	60 m	6 m	20 m	40 m	60 m	6 m	20 m	40 m	6 m	20 m	40 m
Symbiodiniaceae n/cm²	2.60E+06	2.10E+06	3.10E+06	2.90E+06	1.80E+06	2.10E+06	3.10E+06	2.60E+06	3.20E+06	2.70E+06	3.20E+06	2.20E+06	2.90E+06	3.10E+06
Chl a µg/mL/cm²	10.00	12.00	16.00	16.00	9.10	12.00	25.00	21.00	11.00	15.00	15.00	13.00	20.00	20.00
Chl c₂ µg/mL/cm²	3.10	4.20	5.10	5.50	3.80	4.30	9.10	6.70	4.20	4.90	5.30	5.10	7.30	7.40
Ratio Chl a µg/Symbiodiniaceae	4.20E-06	5.80E-06	5.30E-06	5.50E-06	4.80E-06	7.20E-06	8.40E-06	7.90E-06	3.50E-06	5.70E-06	4.90E-06	5.80E-06	7.10E-06	7.00E-06
Ratio Chl c ₂ µg/Symbiodiniaceae	1.30E-06	1.90E-06	1.70E-06	1.80E-06	2.00E-06	2.60E-06	3.00E-06	2.70E-06	1.30E-06	1.90E-06	1.70E-06	2.30E-06	2.50E-06	2.60E-06
Chls (a+c₂) µg/mL/cm²	13.00	16.00	21.00	22.00	13.00	17.00	35.00	27.00	15.00	20.00	21.00	18.00	27.00	28.00
Chls (a+c ₂) µg/Symbiodiniaceae	5.50E-06	7.80E-06	7.00E-06	7.30E-06	6.80E-06	9.80E-06	1.10E-05	1.10E-05	4.90E-06	7.50E-06	6.60E-06	8.10E-06	9.60E-06	9.60E-06
Chls ratio a/c ₂ µg/Symbiodiniaceae	3.30	3.50	3.20	3.10	2.90	2.80	2.80	3.00	2.70	3.10	2.90	2.60	2.80	2.90
Chls ratio c ₂ /a µg/Symbiodiniaceae	0.31	0.35	0.32	0.33	0.39	0.36	0.36	0.34	0.38	0.33	0.34	0.39	0.36	0.35
Size corallites basal (mm)	0.67	0.63	0.71	0.73	0.71	0.64	0.72	0.88	0.66	0.66	0.70	0.68	0.61	0.73
Size corallites apical (mm)	0.74	0.81	0.79	0.85	0.79	0.77	0.79	0.87	0.71	0.76	0.79	0.75	0.81	0.85
Distance corallites basal (mm)	0.42	0.63	0.55	0.70	0.44	0.59	0.61	0.65	0.42	0.56	0.62	0.42	0.67	0.57
Distance corallites apical (mm)	0.16	0.26	0.23	0.24	0.21	0.24	0.26	0.17	0.26	0.29	0.31	0.19	0.24	0.28
δ¹³C Polyps or host‰	-15.00	-17.00	-19.00	-18.00	-16.00	-16.00	-17.00	-18.00	-15.00	-16.00	-18.00	-15.00	-17.00	-18.00
δ ¹³ C Symbionts ‰	-14.00	-18.00	-18.00	-18.00	-15.00	-16.00	-17.00	-19.00	-15.00	-16.00	-18.00	-15.00	-16.00	-18.00
δ ¹⁵ N Polyps or host ‰	3.70	5.50	3.60	5.80	9.60	5.50	4.80	3.90	10.00	9.40	10.00	8.50	7.10	8.60
δ ¹⁵ N Symbionts ‰	4.90	5.30	3.70	3.70	4.40	5.00	5.20	4.20	11.00	9.40	10.00	9.50	8.10	9.10
Ratio δ ¹³ C / δ ¹⁵ N Polyps ‰	3.90	3.20	4.10	4.50	2.50	3.40	3.10	2.40	4.30	3.70	3.90	3.30	3.00	3.20
Ratio δ ¹³ C / δ ¹⁵ N Symbionts ‰	6.00	5.60	6.30	6.20	5.70	5.80	5.50	5.30	6.10	5.50	5.60	6.50	6.00	5.70
Delta 13C Polyps – Symbionts ‰	-0.63	0.28	-0.05	-0.03	-0.25	0.41	0.27	0.36	-0.09	-0.10	0.37	-0.47	-0.12	0.38
δ ¹⁵ N Polyps – Symbionts ‰	-1.20	0.23	-0.06	2.10	5.20	0.54	-0.47	-0.23	-1.20	-0.05	0.09	-0.99	-0.94	-0.54

Table S4.3: Quantitative measures of *Pachyseris* “speciosa” spp. Mean values for each site and depth among the different replicates. The variables (in bold) are the ones whose slope of the Bayesian model, interval confidence 95% (IQ 2.5 and IQ 07.5), does not go across zero.

Archipelago	Society Islands					Tuamotu Archipelago						
Island	Moorea		Bora Bora			Rangiroa			Tikehau			
Depth / Parameter	40 m	60 m	40 m	60 m	90 m	40 m	60 m	90 m	20 m	40 m	60 m	90 m
Symbiodiniaceae n/cm²	7.10E+06	9.50E+06	8.40E+06	1.10E+07	1.40E+07	5.60E+06	6.60E+06	1.60E+07	9.20E+06	1.20E+07	6.00E+06	1.10E+07
Chl <i>a</i> µg/mL/cm²	20.00	29.00	26.00	23.00	53.00	18.00	20.00	53.00	25.00	40.00	16.00	57.00
Chl <i>c</i>₂ µg/mL/cm²	9.20	12.00	11.00	10.00	21.00	6.80	7.70	25.00	7.80	13.00	5.60	22.00
Ratio Chl <i>a</i> µg/Symbiodiniaceae	3.00E-06	3.00E-06	3.10E-06	2.10E-06	3.80E-06	3.10E-06	3.10E-06	3.30E-06	2.70E-06	3.40E-06	2.60E-06	5.10E-06
Ratio Chl <i>c</i> ₂ µg/Symbiodiniaceae	1.30E-06	1.30E-06	1.30E-06	9.40E-07	1.50E-06	1.20E-06	1.20E-06	1.60E-06	8.50E-07	1.10E-06	9.50E-07	2.00E-06
Chls (<i>a</i>+<i>c</i>₂) µg/mL/cm²	30.00	41.00	37.00	33.00	74.00	24.00	28.00	78.00	32.00	52.00	21.00	79.00
Chls (<i>a</i> + <i>c</i> ₂) µg/Symbiodiniaceae	4.30E-06	4.30E-06	4.50E-06	3.10E-06	5.30E-06	4.30E-06	4.20E-06	4.90E-06	3.50E-06	4.50E-06	3.60E-06	7.20E-06
Chls ratio <i>a</i> / <i>c</i> ₂ µg/Symbiodiniaceae	2.20	2.30	2.30	2.30	2.50	2.70	2.60	2.10	3.20	3.10	2.80	2.60
Chls ratio <i>c</i> ₂ / <i>a</i> µg/Symbiodiniaceae	0.45	0.43	0.43	0.44	0.41	0.38	0.38	0.47	0.32	0.32	0.36	0.39
Septa Distance (mm)	0.03	0.04	0.05	0.04	0.03	0.06	0.07	0.03	0.05	0.07	0.06	0.03
Width Valley (mm)	0.13	0.08	0.16	0.15	0.13	0.18	0.16	0.25	0.16	0.35	0.15	0.09
Height Septa (mm)	2.80	2.10	2.80	3.10	1.60	2.50	2.20	1.30	2.70	1.40	2.10	1.10
δ ¹³ C Polyps or host ‰	-19.00	-19.00	-18.00	-19.00	-21.00	-17.00	-17.00	-20.00	-18.00	-18.00	-18.00	-20.00
δ ¹³ C Symbionts ‰	-18.00	-19.00	-19.00	-20.00	-21.00	-17.00	-16.00	-21.00	-18.00	-18.00	-18.00	-20.00
δ ¹⁵ N Polyps or Host ‰	3.00	4.50	4.90	6.00	6.00	7.30	9.90	7.50	9.20	7.90	7.80	7.60
δ ¹⁵ N Symbionts ‰	3.00	4.40	5.20	5.80	5.90	9.30	8.90	8.30	9.70	8.30	8.50	9.10
Ratio δ ¹³ C / δ ¹⁵ N Polyps ‰	5.10	5.20	4.10	5.00	4.10	6.00	5.90	4.20	7.30	3.80	5.60	5.50
Ratio δ ¹³ C / δ ¹⁵ N Symbionts ‰	7.50	7.50	5.80	6.50	6.00	6.20	6.40	5.40	7.20	5.40	6.70	6.90
Delta 13C Polyps – Symbionts ‰	-0.46	0.18	0.51	0.73	0.13	-0.14	-0.32	0.26	0.17	0.40	0.07	-0.06
δ ¹⁵ N Polyps – Symbionts ‰	-0.02	0.02	-0.39	0.22	0.18	-2.00	1.10	-0.83	-0.47	-0.47	-0.73	-1.40

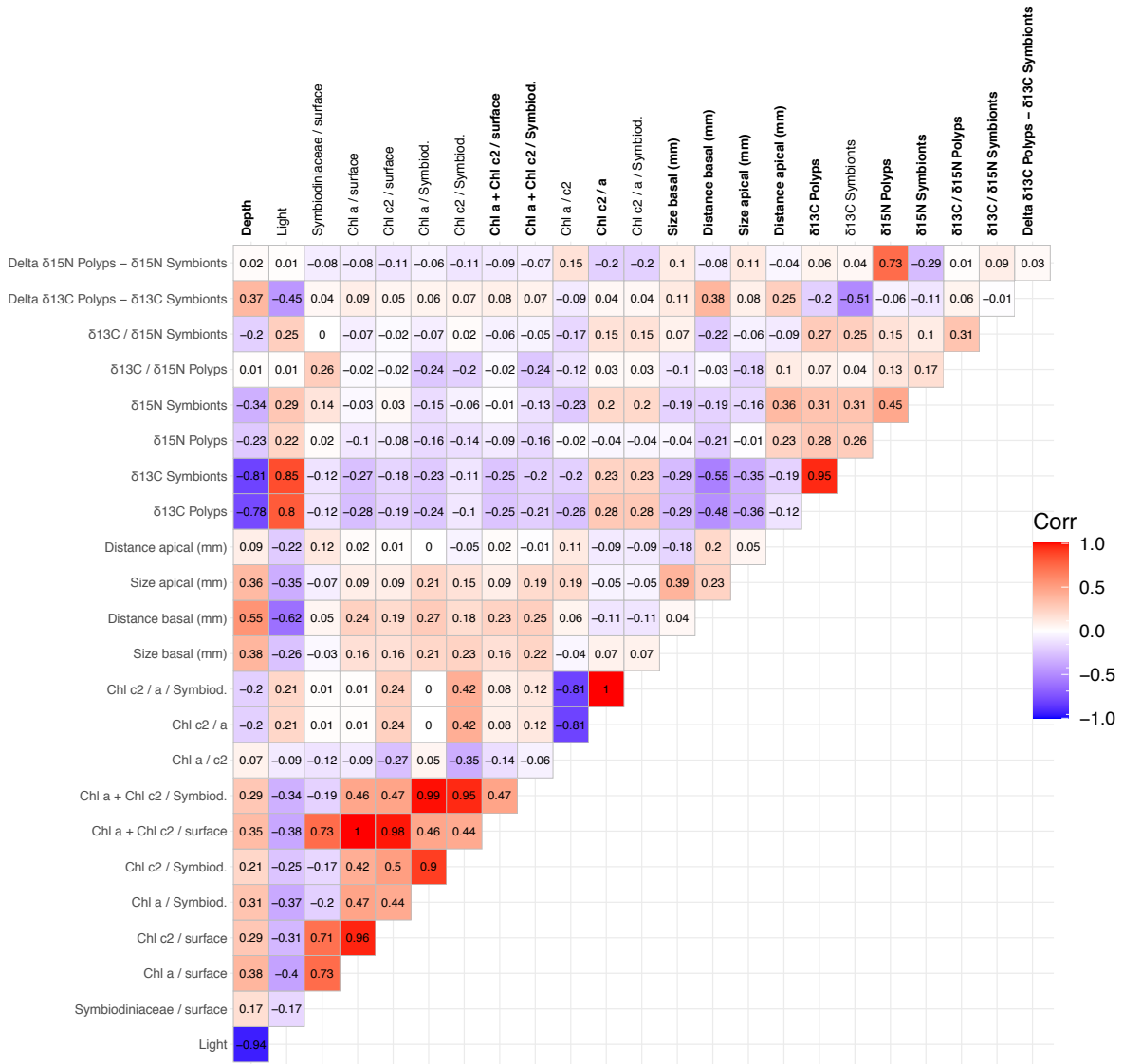


Figure S4.4: Correlations of all quantitative variables with depth, relative index light and in between for *Pocillopora cf. verrucosa*. When variables correlations were above 0.75, these were omitted from the Bayesian model to avoid collinearity.

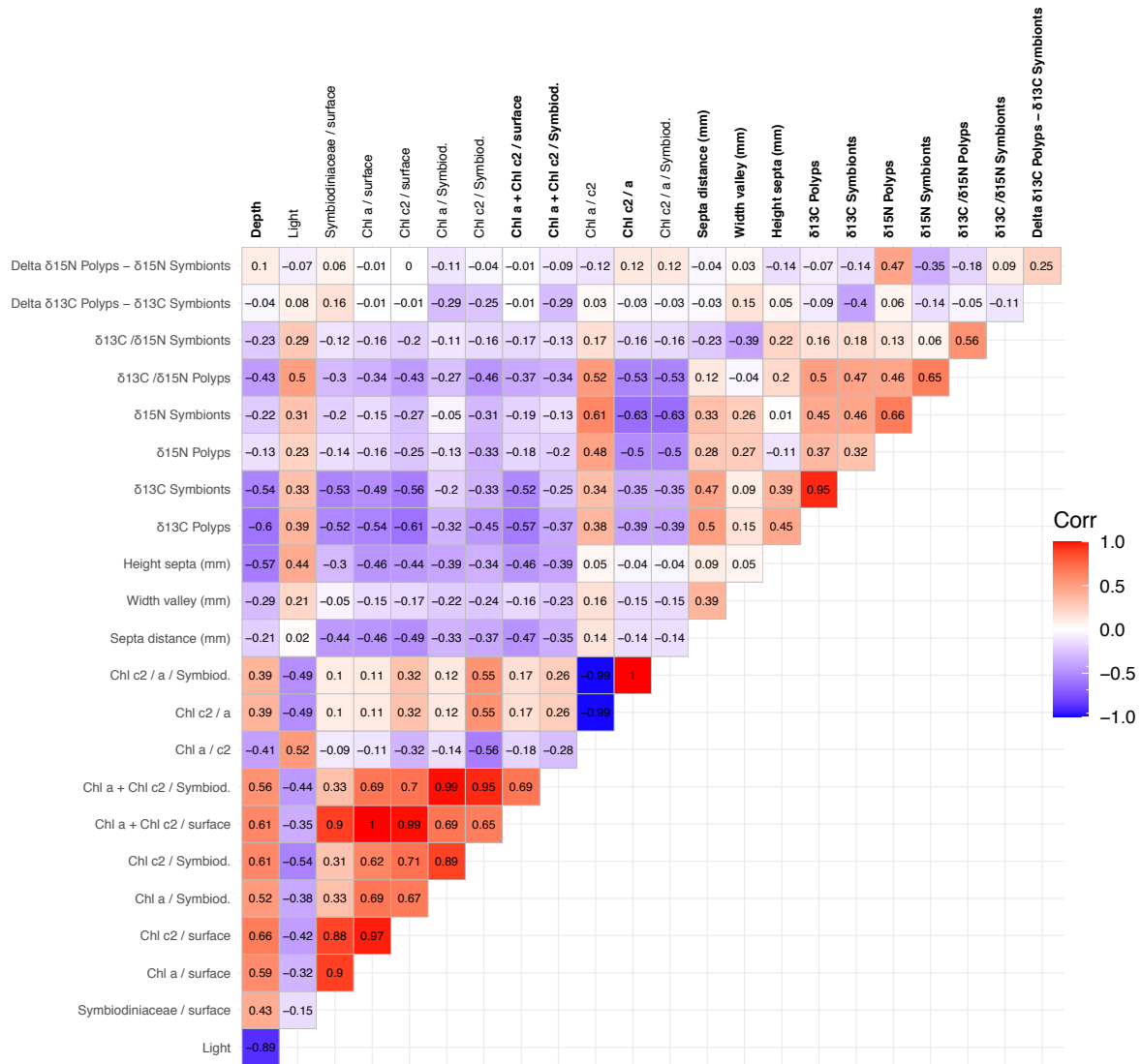


Figure S4.5: Correlations of all quantitative variables with depth, relative index light and in between for *Pachyseris "speciosa" spp.* When variables correlations were above 0.75, these were omitted from the Bayesian model to avoid collinearity.

V. Chapter 5: Coral bleaching with increasing depth

This chapter is published in *Royal Society Open Science* as:

Pérez-Rosales G, Rouzé H, Torda G, Bongaerts P, Pichon M, Under The Pole Consortium, Parravicini V, Hédouin L. 2021 Mesophotic coral communities escape thermal coral bleaching in French Polynesia. *R. Soc. Open Sci.* 8: 210139. <https://doi.org/10.1098/rsos.210139>

5.1. Abstract

Climate change and consequent coral bleaching are causing the disappearance of reef-building corals worldwide. While bleaching episodes significantly impact shallow waters, little is known about their impact on mesophotic coral communities. We studied the prevalence of coral bleaching two to three months after a heat stress event, along an extreme depth range from 6 to 90 m in French Polynesia. Bayesian modelling showed a decreasing probability of bleaching of all coral genera over depth, with little to no bleaching observed at lower mesophotic depths (greater than or equal to 60 m). We found that depth generalist corals benefit more from increasing depth than depth specialists (corals with a narrow depth range). Our data suggest that the reduced prevalence of bleaching with depth, especially from shallow to upper mesophotic depths (40 m), had a stronger relation with the light-irradiance attenuation than temperature. While acknowledging the geographical and temporal variability of the role of mesophotic reefs as spatial refuges during thermal stress, we ought to understand why coral bleaching reduces with depth. Future studies should consider repeated monitoring and detailed ecophysiological and environmental data. Our study demonstrated how increasing depth may offer a level of protection and that lower mesophotic communities could escape the impacts of a thermal bleaching event.

Keywords: Coral bleaching, mesophotic coral communities, spatial refuge, climate change, French Polynesia

5.2. Introduction

Warming sea surface temperature leading to spatially and taxonomically widespread bleaching events is one of the major drivers of the loss of reef-building corals (Hughes, Anderson, *et al.*, 2018). Corals, the habitat engineers of one of the most diverse marine ecosystems of our planet, live in obligate symbiosis with unicellular dinoflagellates from the family Symbiodiniaceae. This symbiosis readily breaks down under unfavourable environmental conditions, most commonly during anomalously high temperature and light-irradiance exposure events (Hoegh-Guldberg and Smith, 1989; Brown, 1997; Suggett and Smith, 2020). With the loss of dinoflagellates from the host tissue, corals are nutritionally compromised and, unless the environmental conditions improve, they die (Weis, 2008; Baird *et al.*, 2009). Bleaching susceptibility is taxon- and location-specific (Loya *et al.*, 2001; van Woesik *et al.*, 2011; Madin, Hoogenboom, *et al.*, 2016; Muir, Done and Aguirre, 2021) and mass bleaching events lead to rapid compositional shifts in the benthic community (Hughes *et al.*, 2019). With the ever-increasing frequency and severity of bleaching events, shallow corals are disappearing at an alarming rate (Claar *et al.*, 2018; Hughes, Anderson, *et al.*, 2018; Eakin, Sweatman and Brainard, 2019; Sully *et al.*, 2019), and the quest to identify thermally tolerant corals and coral reefs is of great interest for conservation and management (Palumbi *et al.*, 2009; Camp *et al.*, 2018).

Because temperature and light attenuate with depth, it has been proposed that mesophotic coral assemblages (*i.e.* below 30 m; (Bongaerts *et al.*, 2019)) may act as a spatial refuge for corals during global and local bleaching events (Bongaerts *et al.*, 2010). However, despite extensive debate regarding the overlap in community structure (Laverick *et al.*, 2018; Rocha *et al.*, 2018) and connectivity between shallow and mesophotic coral habitats (Holstein *et al.*, 2016; Bongaerts and Smith, 2019), there are very few studies that actually assess bleaching well into lower mesophotic depths (Lang, Wicklund and Dill, 1988; Bunkley-Williams, Morelock and Jr., 2011). Here we address this knowledge gap by conducting scleractinian coral surveys to 90 m depth during a mass bleaching event in French Polynesia in 2019. We test the hypothesis that bleaching impacts decrease with depth; assess taxonomic patterns in bleaching susceptibility over depth; and determine whether a decrease in bleaching impacts over depth leaves deeper mesophotic communities unaffected.

5.3. Material and methods

5.3.1. Study locations and sampling protocol

Benthic bleaching surveys were conducted at two locations in French Polynesia: Moorea (Society Archipelago: 17°28.631'S;149°51.067'W) and Makatea (Tuamotu Archipelago: 15°49.383'S,148°16.758'W) from 6 to 90 m depth (**Sup. Fig. S5.1a**). The forereefs of the North coast of Moorea are characterised by a gentle slope (40-60°) from the surface down to 70-80 m depth, where it drops almost vertically. The reefs of the North-West side of Makatea are characterised by a very gentle upper slope (<10°) until about 10 m depth, where it drops off almost vertically. Coral bleaching surveys were done once at each location on the 14-15th of June 2019 in Makatea and 12-13th of July 2019 in Moorea, 2-3 months after the peak in sea surface temperature that triggered a mass bleaching event in March-April 2019. Thirty photo-quadrats (0.75 x 0.75 m) were randomly taken at each of five different depths (6, 20, 40, 60 and 90 m; a total of 150 photos at each location), with constant sampling effort at each depth, covering around 17m² per isobath and 85m² per location (**Fig. 5.1a**). Deep dives were done by the Under the Pole team using mixed-gas and closed-circuit rebreathers. Quadrat photos were white balance corrected using a white reference plate attached to each quadrat.

5.3.2. Environmental parameters

We characterised the temperature regime that induced bleaching at our sites using different techniques. First, we computed the cumulative heat stress as Degree Heating Weeks (DHW) from NOAA Satellite Sea Surface Temperatures (Liu *et al.*, 2013, 2018). Second, because satellite measurements are relevant only for shallow waters, we also deployed *in situ* temperature (HOBO Water Temperature Pro v2 Data) and light (DEFI2-L JFE Advantech) loggers that measured light for Photosynthetically Active Radiation (PAR) at the different sampling depths. A detailed explanation of how these data were collected, normalised according to 6 m depth because it was the departing reference for loggers and bleaching assessments, and processed using the Beer-Lambert equation (Gordon, 1989; Rouzé *et al.*, 2021) are available in the electronic supplementary material (**Sup. Fig. S5.2 and S5.3**).

5.3.3. Coral bleaching classification and statistical analysis

We were interested in exploring the relationship between depth and the likelihood of corals to bleach. In each photo-quadrat, we counted the number of colonies larger than 5 cm (Muir *et al.*, 2017) and identified them to the highest taxonomic resolution possible (*i.e.* at least genus level and, in several cases, species level). We classified each colony using reference colour cards (Siebeck *et al.*, 2006). Although natural changes of colouration can vary with depth, we considered as references the previous healthy colours observed in the photo-quadrats of the DEEPHOPE expedition (Pichon *et al.*, 2021). Coral colonies were considered “healthy” when fully pigmented with their normal colour; “pale” when colonies had lost part of their pigmentation, but Symbiodiniaceae were still visible in their tissues; “bleached” when completely white showing their skeleton through the tissue; and “recently dead” when no living tissues remained over the skeleton, but still had discernible skeletal structure even if colonies started to be covered by turfing algae to varying extents. By contrast, colonies overgrown by thick and dark turf, crustose coralline algae and boring organisms were excluded from the analysis as their mortality likely predates the studied thermal coral bleaching event. Finally, when colonies were patchily pigmented, they were classified by the most severely bleached patch (e.g., a colony 25% bleached and 75% pale was considered as bleached and colonies 30% pale and 70% healthy as pale). To prevent potential observer bias, all photo-quadrats were analysed and scored by a single observer who had been previously trained with the analysis of 2,880 quadrats from the DEEPHOPE expedition (Pichon *et al.*, 2021).

To explore the relationship between the likelihood of bleaching and depth, we fitted a Bayesian model in R, using the brms package (P.-C. Bürkner, 2017; Bürkner, 2018) with a multinomial logit link function, a random intercept for the ‘location’ factor, and a random intercept and a random slope for the ‘genus’ factor. We used uninformative priors and ran the model for four MCMC chains using 7,000 iterations per chain after 3,000 iterations of warmup. We used the posterior likelihood of being healthy at the shallowest occurrence of each genus as a benchmark to account for genus-specific bleaching resistance. Similarly, for each genus, we calculated the posterior likelihood of being healthy at their deepest occurrence to evaluate depth-driven health benefits. All analyses were performed in RStudio. Data and codes are available in https://github.com/gonzalopr/Deep_Bleaching_French_Polynesia.

5.4. Results

5.4.1. Environmental characteristics

Both locations experienced heat stress with sea temperatures above their bleaching threshold (BT). Peak sea surface temperature anomalies occurred at the end of March-April 2019 both in Moorea and Makatea. During the bleaching event, Moorea experienced a cumulative heat stress of 3.5 DHW and Makatea of 2.9 DHW (**Fig. 5.1a**). During the bleaching survey, sea surface temperatures had decreased below the bleaching threshold. Temperatures were similar at both locations, with circadian variations of 0.3°C down to 40 m and high variability below 60 m (**Sup. Fig. S5.2**). Vertical profiles revealed that temperatures slightly decreased or were constant from the surface to 60 m depth (> 95% of surface temperatures). These temperature values were consistent with the vertical CTD profile in Makatea (Pearson = 0.95, p-value = 0.0007) (**Sup. Fig. S5.3**). Light decreased exponentially with increasing depth. Relative to the value at 6 m, PAR was about 25% at 40 m and only 4% at 90 m. These light values were also consistent with the results obtained from a vertical CTD profile (PAR was < 20% of the surface light at 40 m and < 3% at 90 m; Pearson = 0.99, p-value = $4.8e^{-7}$) and well fitted with the Beer-Lambert equation (**Sup. Fig. S5.2 and S5.3**).

5.4.2. Bleaching along the depth gradient

The proportion of colonies impacted by bleaching dramatically declined with depth at both locations (**Sup. Fig. S5.1b**). Despite differences between the two locations in the numbers of colonies over depth (e.g., decreasing in Moorea below 40 m, and remaining constant in Makatea with a maximum number at 60 m), they did not significantly affect the proportional measures of coral bleaching with depth. Consistently, our model shows that the overall probability of bleaching across all coral genera, or dying shortly before the survey period, presumably due to bleaching, decreases with depth (**Fig. 5.1b**). At 6 m, the probability for a coral colony to be bleached or healthy is almost identical (0.25), while at 20 m, the probability of bleaching reduces by more than half and the probability of being healthy doubles to 0.44 ± 0.2 Standard Error Estimate (SEE). At 40 m, the probability of being healthy is 0.73 ± 0.2 SEE, and at 90 m, 0.98 ± 0.02 SEE.

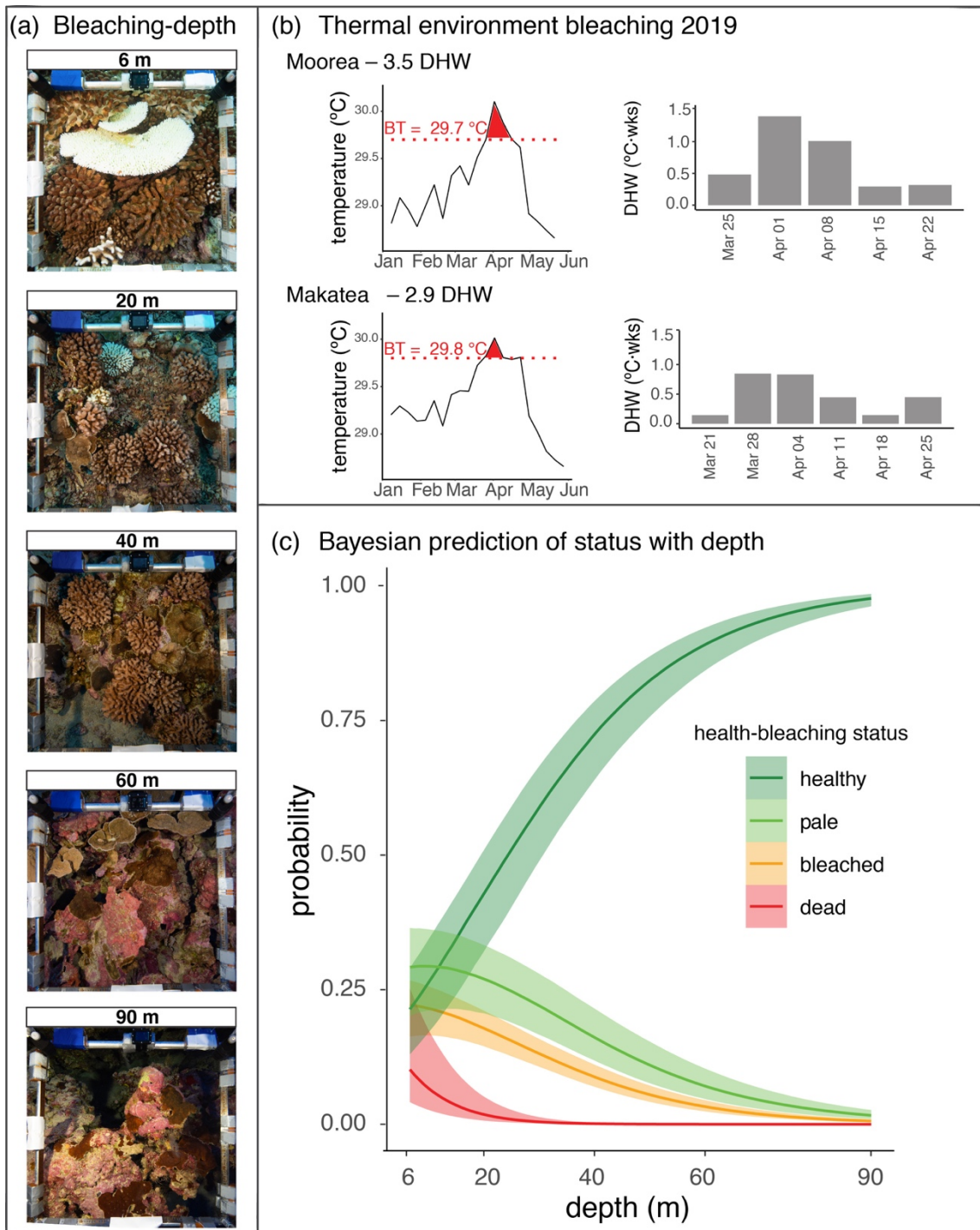


Figure 5.1: (a) Sample photo-quadrats at different depths. (b) Thermal environment with degree heating weeks (DHW) values using Satellite Coral Reef Watch Temperature. (Left) Sea surface temperatures during the bleaching episode. Red fill colour shows the exposure period above the bleaching threshold marked with a dotted line. (Right) Weekly development of the DHW. (c) Bayesian prediction probability of the likelihood of corals to be healthy, pale, bleached or dead as a function of depth.

Additionally, our model detected a remarkable variation in the bleaching sensitivity among genera (Fig. 5.2). Accounting for genus-specific zonation patterns (*i.e.* upper and lower depth limits of coral genera), we found that corals only present at

mesophotic depths were the least sensitive to bleaching (*i.e.* *Echinophyllia* (0.94 ± 0.05 SEE and *Pachyseris* 0.91 ± 0.05 SEE). Among the genera present at 6 m, *Porites* (0.51 ± 0.06 SEE) and *Leptoseris* (0.42 ± 0.09 SEE) were the most resistant to bleaching, while *Astrea* (0.2 ± 0.09 SEE), *Acropora* (0.21 ± 0.07 SEE) and *Montipora* (0.21 ± 0.05 SEE) were the most sensitive. Colonies of all coral genera were healthier at their lower depth limits and the benefit of depth was stronger for depth generalists than for genera with narrow depth ranges. For instance, the probability of a *Pocillopora* colony to be healthy increased by 0.7 from its upper limit at 6 m (0.22 ± 0.02 SEE) to its lower limit at 60 m (0.92 ± 0.03 SEE). In contrast, the probability of an *Astrea* colony only increased by 0.16 from 6 m (0.2 ± 0.09 SEE) to 20 m (0.36 ± 0.11 SEE) (**Fig. 5.2a**). Although the increasing probability of being healthy, and a decreasing probability of suffering bleaching effects with depth was a trend shared by all coral genera, there were genus-specific differences in the benefits provided by depth regardless of the extent of the depth range. For instance, despite *Acropora* and *Montipora* having similar depth distributions and thermal sensitivities in shallow waters, *Acropora* benefited from depth more than *Montipora*. at 40 m, *Acropora* already had a ~ 0.75 probability of being healthy, while the probability of *Montipora* colonies to be healthy was still less than 0.5 (**Fig. 5.2b**).

5.5. Discussion

This study shows a decrease in the incidence of coral bleaching across an extreme depth range (*i.e.* 6 to 90 m) in French Polynesia, as measured 2-3 months after the peak of a heat stress event. Consistent with previous findings, our results suggest that the probability of coral bleaching is reduced with increasing depth (Muir *et al.*, 2017; Baird *et al.*, 2018; Frade *et al.*, 2018; Giraldo-Ospina, Kendrick and Hovey, 2020). However, while previous studies were limited to the boundaries of non-technical diving (*i.e.* 30-40 m depth), we surveyed coral assemblages down to 90 m (Lang, Wicklund and Dill, 1988; Bunkley-Williams, Morelock and Jr., 2011; Smith *et al.*, 2016). In the upper mesophotic zone (40 m), we found no signs of recent mortality, and bleaching (*i.e.* bleached or pale) was 3.4-fold less common than in shallow-water, in concordance with previous studies (Muir *et al.*, 2017; Frade *et al.*, 2018). At the mid-lower mesophotic zone (60 m) and below, we found no signs of recent mortality and bleaching was virtually absent.

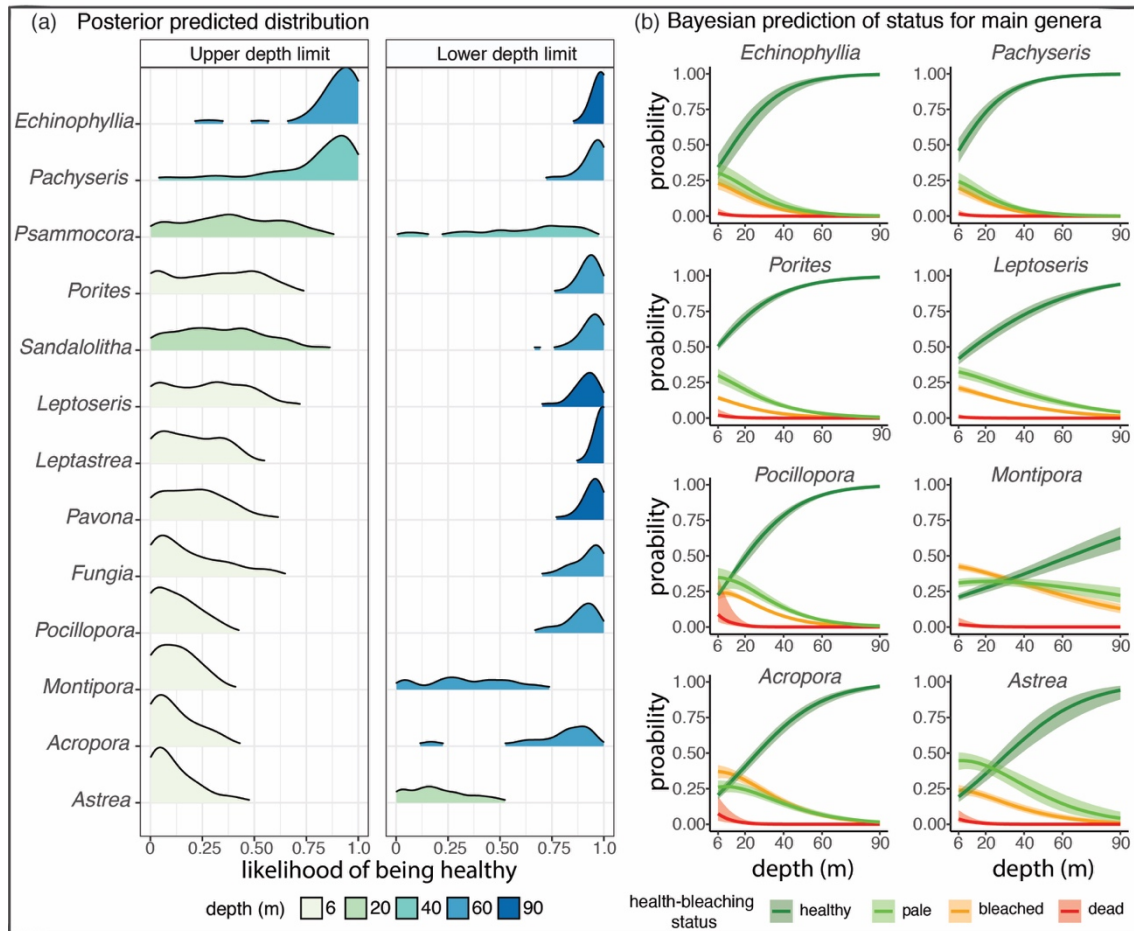


Figure 5.2: (a) Bleaching sensitivity of coral genera based on the posterior likelihood of being healthy. Predictions are displayed for the extremes of the depth range specific to each coral genus (i.e. upper and lower depth local limits). Cases with less than 25 replicates per depth and/or less than 100 replicates total were removed. (b) Bayesian prediction probability of the likelihood of corals to be healthy, pale, bleached or dead as a function of depth. The most bleaching-tolerant coral genera are *Echinophyllia* and *Pachyseris*. The most bleaching-sensitive genera are *Acropora* and *Astrea*. *Porites*, *Leptoseris*, *Pocillopora* and *Montipora* are the most common genera in the coral assemblages of the surveyed sites.

Our Bayesian model predicts taxon-specific sensitivity of corals to bleaching along their respective depth ranges. We show that the reduction in the prevalence of bleached colonies is not simply an effect of taxonomic zonation (Edmunds and Leichter, 2016), at least not at genus level. Coral genera inhabiting exclusively the mesophotic zone, from 40 to 90 m, often suffer bleaching at the upper end of their depth range and decrease in bleaching towards their deepest occurrence. While several studies have tried to classify the sensitivity of corals to bleaching (Marshall and Baird, 2000; Loya *et al.*, 2001; van Woesik *et al.*, 2011; Guest *et al.*, 2012; Furby, Bouwmeester and Berumen, 2013; Swain *et al.*, 2016; Hughes *et al.*, 2017), few studies have so far explored how bleaching sensitivity varies across the depth gradient (Frade *et al.*, 2018; Crosbie *et al.*, 2019). Incorporating random intercept and slope for taxon allowed us to isolate the

probability of coral bleaching from the depth distribution of a given genus. Our predicted results corroborated earlier studies that Acroporidae (for the purposes of this study, *Acropora* and *Montipora*) are extremely sensitive to bleaching (Marshall and Baird, 2000; Pratchett *et al.*, 2013), but also showed that *Montipora* benefits less from the effect of depth than *Acropora*. Moreover, we found that higher probability of detecting healthy colonies with increasing depth was a common trend for all genera regardless of their depth distribution (extending the work by Frade *et al.* (2018); but see Crosbie *et al.* (2019)). Finally, we found that depth-specialist coral genera were the least sensitive to bleaching; and that the health status of depth-generalists improved more with increasing depth than that of depth-specialists. Such generic patterns could be elaborated in future studies, including the inter-specific bleaching variability within genera (McClanahan *et al.*, 2020).

The reduction of coral bleaching from the surface to depth can be attributed to changing environmental conditions, the physiological capacities of corals, or the interplay of the two (Page *et al.*, 2019). By assessing the impact of bleaching 2-3 months after the peak of heat stress, we have a snapshot view of the effect of heat stress on corals along the depth gradient. The timing of our surveys does not allow us to differentiate unaffected corals from those that recovered quickly following the peak of the thermal stress (Claar and Baum, 2018). Nevertheless, we reliably identify the most susceptible coral genera to bleaching along an unprecedented depth gradient because corals severely bleached during the heat stress will die or remain bleached for months before the symbionts come back (Claar and Baum, 2018; Sakai, Singh and Iguchi, 2019). During the survey, sea surface temperatures were below the bleaching threshold, and it is unlikely to see healthy corals bleach because of temperature without heat stress. Anomalously high sea surface temperatures are usually considered the primary driver of coral bleaching but are not the only abiotic parameter involved (Hoegh-Guldberg and Smith, 1989; Brown, 1997; Suggett and Smith, 2020). For instance, the severe bleaching observed in shallow coral assemblages, despite the relatively low values of DHW (Liu *et al.*, 2013), was most likely due to the interaction between temperature and light-irradiation. This interaction could explain why corals bleached, with no mortality, in 2016 at even lower DHW values at some sites of French Polynesia (Donovan *et al.*, 2020; Hédouin *et al.*, 2020; Pérez-Rosales, Brandl, *et al.*, 2021). Vertical profiles from the limited environmental data at our study sites showed stable temperatures from the surface to 40 m and significant temporal variability at lower-mesophotic depths (60-90 m). This high variability (*e.g.* up to one or

two °C within minutes; **Sup. Fig. S5.2**) may provide relief from high temperatures and/or increase organisms' stress tolerance (Wall *et al.*, 2015; Safaie *et al.*, 2018; Reid *et al.*, 2019). The variability is likely associated with the common internal tidal/gravity waves of the Pacific Islands (Wolanski and Delesalle, 1995; Talley *et al.*, 2011; Leichter *et al.*, 2012; Pichon, 2019), which have proved to reduce heat stress in several locations (Schmidt *et al.*, 2016; Reid *et al.*, 2019; Wyatt *et al.*, 2020). Additionally, the thermocline's depth recorded in our study corresponded to depths reported for the region (Leichter *et al.*, 2012; Schramek *et al.*, 2018; James *et al.*, 2020). Although both phenomena appear too deep to have an effect at the timepoint of observations, they might have provided extensive heat relief before our measurements. Therefore, more rigorous and long-term studies are necessary to understand the role of oceanographic processes in reducing heat stress on corals and, hence, identify reefs less affected by coral bleaching (Colin, 2009; Schmidt *et al.*, 2016; Hock *et al.*, 2017; Hughes *et al.*, 2017; Reid *et al.*, 2019; Wyatt *et al.*, 2020).

Coral bleaching is a stress response to the increasing concentration of toxic by-products of photosynthesis, most commonly brought about by high temperature, compounded by other factors such as light intensity and water chemistry (Hoegh-Guldberg and Smith, 1989; Smith, Suggett and Baker, 2005; Weis, 2008; Baird *et al.*, 2009). In contrast to temperature, and in accordance with the Beer-Lambert Law (Gordon, 1989), light levels decreased exponentially with depth (**Sup. Fig. S5.2**). This reciprocal trend to the likelihood of being healthy suggests that light was a stronger predictor of bleaching than temperature in this study (**Sup. Fig. S5.4**). The reduction of PAR with depth (Warner, Fitt and Schmidt, 1999; Bongaerts and Smith, 2019) implies that corals experienced less stress with the decrease of excessive photosynthetic activities (Smith, Suggett and Baker, 2005), indicating that light might be a key contributor to deep coral refuges (Muir *et al.*, 2017). In this context, recent literature suggested that Ultra Violet (UV) radiation might be more important than PAR alone to explain bleaching (Fitt and Warner, 1995; D'Croz L; JL Maté, 2002; Courtial *et al.*, 2017). While challenging to undertake such studies over large depth ranges (Pyle, 2019), future work should include repeated monitoring surveys and endeavour to integrate additional environmental and biological parameters to further understand the observed decrease in bleaching over depth.

Mesophotic coral ecosystems are unlikely to provide long-term refugia from the ever-increasing frequency of thermal stress events (Camp *et al.*, 2018; Bongaerts and Smith, 2019). However, they may still play a role as short-term refuges from bleaching. Our study has contributed to this still controversial concept by extending the depth-related decrease in bleaching incidence to lower mesophotic depths and demonstrating that bleaching is less prevalent towards the lower end of the depth range of coral taxa. While recognising the geographical limitations of this study, and acknowledging the variability in bleaching susceptibility among genera, species and regions, the dampening impact of bleaching over depth may nonetheless be critical in preventing local species extinctions and safeguarding the unique fauna associated with mesophotic depths in some locations.

5.6. Extra information

5.6.1. Acknowledgements

We sincerely thank the team of the Under The Pole Expedition III. Under The Pole Consortium: G. Bardout, J. Fauchet, A. Ferucci, F. Gazzola, G. Lagarrigue, J. Leblond, E. Marivint, A. Mittau, N. Mollon, N. Paulme, E. Périé-Bardout, R. Pete, S. Pujolle, G. Siu.

5.6.2. Data availability

Data and relevant code for this research work are stored in GitHub: https://github.com/gonzalopr/Deep_Bleaching_French_Polynesia and have been archived within the Zenodo repository: <https://doi.org/10.5281/zenodo.5211676>.

5.6.3. Funding

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5.6.4. Supplementary information

Supplementary figures

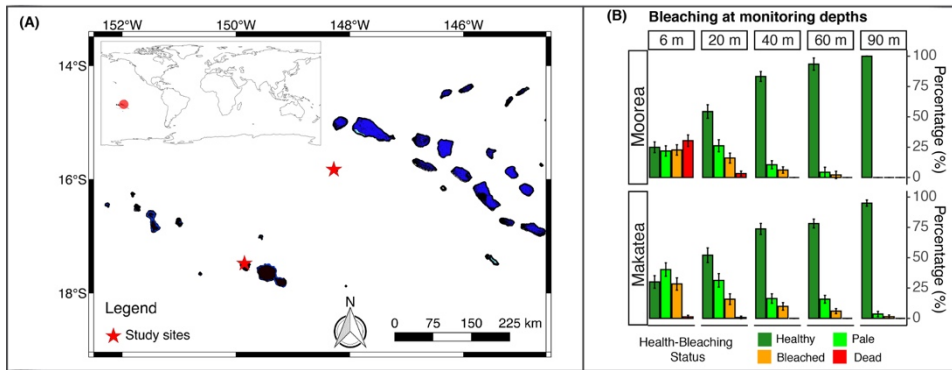


Figure S5.1: (A) Map of the locations of this study. (B) Proportions of each health-bleaching status at each survey depth. Error bars show standard errors using 95% CI. (D) Bayesian prediction probability of the likelihood of corals to be healthy, pale, bleached or dead in function of depth.

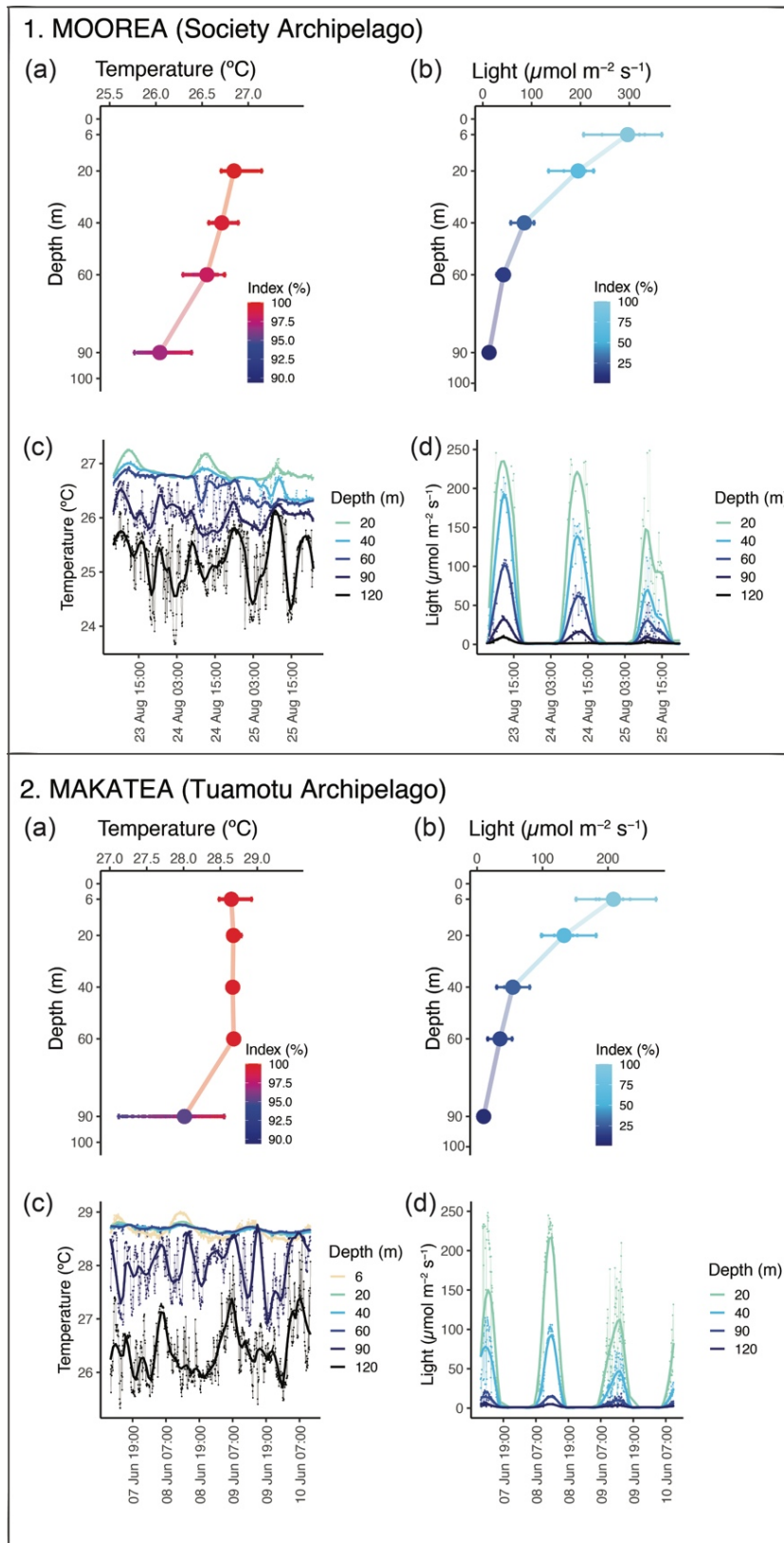


Figure S5.2: Thermal and irradiance environment of the study sites. (a) Temperature (HOBO Water temperature Pro v2 Data, °C) vertical profiles with the relative loss compared to 6 m depth. (b) Light (DEFI2-L JFE Advantech Logger with $0.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ resolution) vertical profiles with the relative loss compared to 6 m depth. (c) In situ temperature loggers at the different depths of our study sites. (d) In situ light loggers at the different depths of our study sites. Data from Moorea do not correspond with the survey period.

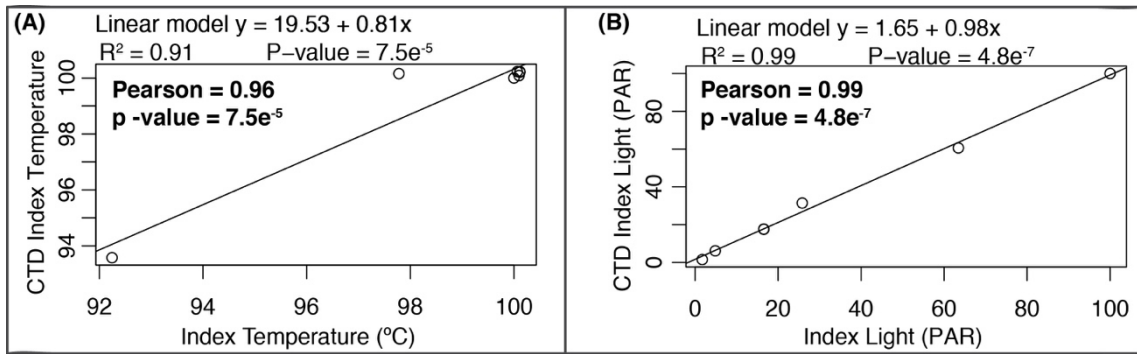


Figure S5.3: Pearson correlations between: (A) the CTD index temperature and the logger index temperature (HOBO Water temperature Pro v2) relative to the surface. (B) the CTD index light and the logger index light (DEFI2-L JFE Advantech Logger) relative to the surface.

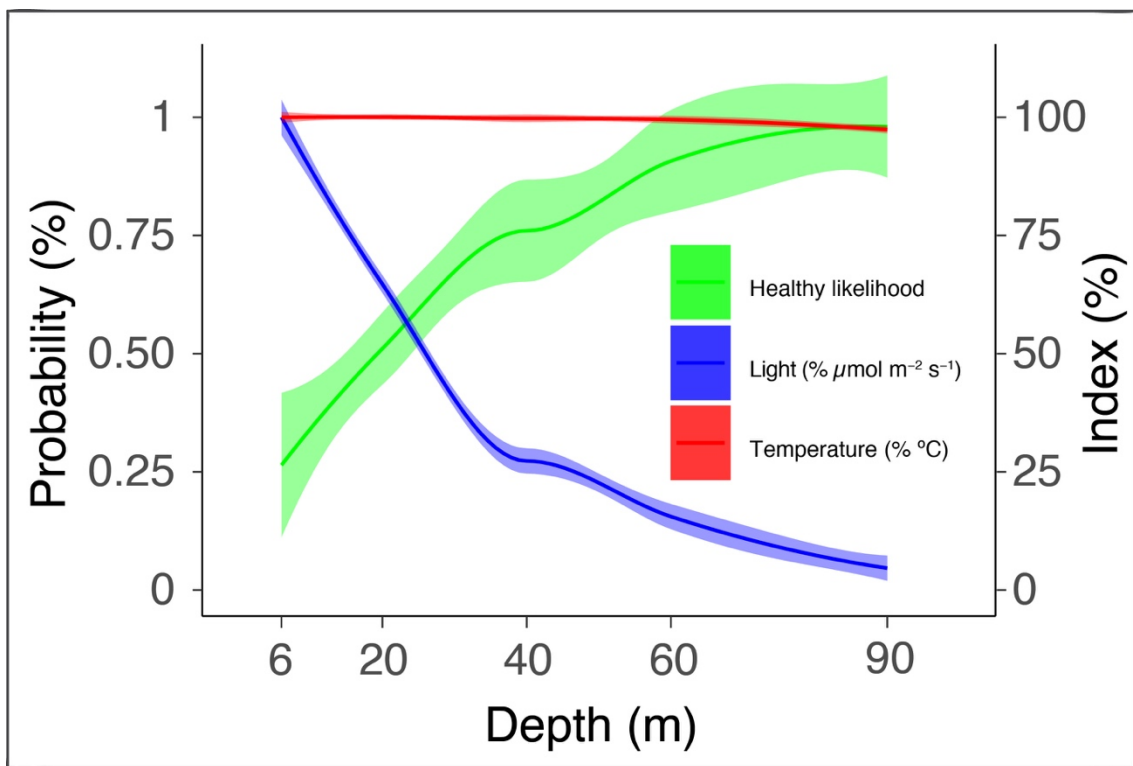


Figure S5.4: Relationship between the Bayesian prediction probability of the likelihood of corals to be healthy and the index profile of temperature and light.

Supplementary material:

Degree Heating Weeks

Sea surface temperature was downloaded from NOAA Coral Reef Watch with a 5 km spatial resolution (0.05 degrees) (Roberts-Jones, Fiedler and Martin, 2012; Maturi *et al.*,

2017). We computed heat stress using the Degree Heating Weeks (DHWs) index (Glynn, 1996; Eakin *et al.*, 2010; Liu *et al.*, 2018). First, we calculated the Monthly Maximum Mean (MMM) for our sites over the climatological period suggested by NOAA (*i.e.*, from 1985 to 1993 – excluding 1991 and 1992 because of the eruption of Mt. Pinatubo volcano). Second, we calculated heat stress as the weekly sea surface temperatures that exceeded the Monthly Maximum Mean by more than 1 °C. This corresponded to the Bleaching Limit Threshold (BLT = weekly SST-MMM \geq 1°C). Third, we computed DHW index values as the sum of the 12 precedent weeks (Glynn, 1996; Eakin *et al.*, 2010; Liu *et al.*, 2013) which represents the accumulation of heat stress and time of exposure over the bleaching threshold. Bleaching levels and expected impacts on corals can be found in Liu *et al.* (2018).

Temperature and light loggers

We deployed *in situ* temperature (HOBO Water temperature Pro v2 Data) and light (DEFI2-L JFE Advantech) loggers that measured temperatures and irradiance for Photosynthetically Active Radiation (PAR) at the different sampling depths over 48 hours. With the available data, we calculated relative vertical profiles of temperature and light from logger data compared to 6 m depth. We standardised according to 6 m instead of the surface because it was the shallowest depth of our loggers and on which we could measure coral bleaching for logistic technical diving reasons. Considering the clear oceanic water and the narrow wavelength band at mesophotic depths, we estimated light missing data from studied depths using Beer-Lambert equation law: $PAR_z = PAR_0 \times e^{-kz}$, where PAR_z is the irradiance at the predicted depth, PAR_0 the irradiance reference, k the light attenuation coefficient estimated with all depths and z the predicted depth (Gordon, 1989; Rouzé *et al.*, 2021). For the light computation we only considered daytime hours from 09h00 to 16h00 (S2). We corroborated estimated values with a vertical temperature and light profile using a CTD (Conductivity, Temperature and Depth – Valeport Midas) deployed in Makatea (**Sup. Fig. S5.3**). Data from Moorea do not correspond with the bleaching survey period and we used data from August 2018. For all these reasons, we did not include temperature and irradiance in the Bayesian model because we believe they were not robust enough. Therefore, we only used logger data as a proxy to interpret the reduction of bleaching prevalence with depth of our Bayesian results.

VI. Chapter 6: General Discussion

Summary of main overall results

Reducing human-induced global warming is the primary action to maintain scleractinian coral reefs. Yet ‘business as usual’ continues and climate change triggering Mass Coral Bleaching Events compromises the future condition of reefs (Hughes, Anderson, *et al.*, 2018). Although the interest in MCEs continues to increase (Bongaerts *et al.*, 2019 - **Appendix 1**), the “twilight zone” remains poorly studied around the world (Loya, Puglise and Bridge, 2019). The present thesis aims at understanding the ecological importance and physiological functioning of scleractinian corals by *Diving deep on the reef slopes in French Polynesia: to reveal new insights into MCEs* at a local scale with potential implications on a global scale. Indeed, this thesis joins the already numerous studies claiming the importance of MCEs (Bridge *et al.*, 2013; Kahng, Copus and Wagner, 2014; Soares *et al.*, 2020) because its findings might bring some hope from the depths for the future of coral reefs.

In summary, during this thesis, I quantitatively studied the MCEs of French Polynesia along a rare – but hugely valuable – depth range (6-120 m, and eventually 172 m) and on a broad spatial scale (covering a total area of ~1,600,000 km²). With a particular focus on Scleractinia and benthic communities, **chapter 2** shows that MCEs are hotspots of scleractinian generic diversity in French Polynesia despite coral cover decreasing with depth. **Chapter 3** shows that notwithstanding the general decreasing trend of coral cover, mesophotic depths hide communities with unexpectedly high coral cover, in some cases, higher than on shallow reefs. **Chapter 4** shows the multiple trait strategies that two complex scleractinian species have developed to cope with low-light environments, suggesting that scleractinian corals have the capacity to live throughout broader depth ranges. **Chapter 5** demonstrates that mesophotic coral communities escaped the consequences of a thermal coral bleaching episode in French Polynesia. Therefore, the thesis brings supporting evidence to suggest that MCEs (and particularly the 40-60 m zone) are key depths for conservation planning because they can increase the overall coral reef ecosystem resilience. Nevertheless, it also joins forces with the multiple

studies claiming that climate action (from individuals to our world leaders) is the primary solution for the future of coral reefs (Hoegh-Guldberg, Kennedy, *et al.*, 2018).

Planning of the discussion

Having summarised the main findings of this thesis, I will discuss the relevance of our results in terms of Scleractinia and benthic communities. I will characterise the MCEs of French Polynesia according to **chapters 2 and 3** and some preliminary results of DEEPHOPE. I will discuss spatial differences in French Polynesia, compare them with other worldwide locations and the potential influence of the environment. I will explain the physiological results of **chapter 4** from an ecological perspective in light of the results of **chapters 2 and 3**. Since **chapters 2, 3 and 5**, and to a certain extent **chapter 4**, demonstrate the importance of MCEs, I will explain how these MCEs might increase the resilience of coral reefs subjected to climate change. Related to the precedent point, I will suggest advice on how conservation planning should consider these key mesophotic depths to face global changes. Finally, I will acknowledge the main limitations and recommend future directions for research and a better understanding of MCEs.

MCEs of French Polynesia, scleractinian diversity and depth zonation

The present thesis, reinforced by some preliminary results of DEEPHOPE, increases local knowledge of the scleractinian diversity and scheme zonation of MCEs in French Polynesia (Pichon, 2019). In general terms, generic richness profiles follow a mid-domain effect with depth, with a peak of richness at about 40 m. Around these mid-depths (20-60 m), most genera converge, allowing the presence/coexistence of shallow and deep coral assemblages at the same time (**Chapter 2**).

From the surface, the composition seems similar from the shallow reefs down to at least 40-45 m depth. In the shallows, the dominant genus in most islands (small beta-diversity, **Chapter 2**) was *Pocillopora* (notably the species *P. cf. verrucosa* and *P. meandrina*). The genus was present down to 40-60 m (maximum depth limits according to the DEEPHOPE expedition were for *P. cf. verrucosa* 90 m in Gambier 2 and for *P. cf. meandrina* 60 m in Makatea 2). Deeper, the species becoming dominant at mesophotic

depths was *Pachyseris* “*speciosa*” *spp.*, especially at the 40-60 m zone. These two complex species (*P. cf. verrucosa* and *P. “speciosa” spp.* (*P. “speciosa” spp.* probably includes three sympatric cryptic lineages; Bongaerts *et al.*, 2021) were used as species models in the physiology study (**Chapter 4**). In the absence of dominance by *Pachyseris*, the community composition at around 40 m was characterised by the highest generic richness (**Chapter 2**) and the highest diversity in morphologies (**Chapter 3**) along the depth slope. A mix of laminar, encrusting and massive forms, and even solitary and branching corals. Among others, these species were *Pavona varians*, *Leptoseris mycetoseroides* and *L. incrustans*, *Porites rus*, *Leptastrea spp.*, *Cycloseris spp.* and some other species from the family Fungiidae. Below 60 m, the genus *Leptoseris* dominated but was also present in encrusting forms at 20 m depth. We found that the gradual transition between the “shallow reef” and the more typically mesophotic fauna was usually in the depth range of 50-60 m. Deeper such a depth, we found laminar *Leptoseris*, *e.g.*, *L. solida*, *L. hawaiiensis*, *L. spp.*, *Montipora spp.*, *Oxypora spp.*, *Echinophyllia spp.*, *Cycloseris wellsi* and *Alveopora spp.* Underneath 120 m, “only” *Echinophyllia* and *Leptoseris spp.* were found, being *L. hawaiiensis* the deepest with a density of 5 colonies/10 m² at 140-150 m depth. The different species of each genus are available in **chapter 3, Table S3.1**.

In addition to the derived results from photo-quadrats (**Chapters 2 and 3**), one of the main findings of the DEEPHOPE expedition was to collect the deepest zooxanthellae scleractinian coral in the world (Rouzé *et al.*, 2021 - **Appendix 2**) (**Fig. 6.1**). Indeed, we settled a new global depth record for light-dependent scleractinian corals: the already defined as the deepest *L. hawaiiensis* collected at 172 m in the Gambier Islands (23° 04.383 S, 135° 00.973 W). This discovery pushed the previous depth limit of 165 m (Maragos and Jokiel, 1986). Together with other collected samples from DEEPHOPE, these findings suggest that the actual depth limits of most scleractinian corals are deeper than currently known and, thus, likely to be extended with further research in the mesophotic zone. For example, the expedition with considerable sampling effort in MCEs increased the depth range zonation of multiple species occurring in French Polynesia from previous knowledge (Pichon, 2019 - Table 24) to Box 1. The results of Box 1 are possible thanks to the work of Professor Michel Pichon, a colleague from DEEPHOPE and co-author of all chapters of my thesis. In particular, he especially contributed to the

preliminary coral identifications and depth ranges of species, which are, to a certain extent, summarised in **Box 6.1**.

Box 6.1: In terms of scleractinian fauna, we collected up to 12 families, 40 genera and over 130 species within the mesophotic range. We found new geographical records for the first time in French Polynesia, such as *Alveopora ocellata* and *A. tizardi* (family Acroporidae), the genus *Cantharellus spp.* (family Fungiidae) and the genus *Goniopora spp.* with the species *G. fruticosa* (family Poritidae), beyond multiple first sight-record for particular archipelagos. Furthermore, we pushed depth range boundaries with 33 new maximum worldwide depths for zooxanthellae species in the Indo-Pacific Ocean. These preliminary results were presented to the scientific community during the International Coral Reef Symposium (ICRS) of Bremen in 2021 (Pichon *et al.*, 2021) and by personal request, and because we will publish these results, they cannot be displayed here.



Figure 6.1: *Leptoseris hawaiiensis* collected at 172 m. (Left) Photo during the sampling (Copyright image: Gael LAGARRIGUE / UNDER THE POLE / Zeppelin Network). (Right) Coral skeleton showing endolithic green algae *Ostreobium* (Copyright image: Gonzalo PÉREZ-ROSALES). These results were published in the ISME journal (Rouzé *et al.*, 2021 - Appendix 2).

MCEs of French Polynesia, spatial differences and worldwide comparisons

This thesis presents enough evidence to suggest French Polynesia as a promising bioregion for the presence of highly diverse and scleractinian covered MCEs (Pichon *et al.*, 2021; Rouzé *et al.*, 2021 - **Appendix 2**). Except for the Marquesas (see below), I

found that the 40-60 m depths of French Polynesia host hotspots of generic richness and coral cover (**Chapters 2 and 3**). Even at lower mesophotic depths, MCEs hosted unexpectedly high scleractinian cover communities of up to 81% at 40 m, 75% at 60 m, 54% at 90 m or 42% at 120 m (**Chapter 3**). However, these results varied across all studied locations because while MCEs with a high scleractinian cover were commonly present until 60 m (14 out of 16 sites with more than 10% coral cover), these were rarer below 90 m (5 out of 16 sites with more than 10% cover; **Table 6.1**). Yet, even if both chapters focused on general patterns, both considered spatial variability for the conclusions. In **chapter 2**, I showed that the Mid-Domain of richness was conserved in all studied islands and that spatial beta-diversity increased with depth. In **chapter 3**, I displayed hotspots as ‘outliers’ of higher coral cover communities than expected for the depths across locations.

Table 6.1: Generic richness (GR) (n) and coral cover (CC) (%) with standard errors (se) for each island, site and depth. All “hotspots” of **chapter 3** with a higher coral cover than expected for the depth are indicated in bold. Differently to Sup. Table S3.3 the table combines generic richness and coral cover.

Depth (m)	Archi- pelago	Society Islands						Tuamotu Archipelago						Gambier Archipelago			
	Island	Moorea		Tahiti		Bora Bora		Tikehau		Rangiroa		Raroia		Makatea		Gambier	
	Site	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
6	GR (n)	11	13	12	13	10	11	11	15	10	11	12	11	11	11	12	15
	CC % (se)	65.91 (5.66)	58.39 (3.6)	57.78 (4.27)	37.51 (2.93)	34.08 (3.35)	53.46 (7.38)	45.06 (5.68)	40.66 (2.15)	17.91 (1.49)	17.06 (1.50)	41.20 (1.88)	18.66 (0.91)	60.35 (3.19)	55.24 (3.45)	10.89 (0.44)	39.15 (2.01)
20	GR (n)	20	22	18	20	17	20	23	20	19	19	15	13	11	11	20	19
	CC % (se)	27.01 (1.06)	38.04 (0.93)	58.75 (2.11)	37.33 (0.63)	46.13 (2.32)	35.06 (1.57)	31.09 (0.65)	33.55 (0.55)	11.11 (0.23)	42.88 (1.90)	55.24 (2.72)	56.09 (3.31)	60.22 (2.10)	66.93 (5.34)	22.17 (0.85)	43.55 (1.04)
40	GR (n)	22	22	19	15	17	22	21	23	24	23	12	18	15	14	17	19
	CC % (se)	27.33 (0.51)	2.84 (0.04)	32.58 (0.79)	32.84 (0.88)	6.75 (0.19)	53.59 (1.13)	29.95 (1.24)	51.42 (2.09)	45.15 (1.86)	26.09 (0.96)	81.86 (7.71)	57.96 (3.13)	46.89 (1.55)	45.51 (1.61)	20.58 (0.58)	43.46 (0.75)
60	GR (n)	17	23	19	10	20	22	17	18	19	20	18	16	15	16	18	17
	CC % (se)	6.22 (0.19)	15.33 (0.34)	11.99 (0.36)	12.66 (0.94)	64.71 (2.19)	68.26 (1.76)	31.40 (1.64)	31.60 (1.48)	21.95 (0.86)	35.77 (1.63)	43.60 (1.48)	18.49 (0.45)	67.11 (3.11)	74.49 (3.05)	35.77 (1.22)	9.37 (0.32)
90	GR (n)	5	6	2	1	5	9	2	10	8	12	11	6	7	9	11	12
	CC % (se)	3.55 (0.32)	1.55 (0.41)	3.07 (1.31)	0.17 (0.0)	0.75 (0.09)	9.91 (0.51)	0.53 (0.13)	9.99 (1.19)	3.42 (0.17)	6.71 (0.30)	14.04 (0.77)	9.06 (0.99)	35.38 (6.94)	30.58 (5.54)	11.55 (1.04)	52.88 (5.12)
120	GR (n)	1	2	2	0	2	2	2	3	4	5	3	2	2	2	8	7
	CC % (se)	0.0	0.31 (0.11)	0.13 (0.02)	0.0	0.13 (0.0)	1.15 (0.04)	0.04 (0.0)	0.27 (0.09)	0.04 (0.0)	1.82 (0.15)	2.89 (0.66)	0.31 (0.11)	3.29 (0.22)	1.82 (0.38)	15.95 (1.54)	42.00 (4.20)

The ‘hotspots’ or positive outliers of coral cover to show how these highly scleractinian-covered MCEs communities look like compared to the ‘coldspots’ or negative outliers are described with environmental and geomorphology in **chapter 3 - Sup. Box 3.1** and **3.2**. Very shortly, the top four hotspots were:

- Raroia Site 1 at 40 m. It was the highest coral-covered ($81.8 \pm 7.7\%$) site among all studied depths. It was composed of a monotypic culture of laminar *Pachyseris speciosa* spp. (85.9 % of the relative composition) in the forms of roses.
- Makatea Site 2 at 60 m. The coral cover was very high for the depth ($74.5 \pm 3.1\%$), and it was composed of encrusting *Leptoseris myscetoseroides* and *Pavona varians*, alternating with laminar *Leptoseris solida*. This site had a garden of laminar roses of *L. solida*, just starting at 60 m and down to 90 m, reaching its maximum values at 80 m. However, this depth was not among the sampled depths, and quantitative data is not available (but see cover photo from page 3).
- Gambier Site 2 at 90 m. The coral cover was high for the depth ($52.9 \pm 5.1\%$). It was composed of a variation between laminar *Montipora* spp. and *Leptoseris* spp. This site was the only one among all at 90 m where branching corals (*Acropora*) were still present. There was a high presence of green encrusting algae (likely from the genus *Ostreobium*).
- Gambier Site 2 at 120 m. The coral cover was unexpectedly high ($42 \pm 4.2\%$) for such a depth. There were large laminar *Montipora* spp. with colonies as big as $\sim 2,500 \text{ cm}^2$.

Most of the ‘hotspots’ were in the islands of Bora Bora and Raroia at 40 and 60 m, in Makatea at 60 and 90 m and Gambier, at 90 and 120 m (**Table 6.1** and **Chapter 3 - Sup. Box. 3.1**). However, the reef conditions at different depths for particular sites could present significant variability along the reef slope, complicating their prediction and suggesting avoiding generalisations, e.g., describing Makatea or Gambier as high coral cover islands all along the depth gradient. To clarify, in other words, I mean that while in one site, a particular depth may harbour high coral cover, adjacent depths for the same site may not. Indeed, this variability reinforces my results suggesting that MCEs are very patchy and tend to differ across locations (high spatial beta-diversity, **Chapter 2**).

However, the statement excluding the Marquesas from highly scleractinian developed MCEs is because the northernmost archipelago differs substantially from the rest of the islands. Indeed, due to their proximity to the equatorial upwelling (Martinez *et al.*, 2020), there are no barrier reefs, and only some fringing scleractinian corals occur on the vertical walls (Sournia, 1976; Fey *et al.*, 2021). Such differences, and again because only shallower data than 40-60 m was available, support the decision not to include the Marquesas in the overall analyses of coral-dominated reef islands (**Chapters 2 and 3**). Yet, the absence of corals is also supported by available literature that reported no Scleractinia at mesophotic depths (Benzoni and Pichon, 2016). Conversely, the Austral Archipelago nor included in my thesis because the lack of data is likely to support the potential of MCEs for French Polynesia. Regardless of different biogeographic stocks and oceanographical conditions, there are some good insights into the highly rich and covered mesophotic scleractinian fauna for Tubuai and Rapa (Chevalier, 1980; Adjeroūd *et al.*, 2012).

The additional information from this thesis on MCEs in French Polynesia (also considering preliminary results from DEEPHOPE) upgrades this region from being poorly studied to being now closer to other studied locations for MCEs across the Indo-Pacific. With over 800 dives below 100 m for taxonomic, genetic and ecological studies. In numbers, more than 1,800 taxonomic scleractinian skeletons, 3,800 genetic samples, and over 1,080 m² of benthos explicitly analysed with photo-quadrats below 30 m were gathered (data for other locations unknown). However, the comparison of community structure from the MCEs of French Polynesia with other worldwide locations gets rapidly limited by geographical distance and the little amount of data from other reef areas across the Pacific archipelagos (except Hawaii (Spalding, Copus, *et al.*, 2019), American Samoa (Montgomery *et al.*, 2019) and Palau (Colin and Lindfield, 2019)). The four locations shared similar mesophotic scleractinian compositions, with *Leptoseris sp.* and *Pachyseris sp.* dominating at MCEs, and these results are also valid for the GBR and the Gulf of Eilat (Bridge *et al.*, 2019; Eyal *et al.*, 2019).

Extensive comparisons between French Polynesia and well-studied locations with available information on MCEs, e.g., Hawaii, the Gulf of Eilat, the Great Barrier Reef, Ryukyus or some Caribbean islands, would be one-sided in terms of global biodiversity patterns (Bellwood and Hughes, 2001; Bellwood *et al.*, 2005). However, it could be done

descriptively with the few locations where coral cover and diversity were assessed. For instance, and as mentioned in **chapter 3**, the high substratum cover by laminar scleractinian corals in MCEs of this thesis is similar to (i) the findings of 100% cover of *Leptoseris sp.* at 65 m at Myrmidon reef, Great Barrier Reef (Hopley, Smithers and Parnell, 2007); (ii) The dominance of *L. hawaiiensis* at 60, 90 and 120 m (at 120 m there is dominance, but the cover is low) in the Au'au channel, Hawai'i (Kahng and Kelley, 2007; Rooney *et al.*, 2010; Pyle *et al.*, 2016); (iii) The defined as the *Echinophyllia* and *Leptoseris* zone in the Marshall Islands (Wells, 1954); (iv) The *L. fragilis* deeper than 80 m in the Gulf of Eilat (Fricke, Vareschi and Schlichter, 1987; Tamir *et al.*, 2019); (v) The *Echinophyllia* and *Leptoseris* zone (defined by Wells; 1954) in Madagascar (Pichon, 1978); Or (vi) the dominance (no quantitative data available) of *Agariciidae* at 75 m in Curaçao (Dutch West Indies) in the Caribbean (Hoeksema, Bongaerts and Baldwin, 2017). Lastly, they are also similar to previous findings in the Tuamotu Archipelago in French Polynesia (Bouchon, 1983; Chevalier and Kühlmann, 1983; Faure and Laboute, 1984; Kühlmann and Chevalier, 1986).

Finally, comparing data from shared species between shallow and mesophotic depths, I found that while in French Polynesia > 130 out of ~210 species of corals occur in MCEs (before DEEPHOPE 96 out of ~208; Pichon, 2019), in American Samoa, about 110 out of 300 species of corals occur in MCEs (no available data for Palau). This percentage of shared species was similar to other locations before DEEPHOPE; now, according to preliminary results, it is the highest across locations due to the high sampling effort of DEEPHOPE (Muir *et al.*, 2018) (Table 6.2). Although such high percentages of shared species between shallow and mesophotic could add some insights to the overlap and “refugia” theory (Laverick *et al.*, 2018; Bongaerts and Smith, 2019), these results need molecular genetic confirmation of species (Baird *et al.*, 2022) and connectivity studies to validate the DRRH (Bongaerts and Smith, 2019).

Table 6.2: Adapted from (Muir *et al.*, 2018). Species richness of scleractinian corals in MCEs (depths 30 to approximately 150 m). ^a designates sites well documented. ^b potential preliminary results subject to possible changes.

Region	Mesophotic species	Total species	Proportion (%)
Red Sea ^a	93	310	30.9
Maldives	34	292	8.7
Great Barrier Reef	32	421	7.6

New Caledonia	72	438	16.6
Japan	17	418	4.1
Micronesia	71	431	16.5
Austral Is. Polynesia	62	153	43.8
Northeast Pacific, Hawaii ^a	23	77	29.9
Honduras/Belize ^a	29	60	48.3
Jamaica ^a	38	59	64.4
French Polynesia before DEEPHOPE	96	210	45.7
French Polynesia after DEEPHOPE^{ab}	~130	210	61.9

MCEs of French Polynesia, the environmental influence

In terms of environmental parameters, we found that waters are very clear among most locations (except the Marquesas) in French Polynesia (**Fig. 6.2 a, b and c**) (Pichon *et al.*, 2021), likely explaining the highly rich and covered communities (**Chapters 2 and 3**). For example, amounts of relative light (according to 6 m as 100% reference point) were at 40 m between 22.6 and 24.5% (Marquesas < 3%), at 60 m between 7.07 and 12% (Marquesas < 0.1 or NA) and at 120 m between 2 and 0.67% (Marquesas NA). Despite not being developed in this thesis, such differences may explain the minor presence of scleractinian communities reported in the Marquesas (Sournia, 1976; Fey *et al.*, 2021) also at mesophotic depths (Benzoni and Pichon, 2016). Back to the studied islands, although light-irradiance profiles showed that only between 2 and 0.7% reached 120 m, we estimated with the Beer-Lambert equation (Gordon, 1989) that still 0.4% of light reached 172 m in Gambier at the depth limits of zooxanthellae scleractinian corals (Rouzé *et al.*, 2021 - **Appendix 2**). This pattern showed an exponential decrease of light with a sharp decrease in shallow waters and a gentle decrease at lower mesophotic depths.

Temperatures recorded by loggers ranged between 21.5 and 23.5°C (lower limits) and 23.7 and 29.9 (hotter limits), and I only found a slight decrease with depth. However, at several locations, I found very significant short-term variations (up to 2-3 °C within 5-10 min) that we associated with internal gravity waves (**Fig. 6.2 d**) (Wolanski and Delesalle, 1995; Talley *et al.*, 2011). Such a tiny decrease in temperature along the slope suggests that the bleaching reduction with depth (**Chapter 5**) might be more associated with reducing light than temperature. At the same time, whether the internal waves could

have released heat stress during the bleaching event was raised as a potential hypothesis explanation (**Chapter 5**)(Wyatt *et al.*, 2020).

A posteriori, I extracted satellite sea surface temperatures from the NOAA Coral Reef Watch (Maturi *et al.*, 2017) from 1985 to 2018 (*i.e.*, before the start of the expedition and when the data were collected). The studied territory showed average temperatures ranging from (20-21°C in Gambier during winter to 30-31°C in Raroia (Tuamotus) during summer). I also studied heat stress by calculating Degree Heating Weeks (DHWs) (Liu *et al.*, 2018). DHWs reached maximum values during the mass bleaching event of 2015-2017 (4.22 °C-weeks in the Society Islands, 8.3 °C-weeks in the Tuamotu Archipelago, 11.72 °C-weeks in the Gambier Islands in 2016 and 12.64 °C-weeks in the Austral Archipelago in 2017) (**Fig. 6.2 e and f**). The heat stress during the thermal bleaching event of 2019 is not displayed here because it occurred after collecting the data during the expedition (but see: **Chapter 5** - Pérez-Rosales, Rouzé, *et al.*, 2021). Whether these bleaching or other disturbances might have affected shallow reefs more than MCEs, and, therefore, may have influenced the general patterns (**Chapter 2**) remains an open question because we do not have time-series of benthic data.

However, since the *in situ* environmental data were not collected during the same period of time, I preferred to avoid further environmental comparisons between locations (spatial differences) because the results are likely influenced by seasonality and different weather conditions. Yet, these environmental data could be used to support some ecological data. The only ecological-environmental modelling performed is available in **chapters 3** and, to a relative extent, **4** and **5**. In this sense, using the relative values according to the surface (*i.e.*, to “avoid” seasonality, but not weather conditions or differences by the time-length of collected data) and geomorphology, predictions of the likelihood of coral cover and explanations of the community structure according to some unique environmental parameters for the depth (*i.e.*, not unique values for the site at all depths) are provided (**Chapter 3**). Following the same strategy, results in **chapters 4** and **5** are supported by light and temperature data but always from the discussion perspective and never to set comparisons between islands.

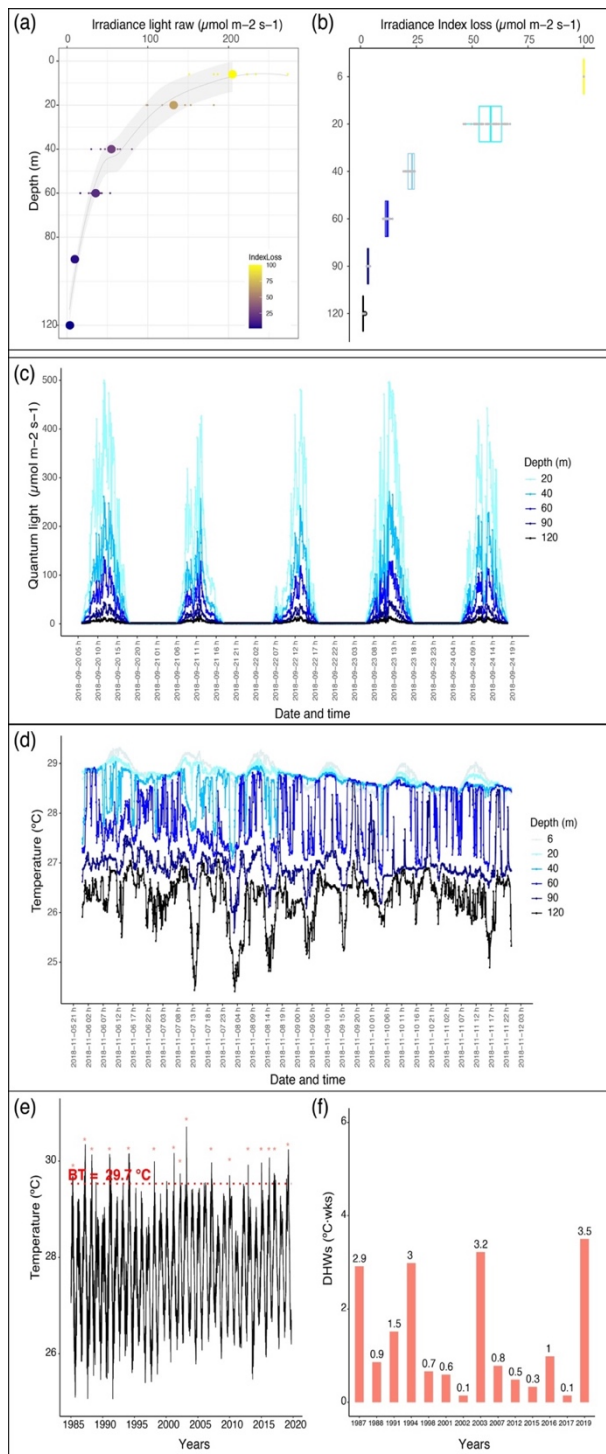


Figure 6.2: Some examples from the environmental data collected during the DEEPHOPE expedition. (a) Light irradiance ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) vertical profile from Makatea. (b) Relative light irradiance index loss ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in %) according to the surface from Makatea. (c) Quantum light ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) measured with the loggers DEFI at different depths during several days in Bora Bora. (d) Temperatures ($^{\circ}\text{C}$) measured with the loggers Quantum HOBO at different depths during several days in Rangiroa. (e) Satellite sea surface temperatures (NOAA – Coral Reef Watch) from 1985 to 2020 in Moorea. Bleaching Threshold (BT) represents the temperature from which corals start experiencing thermal stress and consequently bleach. (f) Degree heating weeks ($^{\circ}\text{C} \cdot \text{weeks}$) measured from sea surface temperatures (e) representing the different bleaching episodes of Moorea.

This strategy allowed us to display that high scleractinian cover occurred on hard substrates with moderate/steep slopes (**Chapter 3, Fig. 3.2**), likely, the best trade-off between high light levels and low sediments, which are detrimental to scleractinian (Hopley, 1982; Bridge *et al.*, 2011; Sherman *et al.*, 2016, 2019; Englebert *et al.*, 2017). Although the amount of relative light is given and certainly one of the most influencing variables for Scleractinia, relative light (according to 6 m) was not used for the

environmental modelling for two reasons: (a) the collinearity with depth and (b) the seasonal differences on which the data was recorded. The same occurred with raw temperatures influenced by the different seasons and the coast orientation because all sites were located on the leeward side (NE-NW), protected from swells and winds. Accordingly, these parameters were omitted for the model of the likelihood of scleractinian coral cover with depth. Although coast orientation likely influences coral communities, neither relative temperatures (according to 6 m) nor temperature variability (collinear with depth) seemed to influence the likelihood of coral cover. Yet, long-term studies of at least one year are recommended for light and temperature data at particular depths because they are likely to influence coral communities (Kahng *et al.*, 2019). Contrary to the ‘hotspots’ of high scleractinian cover (**Fig. 6.3**), the mesophotic landscapes were characterised by sediment and rubble or uncolonised CCA, turf, and sponges. Otherwise, by other typical mesophotic benthic components such as gorgonians and antipatharians when more associated with sandy bottoms or vertical or overhanging walls with caves (**Chapter 3 - Sup. Box. 3.2**).



Figure 6.3: Examples of scleractinian dominated landscapes at MCEs of French Polynesia. (a) Raroia Site 1 at 40 m. (b) Bora Bora Site 2 at 60 m. (c) Makatea Site 2 at 60 m. (Copyright image: Left: Gonzalo PÉREZ-ROSALES; Centre: Franck GAZZOLA / UNDER THE POLE / Zeppelin Network; Right: Julien LEBLOND / UNDER THE POLE / Zeppelin Network).

Relating physiological with ecological results

The physiological capacities of corals to cope with different light environments should determine their depth range, performance and role in the community structure (Kahng *et al.*, 2019). I found shared (*e.g.*, an increase in symbionts and chlorophyll; (Wyman *et al.*, 1987; Padilla-Gamiño *et al.*, 2019) and individual morphological strategies (*e.g.*, increase of corallites distance and size for *P. cf. verrucosa* or decrease of the height of septa for *P. “speciosa” spp.*; Soto *et al.*, 2018; Kramer *et al.*, 2021) to deal with low-light environments. Conversely, I found no specific shifts in the symbiotic communities along the depth gradient (Bongaerts *et al.*, 2011; Polinski and Voss, 2018; Eckert *et al.*, 2020),

and my data could not evidence a switch to heterotrophy (despite a decrease in $\delta^{13}\text{C}$) with depth (Muscatine *et al.*, 1989; Williams *et al.*, 2018; Radice, 2019) (**Chapter 4**). Additionally, all results presented considerable variability of trait performances with and within species and locations, reinforcing the multi-strategy capacities to live along with large depth ranges. These were brought to the extreme by collecting and studying the deepest (172 m) photosynthetic scleractinian coral (Rouzé *et al.*, 2021 - **Appendix 2**). Together with other replicates collected at 168 m (1 specimen), 154 m (1 specimen) and 142 m (3 specimens), they all hosted similar symbiotic communities *Cladocopium* and microbiome to shallow-water corals. Yet, they all came with the association of the coral host with the green endolithic alga *Ostreobium sp.*, which might help Scleractinia live in lower light environments (Gonzalez-Zapata, Gómez-Osorio and Sánchez, 2018; Iha *et al.*, 2021).

The combination of results between the two species model used in the physiology (**Chapter 4**) with the quantitative data from photo-quadrats (**Chapters 2 and 3**) shows how the two species/genus are not equally taking advantage of these strategies. While the genus *Pocillopora* was widely spread between 6 and 40-60 m across all locations (in presence-absence in 16 out of 16 sites at 6 and 20 m, 15/16 at 40 m and 11/16 at 60 m; and relatively high contribution to the total scleractinian cover between 30-90% at 6 m and ~0-50% at 40 and 60 m), the genus *Pachyseris* was more limited in its distribution. Indeed, *Pachyseris* was commonly present in the Tuamotus but less in the Society and Gambier archipelagos (7/16 sites at 20 m, 12/16 at 40 m, 14/16 at 60 m and 4/16 at 90 m; and with a relatively lower contribution to the total scleractinian cover –except at two particular depths 40 and 60– with values between 0-3.7% at 20 m, 0-21% at 90 m and ~0-85% at 40 m and 60 m) (**Fig. 6.4 & Chapter 2, Fig. S2.5 and S2.7**).

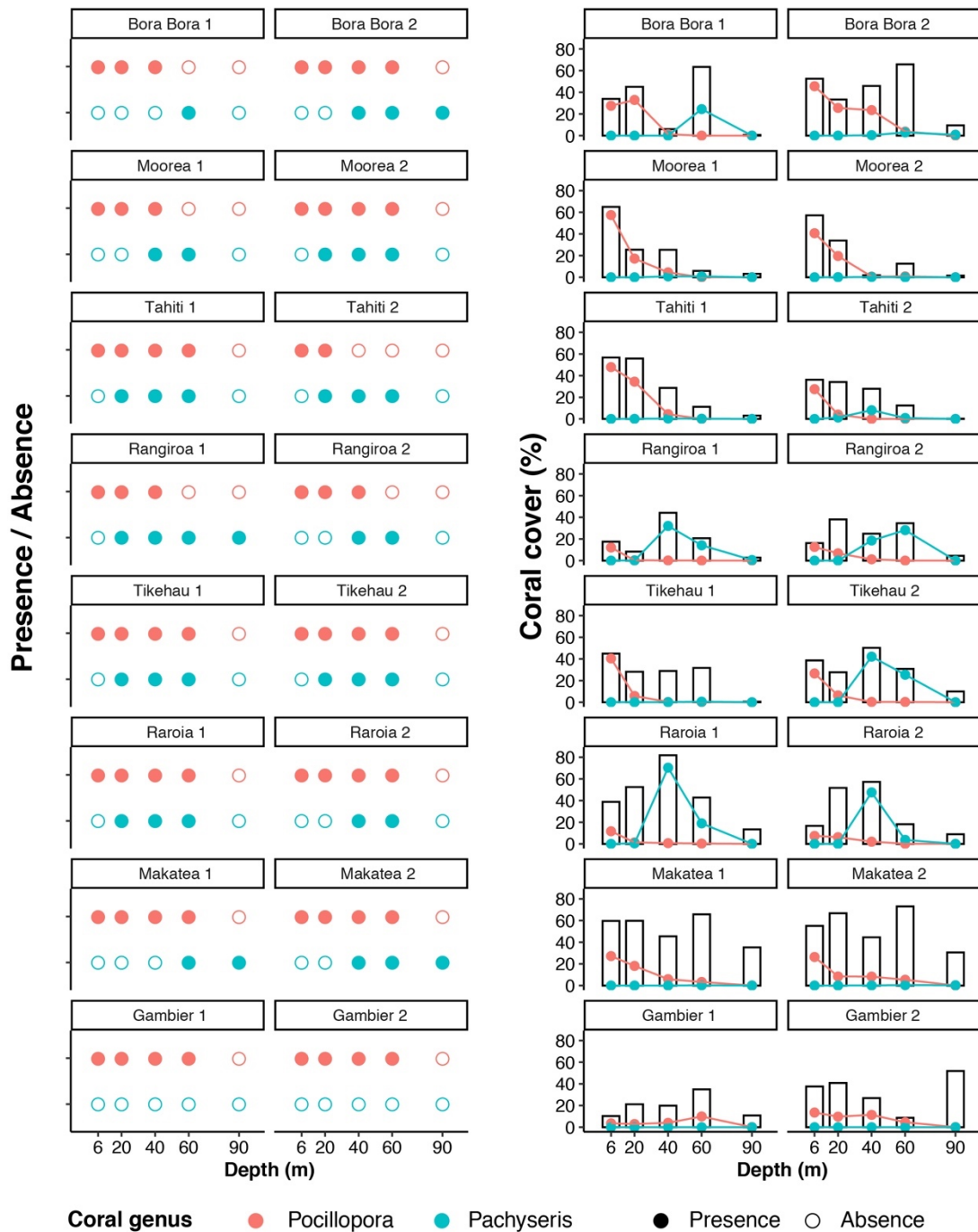


Figure 6.4: Left - Presence (solid) and absence (empty) for the genus *Pocillopora* and *Pachyseris* across the studied sites in chapters 2 and 3. Right - total coral cover (bars) with the relative percentage of the genus *Pocillopora* (red) and *Pachyseris* (green-blue).

These differences in distributions and coral community structure occurred even if *Pachyseris*, with its laminar morphology, goes deeper than *Pocillopora*. The maximum depth observed for *P. cf. verrucosa* by active searching during DEEPHOPE (*i.e.*, information not derived from photo-quadrats, so here the constant sampling effort is not

respected) was 90 m in Gambier; and for *P. "speciosa" spp.* 106 m in Rangiroa. Nevertheless, *Pachyseris* was absent in some sites, and its relative cover was lower on average than for *Pocillopora*. These might reveal some second thoughts about the labels “depth-specialists”, either for shallow or deep and the “depth-generalist”, which are defined according to their depth ranges. Stick to this definition, the most depth generalist corals today are *Leptoseris hawaiiensis* (3 – 172 m) and *Leptoseris scabra* (5 – 127 m) (Muir and Pichon, 2019; Rouzé *et al.*, 2021 - **Appendix 2**). However, if the goal is to differentiate between species with specific adaptations to narrow depth ranges or species with a more plastic eco-physiology to wide depth ranges, these concepts should be reviewed to consider quantitative abundances and geographical distributions. Yet, the lack of data likely influences the hitherto reported depth ranges, suggesting that the upper and lower limits might be underestimated for all species. In other words, the current depth ranges are based on current knowledge. Increasing sampling effort and observations will likely expand such ranges, as observed with DEEPHOPE (**Box 6.1**).

Something similar occurs with the boundaries of “upper” and “lower” mesophotic depth zones. Indeed, several studies tried to define these boundaries according to depths, light and ecology (Kahng, Copus and Wagner, 2014; Laverick, Andradi-Brown and Rogers, 2017; Tamir *et al.*, 2019; Laverick *et al.*, 2020). However, these limits are still controversial because of geographical variations and different opinions. Although the simplification of setting those boundaries according to particular depths or light levels is useful to tackle their study, these terms should be used with extreme caution, especially ascribing particular species to those limits with our lack of knowledge. Notwithstanding, setting artificial boundaries may lead to confusion because, in reality, species go across these boundaries, and habitats and ecological communities blend together (Pyle and Copus, 2019). For example, this thesis suggests that the “upper mesophotic” is the transition zone (**Chapter 2**), with the peak of the mid-domain in generic richness occurring between shallow and deep scleractinian communities. Besides, it might question the controversial lower limits of MCEs (approximately 150 m), with the finding of the deepest light-dependent scleractinian coral today at 172 m (Rouzé *et al.*, 2021 - **Appendix 2**).

Importance of MCEs for coral reef resilience

The ecological importance and the potential contribution of MCEs to strengthen overall coral reef resilience are quantitatively demonstrated in this thesis. Our results suggest that the 40-60 m depths are key zones across the whole depth range of scleractinian corals. I showed (**Chapters 2 and 3**) that this zone has the maximum generic richness (mid-domain) and the highest coral cover. In **chapter 5**, I provided evidence that these depths are less impacted by coral bleaching than shallow reefs. Additionally, I showed that this 40-60 m zone is the transition zone where generic coral composition overlaps/coexists with the shallow (< 30 m) and deep (> 60 m) coral communities (**Chapter 2**). This overlap means that if we lose shallow or deep corals, this zone could act as a safeguard for eventually reseeding the adjacent depths (Bongaerts and Smith, 2019; Montgomery *et al.*, 2021). These mid-depths are also the perfect compromise for (a) the increase of β -diversity with depth across locations (**Chapter 2**); (b) the reduction of coral bleaching prevalence with depth (**Chapter 5**); and (c) the fact that below 60 m, corals were anyway very scarce (but see some positive outliers ‘hotspots’ of **Chapter 3**). In other words, the point (a) means that when comparing sites, the best balance between the shallow communities that were similar in genus composition and the deeper communities that differed from site to site was this transition zone of the mid domain (40 m) if the goal is to consider the overall coral regional diversity.

The supporting reasons for highlighting the importance of MCEs, particularly in the 40-60 m zone, are less evident in the physiological **chapter 4**. However, the multiple strategies developed by corals to be present at different depths and the fact that these barely differ between them can, to a certain extent, suggest MCEs’ importance. Indeed, in this chapter, I show for a typical shallow (*P. cf. verrucosa*) and mesophotic species (*P. “speciosa” spp.*) species, the high capacity of corals for vertical colonisation along with their depth range. Therefore, seeing that the two studied and contrasted (shallow and mesophotic) species overlap in this region (**Chapter 2**) and the high plasticity of corals to inhabit at different depths (**Chapter 4**), I suggest that MCEs depths are already the most important or will become more important in the future. Especially if shallow scleractinian reefs continue to disappear with climate change, and corals will only survive at deeper depths, although this has not been yet demonstrated.

The high scleractinian richness and diversity of MCEs are already reported in the literature (Englebert *et al.*, 2017; Muir *et al.*, 2018; Muir and Pichon, 2019). From an ecological point of view, more scleractinian diversity, the foundation of coral reefs (Loya, 1972; Pichon, 1972; Darling *et al.*, 2019), means more functions and more functions mean more ecological productivity (niches) and resilience (Connell, 1973; Baskett *et al.*, 2010; Brandl *et al.*, 2019; Benkwitt, Wilson and Graham, 2020). More diversity translates into more forms increasing the 3-dimensional complexity and habitat creation for the associated coral reef animals (Graham and Nash, 2012; Darling *et al.*, 2017). The future and resilience of most biodiversity living in coral reef ecosystems (approximately a quarter of all known marine life even if coral reefs only cover 0.1 % of earth's upper oceans; Burke *et al.*, 2011) rely on the scleractinian corals that sustain and construct coral reefs (Stachowicz, 2001; Hoegh-Guldberg, Pendleton and Kaup, 2019). This thesis demonstrates hotspots of scleractinian diversity and high coral cover communities in MCEs. One may expect that as shallow coral communities continue to suffer degradation due to climate change (Hughes *et al.*, 2017), the importance of these mesophotic communities, often with high diversity and cover, is likely to increase. For instance, with the ability of species to adapt to lower depths looking for shelter habitat or because these depths could act as diversity safeguards (Muir *et al.*, 2018) or coral sanctuaries while shallow coral reefs continue to degrade (Muir *et al.*, 2017; Baird *et al.*, 2018; Giraldo-Ospina, Kendrick and Hovey, 2020; Hernandez-Agreda *et al.*, 2022).

Take, for example, the case of French Polynesia. Over the past recent years, several disturbances, notably Crown-of-Thorns (COTs), cyclones and coral bleaching, have impacted the reefs (Adjeroud *et al.*, 2009; Kayal *et al.*, 2012; Vercelloni *et al.*, 2019; Hédouin *et al.*, 2020 - **Appendix 5**; Pérez-Rosales, Brandl, *et al.*, 2021 - **Appendix 3**; Pérez-Rosales, Rouzé, *et al.*, 2021 - **Chapter 5**). We have supporting evidence that these perturbations impacted shallow waters in several locations. However, we ignore whether MCEs were equally affected. In this thesis, I showed that bleaching impacts reduce with depth (**Chapter 5**), in agreement with supporting literature (Muir *et al.*, 2017; Baird *et al.*, 2018; Giraldo-Ospina, Kendrick and Hovey, 2020) but also in contrast to other studies (Smith *et al.*, 2016; Frade *et al.*, 2018). Although the wave strength of cyclones reduces with depth, there are impacts of cyclones on MCEs (Harmelin-Vivien and Laboute, 1986; Bongaerts *et al.*, 2013). For instance, these events trigger mass-scale sediment movements or cascading downslope of large massive shallow structures smashing lower

coral communities (Harmelin-Vivien and Laboute, 1986; Sherman *et al.*, 2019; Smith, Holstein and Ennis, 2019). On the other hand, we lack data on whether COTs impacts increase or decrease with depth (Pratchett *et al.*, 2014; Bridge *et al.*, 2019), except for impacts reported in American Samoa at 40 m (Montgomery *et al.*, 2019) or while writing the end of this thesis in Makatea (Pers. Comm. Laetitia Hédouin thanks to a second expedition). While an assessment of different disturbances in MCEs is available for the Caribbean, it is missing in the Indo-Pacific (Bongaerts *et al.*, 2010). Nevertheless, and back to the example in French Polynesia, it is clear that, in the shallows, the coral cover went from 1-5% in several locations at ~12 m in 2012 to more than 60-80% at 6 and 20 m during the DEEPHOPE expedition in 2019 (**Chapter 3**; Pérez-Rosales, Brandl, *et al.*, 2021 - **Appendix 3**). Such recovery demonstrated an exceptional resilience which still questions where did these coral baby recruits come from? Nonetheless, if a high resilience is documented for shallow reefs, there is a lack of knowledge on the potential resilience of MCEs (Pyle and Copus, 2019).

Although this **thesis** could not demonstrate the importance of MCEs in relation to the ‘Deep Reef Refugia Hypothesis’ (DRRH) (Glynn, 1996; Bongaerts *et al.*, 2010) because time-series data during disturbances and genetic data for connectivity studies are missing, it can suggest the potential importance of this mid-depth zone (40-60 m). However, instead of deep scleractinian communities acting as ‘refugia’ for shallow reefs under disturbances (Bongaerts *et al.*, 2010; Bongaerts and Smith, 2019), we surmise that these communities (40-60 m) may act as a safeguard for shallow and deep communities, simultaneously (i.e., increasing the survival chances of species). For all these reasons, I propose that regardless of the reseeded potential and whether MCEs might or might not share species with shallow reefs, these MCEs are likely to play a critical role in the overall resilience of coral reef ecosystems. There is a need to focus more on the patterns along the reef slope because growing literature suggests that MCEs might be richer and with a higher unique community composition than expected (Bridge *et al.*, 2013; Rocha *et al.*, 2018; Soares *et al.*, 2020). At any rate, one can suggest that MCEs are important in their own right, without the need to compare them with their shallow counterparts.

Conservation planning of coral reefs considering MCEs

According to the findings of this thesis, I suggest that MCEs, particularly the depths between 40 and 60 m, should be considered priority depths for systematic conservation planning of coral reefs. Indeed, coral reefs are currently facing an unprecedented crisis as a consequence of global and local stressors (Hughes *et al.*, 2017). With the present crisis intensified by climate change, coral reef scientists started suggesting conservation planning for coral reefs based on assessments of ecosystem resources and risk sensitivity (Cinner *et al.*, 2016; Beyer *et al.*, 2018; Bellwood *et al.*, 2019). Although these global efforts considered all available data, the extreme, marginal and understudied environments like MCEs were ignored (Bridge *et al.*, 2013; Camp *et al.*, 2018; Soares *et al.*, 2020). Consequently, MCEs are in a very poor state of conservation and are too often not yet considered at all in the conservation planning of coral reefs (Loya, Puglise and Bridge, 2019).

However, if the decisions on conservation areas are based on the criteria mentioned above, MCEs emerge as worthy of consideration. Repeating shortly, in this thesis, I demonstrate with quantitative data why focusing on MCEs will be the best for deciding the potential conservation locations for scleractinian corals. I showed that MCEs, particularly between 40 and 60 m, are hotspots of diversity (**Chapter 2**) and coral cover (**Chapter 3**), and decrease the risk of coral bleaching (**Chapter 5**) (but see; Frade *et al.*, 2018), which is the major threat of coral reefs in the Anthropocene (Hughes *et al.*, 2017; Hoegh-Guldberg, Pendleton and Kaup, 2019). My suggestion has important additional implications because if conservation efforts for corals of French Polynesia focused only on the shallows, without considering MCEs, we could think that conserving a single island would preserve the region's diversity. After all, coral communities are similar across islands in shallow waters (*i.e.*, small β -diversity). However, we would completely miss the richest areas and most of the regional coral diversity. Instead, to preserve the total coral diversity, including the unique sites at MCEs (*i.e.*, high β -diversity) (**Chapter 2**), I suggest focusing on this depth range (40 – 60 m) and expanding to different locations across French Polynesia. It is like the Single Large or Several Small (SLOSS) Marine Protected Areas debate (Diamond, 1975; Fahrig, 2020). Additionally, if we only consider the shallows, we will completely disregard the unexpected but not so rare high coral cover communities of MCEs in French Polynesia (**Chapter 3**). Finally,

by building conservation planning focusing only on the shallows, we are always at risk of seeing our efforts ruined by a bleaching event (Jones *et al.*, 2021; Richards, Juszkievicz and Hoggett, 2021). Yet, if we develop conservation strategies including MCEs, we can expect that bleaching is less severe at MCEs depths and that they are now acting as safeguards of biodiversity (**Chapter 5**).

However, beware, extending studies and conservation to other unknown mesophotic locations might turn into finding even more unique diversity hidden at MCEs (Rocha *et al.*, 2018). We can only protect what we know or, even better, understand, and we are far away from reaching this point at mesophotic depths (Loya, Puglise and Bridge, 2019). Being conscious that those depths are difficult to access, I suggest that future conservation decisions should compromise between shallow waters data and the available data from mesophotic depths. Yet, I also suggest that future studying efforts should give a higher priority to MCEs (Bridge *et al.*, 2013).

Limitations

Each chapter individually explains the limitations. However, since I am the first interested in acknowledging them, these limitations can be grouped and summarised as follow.

The main limitation is the lack of temporary data. My collected data consisted of a single snapshot of when the fieldwork was done. Accordingly, caution is advised in interpreting results because I do not know whether these were also true in the past and will be in the future. I strongly suggest starting long-term monitoring programs in mesophotic depths to understand the current trends and make better predictions on where we are going. A second limitation is that most sites were located in the West-North East coast orientations at the leeward of strong swells and winds for safety and technical diving reasons. Even if TEK diving requires calm conditions, I suggest future studies investigate more sites around particular islands rather than more islands in fewer sites.

A third limitation is the lack of high taxonomic levels by using photo-quadrats. **Chapters 2** and **5** were at the genus level, even if, for **chapter 5**, I collected data at the species level. The same occurred in **chapter 3**, where I grouped corals according to their morphologies. Yet, I provided a list of the genera and species among the different coral

groups (**Chapter 3, Table S3.1**). However, I showed that genus and species levels are highly correlated (**chapter 2, Fig. S2.2**). In most cases, conclusions should also be valid at more accurate taxonomic levels, and if not, these were particularly mentioned (Balmford, Green and Murray, 1996; Heino and Soininen, 2007). Nevertheless, without genetics, visually identifying species levels is inaccurate, even *in situ*, because of the inter and intraspecific morphological variability (Bongaerts *et al.*, 2021). Potential misidentifications are possible, even at the genus level. Yet these were systematic (*i.e.*, repeated everywhere) because all visual analyses were done by the same observer, previously trained and supervised by experienced coral taxonomists. Therefore, misidentifications should not modify the general patterns. If the objective of this thesis had been devoted to taxonomy, depth ranges and species overlap, species-level would have been required. However, the goals of my thesis are to assess general patterns across depths and spatial gradients with implications in general macroecology and conservation at the regional level. Therefore, and according to literature, I believe the genus level should be enough (Ateweberhan and McClanahan, 2016; Hughes, Kerry, *et al.*, 2018; Darling *et al.*, 2019).

Despite the potential limitations of photo-quadrats, this passive methodology allowed us to have an equal sampling effort at all depths independently of decompression limitations, which is essential in quantitative ecology (Chen *et al.*, 2021) (**Fig. 6.5**). Additionally, to study generic richness diversity, I compensated for the limitations of only identifying the benthos underneath the random points by doing the presence-absence in each quadrat. In conclusion, since the purpose of these chapters was to study the ecology of mesophotic corals on a wide vertical and spatial scale all across French Polynesia, I believe I used the best alternative technique and photo-quadrats are widely used in the literature for ecological studies (Hill and Wilkinson, 2004; Pawlik *et al.*, 2022).

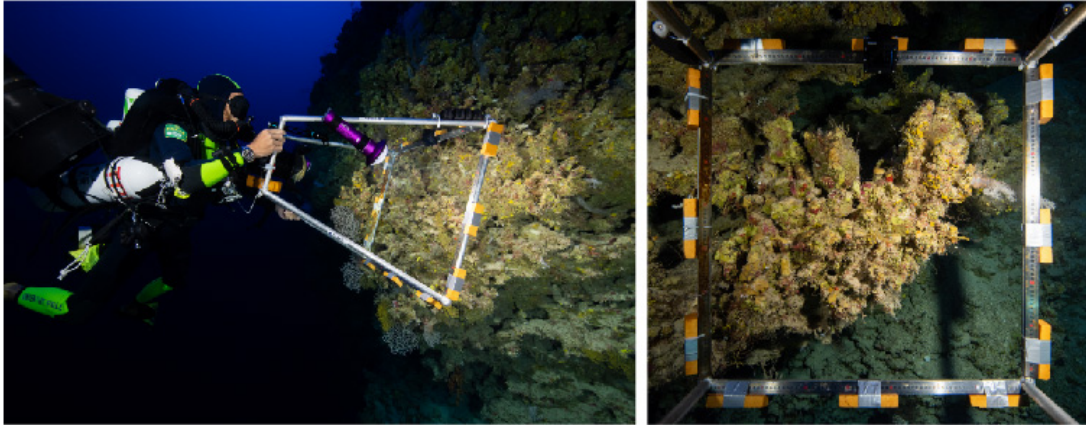


Figure 6.5: The photo-quadrat technique allows analysing the benthos with a constant sampling effort independently of the depth (Copyright image: Ghislain BARDOUT / UNDER THE POLE / Zeppelin Network).

To conclude, all limitations can be justified by the technical challenges of studying within the mesophotic depth range (Pyle, 2019). Accordingly, we need to focus on collecting as much data as possible and accept the passive study techniques afterwards. I used this technique in **chapter 4** with cryopreserved coral fragments and a posterior physiology study. Also, in **chapter 5**, I analysed bleaching levels using reference cards and white balance corrections from images rather than *in situ* techniques studying the density of symbionts or stress levels (Downs *et al.*, 2000; Lesser, 2006). Although I agree that long term experimentation or more sophisticated analyses may have provided more accurate results, my results are already valuable data for MCEs research, considering the little knowledge and the difficulties of studying MCEs (Pyle and Copus, 2019). Furthermore, MCEs are still largely unknown; any kind of data (as long as collected following scientific criterium and transparent/aware of the limitations) has to be considered valuable because, in some way or the other, they increase MCEs' knowledge.

Perspectives and future directions

The results presented in this thesis should motivate future research on MCEs. Although our findings in **chapters 2, 3 and 5** are likely to be valid in other locations, we need similar studies worldwide with quantitative assessments and constant sampling effort all along the depth gradient (Chen *et al.*, 2021). These future results will prove or reject our conclusions, which might be crucial for the conservation planning of coral reefs

(Bellwood *et al.*, 2019; Morrison *et al.*, 2020). We also need accurate assessments of disturbances with depth and establish a worldwide compilation of disturbances in MCE, similar to what was done in 2010 in the Caribbean (Bongaerts *et al.*, 2010). In addition, we need to implement monitoring time series in MCEs (Pyle and Copus, 2019). In the absence of temporal datasets of coral cover and composition trajectories (i.e., ecosystem shifts), the conservation status of these MCEs are poorly known (but see: de Bakker *et al.*, 2016). Our research did not have a starting point (baseline data) to understand the direction of coral trajectories because the past was mostly unknown for French Polynesia (Pichon, 2019). I hope our data (open access) will provide a reference point for future locally and comparative studies with other locations.

With the ongoing climate change, the unprecedented decline of shallow coral reefs (Hughes, Anderson, *et al.*, 2018; Souter *et al.*, 2021), and the potential differential effects along the depth gradient slope (Muir *et al.*, 2017; Baird *et al.*, 2018; Pérez-Rosales, Rouzé, *et al.*, 2021 - **Chapter 5**), identifying and preserving high coral diversity (**Chapter 2**) and cover (**Chapter 3**) MCEs is necessary. We need to investigate if the depth perspective provided by MCEs might give us extra time to maintain scleractinian coral dominated reefs and some of the ecosystem functions of coral reefs (see: Holstein *et al.*, 2019). In the shallows, coral reef-associated animals rely on the three-dimensional habitat complexity provided by scleractinian corals (Graham and Nash, 2012). Although how other reef states (e.g., macroalgae, sponges or soft-coral dominated reefs) might influence biodiversity, fisheries, coast protection, and tourism are still in the debate (Graham *et al.*, 2013; Hoegh-Guldberg *et al.*, 2017), most literature agrees on the high interest of keeping scleractinian-dominated reefs (Bellwood *et al.*, 2019). By now, we can only hypothesise that this is also true in mesophotic depths, therefore, requiring future studies. The literature has broadly focused on whether depth might provide “refugia” for scleractinian and other animals (Bongaerts and Smith, 2019) while rarely mentioning the role of structural complexity. To fully understand the ecological role, functioning and conservation needs of these MCEs, we need first to identify these thriving MCEs and then unveil (1) the long-term dynamics and resilience status; (2) how high diversity and coral cover communities influence associated-marine life at such depths (i.e., despite often being monotypic laminar stands with less structural complexity than the shallows); (3) what threatens their persistence; and (4) whether they could provide “refugia” for marine

life associated with shallow coral reefs. Nevertheless, the future of scleractinian relies on actions to curb climate change (Hughes *et al.*, 2017).

Moreover, this thesis raises the necessity to increase the amount and quality of data from MCEs. The photo-quadrats technique allowed us to study over large vertical and spatial scales to answer regional ecological questions (at the population or ecosystem level) despite the analysis being sometimes at lower taxonomic levels, tedious and time-consuming (Hill and Wilkinson, 2004). Genetic techniques are more accurate than photo-quadrats, but they are expensive, and their high price does not permit the study on large scales. Besides, they require more underwater time to collect the data when bottom times are extremely brief in MCEs (Pyle, 2019). Future studies should make the most of the increasing resolution of pictures and the identification accuracy of genetics, then combine and boost new techniques such as machine learning and artificial intelligence to automatize these data acquisition (González-Rivero *et al.*, 2016). Yet, caution is advised because such techniques are still supposedly inaccurate in mesophotic depths due to the lack of machine training. After all, little data from MCEs is available (Pyle and Copus, 2019). With these new techniques of processing images (*e.g.*, quadrats, transects, videos, photogrammetry), we will significantly increase the amount of available data from MCEs (González-Rivero *et al.*, 2020) and start providing our algorithms with the necessary data to improve our modelling capacity to understand and predict these unique ecosystems (Rocha *et al.*, 2018).

Finally, during this thesis, I studied the coral diversity (**Chapter 2**), the coral cover (**Chapter 3**), the coral physiology (**Chapter 4**) and the coral bleaching (**Chapter 5**) with depth. The coral functionality with depth could not be studied because functional approaches rely on a combination of traits that are unknown for corals in MCEs (Loya, Puglise and Bridge, 2019). For instance, we do not know-how, *e.g.*, the size, growth, reproduction, and carbonate production vary along the depth gradient for the same species. Future studies should try to fill such gaps for different depth levels because these results might show overlap or uniqueness from a functional perspective to reveal areas of special conservation interest for coral reefs.

Conclusion

In summary, this thesis increases the knowledge of MCEs in French Polynesia, suggesting this region as a promising location for the development of MCEs. It presents evidence for raising the importance of mesophotic depths from an ecological point of view. With a particular focus on Scleractinia, this thesis suggests that mesophotic depths are likely to play a role in increasing the overall coral reef resilience with the detrimental effects of global changes. This suggestion is empirically based on quantitative data and the presence of ‘hotspots’ of rich diversity and high coral cover found in MCEs at the zone of 40-60 m, which at the same time are less affected by thermal bleaching events. Such premises are also supported by the physiological capacity of corals to cope with low-light environments, which could allow them to inhabit deeper in MCEs if shallow conditions deteriorate. Thus, while acknowledging the need for future studies, this thesis suggests MCEs as potential key depths to consider in future coral reef conservation planning while waiting on global solutions for climate change. Although this thesis refers to the shallow and MCEs of French Polynesia, the findings presented herein may likely apply to other similar locations worldwide.

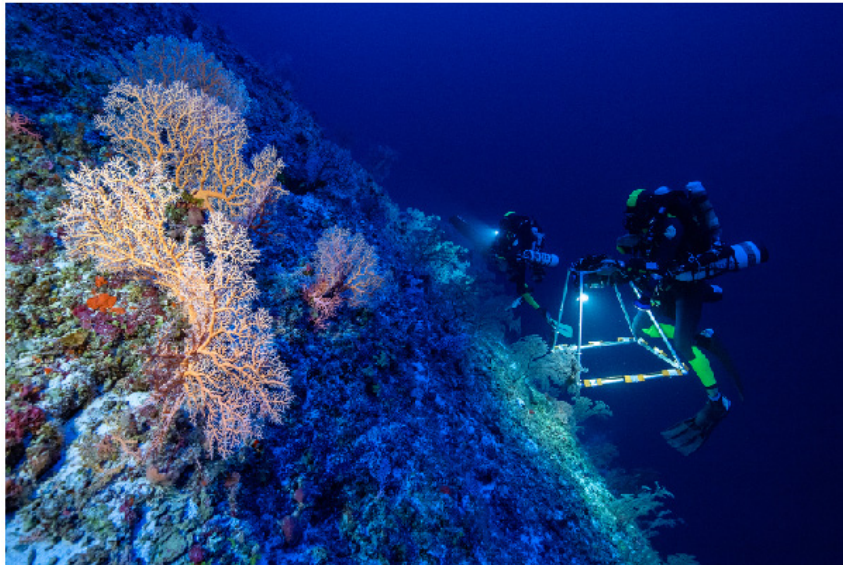
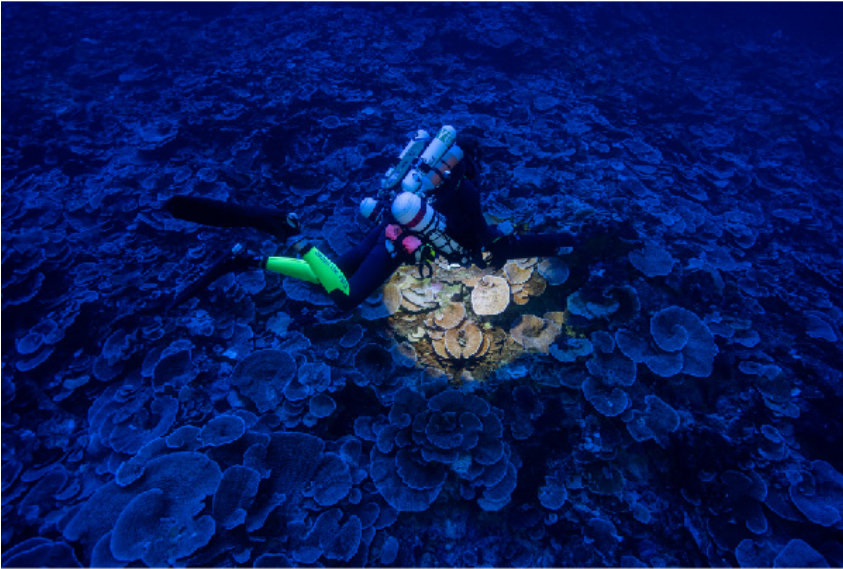


Image 2: Three examples of mesophotic landscapes at the depths of 40, 80 and 100 m from top to bottom. (Copyright image in vertical order: Franck GAZZOLA, Julien LEBLOND and Julien LEBLOND / UNDER THE POLE / Zeppelin Network).

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Appendices

Appendix 1: Manuscript – Mesophotic.org: a repository for scientific information on mesophotic ecosystems

Foreword

This publication regrouped the current state of knowledge of mesophotic coral ecosystems worldwide. Herein, we built a repository database with all the available literature. The original idea was by the corresponding author P. Bongaerts, and I teamed up with him from the very beginning. Up to three years before starting my PhD, I volunteered for him at the University of Queensland and started to compile and add the first selection of literature to the website. Since then, I have contributed to the website, translated into a publication in 2019. During my PhD, I devoted working time to the website and to the publication. Currently, I still work for the website. My current role is as a ‘Coordinator’ of new publications.

The time I worked on the present publication and website allowed me to know the literature, build a mesophotic network with international scientists, and realise the current gaps that should be undertaken in the mesophotic coral ecosystems research.

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Original article

Mesophotic.org: a repository for scientific information on mesophotic ecosystems

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Abstract

Mesophotic coral ecosystems (MCEs) and temperate mesophotic ecosystems (TMEs) occur at depths of roughly 30–150 m depth and are characterized by the presence of photosynthetic organisms despite reduced light availability. Exploration of these ecosystems dates back several decades, but our knowledge remained extremely limited until about a decade ago, when a renewed interest resulted in the establishment of a rapidly growing research community. Here, we present the ‘mesophotic.org’ database, a comprehensive and curated repository of scientific literature on mesophotic ecosystems. Through both manually curated and automatically extracted metadata, the repository facilitates rapid retrieval of available information about particular topics (e.g. taxa or geographic regions), exploration of spatial/temporal trends in research and identification of knowledge gaps. The repository can be queried to comprehensively obtain available data to address large-scale questions and guide future research directions. Overall, the ‘mesophotic.org’ repository provides an independent and open-source platform for the

ever-growing research community working on MCEs and TMEs to collate and expedite our understanding of the occurrence, composition and functioning of these ecosystems.

Database URL: <http://mesophotic.org/>

Background & Summary

Mesophotic coral ecosystems (MCEs) occur in the deeper parts of the ocean's photic zone, beyond the limits of regular scientific diving but shallow enough to still support photosynthetically-active organisms. Traditionally, the term 'mesophotic' (literally 'middle-light') was occasionally used in the scientific literature in referral to aquatic depth layers of low-light (1–3). However, the first published mention in reference to extant coral reef ecosystems was by Robert Ginsburg at a meeting of the Association of Marine Laboratories of the Caribbean in 2007 (4). The term was later officially adopted during an international workshop organized by the U.S. National Oceanic and Atmospheric Administration (NOAA) in 2008 (5), primarily to distinguish deeper sections of (sub)tropical coral reefs from entirely non-photosynthetic deep-sea and cold-water coral ecosystems (6). According to the NOAA definition, 'mesophotic coral ecosystems (MCEs) are characterized by the presence of light-dependent corals and associated communities typically found at depths ranging from 30 to 40 m and extending to over 150 m in tropical and subtropical regions' (5, 7). Following that, the term 'mesophotic' started to be more broadly used to refer to benthic habitats within the depth zone of 30–150 m depth, including in temperate waters (8, 9) where communities at those depths are now characterized as 'temperate mesophotic ecosystems' (10).

Exploration of MCEs began in the 1960s and 1970s by manned submersibles (e.g. 11, 12) and early pioneers of deep scuba diving (13). However, research efforts on MCEs remained extremely limited until its establishment as a 'field of research' about a decade ago (5, 7). The renewed interest in MCEs has been driven by their potential connection with shallow-water coral reef communities as potential 'refuges' from major disturbances (14, 15), their unique and often undescribed biodiversity (6, 16), and their increased accessibility due to the advancement of underwater technologies (e.g. mixed-gas scuba, closed-circuit rebreathers and remotely operated vehicles). Overall, this has led to a major increase in scientific attention over the past decade (17), as evidenced by the rapid growth in the quantity and geographic spread of published scientific literature (Figure 1).

Considering the rapid decline of shallow reefs due to the effects of climate change (18, 19), MCEs have become a common interest among not only the scientific community but also governmental organizations and non-profit groups

(10, 20). There is an emerging consensus that despite their potential role as refuges, MCEs are not immune to disturbance and instead are vulnerable in their own right (16, 21, 22). In order to consider appropriate management for MCEs, it is critical to assess them under different pressures (23). While remaining largely undocumented, MCEs are estimated to occupy similar or larger areas of habitat compared to shallow coral reefs (6, 24, 25), with most of this habitat not included in conservation management efforts (26–28). In order to collate the scientific literature and provide a platform for the growing research community, a basic web repository was launched at the 'International Workshop to Prioritize Research and Management Needs for Mesophotic Coral Ecosystems' organized by NOAA in 2008 (5). The repository has since progressed to form the current iteration of 'mesophotic.org' (<http://mesophotic.org/>): a comprehensive and curated repository of scientific literature on MCEs and TMEs (hereafter referred to as 'mesophotic ecosystems'). The main goals of this repository are to (i) provide a comprehensive and dynamic record of all the published scientific information on these ecosystems and make it queryable through a single web portal, (ii) allow for the exploration of spatial/temporal trends and identification of knowledge gaps through curated metadata for each publication and (iii) act as an institution-independent platform and as a shared resource for and by the research community to accelerate our understanding regarding the occurrence, composition and functioning of these ecosystems.

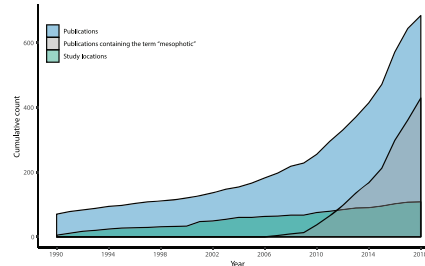


Figure 1. The quantity and geographic spread of scientific literature on mesophotic ecosystems is increasing over time. Series show the cumulative count of scientific publications on mesophotic ecosystems, the subset of those publications using the term 'mesophotic', and unique research locations in the current 'mesophotic.org' database release.

Database information and usage

The current release provides a comprehensive collection of peer-reviewed, scientific articles up to the end of 2018 and incorporates efforts from several other systematic literature reviews (6, 10, 29). The primary contents of 'mesophotic.org' are therefore currently peer-reviewed publications, although the proportion of secondary scientific literature including conference proceedings, technical reports, museum publications, book chapters and (post)graduate theses is growing (as we continue to add these). Each catalogued publication is first identified as 'mesophotic', depending on whether it presents data from or a discussion on the mesophotic depth zone (defined by the most commonly considered depth range of 30–150 m depth; 30) or whether it is relevant despite not occurring in this depth range. Next, where relevant, the publication is tagged either as 'mesophotic coral ecosystem' or 'temperate mesophotic ecosystem' to facilitate separate searches and summaries for these distinct systems. The publications are identified by type (scientific, technical and popular), format (article, review, report, chapter, book and thesis) and whether they present original data and/or report new species.

In addition to standard citation information, additional metadata are manually extracted from each publication (an up-to-date overview of fields and categories can be found on <http://mesophotic.org/metadata>), including the minimum and maximum study depth, the geographic location(s) (each defined by a latitude and longitude), the research platform(s) (e.g. 'rebreather'), the research field(s) (e.g. 'physiology') and the focal taxa (e.g. 'Scleractinia'). The abstract and full text are automatically indexed to extract the occurrence (frequency) of custom keywords (e.g. 'mesophotic'), species known to occur at mesophotic depths (through a curated list: <http://mesophotic.org/species>) and metadata categories (as mentioned above). The article is also summarized through a 'word cloud' (eliminating undesired stop words through a custom 'stop list'). This also allows keywords in the abstract and word cloud to be hyperlinked to other pages on the website. Full-text contents are stored in the database for indexing and searching purposes but are not accessible to comply with copyright regulations. An advanced search function is available to search across publications and their associated metadata, and the results can be browsed through the website or downloaded as a comma-separated values (CSV) file. If a search term is queried, publications are ordered by the number of occurrences of that term in the full text, which can be helpful in identifying the most relevant references. In addition, each metadata field has a separate entry page to summarize literature by category (e.g. geographic region, research platform or focus taxon).

New publications are added by the content editors but can be suggested (as well as any corrections) by any website visitor through email (info@mesophotic.org). After extracted metadata are entered, they are considered 'validated' when verified by at least two different content editors using an internal validation system. If a content editor changes any of the metadata, the system will expire existing validations prompting the other content editors for revalidation. In addition to scientific publications, the website maintains a moderated list of people working on mesophotic ecosystems, a gallery of member photos (with the option of sharing photos for reuse with the Creative Commons License; CC BY-NC 4.0) and a regular blog featuring scientists and their publications in 'Behind the Science' posts.

The current release of all the validated metadata associated with publications can be downloaded in CSV format from anywhere in the 'mesophotic.org' repository. Data can be directly imported into R for analysis by using the 'read.csv' option (www.r-project.org) and pointing to the URL of the dynamically generated CSV files on the website (e.g. <http://mesophotic.org/publications.csv>). Alternatively, CSV files of specific queries can be downloaded, saved and imported in the same way. An electronic notebook with usage examples, including reproductions of the figures included with this manuscript, can be found on <http://mesophotic.org/tutorial>. Metadata can also be explored through the Statistics page (<http://www.mesophotic.org/stats>), to provide general summaries of the data, such as the number of publications over time (Figure 1) and over depth (Figure 2) and the most commonly studied focal taxa, research fields, geographic locations or research platforms (Figure 3).

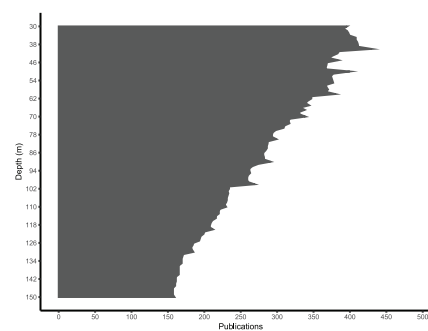


Figure 2. Number of scientific publications decreases over depth (30–150 m). The number of publications at each (1 m) depth interval is determined by assuming the entire depth range from minimum to maximum depth for each publication in the current release.

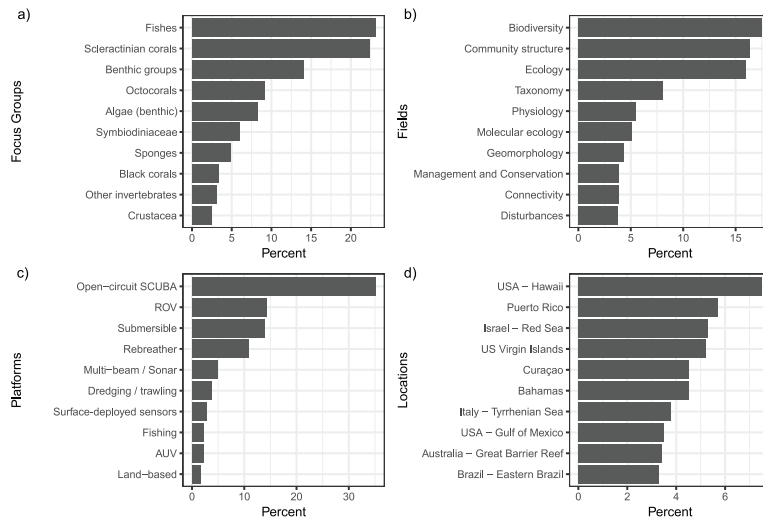


Figure 3. Top 10 fields of metadata categories of the curated literature on mesophotic ecosystems. a) 10 most-studied focus groups of mesophotic publications, b) 10 most-studied fields of research in mesophotic publications, c) 10 most common platforms used to conduct research at mesophotic depths and d) 10 locations with the greatest number of publications focused on mesophotic research.

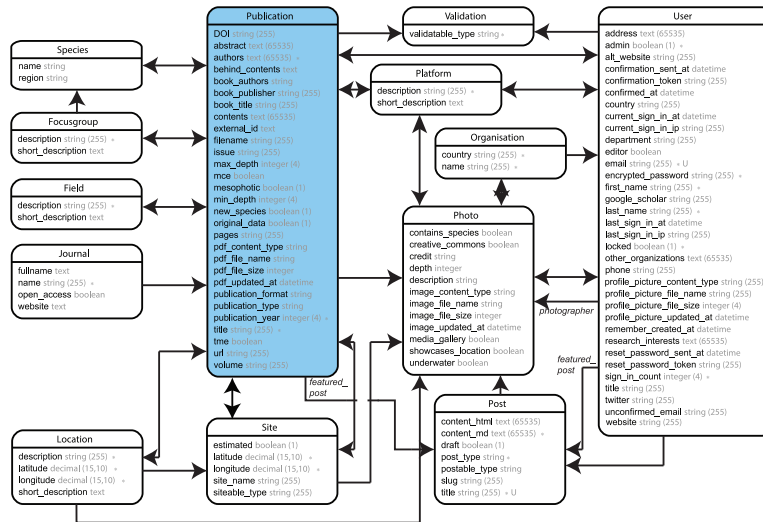


Figure 4. Entity Relationship Diagram (ERD) of the 'mesophotic.org' database release.

Code Availability

The source code for 'mesophotic.org' was written in Ruby (2.5.0) on Rails (5.2.0) and is freely accessible through

<http://www.github.com/pimbongaerts/mesophotic>. The source code is open-source and free to be used, shared and modified under the MIT License. The application relies on

a wide range of Ruby gems and JavaScript packages that are detailed in the README file of the code repository. The database structure is visualized through an Entity Relationship Diagram (ERD; Figure 4), with the most recent version also accessible through the README file. Issues and bugs can be reported through the <https://github.com/pimbongaerts/mesophotic/issues> page.

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Appendix 2: Manuscript – Symbiotic associations of the deepest recorded photosynthetic scleractinian coral (172 m depth)

Foreword

This publication reported the main findings of the deepest ever recorded photosynthetic scleractinian coral, collected at 172 m depth in the Gambier Islands. Although my role as a co-author was to collect the field data and help write the manuscript, I wanted to include the publication because it justifies the one-year time that I spent on the boat also collecting data for other scientists of the consortium DEEPHOPE. The present manuscript allowed me to gain even more knowledge of the molecular ecology techniques implied by corals to inhabit deep mesophotic depths. In my opinion, it fits very well in the storyline of my PhD because it pushes some of the physiological findings of **chapter 4**.

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Symbiotic associations of the deepest recorded photosynthetic scleractinian coral (172 m depth)

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Abstract

The symbiosis between scleractinian corals and photosynthetic algae from the family Symbiodiniaceae underpins the health and productivity of tropical coral reef ecosystems. While this photosymbiotic association has been extensively studied in shallow waters (<30 m depth), we do not know how deeper corals, inhabiting large and vastly underexplored mesophotic coral ecosystems, modulate their symbiotic associations to grow in environments that receive less than 1% of surface irradiance. Here we report on the deepest photosymbiotic scleractinian corals collected to date (172 m depth), and use amplicon sequencing to identify the associated symbiotic communities. The corals, identified as *Leptoseris hawaiiensis*, were confirmed to host Symbiodiniaceae, predominantly of the genus *Cladocopium*, a single species of endolithic algae from the genus *Ostreobium*, and diverse communities of prokaryotes. Our results expand the reported depth range of photosynthetic scleractinian corals (0–172 m depth), and provide new insights on their symbiotic associations at the lower depth extremes of tropical coral reefs.

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The ecological success of scleractinian corals, the engineers of one of the most productive and diverse ecosystems on Earth, relies on a myriad of symbiotic associations with microorganisms [1]. Among these symbioses, the association between the coral host and unicellular algae from the family Symbiodiniaceae is central to coral health and powers the metabolically expensive process of calcification [2]. The coral host provides limited inorganic nutrients, while Symbiodiniaceae share essential organic compounds derived from their photosynthetic activity [3]. This light-dependent association has mainly been studied in shallow waters (<30 m) because of technical limitations imposed by traditional scientific scuba diving. However, photosynthetic scleractinian corals have been observed in the mesophotic reef slope down to 150–165 m depth [4, 5].

As depth increases, the waveband of solar radiation used by most algae for photosynthesis (from 400–700 nm) becomes attenuated in both intensity and width. Even in clear tropical waters, the irradiance levels below 120 m depth can be less than 1% of surface values, and the light spectrum is shifted toward the blue and blue–green wavelengths (~475 nm) (e.g. [4]). These light limitations pose a major constraint for the productivity of benthic organisms that rely on photosynthetic symbionts [6],

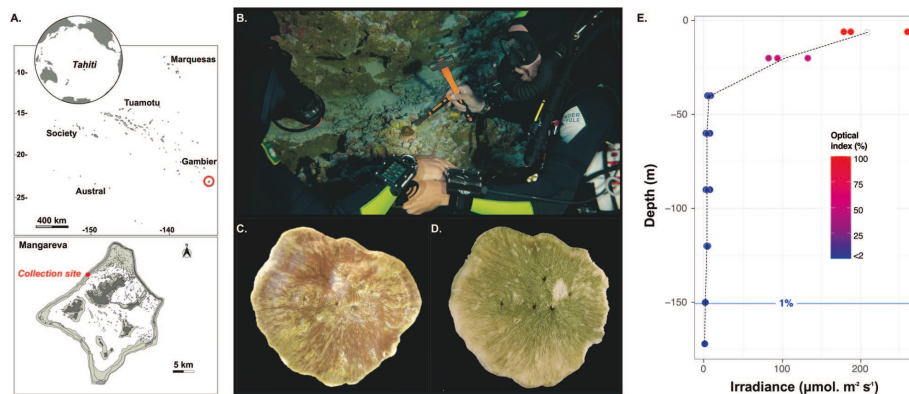


Fig. 1 Sampling location of the deepest photosymbiotic scleractinian coral recorded to date. **A** Map of the Gambier archipelago, French Polynesia. Pictures of *Leptoseris hawaiiensis* collected at 172 m depth in the Gambier archipelago (**B**) during the in situ sampling (screenshot of video © UTP III), (**C**) after reaching the surface and (**D**) after bleaching for taxonomic identification with the green color indicating the presence of endolithic algae. **E** Variation of the optical

index of irradiance (in PAR) along the coral reef depth gradient from 6 to 120 m depth (predictions for 150 and 172 m depths) at Mangareva. For each depth, the three values represent a mean value for 3 days of measurements recorded every 5 min with a PAR logger (DEFI2-L Advantech) at three different time periods of the day (9 h30–10 h00, 12 h30–13 h00 and 15 h30–16 h00).

including reef-building corals (scleractinians). While the scleractinian coral species *Leptoseris hawaiiensis* has been reported to occur as deep as 153 m in Hawaii and 165 m at Johnston atoll (reviewed in [4]), no live specimens were collected at these extreme depths. The fact that Symbiodiniaceae have been found at much greater depth in association with Antipatharians (396 m) [7], raises the possibility that they might also be present in scleractinian corals deeper than 165 m. Previous studies have genetically confirmed and identified endosymbiotic Symbiodiniaceae in *Leptoseris* down to 70 m on the Great Barrier Reef [8] and down to 125 m depth in Hawaii [9–11]. A specific host-Symbiodiniaceae association was reported between deep *L. hawaiiensis* and a *Cladocopium* from the ancestral C1 radiation [9–11], which represents a diverse group of Symbiodiniaceae commonly found in association with scleractinians on shallow coral reefs [8, 9, 12, 13]. To better understand how scleractinian corals can survive so far away from their presumed light optimum, it is critical to determine if these deep specimens (1) maintain their association with photosynthetic algae and/or (2) if their survival in the deepest mesophotic coral ecosystems requires a shift in their microbial communities, including Symbiodiniaceae and other microorganisms such as endolithic algae and bacteria.

Here we report on the observation and collection of the deepest scleractinian corals in association with Symbiodiniaceae and other photosymbionts. Technical divers using closed-circuit rebreathers recovered three *L. hawaiiensis* colonies from the Gambier archipelago (French Polynesia,

Fig. 1A) at 154, 168, and 172 m depth ($n = 2$ subsamples for each depth; Fig. 1B–D). Irradiance measured at 120 m depth was <2% of that recorded at 6 m depth and irradiance at 172 m was predicted to be <1% (Fig. 1E and S1). ITS2 sequencing revealed Symbiodiniaceae presence in all three lower mesophotic colonies sampled, with nearly all of the retrieved amplicon sequence variants (ASVs; with most of these representing intragenomic sequence variants) classified as *Cladocopium* (Fig. 2). The most common ITS2 ASV representative sequence associated with these *Leptoseris* hosts (S-01, Fig. 2 and S2; 50–57% of total ASVs in each sample) was C1 (GeoSymbio and SymPortal databases; see supplementary methods). This represents one of the most common groups of Symbiodiniaceae, and it has previously been reported in *Leptoseris* [9, 10, 14], as well as other host species at depths ranging from the surface to 125 m [8, 10, 11, 13–15]. As a complementary approach, ITS2 profiles predicted by SymPortal were used as proxy for Symbiodiniaceae genotypes ([16]; see supplementary methods and data files S1–S4). These predicted ITS2 profiles were largely consistent among replicates but confirmed a different profile for the colony at 172 m depth compared to those at 154 and 168 m depth (Fig. S2). Nonetheless, the Symbiodiniaceae communities shared three ASVs that exactly matched C89 (S-02: 5% at 172 m vs. 17–19% at 154–168 m) and two different C variants (both S-05 and S-07: 7% at 172 m vs. ~2% at 154–168 m) in public databases (Fig. S3; GeoSymbio, SymPortal or Genbank). Of the 26 ASVs identified across all samples, one sequence originated

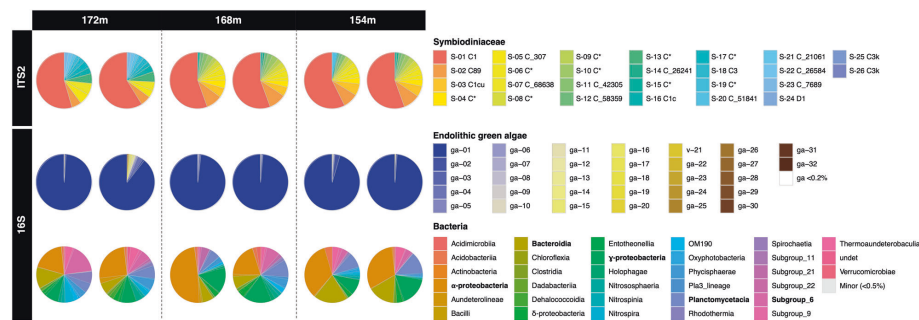


Fig. 2 Microbial communities harbored by the three deep colonies. Composition of the microbial community in *Leptoseris hawaiiensis* collected at 172, 168, and 154 m. At each depth, two subsamples were analyzed for each colony. The ITS2 marker shows the relative proportion of different Symbiodiniaceae ASVs (with GeoSymbio and

SymPortal v.2020-05-19_07-23-40 affiliations). The 16S rDNA marker shows the relative proportions of different ASVs for endolithic algae chloroplast composition and bacteria classes. Asterisk represents sequences with no exact match in the SymPortal database for Symbiodiniaceae.

from *Durusdinium* (S-24 D1 with GeoSymbio and SymPortal databases). This sequence is found in multiple heat-tolerant *Durusdinium* species including the enigmatic, cosmopolitan [17], host generalist *D. trenchii* [18]. However, whether or not the Symbiodiniaceae sampled here is *D. trenchii* or indeed thermally tolerant cannot be confirmed without further genetic and phenotypic data. Low abundance ASVs were observed at all three depths (172 m: 8 ASVs, 154 and 168 m: 10 ASVs, Fig. S3), including nine ASV sequences (Fig. 2) that have not been reported previously in the GeoSymbio [13] and SymPortal (access date: 2020-05-19_07-23-40) [16] databases (Fig. S3). Comparison of the overall Symbiodiniaceae SymPortal predicted ITS2 profiles (Fig. S2) did not confidently identify matches with previously encountered profiles (predominantly from shallow reef environments), indicating that they might be specific to this species and/or mesophotic environment. Given the extreme paucity of light at these depths, we hypothesize that lower mesophotic *L. hawaiiensis* may use different strategies to photoacclimate. Morphologically, the coral species were characterized by a thin flat skeleton (Fig. 1B–D), which is optimal for light harvesting and reducing skeletal carbonate deposition [19]. *Leptoseris hawaiiensis* has also been shown to display depth-associated physiological specialization and trophic plasticity (acquiring energy from different food sources) [9], and an unusual light-harvesting system, which enlarges the spectrum of wavelengths for photosynthesis by transforming the short, blue-shifted wavelength with their autofluorescent pigments [19].

To identify other microorganisms associated with our lower mesophotic scleractinian colonies, we targeted the 16S rRNA gene (V4–V5 region; see supplementary methods). Sequencing data revealed the presence of green algal chloroplast sequences belonging to the genus *Ostreobium*

(Fig. 2). This endolithic alga was abundant in the deep coral colonies as suggested by the marked green color observed below the living tissues (Fig. 1C) and within the skeleton after removing the soft tissues in bleach (Fig. 1D). We identified a single *Ostreobium* species (ASV ga-01), belonging to clade 2, that was dominant in all the colonies (Fig. 2 and S4), and has been previously reported across the depth gradient in scleractinian corals and octocorals worldwide [20, 21]. The nature of the interaction between corals and *Ostreobium* has been debated. Evidence supports a mutualistic association under extreme conditions such as coral stress (inducing bleaching) [22] or drastically reduced light exposure [23]. Under the low light conditions of the deep mesophotic fore reef slope, *Ostreobium* might complement Symbiodiniaceae’s function by providing photosynthates to the host. These endolithic algae are adapted to photosynthesize in near-darkness with increased numbers of light-harvesting xanthophyll pigments that can use shorter wavelengths compared to other green algae and optimize light capture (e.g. [24]).

Bacteria associated with the lower mesophotic scleractinian colonies had an observed richness ranging from 106 to 211 ASVs per sample (Fig. S5). These bacteria mainly belonged to the classes Alpha- (19–49%) and Gamma-proteobacteria (8–17%), Bacteroidia (6–20%) and subgroup-6 of Acidobacteria (1–17%) (Fig. 2), which are known to associate with corals [25]. In total, we detected 843 different bacterial ASVs, among which 67–89% were unique to one colony or even unique to one subsample (Fig. S6 and Table S1). Our data suggest that the coral hosts displayed individual microbial signatures with some common ASVs shared between subsamples of the same colony (Fig. S6). However, this result might have been affected by the low-sequencing depth of the microbiome following the removal of

the *Ostreobium* reads. Our results corroborate previous reports describing the high intra-specific variability of coral-associated bacterial communities at different spatial scales (e.g. [25, 26]), which might be driven by biological traits, such as the age [27] or diets of the colonies [28].

This study reports a new depth record for scleractinian corals associated with symbiotic algae at 172 m. Similar to conspecifics previously sampled in mesophotic environments between 115 and 125 m depth [10], the deepest *L. hawaiiensis* reported here associated with symbiotic-microalgae belonging to the highly diverse C1 lineage. The deep colonies were also characterized by the presence and abundance of a single species of endolithic alga from the genus *Ostreobium* (clade 2). These filamentous green algae adapted to thrive in extreme low light conditions [24] might highly contribute to the survival of *L. hawaiiensis* at depth through photosynthates translocation [29]. In addition, bacterial communities were diverse, with intraspecific differences in community composition. Our findings provide new insights into the symbioses of scleractinian corals at depth, through the conservation of their associated photosymbiotic algae, raising important questions about the nature and mechanisms involved in the interactions between host and Symbiodiniaceae and/or *Ostreobium* (e.g. evolutionary theory of symbiosis [30]). Future studies should establish the contribution of photosynthetic symbionts to the energy budget of mesophotic corals. Understanding the biology of ecosystem engineers, such as tropical reef corals, living at the edge of their habitat range is important to determine the plasticity of these organisms and their ability to withstand environmental pressure.

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Author contributions All authors conceived and designed this study; LH and HR coordinated the study; HR, GP-R, MP, UTP III

consortium and LH collected field data; MP identified coral species; HR carried out analysis and graphics and drafted the manuscript; HR, PG, MM, JBR, PB, and LH wrote the manuscript. All authors commented on the manuscript and gave their approval to submit.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Appendix 3: Manuscript – Documenting decadal disturbance dynamics reveals archipelago-specific recovery and compositional change on Polynesian reefs

Foreword

This publication documented the last 25 years of the shallow coral reefs of several islands of French Polynesia. The long-term study shows how multiple disturbances impacted shallow coral reefs and the high recovery capacity despite significant changes in genus composition. This publication was the subject of my Masters 2 internship. I was given access to the long-term monitoring database Polynesia Mana from the CRIOBE, analysed the data, wrote a manuscript, and the publication is the final result. During my PhD, I devoted significant time to the reviewing processes. The publication is included in the thesis because it perfectly fits the context of shallow coral reefs in French Polynesia.

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Documenting decadal disturbance dynamics reveals archipelago-specific recovery and compositional change on Polynesian reefs

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ABSTRACT

Coral reefs are declining at an unprecedented rate as a consequence of local and global stressors. Using a 26-year monitoring database, we analyzed the loss and recovery dynamics of coral communities across seven islands and three archipelagos in French Polynesia. Reefs in the Society Islands recovered relatively quickly after disturbances, which was driven by the recovery of corals in the genus *Pocillopora* (84% of the total recovery). In contrast, reefs in the Tuamotu and Austral archipelagos recovered poorly or not at all. Across archipelagos, predation by crown-of-thorns starfish and destruction by cyclones outweighed the effects of heat stress events on coral mortality. Despite the apparently limited effect of temperature-mediated stressors, the homogenization of coral communities towards dominance of *Pocillopora* in the Society Archipelago and the failure to fully recover from disturbances in the other two archipelagos concern the resilience of Polynesian coral communities in the face of intensifying climate-driven stressors.

1. Introduction

Coral reefs are rapidly changing as a consequence of natural and anthropogenic stressors (Hughes et al., 2018). Human-induced climate change and ocean acidification are commonly identified as the most existential threats to coral reefs (Walther et al., 2002; Hoegh-Guldberg et al., 2007; Foden et al., 2013). Global warming, for instance, can reshape entire coral reefs at a regional scale through Mass Coral Bleaching Events (MCBE), which result in large-scale mortality of corals to produce fundamentally different ecosystem dynamics that can be difficult to reverse (Heron et al., 2016; Hughes et al., 2017). In addition, there are various natural (e.g., cyclones, crown-of-thorn starfish [COTS] outbreaks) and anthropogenic (e.g., fishing, pollution and sedimentation) local stressors that affect coral reef communities (Roberts, 1995; Fabricius, 2005; Bégin et al., 2016). The presence of several different stressors at various scales and their complex interactive effects suggest that reefs face an uncertain future (Darling et al., 2013). Already, many coral reefs across the globe have undergone ecosystem transitions to less-desirable states (Graham et al., 2015) and with global warming

predicted to surpass 1.5 °C by 2100 (IPCC, 2018), even more severe and larger-scale shifts stand to occur.

Understanding, predicting, and counteracting consequences of disturbances caused by cyclones, COTS, and temperature-mediated stress requires a thorough grasp on their isolated and combined effects on organisms, communities, and ecological processes on coral reefs (Brandl et al., 2019). By recording biotic and abiotic parameters over time, long-term monitoring programs permit the documentation of reef community dynamics and their drivers at a large temporal and spatial scale. This documentation is particularly relevant for scleractinian corals, which, as the primary reef builders, hold a dominant role in determining the status of coral reef ecosystems. Monitoring changes in coral communities as well as their potential causes over extended time periods is, therefore, useful to identify the main drivers of coral mortality and their role for shifts in community-wide properties following disturbances (Bjornstad and Grenfell, 2001; Gardner et al., 2003; Pandolfi et al., 2003; De'ath et al., 2012). In this study, we will consider resilience as the capacity of an ecosystem to return to its original state after a disturbance in terms of coral cover and composition (Holling, 1973), while we will consider

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recovery as the rate at which coral cover (in particular) returns to its pre-disturbance levels. The recovery of a coral reef after disturbances depends on the settlement of new larval recruits, their growth, and the survival of established coral colonies (Gilmour et al., 2013; Adjeroud et al., 2018). Mortality events usually create unoccupied space in the benthic community, after which recovery hinges on the dynamics between newly recruited corals and their algal competitors (Diaz-Pulido et al., 2009). However, these are often relatively slow processes that require long-term monitoring datasets that can trace the respective representation of benthic taxa before, throughout, and after disturbances.

Beyond the island of Mo'orea (Galzin et al., 2016), coral reefs in French Polynesia are relatively poorly studied. Yet, Polynesian reefs represent an excellent opportunity to assess how reefs may change as a consequence of physical and/or biological impacts and temperature-mediated stressors. Because they are remote islands in various geomorphological settings (i.e., from high volcanic islands to atolls), many Polynesian reefs are subject to relatively low local anthropogenic pressures (Cinner et al., 2018). Indeed, beyond the heavily populated island of Tahiti (189,500 inhabitants, INSEE-ISPF), most Polynesian islands are sparsely or not inhabited, creating a seascape of coral reefs with varying conditions, where most disturbances can be attributed to acute events such as physical storm and cyclones or COTS outbreaks (Adjeroud et al., 2009). Nevertheless, the global footprint of anthropogenic warming also affects reefs across French Polynesia, creating a second group of stressors of fundamentally different scale and nature (Donovan et al., 2020). Since 1993, the Center of Insular Research and Observatory of the Environment (CRIOBE) has monitored coral reefs across seven islands in French Polynesia (SO CORAIL, Polynesia Mana).

During this time, the studied coral reefs have experienced three main types of disturbances: (i) predation by COTS (*Acanthaster planci*) in 2007–2009; (ii) tropical cyclones Martin and Osea in 1997 and cyclone Oli in 2010, and (iii) various heat stress periods. The effects of these disturbances are documented in detail for reefs surrounding the island of Mo'orea in the Society Archipelago (Adjeroud et al., 2009; Lamy et al., 2016), where reefs have shown a remarkable capacity to recover from disturbances in terms of overall live coral cover (Berumen and Pratchett, 2006; Edmunds et al., 2018, 2016). This suggests that, in certain environmental settings, a lack of strong local anthropogenic impacts may facilitate resilience and recovery from natural and climate-induced degradation. Yet, it is unknown whether this island-level trend can be extended to other islands in the Society Archipelago or different Polynesian archipelagos (i.e., Tuamotu, Marquesas, Gambier and Austral).

In the present study, we aimed to understand disturbance and recovery dynamics in coral communities across a range of Polynesian reefs. Specifically, using a long-term monitoring database across three archipelagos, our goals were to (1) document decadal disturbance and recovery dynamics across three different archipelagos, (2) examine how compositional patterns differ across space and time, and (3) evaluate the comparative impacts of acute disturbances (cyclones, COTS and thermal stress).

2. Materials and methods

2.1. Locations and coral monitoring

Permanent monitoring sites were located at 10 m depth on the forereefs of seven islands from three archipelagos in French Polynesia. In

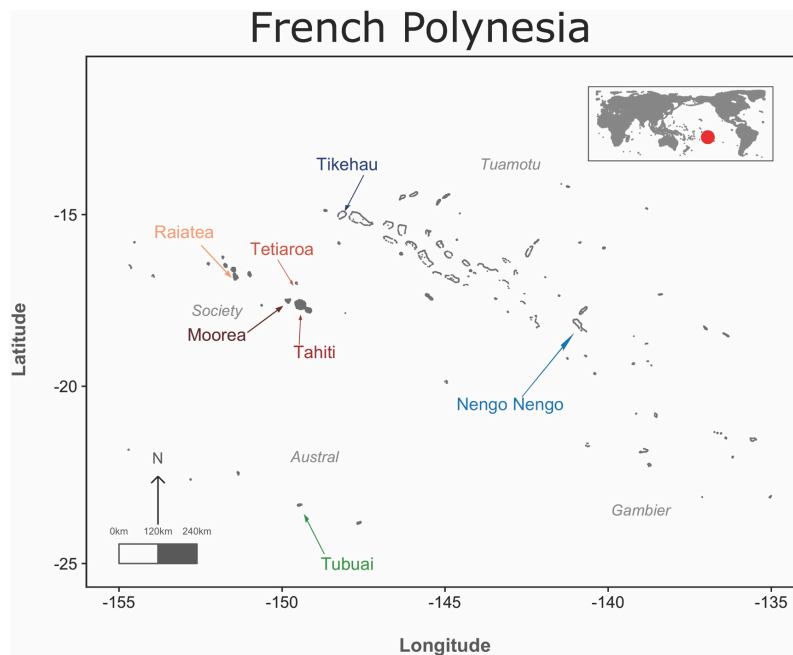


Fig. 1. Map of French Polynesia, with the studied islands indicated. Color palettes indicate different archipelagos: Red = Society Archipelago; Blue = Tuamotu Archipelago; Green = Austral Archipelago. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the Society Archipelago, we studied the high-volcanic islands Mo'orea (17.479°W, 149.852°S), Tahiti (17.5425°W, 149.619°S) and Raiatea (16.732°W, 151.504°S) and the atoll Tetiaroa (17.031°W, 149.563°S). In the Tuamotu Archipelago, we surveyed the atolls Tikehau (15.014°W, 148.285°S) and Nengo Nengo (18.707°W, 141.867°S). In the Austral Archipelago, we surveyed the high-volcanic island Tubuai (23.344°W, 149.404°S) (Fig. 1).

Overall, 87 surveys were performed over the past 26 years (1993–2019) by the SO Coral Monitoring Program (Polynesia Mana). Each site was monitored every two years. This biannual survey method was set as a rule since 1997, after the beginning of the time series. Surveys in Nengo Nengo were stopped after 2015 because of administrative problems. All sites were outside protected areas and chosen according to fieldwork logistics (i.e., away from passes between the foreereef and lagoon to minimize their effect, navigation time, wave exposure, and a compromise between deep and shallow diving constraints, etc.).

Surveys were performed using permanent photo-quadrats. Each survey consisted of the identification of points defined by a superimposed grid (10 × 10 cm mesh) placed on each photo-quadrat (1 m², n = 20 per survey), aligned consecutively along a 20 m transect laid parallel to the reef crest (Hill et al., 2004). In order to analyse these data, we used an approach similar to that used by other authors working with the same dataset (see Adjeroūd et al., 2005; Vercelloni et al., 2019). The approach consists of measuring coral cover at the genus level and pooling observations over 5m² of reef area, thus obtaining four replicates of 5m² for each 20m² transect. However, contrary to previous studies, we applied a permutational approach where we randomly select five non-contiguous quadrats for each transect and repeated this random selection 1000 times. The statistical tests (either *t*-tests or pairwise PERMANOVA, see below) are calculated at each permutation and significance is calculated on the basis of the full distribution of the statistics obtained by the random draw. We grouped corals into five main genera (*Acropora*, *Astreopora*, *Montipora*, *Pocillopora* and *Porites*) and an "Other" category that included all remaining genera of lower abundance (<5%, Fig. 2 & 1 SD).

2.2. Environmental context

We collated information concerning the occurrence of COTS outbreaks and cyclones over the studied period through different sources. First, we gathered COTS occurrence data from field observations over the 26-year monitoring period and supplemented these data with COTS population dynamics described in the literature (Chin et al., 2011; Vieux et al., 2004). We extracted occurrences of cyclones from records published by Météo France (Laurent and Varney, 2010), the European Centre for Medium-Range Weather Forecasts (ECMWF), and the Global Forecast Systems (GFS) from the National Oceanic and Atmospheric Administration (NOAA). We compared the resulting data with the available information from published sources (Canavesio, 2019; Duvat and Pillet, 2017) (Fig. 2).

To establish thermal context and calculate heat stress, we extracted daily satellite-derived sea surface temperature (SST) recordings from the NOAA Coral Reef Watch from 1985 to 2018, with a 5 km spatial resolution (0.05 degrees) (Maturi et al., 2016; Roberts-Jones et al., 2012). We compared the accuracy of satellite observations with in situ recorded temperatures from 56 temperature sensors (SeaBird thermometer) deployed at the depth of the coral monitoring (i.e., ~10 m) using direct comparisons. From the matched daily temperatures, we calculated root mean square errors (RMSE) and biases (i.e., average of satellite - logger) (DeCarlo and Harrison, 2019). In light of consistently low RMSE <0.33 and bias <0.08 between remotely-sensed and empirically-derived temperature, we preferentially used satellite SST observations because (1) several gaps existed in the in situ temperature database due to technical or logistical issues, and (2) standard heat stress calculations are primarily based on satellite observations. We computed heat stress using

the Degree Heating Weeks (DHWs) index (Glynn, 1996; Eakin et al., 2010; Liu et al., 2018, 2013). To do so, we first calculated the Monthly Maximum Mean (MMM) for each location over the climatological period suggested by NOAA (i.e., from 1985 to 1993 – excluding 1991 and 1992 because of bias caused by the volcano Mt. Pinatubo). Then, we calculated heat stress as the weekly sea surface temperatures that exceeded the MMM by more than one-degree °C. This temperature (MMM + 1 °C) is generally considered as the bleaching threshold. DHWs represent the accumulation of heat stress and time of exposure over the bleaching threshold for the twelve preceding weeks. When DHWs were above 4 (generally termed "bleaching alert level 1" (Liu et al., 2018)), we considered the event as major thermal stress and as a main disturbance independently of changes in coral cover. When DHWs were below 4, we considered them as a minor disturbance. More details on the DHW calculation and its values are available in the Supplemental Information (Fig. 2 SD).

2.3. Statistical analysis

We defined main disturbances as the occurrence of an environmental perturbation or a major thermal stress event causing abrupt changes in coral cover. We analyzed the effects of each of these main disturbances in isolation, assessing the change of coral cover before and just after the particular perturbation for each island (Δ coral cover - Fig. 3). In addition, we studied changes in coral cover and community composition after recovery of main disturbances in the affected islands. For each disturbance that caused an abrupt change in coral cover, we defined two periods, denominated as 'before' and 'after recovery'. The period defined as 'before' corresponded to the survey immediately before the identified abrupt change in coral cover caused by the disturbance. The period defined as 'after recovery' corresponded to the maximum value of coral cover after disturbance. Because of the biannual survey method, we analyzed some disturbances as a combined effect of two disturbances, and the defined periods for 'before' and 'after recovery' were specific for each island.

We used parametric Student's *t*-tests for paired samples to examine changes in total coral cover caused by each specific main disturbance and to assess the periods 'before' and 'after recovery' of disturbances at each location. We selected *t*-tests depending on the assumptions of normality in the response and the homogeneity of the variance, which we assessed using Shapiro-Wilk test (for normality) and *F*-tests (for variance). Furthermore, we assessed changes in coral cover (Δ coral cover) as a function of the different disturbance types, i.e. 'cyclone', 'COTS', 'COTS and cyclones simultaneously', and 'thermal stress'. Δ coral cover was fitted using ANOVAs across disturbance types. To examine shifts in the community composition of coral genera (i.e., the relative abundance of each genus), we used a PERMANOVA on the Bray-Curtis distance matrix of the data with pairwise comparisons (Martinez Arbizu, 2019), with each island and time period specified as fixed effects.

We also computed coral recovery rate (% coral cover-year⁻¹) after disturbance with a modification of the geometric rate of change (Côté et al., 2005) using Eq. (1). Specifically, Post.Dist.cover (%) was the maximal coral cover value recorded during the 'after recovery' period of a given disturbance event, corresponding to a specific year. Min.cover (%) was the lowest coral cover observed in a particular year just after the focal disturbance. Time (years) was the number of years necessary for coral cover to transition from its lowest (Min.cover) to highest (Post. Dist.cover) value. In the case of multiple main disturbances, we separately calculated recovery for each transition event (Table 1). The contribution of each genus to the total coral recovery rate was calculated using linear regressions.

$$\text{Coral recovery rate} = \frac{\text{Post.Dist.cover} - \text{Min.cover}}{\text{Time}} \quad (1)$$

To investigate overall compositional changes in the coral community

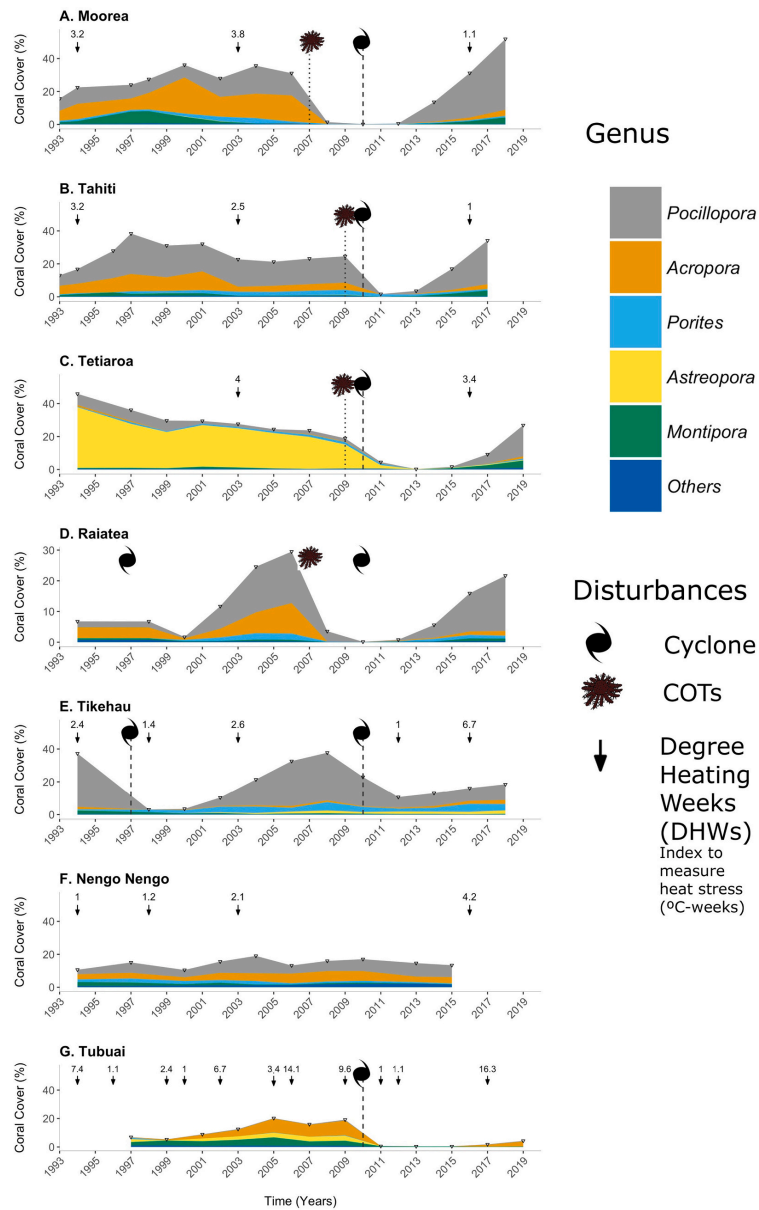


Fig. 2. Cumulative plots per genus highlighting coral cover dynamics and main disturbance events across the seven islands. Points indicate years of sampling and total coral cover. Disturbances are included as cyclones, COTs outbreaks, and DHWs (arrows with numbers).

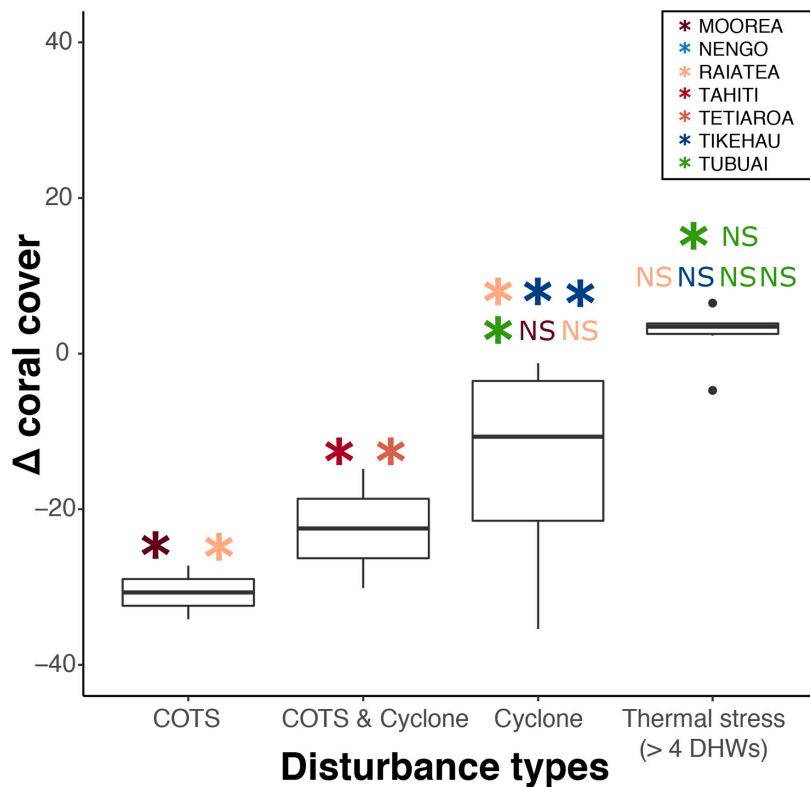


Fig. 3. Effects of disturbance types on the change in coral cover (Δ) across the studied islands. Boxplots show interquartile ranges (IQRs), while external points are statistical outliers. An ANOVA revealed a significant effect of the type of disturbance ($F = 13.93$, $p = 0.007$) in coral cover. The t -test results of particular disturbance types in the change of coral cover are displayed for each island, with '*' when the change was significant and with 'NS' when not significant.

across the seven islands and over the monitored period, we performed a non-metric multi-dimensional scaling (nMDS) ordination on a Bray-Curtis dissimilarity matrix (Kruskal, 1964; Shepard, 1962). Percent cover estimates of the most abundant coral genera were square root transformed to adjust for unequal representation of the genera (Edmunds et al., 2016). We validated the convergence of the ordination by examining stress values. Furthermore, we applied a permutational multivariate analysis of variance (PERMANOVA) to the distance matrix to test for the effects of temporal (i.e., year) and spatial (i.e., island) differences on coral community dissimilarities. All analyses were conducted using R and the 'vegan' package (Oksanen et al., 2013).

3. Results

3.1. Disturbance effects on coral cover

Overall, coral cover on observed Polynesian reefs ranged from 2% to 55% across the examined time period and was affected by tropical cyclones, COTS and heat stress anomalies (Fig. 2). The islands of the present study were not equally impacted by these disturbances.

In the Society Archipelago, cyclones Martin and Osea affected only the island of Raiatea. Coral cover fell from 8.27% (Standard Deviation =

0.55) to 2.16% (0.39) causing a significant decline (Student t -test, $t = -5.13$, $p = 0.01$). After the cyclones, the recovery rate in Raiatea was 4.8% coral cover-year⁻¹ and in 2005–2006 (the 'after recovery' time point for Martin and Osea), coral cover was significantly higher than before the disturbance ($t = 8.43$, $p < 0.005$). On the other hand, the COTS outbreak from 2007 to 2009 heavily impacted Mo'orea ($t = -18.7$, $p < 0.005$) and Raiatea ($t = -10.53$, $p < 0.005$), and together with cyclone Oli was particularly strong in Tahiti ($t = -9.32$, $p < 0.005$), but also affected Tetiaroa ($t = -4.08$, $p = 0.03$). While maximum pre-disturbance coral cover ranged from 25.7% to 36.1%, coral cover declined to less than 2% in 2010–2012 (a 99% loss). Reefs in Tetiaroa differed from Mo'orea, Tahiti and Raiatea by continuously declining from 45.9% (0.8) in 1994 to 18.92% (0.68) in 2009, but also exhibited a steep decline in 2010. After these disturbances, reefs in Mo'orea, Tahiti, Raiatea, and Tetiaroa showed recovery trajectories of 6.8%, 5.9%, 3.1 and 5.4% increases in coral cover-year⁻¹, respectively. In 2017–2019 (the 'after recovery' time point for these disturbances), estimates of coral cover did not significantly differ from 'before' disturbance values in Tahiti (from 27.4% to 37.3% [$t = 2.14$, p -value = 0.14]), Tetiaroa (from 25.6% to 32.7%; [$t = 1.65$, $p = 0.24$]) or Raiatea (from 31.8% to 25.25% [$t = -1.56$, $p = 0.25$]), despite the slower recovery. However, a significant difference was present for Mo'orea (36.01% to 54.63% [$t = 5.79$,

Table 1
Summary of coral cover values and recovery dynamics 'before' and 'after recovery' the main disturbances.

Island	Disturbance type (year)	Type (Genus)	Pre-disturbance cover (%) and (year)	Min. cover after disturbances (%) and (year)	Max. post-disturbance cover (%) and (year)	Minimum below 1% time (years)	Recovery (coral * year ⁻¹) (mean ± se)
Moorea	COTS (2007, 2008) & Cyclone (2010)	All genera	36.01 (2006)	0.18 (2010)	54.63(2018)	4	6.8 ± 0.31
		<i>Pocillopora</i>	13.52 (2006)	0 (2010)	43.02 (2018)	6	5.38 ± 0.3
		<i>Acropora</i>	15.8 (2006)	0 (2010)	3.64 (2018)	8	0.45 ± 0.1
		<i>Porites</i>	1.97 (2006)	0.12 (2010)	1.726 (2018)	6	0.2 ± 0
Tahiti	COTS (2008, 2009) & Cyclone (2010)	All genera	27.4 (2005)	1.85 (2011)	37.3 (2017)	0	5.91 ± 0.8
		<i>Pocillopora</i>	14.63 (2005)	0.06(2011)	26.54 (2017)	1	4.41 ± 0.5
		<i>Acropora</i>	3.58 (2005)	0 (2011)	2.9 (2017)	4	0.48 ± 0.1
		<i>Porites</i>	4.44 (2005)	1.48(2011)	1.79 (2017)	0	0.05 ± 0.2
Tetiaroa	COTS (2009) & Cyclone (2010)	All genera	25.63 (2005)	0.31 (2013)	32.70 (2019)	1	5.39 ± 0.43
		<i>Pocillopora</i>	1.17 (2005)	0 (2013)	18.95 (2019)	6	3.16 ± 0.3
		<i>Acropora</i>	0.06 (2005)	0 (2013)	1.29 (2019)	8	0.21 ± 0
		<i>Porites</i>	1.11 (2005)	0 (2013)	0.8 (2019)	5	0.13 ± 0
Raiatea	Cyclone (1997)	<i>Astropora</i>	21.48 (2005)	0.18 (2013)	0.37 (2019)	6	0.03 ± 0
		All genera	8.27 (1994)	2.16 (2000)	30.84 (2006)	0	4.77 ± 0.6
		<i>Pocillopora</i>	1.97 (1994)	0.43(2000)	16.79(2006)	1	2.72 ± 0.5
		<i>Acropora</i>	3.46 (1994)	0.49(2000)	9.87 (2006)	1	1.56 ± 0.2
	COTS (2007, 2008) & Cyclone (2010)	<i>Porites</i>	0.06 (1994)	0.43(2000)	2.03 (2006)	6	0.27 ± 0.1
		All genera	31.81 (2006)	0.12(2010)	25.25 (2018)	4	3.14 ± 0.3
		<i>Pocillopora</i>	16.790 (2006)	0.06(2010)	18.02 (2018)	4	2.25 ± 0.2
		<i>Acropora</i>	9.87 (2006)	0 (2010)	1.48 (2018)	8	0.18 ± 0.1
		<i>Porites</i>	2.03 (2006)	0 (2010)	1.91 (2018)	8	0.24 ± 0
		All genera	39.51 (1994)	4.13 (1998)	36.73 (2006)	0	4.08 ± 0.3
Tikehau	Cyclone (1997) & Bleaching (1998)	<i>Pocillopora</i>	32.65 (1994)	0.06(1998)	27.40 (2006)	4	3.42 ± 0.2
		<i>Acropora</i>	1.35 (1994)	0.06(1998)	0.98 (2006)	12	0.11 (0.1)
		<i>Porites</i>	0.67 (1994)	1.54(1998)	4.81 (2006)	0	0.4 ± 0.1
		All genera	36.72 (2006)	14.24 (2012)	19.62 (2018)	0	0.89 ± 0.4
Cyclone (2010)	<i>Pocillopora</i>	27.4 (2006)	6.48(2012)	9.63 (2018)	0	0.52 ± 0.3	
	<i>Acropora</i>	0.99 (2006)	0.49 (2012)	2.4 (2018)	8	0.32 ± 0.2	
	<i>Porites</i>	4.81 (2006)	3.70 (2012)	3.94 (2018)	0	0.04 ± 0.1	
	All genera	25.26 (6.5)	0.43 (2013)	4.37 (2019)	6	0.65 ± 0.1	
Tubuai	Cyclone (2010)	<i>Pocillopora</i>	0.37 (2005)	0 (2013)	0.49 (2019)	12	0.08 ± 0
		<i>Acropora</i>	9.63 (2005)	0 (2013)	3.52 (2019)	6	0.59 ± 0.1

$p = 0.006$]). In contrast to the effects of physical and biological disturbances associated with the two perturbation events, the minor temperature-mediated stress events recorded in Moorea, Tahiti, and Tetiaroa had no visible effect on coral communities. While major temperature-mediated stress events (above 4 DHW) occurred in Raiatea, coral cover did not significantly change following this event ($t = 2.23$, $p = 0.13$).

In the Tuamotu Archipelago, the two islands differed markedly in how they were affected. Tikehau was impacted by two cyclones and temperature stress. First, the cyclones Martin and Osea (1997) reduced coral cover from 39.5% (1.1) to 4.1% (0.3), causing a significant decline ($t = -19.48$, $p < 0.005$). Then, a recovery rate of 4.1% coral cover⁻¹ returned the reef to its pre-disturbance value ($t = -1.04$, $p = 0.44$). Second, cyclone Oli (2010) caused a less extreme, but still significant ($t = -5.79$, $p = 0.007$) decrease, from 39.57% (1.1) to 14.27% (0.95), followed by a slower recovery rate of 0.9% coral cover⁻¹. Consequently, coral cover 'after recovery' remained significantly lower in 2018 than before the disturbance in 2006 (from 36.72% to 19.6% [$t = -5.29$, $p = 0.01$]). Conversely, Nengo Nengo was the only undisturbed reef. Being spared by major disturbances, its reefs exhibited a relatively stable trajectory over the past 25 years, with a slight but significant increase in coral cover from 15.3% (0.53) in 1994 to 26.9% (1.6) in 2015 ($t = 3.92$, $p = 0.036$). As for the island of Raiatea, thermal stress events occurred for Tikehau and Nengo Nengo (DHW = 6.7 °C-weeks and DHW = 4.2 °C-weeks, respectively) but these events did not cause a clear decrease in coral cover ($p > 0.05$). The contribution of the minor thermal anomaly of 1998 in Tikehau might have affected simultaneously to the coral decrease after the cyclone.

Finally, reefs in the Austral Archipelago (island of Tubuai) reached 25% (1.8) coral cover in 2005, but the 2006 bleaching event (DHW = 14.1 °C-weeks) led to a 20% loss of coral cover (from 25.2% [1.8] to 20.4% [1.4]). After this, the impact of cyclone Oli in 2010 further caused

a 97% loss of coral cover ($t = -8.65$, $p = 0.006$). Here, the recovery rate after the disturbance was the lowest across all islands and disturbance events (0.65% coral cover⁻¹) and resulted in a coral cover after recovery (2019, 4.4%) that was significantly lower than before (2005, 25.4%, $t = -7.29$, $p = 0.01$). Reefs around Tubuai suffered from multiple heat stress events (7 total, Figs. 2 SD & 3 SD) ranging from 1 up to 16.3 °C-weeks in 2017 that did not cause further significant declines in coral cover ($p > 0.05$) but potentially compromised recovery.

Overall, disturbance type had a significant effect on Δ coral cover ($F = 13.93$, $p = 0.007$; linear model: $se = 7.23$, R-squared: 0.92, p -value: 0.03) (Fig. 3), with Δ coral cover showing more pronounced declines following COTS outbreaks ($t = [-18.7$ to $-10.5]$, and $p < 0.005$), COTS & cyclones simultaneously ($t = [-9.32$ to $-4.08]$, and $p = [0.002$ to $0.03]$) and cyclones alone ($t = [-19.48$ to $-2.11]$, and $p = [0.0004$ to $0.16]$) than when compared to heat stress ($t = [-1.17$ to $6.4]$, and $p = [0.009$ to $0.566]$), which did not cause universal declines (Fig. 3).

3.2. Disturbance effects on coral community composition

Following cyclones Martin and Osea of 1997, the community composition of Raiatea changed (PERMANOVA: $F_{\text{Statistic}} = 9.336$, $p = 0.034$) but remained similar in Tikehau (PERMANOVA: $F_{\text{Statistic}} = 3.803$, $p = 0.066$). The dominant genera in Raiatea switched from *Acropora* to *Pocillopora*. Their contribution changed from 43% and 16% to 33% and 56%, respectively. In Tikehau, the relative contribution of *Pocillopora* decreased from 83% to 75% but the genus remained dominant (Fig. 4A).

Following the COTS episodes and cyclone Oli in the 2000s, all islands exhibited shifts in coral community composition (PERMANOVA: $F_{\text{Statistic}} = [94.05$ to $5.62]$, $p < 0.05$) (Fig. 4B). In the four islands of the Society Archipelago, the relative contribution of *Pocillopora* was consistently higher in 2017–2019 (78.4%, 71.1%, 59.8% and 72.1%, respectively) compared to 2004–2005 (36.3%, 46.3%, 7.43% and 48.2%,

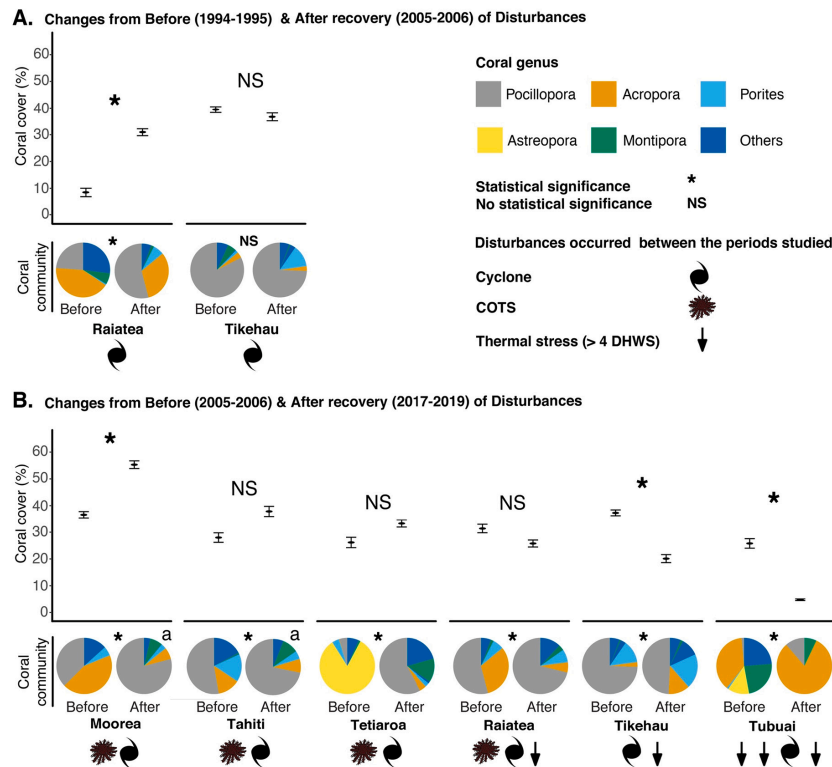


Fig. 4. Changes in peak coral cover and coral community composition 'before' and 'after recovery' from disturbances that affected French Polynesia during our study. Panel (A) refers to the period between 1995 and 2005; panel (B) refers to the time between 2006-07 and 2017-2019. Colors in the coral community represent each coral genus. * = significant, NS = not significant.

respectively). Mo'orea showed a particularly strong shift towards new domination of *Pocillopora* ($F = 94.05$, $p = 0.03$). The same occurred in Tetiaroa, driven by the near-complete loss of *Astreopora* ($F = 74.04$, $p = 0.03$), which was also replaced by *Pocillopora*. In contrast, in the Tuamotu Archipelago, Tikehau showed a considerable decrease in *Pocillopora* after the impact of cyclone Oli, from 75.6% in 2006 to 46.6% in 2018 ($F = 5.62$, $p = 0.04$). Notably, even in the relatively disturbance-free reefs of Nengo Nengo, where coral cover was stable, significant shifts in community composition occurred, mostly due to increases in the *Other* category ($F = 16.06$, $p = 0.029$). Finally, in the Austral Archipelago, which was also unaffected by COTS, Tubuai experienced a significant shift towards a more pronounced dominance of *Acropora* corals than before the cyclonic disturbance ($F = 25.149$, $p = 0.03$).

In accordance with the observed genus-specific dynamics, the nMDS ordination revealed considerable temporal and spatial differences in coral communities (PERMANOVA $F = 3.27$, $p = 0.002$ for year; $F = 7.91$, $p = 0.001$ for island). Only Mo'orea and Tahiti showed similarities in coral community composition (PERMANOVA-pairwise comparisons; $F = 2.38$, $p = 0.059$). As expected, Nengo Nengo reefs and Tikehau showed the least pronounced compositional changes over time, while temporal trajectories were particularly expansive for Tubuai, Tetiaroa, and Mo'orea. Aside from reefs in Tubuai, all surveyed islands converged towards coral communities dominated by *Pocillopora* colonies, which

had high recovery rates (e.g., 5.38 and 4.41 *Pocillopora* cover-year⁻¹, contributing up to 78.4% to 71.1% of the total recovery, respectively, in Mo'orea and Tahiti) (Fig. 5). Consequently, *Pocillopora* increased the contribution after recovery because the genus accounted for between 7.4 and 48.2% of cover before the COTS and cyclone disturbances in 2007-2010 and between 59.8 and 78.4% of cover after recovery across all islands, with the exception of Tikehau and Tubuai. *Pocillopora* represented between 57% and 84% of the overall recovery rate for all studied islands, except for Tubuai (Fig. 4 SD). This strong recovery of *Pocillopora* offset the very low recovery rates of *Acropora* (<0.6% *Acropora* cover-year⁻¹) and *Porites* (<0.3% *Porites* cover-year⁻¹).

4. Discussion

Disturbances of fundamentally different nature and magnitude can severely influence coral reef ecosystems by restructuring scleractinian coral assemblages. By analyzing long-term monitoring data on coral assemblages across French Polynesia, we reveal distinct causes of coral mortality and recovery dynamics over 26 years. Of the seven studied reefs, six were severely impacted by COTS predation and cyclones, which appear to represent the major drivers of coral mortality over the surveyed period from 1993 to 2018. In contrast, heat stress had limited impacts on the studied reefs during the survey period, except for reefs in

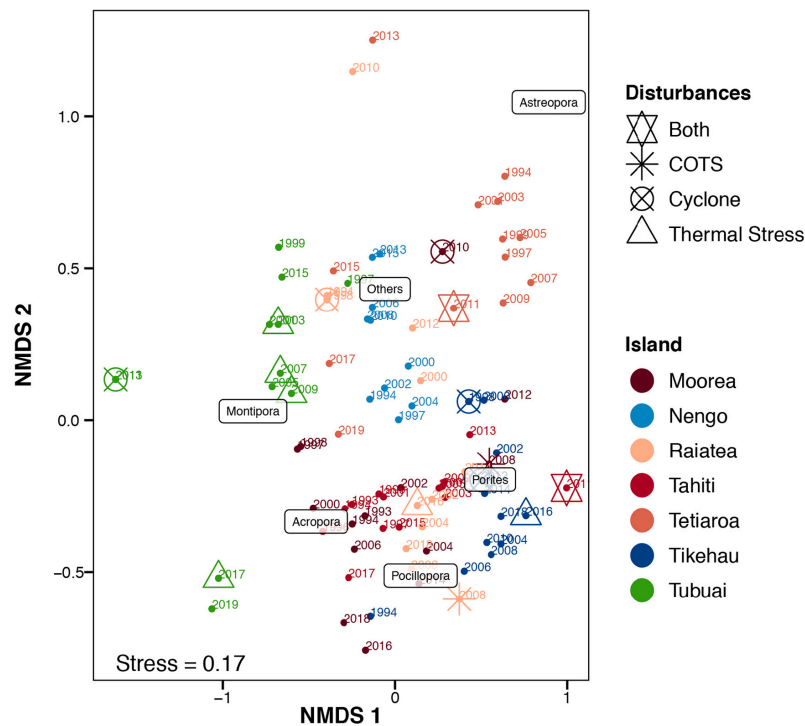


Fig. 5. nMDS ordination on the Bray-Curtis dissimilarity matrix of coral community composition across space and time. Symbols display the different disturbances. The disturbances correspond to the first survey after the disturbances, not the year the disturbance occurred. Coral genera are displayed in black inside labels.

Tubuai, especially during La Niña events. Furthermore, heat stress events may have compromised ongoing recovery across different islands. While coral cover showed distinct pulse dynamics in synchrony with disturbances, coral community composition exhibited more linear dynamics with a relatively consistent (five out of seven islands) convergence towards communities dominated by *Pocillopora* colonies.

4.1. Spatially divergent recovery dynamics

Our study revealed distinct temporal dynamics in coral cover across the seven islands. Specifically, while Mo'orea, Tahiti, Tetiaroa and Raiatea exhibited good recovery after disturbances, and values of coral cover in 2018 were close to the maximum observed since 1993, Tikehau and Tubuai fell significantly short of these values. Given the comparable nature and intensity of disturbances, these results suggest that reefs in different archipelagos are subject to fundamentally divergent ecological processes pertaining to the recovery of coral populations.

One explanation for the differences in coral recovery may lie in different connectivity and/or distinct local environmental conditions resulting in diverse coral settlement and recruit survival patterns. The fast and extensive recovery in the four Society islands mirrors previous results from Mo'orea (Adjeroud et al., 2009; Bramanti and Edmunds, 2016; Trajon et al., 2011; Lamy et al., 2016), and might be facilitated by strong connectivity within the Society Archipelago and a resulting supply of larvae from neighboring islands and/or deeper reefs (Bongaerts et al., 2010; Tsounis and Edmunds, 2016). Genetic evidence

suggests the Society Archipelago as the most likely source of larvae after the disturbances, since *Pocillopora meandrina*, for example, exhibits a strong spatially clustered genetic structure within the Society Archipelago (Magalon et al., 2005). Thus, recovery from natural pulse disturbances appears to be swift in the well-connected Society Archipelago (3.1% to 6.8% coral cover-year⁻¹), supporting the previously suggested high potential for recovery of Indo-Pacific reefs (3% to 9.5% coral cover-year⁻¹; Done et al., 1991; Baker et al., 2008; Graham et al., 2011; Gilmour et al., 2013).

In contrast, more remote islands such as Tubuai (Austral) and Tikehau (Tuamotu) were much slower to recover or failed to do so entirely, which may suggest an important role for seascape configurations in governing recovery dynamics. The distance between reefs in our study generally ranged from 17 km (Tahiti-Mo'orea) to 607 km (Tahiti-Tubuai), thus lying well below the 850 km dispersal distance reported for scleractinian corals (Robitzsch et al., 2015). However, given the largely passive dispersal of coral larvae, oceanographic currents are key determinants of dispersal dynamics (Pineda et al., 2007). In French Polynesia, surface currents flow in average southwestward north of 20°S (South Equatorial Current; Rougerie and Ranchert, 1994), and eastward in the south (South Tropical Counter Current; Martinez et al., 2009). Thus, surface waters are unlikely to transport larvae from the Society and Austral archipelagos to the Tuamotu, potentially limiting the scope for replenishment of the reefs studied in the Tuamotu from the Society. The recovery dynamics in Tikehau lend some support to this hypothesis. The drastic decline in recovery rate from 4.08 to 0.89% coral

cover-year⁻¹ between the cyclones of 1997 and 2010 in Tikehau suggests that, while a large enough regional pool of larvae may have been present to boost recovery after the first event, a resulting lack of recruitment may have stymied recovery after the second event. This insufficient recovery might be associated with inhospitable environmental conditions mediated by heat stress (i.e., DHW = 6.7 °C-weeks), which can impede the survival of coral larvae and recruits while not affecting adult coral cover. The lack of recovery after the cyclone of 2010 in Tikehau deserves further studies to identify whether coral recovery potential has been permanently altered (i.e. reef source of larvae) by changes in larval connectivity, or whether local degradation of environmental conditions is responsible for the lack of recovery.

Conversely, larvae from the Society Archipelago might be advected to the Austral Archipelago, since the average surface currents in the region (Martínez et al., 2009; Tomczak and Godfrey, 2013) can connect the two archipelagos (Martínez et al., 2007). Yet, the potential influx of larvae does not seem sufficient to counterbalance the heat stress suffered by coral larvae and explain the slow recovery. Indeed, since cyclone Oli in 2010, coral communities in Tubuai experienced intense heat stress (e.g., DHW = 16.3 °C-weeks in 2017). While this had limited effects on the already limited coral cover (less than 2% in 2017), these thermal anomalies may have compromised the survival of local coral larvae and recruits during and after the critical settlement phase (Randall and Szmant, 2009). In addition, as the southernmost island in our dataset, corals in Tubuai are exposed to the lowest Polynesian SSTs during winter, which approach the lower coral temperature limits (Kleypas et al., 1999). These cold temperatures may reduce coral growth and recovery capacity after disturbances (Rodolfo-Metalpa et al., 2008; Anderson et al., 2017), but also alter the survival of coral larvae arriving from the Society Archipelago that are less adapted to such a wide range of temperatures. Thus, beyond dispersal, environmental context is critical for the interpretation of the observed recovery dynamics.

4.2. Compositional changes

The compositional changes in coral communities showed similar spatial dynamics as the overall recovery trajectories, with Tikehau and Tubuai being the only islands that were not characterized by a shift towards *Pocillopora* colonies. In contrast, in the Society Archipelago, the loss of corals in the Acroporidae family (*Acropora*, *Astrotopora*) was compensated by a stark increase in the already dominant genus *Pocillopora*. *Pocillopora* is one of the primary reef-building genera on Indo-Pacific reefs (e.g. Carriquiry et al., 2001; Glynn et al., 1972; Veron and Pichon, 1976) and has been dominant in French Polynesia for decades. However, historically, *Acropora* colonies have contributed more substantially to recovery than in the present study (e.g., recovery in 1991; Adjeroud et al., 2009). Our study emphasized this contribution in Raiatea, where the recovery rate of *Acropora* was 1.56% coral cover-year⁻¹ after the cyclone of 1997 but only 0.18% after the COTS of 2007 and cyclone 2010. This dwindling contribution of *Acropora* in recent years in French Polynesia may be driven by a combination of the life-history of acroporid corals and recent developments on Polynesian reefs.

While *Acropora* and *Pocillopora* share similar competitive life-history strategies (Darling et al., 2017), the prevalence of *Pocillopora* on Polynesian reefs is likely attributable to several ecological traits. First, while *Acropora* larvae require specific substrata for settlement (e.g., crustose coralline algae, CCA) to induce metamorphosis (Baird and Hughes, 2000; Baird and Morse, 2004), *Pocillopora* larvae can settle on fairly unconditioned surfaces (Atoda, 1951, 1947a, 1947b; Harrigan, 1972). Since reef colonization by CCA can be slow (Klumpp and McKinnon, 1992), weedy *Pocillopora* corals may enjoy early colonization success in open space and on barren or poorly conditioned reef substrata following disturbances (Connell, 1973; Grigg and Maragos, 1974; Loya, 1976), especially in comparison with other genera (Darling et al., 2012). In fact, after 2010, the loss of corals in Mo'orea was followed by the rapid establishment of turf algae (Díaz-Pulido et al., 2009; Díaz-Pulido and

McCook, 2002). While herbivorous grazing on reefs around Mo'orea is seen as sufficient to prevent the establishment of macroalgae following disturbances (Holbrook et al., 2016), species-specific effects of herbivore grazers on benthic successional dynamics (Burkepile and Hay, 2010) suggest that even nuanced shifts in herbivore composition (Han et al., 2016) could hamper the establishment of CCA. This would likely favor colonization of *Pocillopora* over *Acropora* larvae in the Society Archipelago. Second, *Pocillopora* propagules have the ability to travel long-distances (up to 850 km for *P. verrucosa*; Robitzsch et al., 2015). As such, *Pocillopora* species may boast higher levels of connectivity compared to acroporids across the scattered islands of the Society Archipelago (Magalon et al., 2005). Continental reefs in the Indo-Pacific (Wood et al., 2014), where recovery dynamics do not customarily result in the dominance of *Pocillopora*, are likely to be less prone to the dispersal-driven effects that may underpin *Pocillopora* dominance in French Polynesia.

4.3. Cyclones and COTS impacts vs. temperature-mediated stress effects

Across the studied islands, COTS outbreaks and cyclones appeared to have a more significant impact on coral cover and community composition than heat stress events. While this may suggest a capacity for local management to enhance reef resilience in the face of climate change, our findings need to be interpreted with caution. Chronic stressors, such as warming SSTs may affect recovery processes even under excellent local management. Non-lethal, chronic thermal stress increased during the past 26 years in all sites (even Nengo Nengo, which did not show clear acute disturbances). Across locations, there was an evident decline in mounding and plating corals such as *Astrotopora* and *Acropora*. In contrast, branching/weedy corals such as *Pocillopora* increased in their contribution to coral cover. Thus, similar to the Caribbean, chronic stressors that were not considered in this study may play a role in shifting community composition (Alvarez-Filip et al., 2009). In French Polynesia, this shift is clearly going towards a monoculture of *Pocillopora*, which raises critical questions concerning the functioning and resilience of the newly formed assemblages (McWilliam et al., 2020; Pratchett et al., 2015).

Decades of research have revealed strong effects of both species identity and diversity on ecosystem functioning (Cardinale et al., 2012; Duffy et al., 2017). On coral reefs, the relationship between diversity and functioning is relatively poorly explored (Brandl et al., 2019), but emerging evidence suggests that coral growth is, in fact, promoted by species richness (Clements and Hay, 2019; McWilliam et al., 2018). The observed recovery dynamics on Polynesian reefs suggest a strong contribution of *Pocillopora* corals to functioning (i.e., coral cover); yet, care must be taken not to conflate coral cover with rates of calcification that underpin reef scale functioning (Brandl et al., 2019). At this stage, we are unable to resolve whether the revealed shifts towards *Pocillopora* represent a permanent, stable community shift or a temporary successional shift that will soon give way to a more diverse community. In the latter case, it appears that intervals between disturbances provide insufficient time for the re-establishment of the previous community.

Regardless of the mechanism that has caused the current emergence of *Pocillopora*-dominated reefs, the concept of response diversity suggests a higher vulnerability of monocultures to disturbances such as heat-stress events in the future (Dalin et al., 2009; Lin, 2011). Reefs dominated by a single genus have a more limited range of traits and functions to persist and survive under challenging conditions than those with more diverse reef ecosystems (Aronson and Precht, 1995; Palumbi et al., 2009). Therefore, despite the apparent resilience of Polynesian reefs to climate change to date, the recent shift towards *Pocillopora* dominated states on Polynesian reefs may severely compromise their capacity to cope with future global changes. In fact, recent large-scale bleaching throughout the Society Archipelago in 2019 (pers. obs.) suggests that climatic disturbances will have more dramatic effects than previously observed. This observation highlights the importance of

examining the historical context of coral communities to understand future responses to disturbances.

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CRDiT authorship contribution statement

Gonzalo Pérez-Rosales: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Simon Brandl:** Writing – review & editing. **Yannick Chancerelle:** Data curation. **Gilles Siu:** Data curation. **Eloïdie Martinez:** Data curation, Writing – review & editing. **Valeriano Parravicini:** Formal analysis, Writing – review & editing. **Laetitia Hédouin:** Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix 4: Manuscript – Long-term monitoring of benthic communities reveals spatial determinants of disturbance and recovery dynamics on coral reefs

Foreword

This publication documented the last 13 years of the shallow coral reefs around the island of Moorea in French Polynesia. The long-term study shows spatiotemporal contrasted coral dynamics between the fringing, barrier and outer reefs. I joined this publication after being requested to make similar analyses on community composition and cover dynamics than **Appendix 3**. Before and during my PhD, I devoted significant time to helping write the manuscript and the reviewing processes. The publication is included in the thesis because it perfectly fits the context of shallow coral reefs in Moorea, French Polynesia.

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Long-term monitoring of benthic communities reveals spatial determinants of disturbance and recovery dynamics on coral reefs

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ABSTRACT: Coral reefs across the globe are facing threats from a variety of anthropogenic disturbances. Consequently, the proportional representation of live scleractinian corals in the benthic community has declined substantially in many regions. In contrast, parts of the reef ecosystem around Mo'orea (French Polynesia) have displayed remarkable rebound potential. Nevertheless, detailed studies of when, where, and to what extent reefs have been disturbed and subsequently recovered in the different reef habitats are lacking. Using long-term monitoring data (2004–2018), we reveal that the spatiotemporal dynamics of benthic communities differ markedly between the contiguous inner (fringing and barrier) and outer (fore) reefs. Coral communities on inner reefs vary spatially but were remarkably stable over 15 yr, exhibiting consistent levels of coral and algal cover, with no evidence for disturbance-driven regimes or community transitions. In contrast, the outer reefs showed marked declines in coral cover following consecutive acute disturbances, but coral recovered rapidly thereafter. Nevertheless, community composition changed significantly, with *Pocillopora* replacing *Acropora* as the dominant genus at several sites, indicating a more subtle but potentially critical transition into an alternative state defined by the prevalence of a single, fast-growing genus. Inner reef stability and outer reef recovery provide evidence that the effects of environmental disturbances and chronic anthropogenic stressors can manifest in fundamentally different ways, depending on prevailing conditions. Our results suggest important ecological and physical links between inner and outer reef systems that influence the observed dynamics, emphasizing that reef ecosystem management and conservation strategies need to consider all habitats.

KEY WORDS: Reef habitats · Spatial resilience · Natural perturbations · Pacific · *Pocillopora* · Regime shift

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1. INTRODUCTION

Disturbances are a natural component of ecosystems, shaping the composition of biological communities through time and space (Pickett et al. 1989).

The effects of disturbances depend on their severity, frequency, and environmental context. Due to the ever-increasing human footprint on our planet, many ecosystems are now experiencing altered disturbance regimes that can combine with characteristics

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of the prevailing environment to shift communities into alternative states (Scheffer & Carpenter 2003, Hughes et al. 2013). As a consequence, several shifts between stable states induced by human-mediated disturbances have been reported in recent years, with some of them leading to undesirable ecological and economic outcomes (e.g. biodiversity loss, erosion of resilience, fishing and tourism industry loss of income; Pecl et al. 2017).

Despite being naturally prone to disturbance-driven changes in biotic structure (Madin & Connolly 2006), coral reefs are currently experiencing unprecedented declines due to a combination of natural and anthropogenic stressors at various scales (Bruno & Selig 2007, De'ath et al. 2012, Jackson et al. 2014, Smith et al. 2016, Hughes et al. 2017a,b). Disturbances on coral reefs range from tropical storms and cyclones (Foster et al. 2011, Perry et al. 2014, Gouezo et al. 2015) to outbreaks of predators such as the seastar *Acanthaster planci* (Moran 1986, Sano 2000, Adam et al. 2011, Kayal et al. 2011, 2012), or exposure to extreme environmental variations (e.g. seawater surface temperature anomalies or nutrient pollution; Adjeroud et al. 2009, Hughes et al. 2018a,b, Donovan et al. 2020). Responses of reefs to these disturbances can be measured in the spatial extent and composition of the benthic community. Change in the proportional occupation of the seafloor by corals, as the primary reef-building organisms, is the most common indicator of the status and trajectory of reefs (e.g. Bruno & Selig 2007, Gilmour et al. 2013). As such, examining benthic community composition and coral cover across space and time can inform us about the responses of reefs to disturbances, while providing a framework that allows for broad comparisons of reefs in different geographic regions or with varying prevailing conditions (Darling et al. 2019).

Naturally, there is great variability in how different disturbances affect coral reefs. Nevertheless, even the same disturbance can yield greatly differing responses on reefs, in both close spatial proximity (e.g. same island) or across large distances (e.g. biogeographic regions). For example, reefs on the Great Barrier Reef and in Micronesia that were affected by the same type of disturbances (*A. planci* outbreaks) varied substantially in their post-disturbance composition and recovery trajectories (i.e. the way and extent to which the reefs recovered; Graham et al. 2014, Houk et al. 2014). These divergent responses highlight the natural environmental variability at relatively small spatial scales such as neighboring islands (e.g. Wismer et al. 2009, Williams et al. 2013), which shapes coral reef communities and their inter-

actions with disturbances. On the scale of single islands or reef systems, environmental conditions can differ substantially, both based on the reef zone (e.g. inner and outer reefs) and the dominant wave exposure and direction (e.g. Done 1982, Alevizon et al. 1985). Exposed outer reefs are usually characterized by intense hydrodynamic pressure from wave action, often showing high susceptibility to cyclones and other severe weather events (Done 1992, Harmelin-Vivien 1994). In contrast, sheltered fore reefs or fringing and back reefs are usually dominated by calmer conditions but can be susceptible to disturbances created by nutrient run-off due to coastal development or temperature-induced coral bleaching (Donovan et al. 2020). Despite the important roles of fine-scale environmental conditions for mediating disturbance effects and recovery, there are few long-term assessments of fine-scale spatial differences in reef trajectories around single islands (Madin et al. 2018).

The capacity of each reef habitat to resist and/or respond to disturbances is reflected in the stability of their communities over time. While some reefs have demonstrated a strong capacity to absorb disturbances and remain in or return to a coral-dominant state (Jackson 1992, Pandolfi & Jackson 2006, Graham et al. 2015), others have changed to dominance by either small, weedy coral genera, or other benthic groups such as macroalgae, sponges, or soft corals (McManus & Polsenberg 2004, McClanahan et al. 2007, Bruno et al. 2009, Hughes et al. 2010, Darling & Côté 2018). The frequency and longevity of such phase shifts remains vigorously debated (Bruno et al. 2009, 2014, Graham et al. 2015, Mumby et al. 2016), not least because the recovery following natural and anthropogenic disturbances can exhibit marked variations in temporal and spatial scales (Connell 1997, Jackson et al. 2014). Long-term studies with sufficient resolution to document fine-scale changes in the coral community structure, leading to understanding the recovery dynamics at the island scale, are therefore indispensable (Roff & Mumby 2012).

With a contiguous reef system surrounding the entire island and a long history of research, the island of Mo'orea (French Polynesia) provides an excellent opportunity to evaluate the spatiotemporal dynamics and recovery potential of a coral reef ecosystem facing major disturbances across multiple sites and habitats (Table 1). The effects of major disturbances (e.g. a bleaching event in 1991, an *A. planci* outbreak in 2006–2009, and cyclone Oli in 2010) on the succession of benthic (Adjeroud et al. 2009, Kayal et al. 2012, Adjeroud et al. 2018)

Table 1. Disturbances that occurred in Mo'orea over the past 40 yr

Year	Type of disturbance			Source
	Bleaching	Cyclone	<i>Acanthaster planci</i> outbreak	
1978–1980			All around Mo'orea	Surveyed in Faure (1989) Reported in Bouchon (1985, 1996)
1983	Moderate			Reported in Glynn (1984, 1991), Williams & Bunckley-Williams (1990), Salvat (1992), Salvat & Aubanel (2002)
1987	Moderate			Authors' pers. comm.
1991	Strong			Surveyed by Salvat (1992), Gleason (1993)
1994	Strong			Surveyed by Fagerstrom & Rougerie (1994), Hoegh-Guldberg & Salvat (1995), Adjeroud et al. (2005)
2002	Strong			Surveyed by Carroll et al. (2017), Y. Chancerelle et al. unpubl. data, Penin et al. (2013), Adjeroud et al. (2005)
2006–2009			All around Mo'orea	Reported in Kayal et al. (2012), Lamy et al. (2015), Lamy et al. (2016)
2010		Oli in February		Reported in Lamy et al. (2015), Lamy et al. (2016), Adjeroud et al. (2018)

and fish communities (Lamy et al. 2015, Galzin et al. 2016, Lamy et al. 2016, Martin et al. 2017, Viviani et al. 2019) have been assessed at a few sites on the fore reefs. However, in-depth analyses of the long-term dynamics and transitory states of coral communities across habitats and locations are lacking (Holbrook et al. 2018). Here, we used long-term monitoring data on benthic cover and composition over 15 yr at 13 sites around the island to analyze the spatiotemporal dynamics of reefs from 3 habitats (fringing, barrier and fore reefs) under the consideration of various acute and chronic disturbances. Assessing changes in community composition over time and comparing pre-disturbance and post-disturbance coral reef characteristics, while quantifying the importance of local and broad scale factors on these changes, is key to a better understanding and management of the complex coral reef ecosystem surrounding Mo'orea.

2. MATERIALS AND METHODS

2.1. Study system

Mo'orea (17° 30' S, 149° 50' W) is a volcanic island in the Society Islands archipelago, French Polynesia (Fig. 1a), home to approximately 17 000 people, whose livelihoods are supported by the surrounding reef system through tourism, fishing, and other services. The reef around Mo'orea is structured from the shore to the open sea as follows: (1) the fringing reef, adjacent to the shore, (2) the barrier reef, separated

from the fringing reef by a deeper channel, and (3) the fore reef, from the barrier reef crest outwards.

2.2. Benthic monitoring data

We used data from the Mo'orea marine protected area (MPA) program from 2004 to 2018. This program uses the point intercept transect method (PIT, Hill & Wilkinson 2004) to estimate benthic community cover and composition (e.g. corals, identified to the genus level [Veron 1986, 2000, Bosserelle et al. 2014], algae, composed of macroalgae and turf, and abiotic substrate). For the PITs, points were placed every 0.25 m along 25 m length transects deployed at 10–12 m depth on the fore reef parallel to the reef slope, and at 0.5–2 m depth on the fringing and barrier reefs parallel to the coastline. The MPA program surveyed 13 sectors around Mo'orea, within all 3 habitats (fringing, barrier, and fore reefs; Fig. 1a) surveyed via 3 random transects (total $N = 39 \text{ yr}^{-1}$). This dataset was used here to analyze the dynamics of the benthic community structure across space in the different habitats and time.

2.3. Statistical analyses

To characterize the dynamics of the disturbance–recovery cycle observed during the study period, we calculated the mean coral cover and the mean number of coral genera pre-disturbance (2004–2006) and post-disturbance (2016–2018) at each site across habitats, as well as the number of years when coral

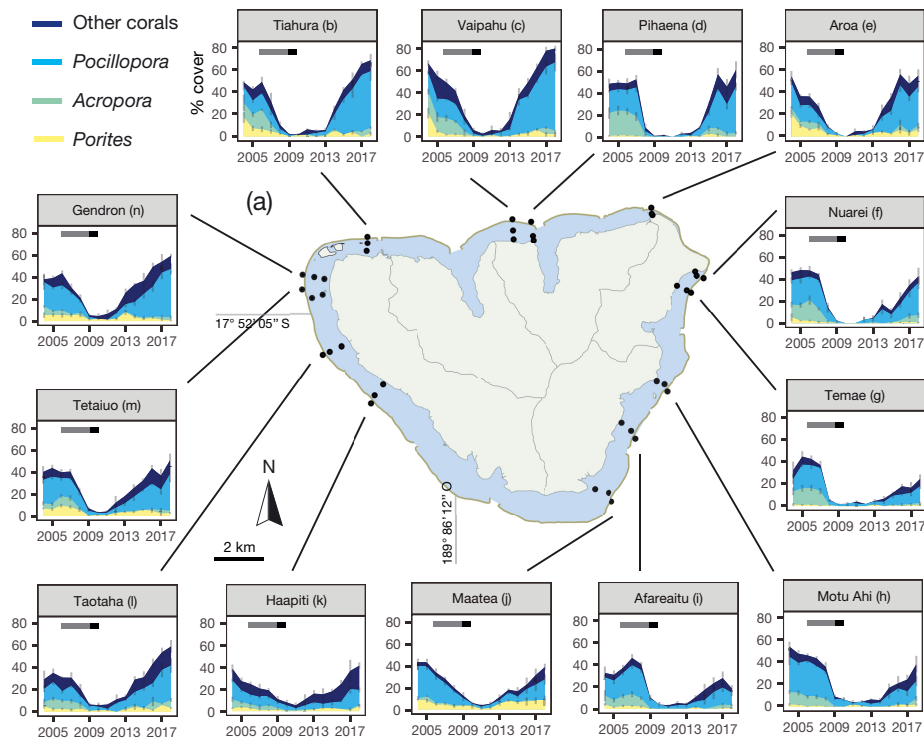


Fig. 1. (a) Map of Mo'orea showing the sampling locations on the continuum fringing, barrier, and fore reef (●). (b–n) Cumulated percent coral cover of the 3 main coral genera and other coral genera on the fore reef. Horizontal grey and black bars indicate, respectively, the 2006–2009 *Acanthaster planci* outbreak and the 2010 cyclone Oli. See Fig. S1 in the Supplement for fringing and barrier reef graphs

cover was $<5\%$ between these periods. For each habitat, we performed a hierarchical cluster analysis based on Euclidean distance between the sites (Gauch & Whittaker 1981) based on the scaled and centered matrix of these reef characteristics. We cut the resulting dendrogram at height = 3. For each habitat, we also used an ANOVA with the factor Period (2 levels: pre-disturbance and post-disturbance) and the factor Site (13 levels, one for each site) on coral cover and diversity to test the hypothesis that there are spatial differences of the surveyed reefs 'before' and 'after' disturbances. We used a Shapiro-Wilk test to assess the normality of the model residuals, which were normally distributed in all cases ($p > 0.05$), and a Bartlett's test to assess homogeneity of variances, which were equal for all samples.

To assess the importance of the variables 'site', 'habitat' and 'year' on the fine-scale coral community composition, a permutational multivariate analysis of variance (PERMANOVA) was performed on a distance matrix generated with the coral genus data. Then, to assess the specific effects of the different habitats on community composition, a permutation test was performed using 'fringing reef', 'barrier reef' and 'fore reef'.

We computed a set of non-metric multidimensional scaling (nMDS) ordinations based on the Bray-Curtis measure of dissimilarity (Shepard 1962, Kruskal 1964) between each year, calculated on Hellinger-transformed coral genus data for the 3 habitats separately to visualize long-term trajectories in coral community composition (genus level) between 2004 and

2018 in each habitat. We ran an ANOSIM (analysis of similarities, in which R statistic > 0.2 provides evidence for strong differences between 2 communities) to test the null hypothesis of no difference in relative genus composition between pre- (2004–2006) and post-disturbance (2016–2018) periods. All statistical analyses were performed in the statistical environment R version 3.1.2 with the *vegan* package (Oksanen et al. 2016, R Core Team 2017).

3. RESULTS

3.1. Coral cover and genus diversity dynamics

Reef habitats within the lagoon displayed heterogeneous benthic communities across sites (Fig. 2a,e), especially on the fringing reef, but showed a high compositional stability of the major groups over time (Fig. 2; fringing: b–d and barrier: f–h). We detected

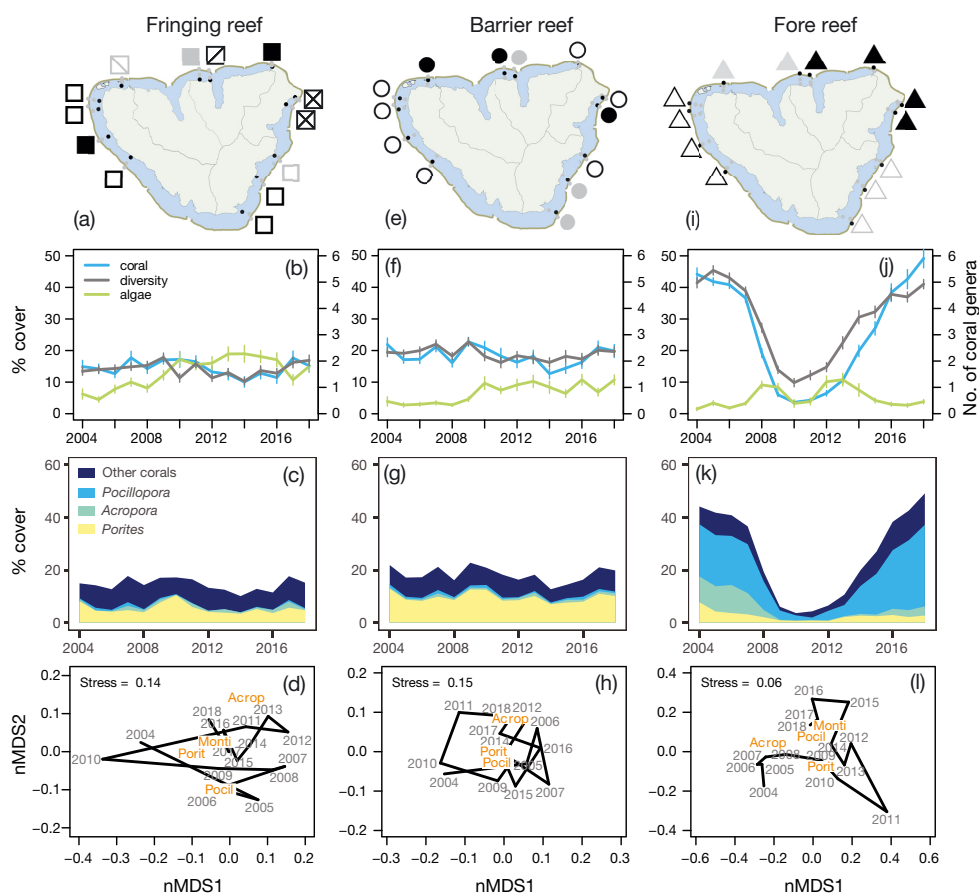


Fig. 2. (a,e,i) Maps of Mo'orea indicating site similarity: symbols filled similarly indicate site similarity (see Section 2 for details) for the 3 habitats (squares, circles and triangles for the fringing, barrier and fore reef, respectively) analyzed separately. (b,f,j) Percent coral cover, number of coral genera (diversity), and percent macroalgae-turf cover averaged across sites and replicates (vertical bars are SE; note the double y-axis scale). (c,g,k) Cumulated percent coral cover of the 3 main coral genera and other coral genera. (d,h,l) Non-metric multidimensional scaling (nMDS) of the coral assemblages showing the temporal trajectory of the coral community composition; the position of the main coral genera in the multidimensional space is indicated (Acrop: *Acropora*; Mont: *Montipora*; Pocil: *Pocillopora*; Porit: *Porites*)

no effects of disturbances on coral cover and coral diversity for these 2 habitats (ANOVA p-value > 0.05 for the Period factor), but sites varied significantly among them in terms of coral cover and diversity (ANOVA p-value for the Site factor < 0.05, and marginally different for coral cover on the barrier reef where p-value = 0.083). Despite a regular increase in algal cover over the study period on both habitats, it never exceeded coral cover on the barrier reef (Fig. 2b,f).

In contrast, the fore reef of Mo'orea displayed a much more dynamic community structure over time (Fig. 2j–l). The prevalence of algae (macroalgae and turf) was opposite to that of coral cover, but algae never permanently replaced coral as the dominant group around Mo'orea despite the acute disturbances (Fig. 2j). Coral cover pre- and post-disturbance showed no significant difference (Period factor p-value = 0.728, F -value = 0.127), and sites were not significantly different (Site factor p-value = 0.137, F -value = 1.915). Indeed, at all sites, the 2011–2018 period exhibited a remarkable recovery in coral cover, which reached $49.2 \pm 18.4\%$ (mean \pm SD) in 2018 on average around the island (Fig. 2j), and up to $80 \pm 4\%$ (mean \pm SD) at Vaipahu (north coast, Fig. 1c). More specifically, 8 yr after the lowest coral cover reported in Mo'orea in 2010, which decreased down to zero at all transects in Aroa and Nuarei, most outer reef sites (10 of the 13 sites investigated) reached similar (Pihaena, Aroa, Nuarei, Maatea, Haapiti, Tetaiuo: Fig. 1d–f,j,k,m) or higher (Tiahura, Vaipahu, Taotaha, Gendron: Fig. 1b,c,l,n) coral cover than recorded before the disturbances. Mean coral diversity, however, was significantly different pre- and post-disturbance (ANOVA p-value < 0.05 for the Period factor) but tended to go back to its original levels (Fig. 2j). Only Temae, Motu Ahi and Afareaitu showed disturbance-driven decreases in coral cover on the fore reef (Fig. 1g–i). Disturbance and recovery dynamics followed a gradient around the island, according to their geographic location (Fig. 2i), which were differently impacted by the disturbances: cyclone Oli mostly affected the northern coast, whereas the *Acanthaster planci* outbreak spread progressively around the entire island (see references in Table 1).

3.2. Coral community composition dynamics

Coral community composition differed significantly among habitats, sites, and years (PERMANOVA: $p = 0.001$: Table 2). However, the stronger effects

Table 2. Results of the PERMANOVA performed on the distance matrix of coral community composition for habitat, site and year. SES: standardized effect sizes

	F -statistic	SES	Pr (perm)
Site	10.16	43.64	0.001
Habitat	208.91	441.91	0.001
Year	49.75	72.46	0.001

were found by far for habitat, followed by year, then site (standardized effect sizes, SES: Table 2). Within habitats, while the fore reef strongly differed from the fringing and barrier reefs (SES < -9), the difference between the fringing and barrier reefs was less pronounced (SES = 2.4, Table 3).

On the fore reef, *Pocillopora* was the dominant genus between 2004 and 2018 at almost all sites, followed by *Acropora*, *Montipora* and *Porites* in various orders (Fig. 3). However, coral community composition differed between 2004 and 2006 (pre-disturbance) and 2016 and 2018 (post-disturbance) at almost all sites (ANOSIM: R ranging from 0.218 to 0.988, p-value from 0.001 to 0.007), except Taotaha ($R < 0.2$, $p > 0.05$). Specifically, contributions of *Pocillopora* increased markedly at most sites, particularly on the northern coast, where *Acropora* corals drastically decreased after the disturbances (e.g. Fig. 3b: *Pocillopora* went from 21.66 to 63.03%, and *Acropora* went from 19.12 to 5.04%). In contrast, sites on the southeastern side of the island, in particular, showed slower recovery and a much less pronounced (or no) increase in *Pocillopora* cover.

On the inner reefs, coral community composition was stable pre- and post-disturbance at most sites (ANOSIM: $R < 0.2$), with the exception of Nuarei on the fringing reef ($R = 0.348$, $p = 0.001$), and Aroa ($R = 0.256$, $p = 0.008$) and Vaipahu ($R = 0.477$, $p = 0.001$) on the barrier reef. *Porites* and *Montipora* characterized most of the inner reef sites around

Table 3. Results of the permutation test performed on the distance matrix of coral community composition in the reef habitats. SES: standardized effect sizes

	F -statistic	SES	Pr (perm)
Overall	86.17	80.80	0.001
Barrier reef – Fringing reef	2.37	2.40	0.015
Barrier reef – Fore reef	-9.70	-9.77	0.001
Fringing reef – Fore reef	-11.77	-11.96	0.001

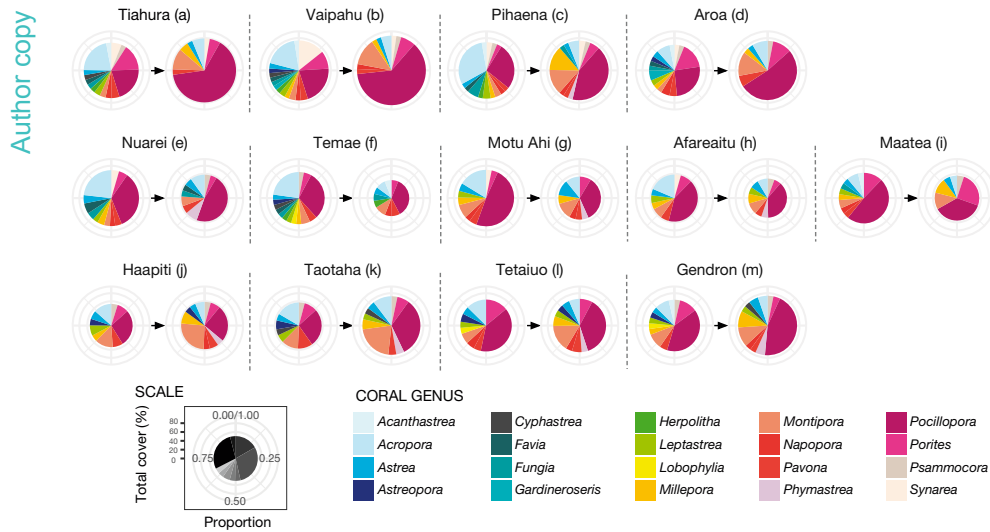


Fig. 3. Proportion of coral genera before (i.e. averaged over 2004–2006; left) and after (i.e. averaged over 2016–2018; right) the *Acanthaster planci* outbreak and cyclone Oli on the fore reef. Circle size is proportional to the coral percent cover. See Figs. S2 & S3 in the Supplement for fringing and barrier reef graphs

Mo'orea (Fig. 2c,g & Figs. S1, S2, S3 in the Supplement; www.int-res.com/articles/suppl/m672p141_supp.pdf). Temae, Nuarei, Vaipahu, Pihaena and Motu Ahi were distinct from their neighbors in terms of coral composition (Fig. S2); *Acropora* dominated in Temae while other genera such as *Montipora* dominated in Motu Ahi (Figs. S1 & S2).

4. DISCUSSION

4.1. Habitat variation in reef dynamics

Although coral reefs are naturally prone to disturbances, increasing anthropogenic pressure has intensified interest in the response of reefs to natural and anthropogenic stressors. Our results show that, on the scale of a single island, disturbance and recovery dynamics depend greatly on the environmental settings of reefs. Specifically, we show fundamental differences between highly dynamic, rapidly recovering outer reefs subjected to acute natural disturbances and relatively stable inshore reefs with low but consistent coral cover (<20%) over 15 yr. Furthermore, we highlight that, despite a relatively consistent recovery on the exposed reefs, the extent and

nature of recovery hinges on contributions of a single genus (*Pocillopora*), for which population dynamics differ spatially. Our results suggest that, while the broad disturbance dynamics of reefs depend strongly on the prevailing ecological dynamics across habitats, more subtle characteristics of recovery trajectories can vary across sites in the same habitat at the scale of a small Pacific island.

Effects of various disturbances have been documented to differ according to the distance of reefs from shore, their depth, and habitats (Berkelmans & Oliver 1999, Fabricius et al. 2008, Baker et al. 2016), with near-shore reefs displaying greater vulnerability to land-based disturbances than offshore reefs (Smith et al. 2008a, Donovan et al. 2020). Reefs around Mo'orea are relatively sheltered from coastal anthropogenic developments compared to some other Pacific islands (e.g. Hawaii: Hunter & Evans 1995; Australia: Smith et al. 2008b), which may explain the stability of coral cover on the inner reefs in the present study. However, spatial differentiation of benthic communities was stronger on inner reefs compared to outer reefs. This suggests that long-standing differences in the geography of the island and the patterns of human development may have shaped these lagoonal reefs over the past few

decades, or even centuries. Recent results, which document interactive effects of nutrients and sea surface temperature on coral bleaching in Mo'orea's lagoon, support this line of evidence (Donovan et al. 2020). It is possible that the observed stability of inner reefs despite a suite of disturbances represents a hysteresis due to long-standing, chronic stressors that have shifted reefs into a stable state of disturbed benthic communities.

Conversely, outer reefs showed a highly dynamic response to disturbance, with dramatic losses but a rapid recovery. This observed recovery of outer reefs may, at least in part, be facilitated by the presence of the expansive lagoon around Mo'orea and its associated reefs. First, lagoonal reefs may absorb much of the human-derived local impacts (e.g. nitrogen pollution), which can facilitate the recovery of further reefs (i.e. closer to the reef crest) after disturbances (Donovan et al. 2020). Second, inner reefs with stable benthic communities may provide a nursery area for coral-dependent organisms that facilitate recovery (Rouzé et al. 2015, Morgan et al. 2016). For example, in Mo'orea, parrotfishes that recruit to stable nursery habitat within the lagoon can move offshore during the course of their ontogeny to reduce macroalgae on the outer reef, thus promoting coral settlement and growth after the reefs were completely denuded (Adam et al. 2011, Lamy et al. 2016, Martin et al. 2017, Viviani et al. 2019). In turn, outer reefs absorbed the brunt of the hydrodynamic damage imposed by the cyclone and suffered much higher damage from the *Acanthaster planci* outbreak, thus safeguarding inner reefs from these acute disturbances. This highlights the interdependence of inner and outer reefs and the importance of considering divergent responses of reef habitats to acute and chronic stressors in synergy (Done 1992).

4.2. Processes underpinning recovery on outer reefs

The coral decline between 2006 and 2010 was the most dramatic reported on fore reefs in Mo'orea and was extremely consistent across sites. Nevertheless, 8 yr later, coral cover reached values similar to pre-disturbance levels at 10 of the 13 sites investigated, with an estimated recovery rate of $6.3\% \text{ yr}^{-1}$. Such fast recovery in Mo'orea is not without historical precedent, with comparable rates reported following an *A. planci* outbreak in 1979 and a cyclone in 1991 (Lamy et al. 2016). These recovery rates appear to be higher than many other reported cases (e.g. Colgan

1987, Connell et al. 1997, Sano 2000, Guzman & Cortés 2007, Gilmour et al. 2013, Morri et al. 2015, Gouezo et al. 2017) and strongly contrast with a complete lack of recovery on many Caribbean reefs (Jackson et al. 2014). There, several biotic and abiotic conditions combined with strong anthropogenic stressors appear to have interrupted recovery dynamics to shift reefs into low coral-cover states (Jackson et al. 2014). This long-term decline of *Acropora* in the Caribbean, where it was replaced by opportunistic, less structurally complex species (Green et al. 2008, Alvarez-Filip et al. 2011), provides a sobering example of stable shifts into alternative benthic compositional regimes, despite relatively consistent coral cover.

Contrasting with the Caribbean case, our results provide some insights into the potential processes that underpin recovery of the fore reefs in Mo'orea. Graham et al. (2015) suggested that high initial bottom complexity (3-dimensional structure) promotes reef recovery, but our results do not support this hypothesis as the recovery was preceded by a near-complete loss of structural complexity after the 2006–2010 disturbances. Instead, a combination of sufficient recruits (Adjeroud et al. 2018, Holbrook et al. 2018), sufficient herbivory (Martin et al. 2017, Viviani et al. 2019) and generally low algal prevalence due to high wave action may have permitted the essentially barren space to be colonized by competitive coral genera rather than algae. Indeed, bare substrate usually promotes the settlement of opportunistic genera, often attracting competitive and/or weedy corals (Darling et al. 2012), and reported peaks of *Pocillopora* recruitment (Adjeroud et al. 2018, Holbrook et al. 2018) support this assumption. In contrast to *Acropora* larvae (Tebben et al. 2015), *Pocillopora* larvae are more flexible and tend to colonize various microhabitats, from healthy reefs dominated by crustose coralline algae to ephemeral and exposed habitats (Riegl et al. 2013) and reefs altered by terrestrial runoff and dominated by macroalgae (Mwachireya et al. 2017). After settlement, a lack of competition on the mostly barren benthos may also have promoted a rapid growth and eventual dominance of young *Pocillopora* colonies, possibly because of the lack of competition with other corals and algae around. At sites where coral cover equaled or even exceeded pre-disturbance cover in 2018 (western and northern outer reef sites), the proportional contribution of *Pocillopora* invariably increased, predominantly at the expense of acroporid corals. Such dominance of *Pocillopora* over *Acropora* has been observed after previous disturbances on a

single reef in Mo'orea (Tiahura on the northern coast; Berumen & Pratchett 2006, Pratchett et al. 2011, Lamy et al. 2016). Our study confirms this dynamic around most (but not all) of the island (this study and Holbrook et al. 2018) and its importance for the recovery of coral cover. Indeed, on the eastern side of the island, the prevalence of *Pocillopora* did not show marked increases, and recovery was comparably poor.

While it is unclear whether dominance by *Pocillopora* after the disturbance is stable or merely a successional stage, the compositional changes have potential implications for the functioning of reefs around Mo'orea. While coral cover is a widely used metric to assess coral health worldwide, it may conceal important underlying ecological processes that are critical to our understanding of underlying ecological processes (Brandl et al. 2019). For instance, while reefs on the northern and western side of the island appeared to have been in excellent condition at the end of our monitoring (based on very good coral cover), the recovery may have been largely driven by the non-selective recruitment patterns of *Pocillopora* (Harriott 1983, Perez et al. 2014) associated with higher fecundity and population turnover than that of other genera (Darling et al. 2012). This may make these reefs functionally depauperate and vulnerable to future disturbance regimes. However, changes in coral community composition are likely to continue over the next decade around Mo'orea, with increasing contribution of the *Acropora* genus. But if the coral community remains monospecific on the mid-term, recovery from future disturbances (e.g. successive bleaching events, Hédouin et al. 2020) may be greatly compromised if conditions are less favorable for *Pocillopora*, as appears to be the case on the eastward side of the island. Monitoring and understanding the nuances of shifts in coral communities for the internal processes that govern coral reef ecosystem functioning and services present a critical objective for coral reef researchers and conservationists in the future.

While the present study is focused on how natural disturbances that occurred in Mo'orea more than 10 yr ago affected the reef, our findings can help mitigate anthropogenic stressors that are currently acting to shape coral reefs around the island. Specifically, by revealing the fundamentally different dynamics that act upon the different reef habitats around Mo'orea (mainly due here to natural disturbances caused by climate change and ocean warming and buffered beyond the barrier reef), our results make it clear that a single reef management plan for

the island is unlikely to succeed. Some levels of protection are already in place in Mo'orea, but there is little distinction between the 3 habitats. It is therefore important that the MPA program, which has been in place since 2004 (PGEM: 'Plan de Gestion de l'Espace Maritime'), considers the clear distinction among habitats in the future. Regular interactions between scientists, the population, consultants, practitioners in Moorea and the Government of French Polynesia regarding the PGEM and its benefits to the biological communities of the reef (e.g. Salvat & Aubanel 2002, Moreau et al. 2014, Moritz 2021) are encouraging to envision future improvement in the Government's management decisions to protect the reef in the long term. Indeed, protecting Mo'orea reefs from local anthropogenic stressors may better promote recovery after natural acute disturbance events, and, in return, understanding how these events shape the reef can allow managers to correctly implement appropriate measures at specific sites and habitats. Simultaneously, because local anthropogenic stressors are adding to the global-scale climate change and ocean warming effects on reef habitat and biological community dynamics, larger scale protection measures (such as reducing pollution at a global level) is now a necessity to increase the beneficial effects of protecting reefs locally by responsible governments.

Data accessibility. Data are available on the website SO CORAIL (http://observatoire.criobe.pf/CRIOBEData/displayMPAMooreaBenthos_PIT.jsp and upon request to Serge Planes (serge.planes@criobe.pf). R scripts are available upon request to Charlotte Moritz (charlotte.moritz@gmail.com).

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Appendix 5: Manuscript – Contrasting patterns of mortality in Polynesian coral reefs following the third global coral bleaching event in 2016

Foreword

This publication revealed the contrasting mortality patterns following the bleaching event that impacted French Polynesia in 2016. The study shows how some islands from the Society Archipelago were barely hit by bleaching (1% mortality) while other northern islands from the Tuamotu Archipelago experienced severe heat stress $9.2^{\circ}\text{C}\cdot\text{weeks}$ and up to 71% mortality. I joined this publication after being requested to make similar analyses on the satellite temperature extraction and calculation of degree heating weeks than **Appendix 3**. Then, I helped analyse additional data and write the manuscript. During my PhD, I devoted significant time to the reviewing processes. The publication is included in the thesis because it perfectly fits the context of how thermal bleaching events are impacting French Polynesia.

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Contrasting patterns of mortality in Polynesian coral reefs following the third global coral bleaching event in 2016

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Abstract In 2016, many tropical corals worldwide were exposed to anomalously high temperatures due to one of the strongest El Niño events ever recorded. Bleaching impacts were reported on 23 islands within three archipelagos of French Polynesia (Tuamotu, Society and Marquesas archipelagos). A detailed study on the effects of elevated temperatures on corals was performed on five islands (Mo'orea, Makemo, Hikueru, Marutea and Katiu) and revealed contrasting patterns of coral bleaching responses between Mo'orea (Society Archipelago) and the four islands of the Tuamotu Archipelago. While some reefs from the Tuamotu lost more than half of their coral cover,

in Mo'orea, less than 1% mortality was recorded 6 months after bleaching. During the 2016 bleaching event, certain reefs at 12 m depth in the outer reef habitats were not exposed to sufficiently long high-temperature periods (heat stress not exceeding 1.1 °C weeks in Mo'orea) to cause large-scale bleaching-related coral mortality. In contrast, other reefs in the Tuamotu Archipelago had DHW reaching up to 9.2 °C weeks and experienced severe mortality (up to 71%). Our study showed how differential heat stress exposure across reefs of French Polynesia led to different impacts on corals. Until now, Mo'orea reefs have been spared abnormally high temperatures leading to mortality and should be considered an important source of larvae to help maintain reefs on the surrounding islands.

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Introduction

The 2015–2016 El Niño event combined with global warming resulted in one of the three strongest ocean warming events since 1950 (L'Heureux et al. 2016). The Third Global Coral Bleaching Event (GCBE3) bleached and killed tropical reef corals throughout the world from mid-2014 through mid-2017 (Eakin et al. 2019 and references therein). Coral bleaching is a physiological response to elevated temperatures, characterized by the breakdown of the mutualistic symbiosis between the coral host and their microalgae of the family Symbiodiniaceae (LaJeunesse et al. 2018). Under normal conditions, microalgae provide coral tissue pigmentation and contribute up to 95% of coral energy requirements (Muscatine 1990). Bleaching is a reversible process, and corals can recover. However, in

the case of chronic or prolonged breakdown of coral-alga partnerships, the bleached corals will ultimately die (Lesser and Farrell 2004). Scientists and managers are still finalizing estimates of damages caused by the 2014–2017 GCBE3. The Great Barrier Reef Marine Park Authority report states that 29% of the shallow-water corals were lost during the 2016 event, and most of the mortality was located in the north of the Great Barrier Reef (GBR) (GBRMPA 2017). This coral bleaching event was the worst experienced by the GBR on record, with only 9% of the reefs escaping bleaching, compared to 42–45% in 1998 and 2002 (Hughes et al. 2017). In the Hawaiian archipelago, the GCBE3 caused approximately 75% of the colonies at A'alapapa Reef to show signs of bleaching (Minton et al. 2015), whereas the coral death toll at a reef in Western Samoa was 100% in mid-2015 (Berthe et al. 2016) due to a combination of abnormally high temperatures and outbreaks of the seastar *Acanthaster planci*. In the central equatorial Pacific, the GCBE3 had catastrophic impacts on certain coral reefs, such as a decline of coral cover from 17.8 (pre-bleaching) to 0.3% (post-bleaching) at Jarvis island, which experienced heat stress of 35.8 °C weeks (Brainard et al. 2018).

Over the last three decades, considerable coral monitoring efforts have been undertaken within specific regions of the Pacific, such as the Great Barrier Reef and the Hawaiian and French Polynesian archipelagos (e.g., Jokiel et al. 2004; De'ath et al. 2012; Lamy et al. 2016). In French Polynesia, most ecological assessments of the coral survivability to unusually warm seawater temperatures have been documented over a short duration (e.g., a snapshot survey in Rangiroa; Mumby et al. 2001) and small and limited spatial scales (e.g., Mo'orea, Penin et al. 2007, 2009). Moreover, most of our knowledge about coral ecology in French Polynesia is derived from the long-term reef monitoring program of coral reefs in Mo'orea, an island in the Society Archipelago (e.g., Adjeroud 1997; Edmunds et al. 2010; Kayal et al. 2012; Rouzé et al. 2015; Fig. 1). This monitoring revealed that the reefs of Mo'orea experienced seven bleaching events caused by heat stress (i.e., temperatures above the thermal threshold of 29.2 °C) following the first record in 1979 (1984, 1987, 1991, 1994, 2002, 2003 and 2007; Adjeroud et al. 2002, 2009; Hoegh-Guldberg and Salvat 1995). Bleaching-related information for these past events is disparate, with some studies solely reporting the proportion of colonies bleached during certain events (Hoegh-Guldberg and Salvat 1995; Penin et al. 2007, 2013) and other works also documenting coral mortality a few months postbleaching (Salvat 1993). However, no complete temporal description of bleaching in Mo'orea (e.g., bleaching occurrence and severity and subsequent mortality) has been done, perhaps because so far, Mo'orea reefs have not been severely damaged by

abnormally elevated temperatures compared to other natural perturbations (Adjeroud et al. 2009; Trapon et al. 2011; Lamy et al. 2016). Indeed, the outbreak of the seastar *Acanthaster planci* from 2006 to 2009 followed by the cyclone Oli in 2010 almost entirely wiped out these reefs (Kayal et al. 2012), with observed coral cover reduced to less than 5%. However, the reefs showed an astonishing capacity for recovery, and in just 4 years, coral cover bounced back to 30% in some fore reef sites (Tsounis and Edmunds 2016).

French Polynesia encompasses 118 islands distributed over 5.5 million km² and is made of five archipelagos. Diverse types of islands are present, ranging from open and closed atolls (e.g., Tuamotu Archipelago) to volcanic islands with or without lagoons (e.g., Society vs. Marquesas archipelagos). The Tuamotu Archipelago harbors the northernmost typical coral reefs in French Polynesia. (There are no well-developed coral reef systems in the Marquesas.) The reefs in the Tuamotu are exposed to warmer annual temperatures than those of the Society Islands and could have a higher propensity for coral bleaching (van Hooedonk et al. 2016). During the 1998 event, severe bleaching-induced mortality was recorded for both the slow-growing genus *Porites* and the fast-growing genus *Pocillopora* in the lagoon of Rangiroa atoll (Mumby et al. 2001). Other than this event, coral bleaching and bleaching-induced mortality during periods of elevated temperature have not been documented.

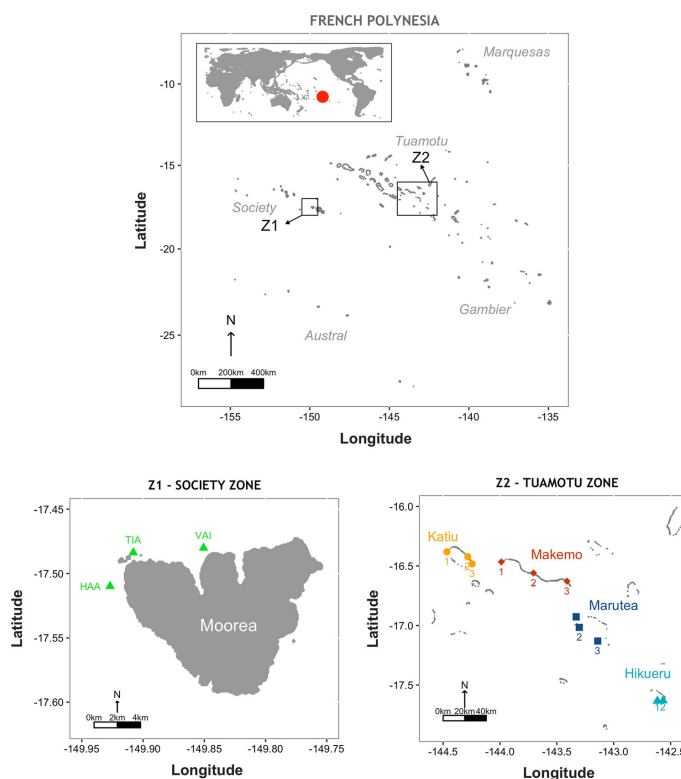
The purpose of our study was to assess whether bleaching during the GCBE3 varied across a range of French Polynesian islands. For that purpose, we provide quantitative and qualitative coral bleaching and mortality information across five islands among the Tuamotu and Society archipelagos for the 6 months following the 2016 bleaching event. This work also comprises a more detailed investigation of Mo'orea reefs, where ecological surveys were performed before, during and after the 2016 bleaching event. Then, we analyzed 32 years of sea surface temperature records obtained from satellite remote sensing to obtain deeper insights into the environmental conditions that corals experienced at the five islands studied. Finally, we compiled underwater observations to document the occurrence of coral bleaching in various islands of French Polynesia.

Materials and methods

Monitored islands

A detailed monitoring of the effects of bleaching was performed on five islands (Mo'orea, Katiu, Makemo, Marutea and Hikueru) of French Polynesia (Fig. 1, ISPF

Fig. 1 Map of French Polynesia and locations of the study zones (Z1 and Z2). The colored icons correspond to the study sites on the fore reefs (3 per island)



2012). Mo'orea Island ($17^{\circ} 29' 13.2''$ S $149^{\circ} 45' 26.4''$ W) in the Society Archipelago is surrounded by a barrier reef, and multiple reef habitats were observed (fringing, barrier and fore reefs). Katiu, Makemo, Marutea and Hikueru are four atolls of the Tuamotu Archipelago. Katiu ($16^{\circ} 25' 144^{\circ} 22'$ W), located 575 km east of Tahiti, and Makemo, 26 km west of Katiu, each have two passes. Marutea ($17^{\circ} 3' 17.23''$ S $143^{\circ} 9' 12.40''$ W), at 26 km to the southeast of Makemo ($16^{\circ} 35' 55''$ S $143^{\circ} 39' 41''$ W), has one pass. Hikueru ($17^{\circ} 32' 41''$ S $132^{\circ} 36' 47''$ W), located 26 km to the southeast of Marutea, has no pass.

Temperature

Sea surface temperature (SST, in $^{\circ}$ C) data were used to characterize the thermal environments in each of the five investigated islands. SSTs were acquired from the NOAA Coral Reef Watch (CRW) at a resolution of 5 km (0.05° latitude and longitude grid, Liu et al. 2017; Maturi et al.

2017; Skirving et al. 2019). Daily SSTs were downloaded from January 1985 to December 2016 (CoralTemp' SST product version 3.1, NOAA 2018). To highlight SST interannual variability, anomaly fields were obtained by subtracting the average maximum monthly values calculated over the 1985–1993 period (excluding 1991 and 1992 because of eruption of volcano Pinatubo) from the time series. Then, the SST data set and its anomalies were extracted from each survey location. Comparison of SST and in situ temperature at 12 m depth indicated a strong regression, with an R^2 of 92% (data not shown), revealing that SST is a good proxy of temperature in shallow reef waters.

Mo'orea surveys

To assess the impact of the 2015–2016 El Niño event in Mo'orea, underwater visual surveys were carried out at three fore reef sites (Tiahura, Vaipahu and Haapiti).

Surveys were performed in three periods: (a) pre-bleaching in November 2015, (b) bleaching in May 2016 and (c) post-bleaching in November 2016. Twenty-meter-long transects ($n = 3$ per site) were deployed randomly at a depth of 12 m. Video transects were recorded with a TG-3 Olympus camera for later analysis. From these videos, the percent cover of the benthos was estimated using the line intercept transect method (Benayahu and Loya 1977; Hill and Wilkinson 2004). Benthic organisms were visually sorted into four main categories: 1/corals (COR), 2/algae (ALG), 3/substrate classified as bedrock (BED), rubble (RUB) or sediments (SED) and 4/other organisms (ORG). Corals were further classified as alive (pigmented), recent dead (REC, dead coral with intact and clearly defined corallite septa) or old dead (OLD, skeleton recolonized by crustose coralline algae and other organisms). Colonies under each transect line were identified to the genus level. Recent mortality characterized by the percentage of recent dead corals, pre- and post-bleaching were used as a proxy of sensitivity to the heat stress caused by El Niño (Lirman et al. 2014).

Additionally, in May 2016 (i.e., during the bleaching), the extent and intensity of bleaching were noted at each site. Three 20 m \times 1 m belt video transects were randomly performed at a depth of 12 m and recorded using a TG-3 Olympus camera. Coral colonies inside each transect were identified to the genus level. The status of each colony was reported in three categories: bleached (total discoloration of coral tissues), pale (slight pigment loss) and normal (whole-colony pigmented).

Six-month post-bleaching surveys in the Tuamotu

The effects of the GCBE3 in Tuamotu were studied in October 2016 (ca. 6 months post-bleaching) on the fore reefs of four atolls: Katiu, Makemo, Marutea and Hikueru (Fig. 1). Three sites were selected for each atoll, except for Hikueru ($n = 2$). Video transects (20 m long; $n = 3$ per site) were recorded at 12 m depth with a TG-3 Olympus camera and analyzed later. The line intercept transect method was performed as described above to assess the percentage of coral cover and health condition, such as recent mortality, which was used as a proxy for bleaching disturbance.

Extent of coral bleaching

Pictures of coral bleaching from 23 French Polynesian islands and atolls were received by CRIOBE scientists during the 2016 austral summer. These observations, provided from different sources (e.g., managers, tourists, fishermen, other scientists), were analyzed to first check the reliability of bleaching occurrence and to avoid confusion

of bleaching with other types of disturbance (coral disease). If reliable, corals were identified to the genus level. Information was mapped to reveal the extent of coral bleaching occurrence in French Polynesia.

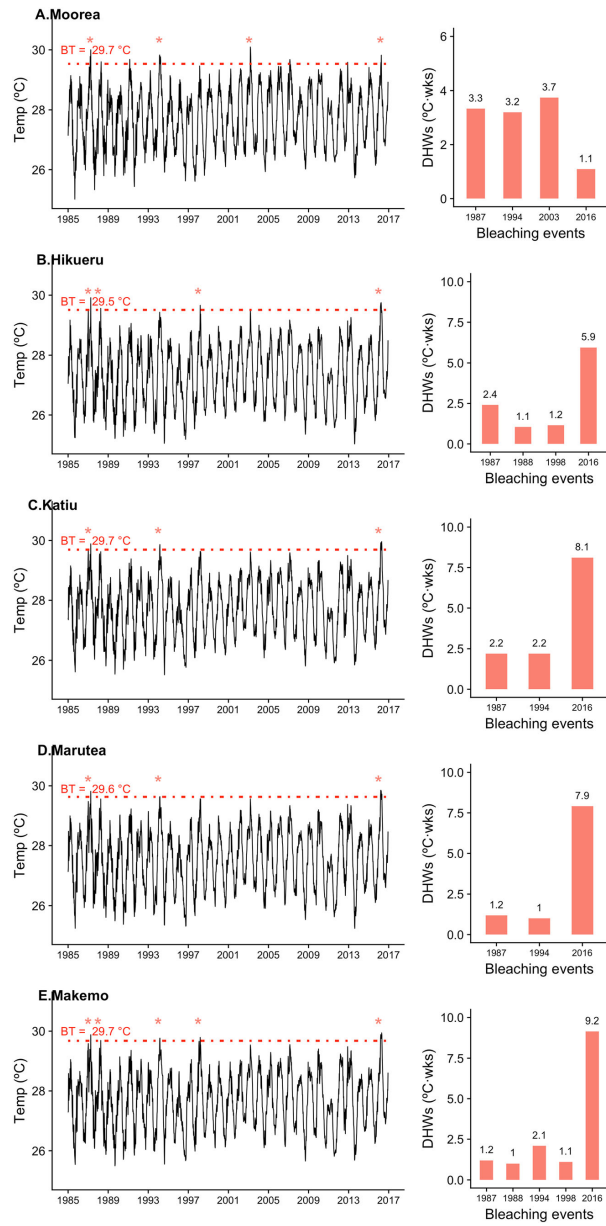
Statistical analyses

Environmental datasets (SST and SST anomalies) from 1985 to 2016 were used to evaluate the conditions experienced during the coral bleaching of 2016 and to compare them with past coral bleaching years (1987, 1994, 1998 and 2003) and among the five monitored islands (presented in “Monitored islands” section) during 2016. We tested for differences in the environmental data among sites using Friedman test, a nonparametric randomized block analysis of variance for SST values, and analyses of variance (ANOVA) for the SST anomalies. In cases of homogeneity of variance and homoscedasticity, we used Shapiro and Bartlett tests on residuals, respectively. Otherwise, we used nonparametric Kruskal–Wallis rank tests. Furthermore, to assess the heat stress occurring during the 2016 bleaching event, the Degree Heating Weeks (DHWs) for each island were computed. To do so, the monthly mean SST was calculated over the 1985–2016 period, and the mean maximum monthly value (referred to as the monthly maximum mean MMM) was extracted for each island. Specific bleaching thresholds (BT) were calculated by adding 1 °C to the MMM (Hoegh-Guldberg 1999a; Hughes et al. 2003). DHWs were measured using the same criteria as Eakin et al. (2010), Glynn (1996) and Liu et al. (2017). DHW is an index that shows how much heat stress has accumulated in an area over the past 12 weeks, by adding up any difference between the SST and the MMM of 1 °C or higher thus combining temperature anomaly and duration of exposure.

The difference between weekly SST and MMM was calculated as $SST - MMM$. Since heat stress normally starts when temperatures exceed the MMM by 1 °C or more, only values with differences ≥ 1 °C were summed to calculate the heat stress for the 12 preceding weeks (Fig. 2). For example, if over a 12-week period, positive SST–MMM values of 0.8, 1.2, 2, 0.9 and 1 °C are recorded for 5 weeks, the resulting DHW value is 4.2 °C weeks (the sum of 1.2, 2 and 1 °C weeks, with no contribution from the 0.8 and 0.9 °C weeks). Expected bleaching levels were predicted according to DHW thresholds (Liu et al. 2018). No bleaching ($DHW \leq 0$); bleaching warning ($0 < DHW < 4$), where bleaching might happen; bleaching alert level 1 ($4 \leq DHW < 8$), where bleaching is likely to happen; and bleaching alert level 2 ($DHW \geq 8$), where widespread bleaching and mortality are both likely.

All statistical analyses were performed using the “Vegan” and “lme4” packages in R software (Bates et al.

Fig. 2 (Right) Temporal trend in sea surface temperature with reported Degree Heating Weeks (*) and calculated bleaching threshold (BT); (Left) Degree Heating Weeks (DHWs, left) for the five islands investigated: **a** Mo'orea, **b** Hikueru, **c** Marutea, **d** Makemo and **e** Katiu



2015; Oksanen et al. 2018). To understand how thermal anomalies have affected benthic communities across different islands, a principal component analysis (PCA) was performed on the log + 1 transformed data (FactoMineR package). Moreover, permutational multivariate analysis of variance (PERMANOVA) was used to estimate the contribution of islands and sites to the dissimilarity matrix (based on benthic categories). The performance of our distance matrix was tested using permutations (the *Adonis* function of the *Vegan* package). Further analyses on coral community variances at the genus level were conducted with nested analysis of variance (ANOVA) from the generalized linear mixed model (the *lmer* function from the *lme4* package) and associated post hoc tests, in which sites were considered as random factors nested within the islands.

Results

Spatiotemporal analyses of SST

SST variability from 1985 to 2016 (Fig. 2) displayed significant differences among islands (Friedman test: $df = 4$, $\chi^2 = 1842$, $P < 0.001$), while median \pm SD values remained close (27.39 ± 1.0 °C in Hikueru, 27.57 ± 1.0 °C in Marutea, 27.77 ± 1.0 °C in Mo'orea, 27.80 ± 0.9 °C in Katiu and 27.74 ± 0.9 °C in Makemo). However, SST anomalies exhibited no significant differential patterns among locations (two-way ANOVA; $P > 0.05$), but a significant interaction effect between locations and time was reported (two-way ANOVA with combined effects of Island \times Year: $df = 116$, $F = 3.1$ and $P < 0.001$). The bleaching thresholds (BTs) calculated over the last 32 years were close, with BT values of 29.7 °C in Mo'orea, Katiu and Makemo, 29.6 °C in Marutea and 29.5 °C in Hikueru.

Despite this environmental similarity, a wide range of DHW values were observed over the last 32 years and their timing varied among the islands. Heat stress was recorded in 1987, 1988, 1994, 1998, 2003 and 2016, all corresponding to El Niño events. All islands studied were affected by the 1987 temperature event, but its impact was low (DHWs varying from 1.2 to 3.3 °C weeks). All islands except Hikueru were impacted by the 1994 bleaching alert (DHWs ranging from 1 to 3.2 °C weeks). The stress event in 1998 only affected reefs of Makemo and Hikueru (1.1 and 1.2 °C weeks, respectively). In contrast, the 2016 temperature event affected all islands studied with DHWs ranging from 1.1 to 9.2 °C weeks. Mo'orea reefs suffered from a disturbance in 2003 (DHWs of 3.7 °C weeks), whereas Tuamotu reefs did not suffer from any reported heat stress.

Coral health assessment in Mo'orea before, during and after the 2016 bleaching event

No significant decline in coral cover (Kruskal–Wallis: $df = 1$, $\chi^2 = 1.9$, $P = 0.171$) and no modification in the taxonomic composition were observed in Mo'orea between pre- and post-bleaching periods (2015 vs. 2016, Table 1). On average, the coral cover of Mo'orea in 2015 (pre-bleaching) and 2016 (post-bleaching) ranged from 34 to 56%, with significant variation among sites (Kruskal–Wallis: $df = 2$, $\chi^2 = 10.3$, $P = 0.006$). For both periods, coral cover in Haapiti (34–39%) was lower than in Tiahura (55–56%, Table 1). All sites were dominated by the genus *Pocillopora*, representing 47–66% of the relative contribution of the genera to the coral cover in the years

Table 1 Total coral cover (in bold) and coral cover of the 7 most important genus (mean and standard deviation) before (2015) and after bleaching (2016) in the three stations around Moorea Island

Percentage (%)	2015		2016	
	Mean	SD	Mean	SD
Haapiti				
Coral cover	34.1	6.1	39.2	3.3
<i>Pocillopora</i>	64.3	3.6	65.5	3.6
<i>Porites</i>	12.7	1.4	11.7	4.8
<i>Acropora</i>	7.6	2.5	7.1	3.2
<i>Montipora</i>	8.3	3.0	8.4	2.8
<i>Pavona</i>	1.0	0.2	0.9	0.2
<i>Astrea</i>	1.7	1.4	2.1	1.3
<i>Others</i>	4.3	4.1	4.3	3.4
Tiahura				
Coral cover	56.4	4.4	55.8	7.0
<i>Pocillopora</i>	66.5	5.9	66.8	5.2
<i>Porites</i>	10.8	6.8	11.8	4.3
<i>Acropora</i>	6.9	2.8	6.1	3.3
<i>Montipora</i>	8.4	1.4	8.7	1.7
<i>Pavona</i>	1.1	0.4	1.1	0.5
<i>Astrea</i>	1.8	1.2	1.7	0.8
<i>Others</i>	4.4	2.2	3.8	1.8
Vaipaho				
Coral cover	38.4	8.4	55.6	10.2
<i>Pocillopora</i>	64.5	6.4	64.9	3.4
<i>Porites</i>	14.8	1.8	10.6	5.7
<i>Acropora</i>	6.6	5.3	7.5	3.8
<i>Montipora</i>	7.4	3.7	8.7	3.1
<i>Pavona</i>	1.0	0.6	1.1	0.4
<i>Astrea</i>	1.5	1.0	2.2	1.5
<i>Others</i>	4.1	1.8	5.1	3.3

2015–2016, followed by *Montipora* (8–17%) and *Porites* (5–16%).

The first signs of bleaching in Mo'orea were reported in early April 2016. In May 2016, coral bleaching surveys revealed significant impact of bleaching in the three studied sites depending on the genus (Table 2 and Fig. 3). The highest proportion of bleached colonies (pale and completely bleached) was recorded at Vaipahu ($61.2 \pm 5.5\%$), followed by Haapiti ($53.1 \pm 7.1\%$) and Tiahura ($44.4 \pm 3.6\%$). The genus *Astrea* had the highest percentage of totally bleached colonies, 32% to 79%. Bleaching was also common in *Pocillopora* (7–20%) and *Montipora* (11–42%) on all three fore reef sites. *Porites* and *Pavona* showed almost no signs of complete bleaching (< 1%) in the three sites of Mo'orea. *Acropora* was more sensitive to bleaching than *Porites* and *Pavona*, with up to 15% of colonies showing signs of complete bleaching. Six months after the 2016 bleaching event, recent mortality was rare (< 1%, Fig. 5).

Post-bleaching effects of the El Niño 2016 event on coral communities in French Polynesia: Mo'orea versus Tuamotu

Benthic communities

Principal component analysis (Fig. 4) showed some differences in benthic communities between Tuamotu and Society islands in October/November 2016. Differences were significant among islands (PERMANOVA: $F_{(4,37)} = 25.8$, $P < 0.005$) and across the "sites" within these islands ($F_{(13,28)} = 24.38$, $P < 0.005$). Specifically, the five benthic categories, "live coral" (COR),

Table 2 Three-way analysis of variance (ANOVA) showing the effects and interactions of 'reef sites' (SITE), 'health state' (STATE) and 'coral genus' (GENUS) on the relative abundance of coral colonies recorded in May 2016 around Moorea

Factor	df	F	P
SITE	2	0.36	0.70 ^{NS}
STATE	1	36.28	< 0.001***
GENUS	5	76.20	< 0.001***
SITE × STATE	2	6.18	0.003**
SITE × GENUS	10	2.75	0.004**
GENUS × STATE	5	27.81	< 0.001***
SITE × GENUS × STATE	10	1.38	0.196 ^{NS}

For the GENUS factor, the analysis considers the six main coral genus categories: *Acropora*, *Astrea*, *Montipora*, *Pocillopora*, *Porites* and *Pavona*. For the STATE factor, only resistance or sensitivity to coral bleaching is considered

NS not significant

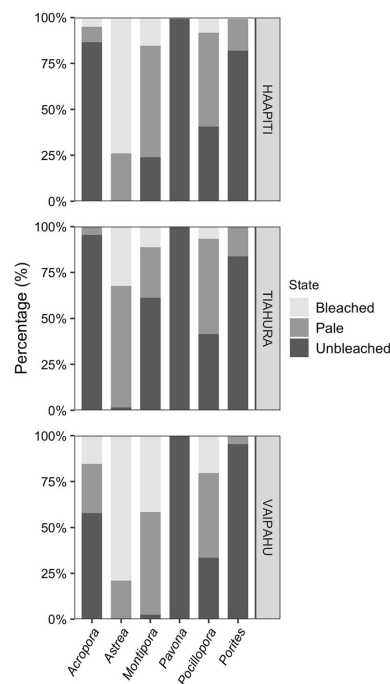
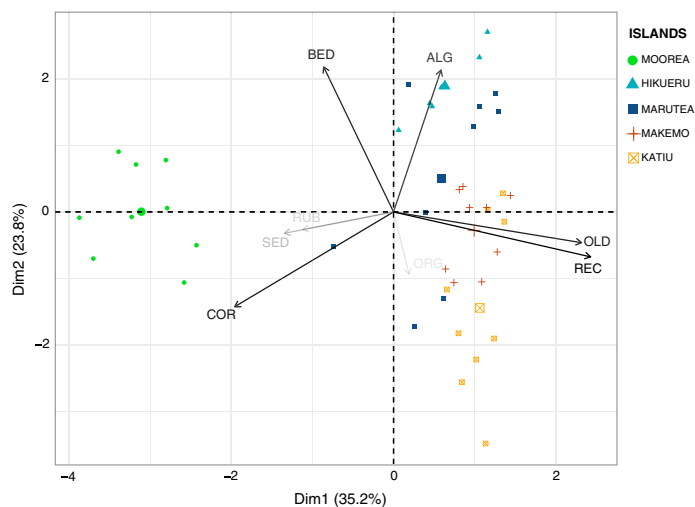


Fig. 3 Relative proportion of bleached, pale and unbleached corals in three sites (Haapiti, Tiahura and Vaipahu) around Mo'orea in 2016. The main genera are shown: *Pocillopora* (POC; number of colonies, $N = 646$, 587 , and 800 , respectively), *Montipora* (MON), *Porites* (POR; $N = 127$, 190 and 87 , respectively), *Acropora* (ACRO; $N = 59$, 45 and 26 , respectively), *Astrea* (AST; $N = 131$, 127 and 71 , respectively), *Pavona* (PAV; $N = 124$, 87 and 36 , respectively)

"macroalgae" (ALG), recent (REC) and old (OLD) dead corals and bedrock (BED), strongly influenced the structure of these benthic communities, with significant variations between and within islands (results ANOVAs, Table 3).

The first dimension of the PCA (35.2%) highlighted a strong and significant separation between the reefs of Mo'orea and those in the Tuamotu islands (Katiu, Makemo, Hikueru and Marutea), where the total benthic community was composed of 50% versus 10–23% of living corals, respectively (Fig. 5). This first axis separated reefs that experienced high recent (REC) and old (OLD) coral mortality (Tuamotu reefs) from those that experienced almost no mortality (Mo'orea reefs). Indeed, reefs from the Tuamotu islands had significantly higher rates of recent (10–37%) and old (10–20%) coral mortality of the total benthic community, corresponding to 34–54% and

Fig. 4 Principal component analysis (PCA) of benthic communities in Mo'orea and the Tuamotu islands (Hikueru, Marutea, Makemo and Katiu). Dimensions 1 and 2 of the PCA according to the main benthic categories of corals (COR), macroalgae (MALG), recent (REC) and old (OLD) dead corals, bedrock (BED), rubble (RUB), sediment (SED) and other organisms (ORG)



24–36%, respectively, of the total coral cover (Fig. 5). The second dimension of the PCA (23.8%) depicted the benthic community structure among Tuamotu islands, showing a clear partition from northwest (Katiu and Makemo) to southeast (Marutea and Hikueru). Indeed, among the four

Tuamotu islands, Katiu had the highest coral cover, equivalent to $23 \pm 8\%$, which was 2 times more than at Makemo ($15 \pm 4\%$) and 2.6 times more than at Hikueru and Marutea ($10 \pm 6\%$ and $11 \pm 4\%$, respectively; Table 3, Fig. 5). On the other hand, Hikueru had a

Table 3 Statistical analysis of the coral cover per island (MOO: Mo'orea; HIK: Hikueru; MAR: Marutea; MAK: Makemo; and KAT: Katiu) and sites (ALG: alga; COR: alive coral; REC: recent dead coral; OLD: old dead coral; SED: sediments; BED: bedrock; RUB: rubble; SED: sediments; ORG: organisms)

Category	Factor	F	P	Tukey post hoc test				
				MOO	HIK	MAR	MAK	KAT
ALG	Island ($df = 4$)	13.41	< 0.001	bc	a	ab	c	c
(log + 1)	Random effect site ($df = 1$)	8.5	0.004**					
COR	Island ($df = 4$)	40.12	< 0.001	a	d	cd	bc	c
(log + 1)	Random effect site ($df = 1$)	11.1	< 0.001***					
REC	Island ($df = 4$)	256.37	< 0.001	c	b	a	a	a
(log + 1)	Random effect site ($df = 1$)	4.84	0.03*					
OLD	Island ($df = 4$)	23.28	< 0.001	b	a	a	a	a
(log + 1)	Random effect site ($df = 1$)	1.26	0.3					
BED	Island ($df = 4$)	10.30	< 0.001	a	a	ab	bc	c
(log + 1)	Random effect site ($df = 1$)	6.54	0.01*					
RUB	Island ($df = 4$)	1.74	0.16					
(sqrt)	Random effect site ($df = 1$)	1.53	0.2					
SED	Island ($df = 4$)	4.64	< 0.005	a	b	ab	b	b
(log + 1)	Random effect site ($df = 1$)	1.31	0.3					
ORG	Island ($df = 4$)	1.40	0.2463					
(log + 1)	Random effect site ($df = 1$)	0.00	1					

Lowercase letters (a-d) indicate significant differences among islands ($p < 0.05$). Different letters represent significant differences at $p < 0.05$ probability level

Significant differences are shown in bold

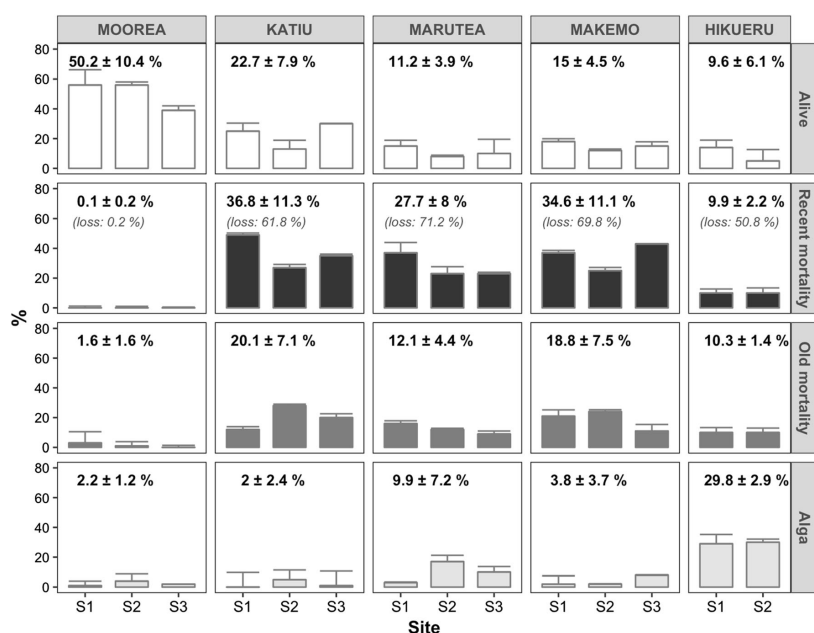


Fig. 5 Mean percentage and standard deviation of coral cover derived from three categories (alive, recently and old dead) and algal cover from the five islands surveyed in October/November 2016

(postbleaching). The number in brackets for recent mortality represents the estimated loss of living corals due to the 2016 bleaching event

significantly different community due to its high macroalgal cover ($30 \pm 3\%$; Table 3, Fig. 5) contrasting with less than 7% and 3% macroalgal cover in Marutea and Katiu/Makemo, respectively.

Coral communities

Differences in coral assemblages were significant among islands (Mo'orea vs. Tuamotu islands, Fig. 6; PERMANOVA: $F_{(4,37)} = 20.8$, $P = 0.001$) and among sites within these islands ($F_{(9,28)} = 2.8$, $P = 0.001$). The genus *Pocillopora* was predominant in the coral composition of Mo'orea ($53 \pm 14\%$), which contrasted with the Tuamotu islands, where *Pocillopora* was lower (Katiu: $30 \pm 13\%$, Hikueru: $27 \pm 17\%$; Marutea: $27 \pm 12\%$ and Makemo: $16 \pm 11\%$; nested ANOVA_{ISLAND}: $F_{(4,37)} = 6.9$, $P < 0.001$) and where a lower coral cover was observed. Additionally, a higher proportion of colonies in the genus *Montipora* was recorded for Mo'orea and the northern Tuamotu islands Katiu and Makemo, reaching up to 14%, compared to the southern Tuamotu islands Marutea and

Hikueru, where it accounted for less than 3% (nested ANOVA_{ISLAND}: $F_{(4,37)} = 6.59$, $P < 0.001$). In the same way, both northern islands, Katiu and Makemo, were significantly predominated by *Porites* ($48 \pm 15\%$ and $48 \pm 19\%$, respectively; nested ANOVA_{ISLAND}: $F_{(4,37)} = 28.9$, $P < 0.001$), while the two Tuamotu southern islands and Mo'orea harbored 0–4% and 11%, respectively, of *Porites* (high variability among sites). In contrast, the two southern islands were distinguished by relatively high abundances of *Dipsastraea* ($23 \pm 6\%$ in Marutea and $28 \pm 12\%$ in Hikueru; nested ANOVA_{ISLAND}: $F_{(4,37)} = 20.4$, $P < 0.001$). Additionally, higher proportions of *Astreopora* and *Pavona* were observed in Hikueru and Marutea, respectively (nested ANOVA_{ISLAND}: $P < 0.05$ of the two coral genera).

Similar trends were observed when calculating the percentage of recent coral mortality of the various genera (i.e., proxy of coral bleaching during the 2016 El Niño event). In Mo'orea, almost no recent mortality (0.1%) was recorded six months after the 2016 event. Hikueru differed from the three other Tuamotu islands due to the lower level

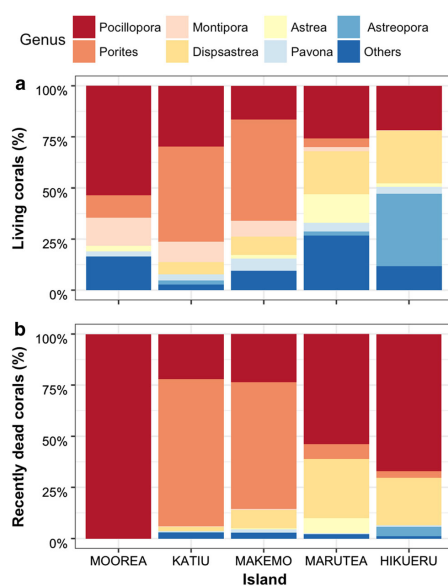


Fig. 6 Relative abundance of **a** alive and **b** recently dead coral colonies surveyed in the five investigated islands (Mo'orea, Hikueru, Marutea, Makemo and Katiu) and representing the following coral genera: *Pocillopora*, *Porites*, *Montipora*, *Dipsastraea*, *Pavona*, *Astrea*, *Astreopora* and other less abundant genera

of total recent mortality recorded (9.9%) compared to 27.7–36.8% in other islands (Table 3, Fig. 5). In addition, the compositional differences in recently dead coral genera were significant among the Tuamotu islands (PERMANOVA: $F_{(3,29)} = 40.5$, $P = 0.001$; Fig. 6) and among sites within these islands ($F_{(7,22)} = 4.5$, $P = 0.00$). The northern islands, Katiu and Makemo, displayed recent high mortality of *Porites* ($72 \pm 14\%$ and $59 \pm 12\%$, respectively), contrasting with the southern islands, Hikueru and Marutea (nested ANOVA_{ISLAND}: $F_{(3,29)} = 38.5$, $P < 0.001$), in which less than 6% of recent mortality was recorded for this genus. In contrast, the southern islands mostly revealed recent mortality of *Pocillopora* corals (Hikueru $67 \pm 27\%$ and Marutea: $56 \pm 17\%$); that in the northern islands was significantly lower, with $25 \pm 7\%$ in Makemo and $22 \pm 16\%$ in Katiu (nested ANOVA_{ISLAND}: $F_{(3,29)} = 17.6$, $P < 0.001$). Recent mortality records of *Dipsastraea* corals were significantly higher (nested ANOVA_{ISLAND}: $F_{(3,29)} = 10.6$, $P < 0.001$) in Marutea and Hikueru ($30 \pm 14\%$ and $22 \pm 28\%$, respectively) than in Makemo and Katiu ($10 \pm 8\%$ and $2 \pm 2\%$).

Extent of coral bleaching

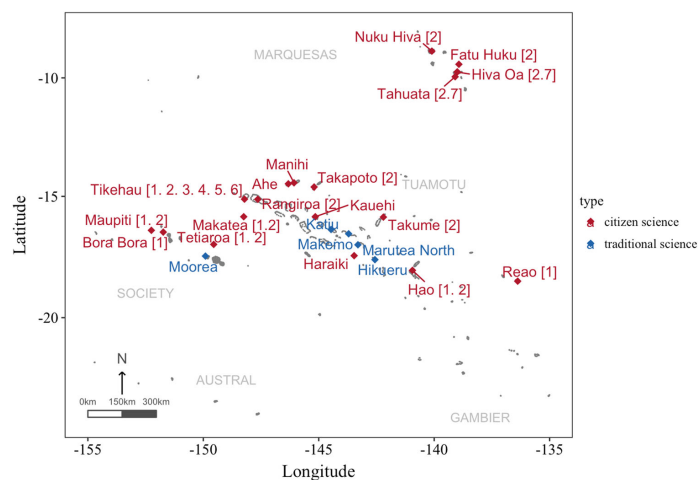
Valuable information on bleaching occurrence in 2016 was received from an additional 18 islands of the Tuamotu, Marquesas and Society archipelagos (Fig. 7). Severe bleaching was observed in seven genera (*Acropora*, *Pocillopora*, *Fungia*, *Montipora*, *Dipsastraea*, *Millepora* and *Porites*), with most information concerning *Acropora*, *Pocillopora* and *Porites*. Coral bleaching was first reported to occur in Marquesas, then in Tuamotu and finally in the Society islands.

Discussion

Here, we revealed that the 2016 bleaching in French Polynesia had contrasting mortality patterns across the French Polynesian islands based on the distinct heat stresses experienced by corals. Coral bleaching generally occurred when the seawater temperature was above the bleaching threshold (BT). BTs calculated from 1985 to 2016 showed values of 29.7°C in Mo'orea (Fig. 2), which is slightly higher than the value reported in Tahiti (29.2°C) by Hoegh-Guldberg (1999b). This is likely due to the use of different datasets (our use of NOAA Coral Reef Watch—CRW—vs. Hoegh-Guldberg's use of Integrated Global Ocean Services System Global SST data from Reynolds and Smith—IGOSS-nmc-blended data from the Lamont-Doherty Climate Center at Columbia University, Reynolds and Smith 1994). No difference was recorded among the BTs estimated for the five islands investigated, which suggests that corals from these islands will bleach at similar levels and intensities of heat stress. However, corals from the Tuamotu islands experienced a higher heat stress (characterized by DHWs reaching 9.2°C weeks) compared to those living in Mo'orea (1.1°C weeks). This definitely led to distinct patterns of post-bleaching mortality. Reefs from the Tuamotu islands suffered from moderate to severe heat stress with DHW values of 5.9 – 9.2°C weeks, with a loss of 50–71% of living coral cover. In contrast, corals from Mo'orea experienced very low heat stress (1.1°C weeks). Nonetheless, during that time, bleaching was recorded in Mo'orea (77% of colonies showed early signs of bleaching), but corals recovered remarkably well, with less than 1% coral loss.

The 32-year long-term monitoring (1985–2016) SST data (and their associated anomalies) revealed that the temperature anomaly and duration of heat stress in Tuamotu drove coral mortality following the summer of 2016. Interestingly, the five islands investigated here were relatively spared from abnormally high temperatures over 1985–2016, except in 2016, which was declared as the third global coral bleaching event (GCBE3) worldwide

Fig. 7 Map of French Polynesia indicating where coral bleaching was reported from the scientific assessment (blue) and from citizen surveys (red). Information relative to the coral genus was reported in the bracket with a number: [1] *Acropora*, [2] *Pocillopora*, [3] *Fungia*, [4] *Montipora*, [5] *Astrea*, [6] *Millepora* and [7] *Porites*



(Eakin et al. 2017). Indeed, only a few episodes of abnormally high temperature were recorded at a moderate level (DHWs ranging from 1.1 to 3.7 °C weeks) during the last 32 years: in 1987 (all five islands), 1988 (in Hikueru), 1994 (in Mo'orea, Katiu, Marutea and Makemo), 1998 (in Makemo and Hikueru) or in 2003 (in Mo'orea), all occurring during El Niño events. This observation is congruent with the recent prediction of van Hooidonk et al. (2016), which revealed that reefs in the southern areas of French Polynesia (e.g., Tahiti and Mo'orea Islands) are among the projected "climate refugia" where corals may experience less severe bleaching this century due to comparatively lower predicted thermal anomalies. Moreover, this trend is also consistent with past recorded bleaching events that have occurred in Mo'orea and that yielded relatively low mortality (Hoegh-Guldberg and Salvat 1995; Adjeroud et al. 2009; Lamy et al. 2016). Nonetheless, 2016 was exceptional in terms of the intensity and duration of elevated temperature, and it was the first time DHWs reaching 9.2 °C weeks were recorded on the Tuamotu islands.

The elevated DHWs in the Tuamotu led to dramatic declines of coral cover in the southernmost islands (50% and 71% in Hikueru and Marutea, respectively). The northern reefs of Katiu and Makemo also displayed recent coral mortality (34–36%, averaged across all genera), apparently driven by the loss of the massive coral *Porites*, the original dominant genus from these islands (accounting for 61–71% of the total recent mortality). However, the massive *Porites*, a slow-growing coral, is typically considered an ecological "winner" or very resistant to heat

stress (Marshall and Baird 2000), as observed during the 1998 bleaching event in Sesoko by Loya et al. (2001), where the sea surface temperature peaked at 2.8 °C above average during August and led to a DHWs of 3.3 °C weeks (Sakai et al. 2019). Nevertheless, mortality for this genus has been previously observed during high DHWs as reported by Mumby et al. (2001). The latter described an unprecedented loss of massive *Porites* (25%) in the Rangiroa atoll (Tuamotu Archipelago) following the strong 1997/1998 El Niño Southern Oscillation, where SSTs exceeded and remained above the average March temperature for a period of three months (which led to a heat stress of more than 5 °C weeks for the Tuamotu regions, see data from Coral reef Watch Virtual Station, NOAA 2018). Since DHWs from Tuamotu recorded in 2016 were the highest ever documented in this region (DHWs from 5.9 to 9.2 °C weeks), the high mortality of *Porites* from Tuamotu reefs is not surprising. Recent studies also shed some light on the susceptibility of massive *Porites* compared to branching corals during severe bleaching events (Guest et al. 2012, 2016; Putschim 2017). As a slow-growing coral, *Porites* colonies have persisted in the population over time under challenging environmental conditions but potentially harbored a slower capacity to naturally evolve compared to fast-growing corals. *Porites* generally suffer more frequently from partial mortality as opposed to whole-colony mortality (Mumby et al. 2001; Roff et al. 2014). Therefore, instead of having a new genetic pool of *Porites* individuals (from thermotolerant parents) colonizing the reefs after bleaching disturbance, most of the colonies that suffer partial mortality recover

by regrowth from tissue expansion (Roff et al. 2014; Furby et al. 2017).

During the GCBE3, reefs from the southern islands of Hikueru and Marutea, already characterized by low coral cover (pre-bleaching estimation of 20% alive corals), lost 50–71% of their total living coral cover. At this location, bleaching and mortality mostly affected branching *Pocillopora*, often described as relatively fast-growing with low stress tolerance (Stimson 1978; Baird and Marshall 2002; Darling et al. 2013). Although bleaching assessment only occurred on Mo'orea during the April 2016 event, here we showed that *Astrea* was the most sensitive genus, with 100% of the colonies harboring signs of bleaching, followed by *Montipora* and *Pocillopora*. However, the bleaching response in Mo'orea did not lead to mortality, as the heat stress was low (1.1 °C weeks) compared to that occurring in Tuamotu. In contrast, in the Tuamotu Islands, where mortality was recorded, *Pocillopora* and *Porites* were the genera most susceptible to bleaching (with high mortality in Hikueru and Marutea and in Makemo and Katiu, respectively). Our work showed that resistance to bleaching mortality is variable among genera and locations and potentially other unidentified factors. Hence, more detailed and spatially explicit studies will be needed to predict how coral communities will evolve under future climate change.

This study documented bleaching and/or recent coral mortality (used as a proxy of bleaching disturbances) across five islands with 18 additional islands represented by a citizen survey in French Polynesia, revealing the widespread impacts of the 2016 bleaching event and the contrasting thermal regimes experienced by corals during this event. The 2015–2016 El Niño event led to anomalously warm conditions with heat stress reaching levels never reported before in this region and with up to 71% coral loss in Tuamotu. In contrast, corals from Mo'orea experienced lower heat stress, leading to bleaching but with extremely low resulting mortality. The temperature anomalies experienced by various reefs across French Polynesia were variable and controlled the severity of bleaching. Even at a local scale of French Polynesia, a geographic mosaic of coral responses to climate change has been observed and provides insights into the future capacity of Polynesia reefs to handle environmental disturbances of the Anthropocene era.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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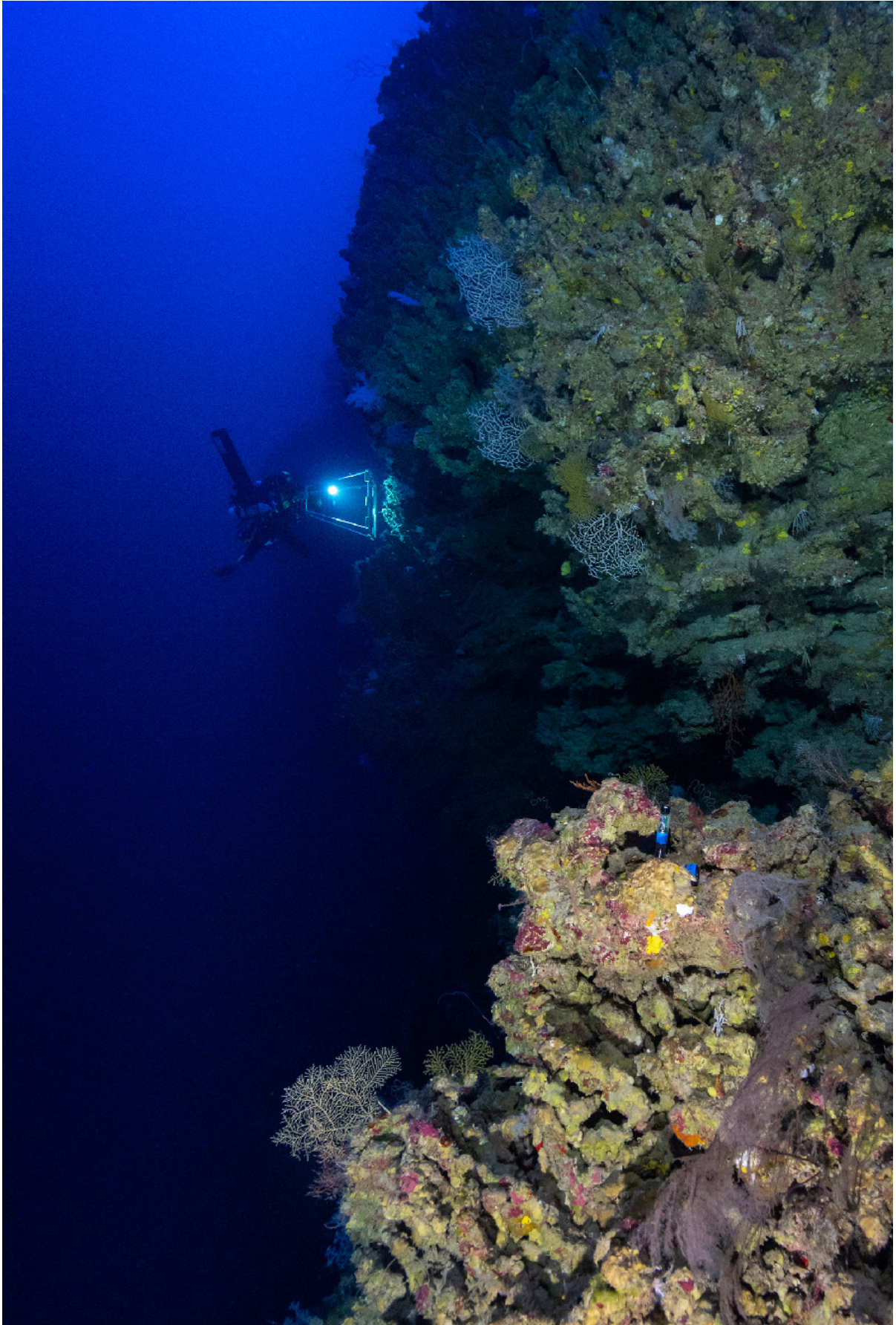


Image 3: Despite increasing efforts, the twilight zone remains understudied around the world (Copyright image: Ghislain BARDOT / UNDER THE POLE / Zeppelin Network).

Résumé substantiel

Le changement climatique, ainsi que divers types de perturbations sont une cause de disparition des récifs coralliens. Au-delà des récifs coralliens superficiels, et malgré une diminution de la lumière avec la profondeur, les Écosystèmes Coralliens Mésophotiques (ECM) sont caractérisés par la présence de coraux scleractiniaires photosynthétiques et de peuplements associés, distribués mondialement dans les mers tropicales et subtropicales entre 30 et 150 m. Bien que leur connaissance et leur capacité à jouer un rôle de refuge pour les espèces récifales superficielles fassent l'objet d'un intérêt croissant, ils demeurent très peu explorés et mal connus en raison de contraintes logistiques affectant les recherches au-delà des limites de la plongée en scaphandre autonome traditionnel. Cependant, l'intérêt pour ces milieux extrêmes et ces écosystèmes marginaux, stimulé par les progrès de la technologie de la plongée a conduit à un développement rapide des recherches au cours des années récentes. Malgré tout, la somme des publications qui leur sont consacrées est mondialement très inégalement répartie. Tandis que des régions telles que le Golfe d'Eilat (Israël), la Grande Barrière de Corail (Australie) ou certaines îles américaines (Porto-Rico, Îles Vierges américaines et Hawaii) ont fait l'objet de recherches considérables, beaucoup d'autres régions telles que la Polynésie Française demeurent peu étudiées.

Le but de cette thèse, laquelle est un des composants du projet DEEPHOPE (une collaboration entre des scientifiques et des plongeurs techniques de « Under The Pole ») est de remédier aux insuffisances dans notre connaissance des Milieux Coralliens Mésophotiques de Polynésie Française, concernant notamment leur écologie et leur physiologie. Dans ce travail, l'attention s'est portée sur les coraux scleractiniaires, afin d'évaluer l'importance des MCE dans la résilience de l'écosystème récifal en général. Dans cette optique, j'ai évalué si la diversité et le taux de couverture corallienne augmentaient avec la profondeur de façon à identifier les zones critiques pour la conservation. J'ai caractérisé l'acclimatation physiologique et l'adaptation des scleractiniaires aux profondeurs de façon à comprendre comment ils peuvent vivre dans de telles conditions de luminosité atténuée. Finalement, j'ai examiné si les coraux mésophotiques étaient autant affectés que les coraux peu profonds par la principale menace pesant actuellement sur eux : un épisode de blanchissement thermique.

Pour vérifier ces hypothèses, j'ai participé à une expédition (DEEPHOPE) d'une durée de 10 mois, incluant 11 îles dans cinq archipels de Polynésie Française, répartis sur 1,600,000 km², expédition durant laquelle environ 800 plongées trimix en recycleur ont été réalisées. Cette expédition a procuré l'occasion de constituer (a) une base de données quantitatives de plus de 3500 photo-quadrats, aux profondeurs de 6, 20, 40, 60, 90 et 120 m, (b) une base de données physiologiques (118 répliques de *Pocillopora cf. verrucosa* de 6 à 60 m, et 115 répliques de *Pachyseris « speciosa » spp.* de 10 ou 20 à 90 m) et (c) une base de données environnementales (par ex. lumière, température, bathymétrie, profils CTD, nutriments) à toutes les profondeurs d'échantillonnage. Finalement, une collection de plus de 1800 spécimens de scleractiniaires rassemblée au cours de l'expédition, a permis la constitution d'une base de données taxonomique ayant servi d'appui à mes propres données.

Chapitre 1. Dans ce chapitre sont introduites les généralités sur les récifs coralliens et les Écosystèmes Coralliens Mésophotiques, à l'échelle mondiale et dans le contexte de la Polynésie Française. J'y présente les conditions de milieu, la structure des communautés des ECM et l'état de nos connaissances sur la physiologie des scleractiniaires vivant dans des conditions de luminosité atténuée. Bien que quelques études antérieures soient disponibles, nos connaissances sur les ECM de Polynésie Française demeurent bien fragmentaires. Les hypothèses de départ faisant l'objet des chapitres suivants ont été développées en prenant en compte les conditions actuellement observées dans les récifs peu profonds et des connaissances préalables concernant les ECM.

Chapitre 2. Dans le chapitre 2, il est démontré que les ECM sont des points chauds de diversité générique en Polynésie Française, malgré la décroissance de la couverture corallienne avec la profondeur. J'ai montré que la richesse générique maximale (diversité α) se situait entre 20 et 60 m en raison d'un effet de « domaine moyen ». Aux environs du maximum de diversité au centre du domaine moyen (40 m) on observe simultanément des assemblages composés de genres de coraux superficiels et profonds (du fait que la dissimilarité et le turnover augmentent avec la distance verticale). Il a également été montré que la diversité spatiale (diversité β) augmentait avec la profondeur, ce qui signifie que, alors que les assemblages en eaux peu profondes sont similaires dans

tous les sites étudiés, les divers peuplements situés à des profondeurs mésophotiques sont différents et uniques. De ce fait, des stratégies de conservation différentes sont requises pour préserver la diversité à l'échelle régionale.

Chapitre 3. Les résultats présentés dans le chapitre 3 indiquent que malgré la tendance générale pour la couverture corallienne à diminuer avec la profondeur, les ECM peuvent également abriter des assemblages présentant de façon inattendue une forte couverture corallienne. Dans la gamme de profondeurs mésophotiques, 20 parmi les 64 sites profonds étudiés présentaient un taux de couverture supérieur à celui attendu (par modélisation) aux profondeurs correspondantes. Ces sites particuliers (dénommés « points chauds » de couverture corallienne) présentaient dans certains cas des taux de couverture corallienne supérieurs à ceux observés dans les récifs peu profonds. J'ai démontré que, à côté de la profondeur et la quantité de lumière relative en fonction de 6 m (colinéarité), une pente d'inclinaison modérée à forte, et un faible taux de sédimentation favorisaient une forte couverture corallienne avec les profondeurs croissantes, en dépit de différences importantes dans la morphologie des coraux. Alors que les coraux de forme lamellaire, établis préférentiellement sur des pentes fortement inclinées dominant dans les milieux les plus profonds, un mélange de formes encroûtantes et lamellaires colonisent préférentiellement les pentes d'inclinaison plus modérée. Enfin, j'ai mis en place les fondations pour développer une modélisation prédictive environnementale du taux de couverture corallienne en milieu mésophotique, tout en reconnaissant le besoin d'améliorer notre capacité de prédiction et la nécessité d'évaluations de vulnérabilité.

Chapitre 4. Dans ce chapitre les multiples stratégies de caractères utilisées par deux espèces de scléactiniaires (*Pocillopora cf verrucosa* et le complexe génétiquement diversifié de *Pachyseris «speciosa» spp*) pour s'accommoder des milieux à éclaircissement réduit sont élucidées et sont de nature à expliquer la capacité des coraux à vivre dans de larges gammes de profondeur. En utilisant des résultats provenant de l'étude de l'hôte animal et de ses symbiotes, d'une part chez une espèce branchue et des espèces accompagnatrices peu profondes, et d'autre part chez une espèce lamellaire et des espèces accompagnatrices mésophotiques, il a été démontré que malgré les changements dans les communautés de symbiotes avec la profondeur, les profils ITS2 dominants (*Cladocopium*, *Durusdinium* et *Gerakladium*) demeuraient les mêmes. J'ai également

observé que l'augmentation de la concentration en pigments chlorophylliens, la densité de symbiotes et les modifications de la morphologie du squelette (pour augmenter la capacité de collecte de la lumière) étaient les stratégies les plus significatives contribuant à maintenir la photosynthèse. Aucune évidence de plasticité nutritionnelle (passage d'un mode autotrophe à un mode hétérotrophe pour satisfaire les besoins en énergie primaire) n'a été détectée, malgré une réduction du $\delta^{13}\text{C}$ des deux espèces avec la profondeur. Cependant, le besoin d'études complémentaires, mettant en œuvre des techniques standardisées a été souligné, de façon à permettre de tirer des conclusions plus définitives sur les capacités d'acclimatation et les stratégies d'adaptation. Celles-ci en effet demeurent encore mal définies, en raison de la variabilité naturelle et spatiale observée. Une telle variabilité, et les multiples réponses observées pourraient fournir des indications sur la capacité des coraux à coloniser des zones plus profondes lorsque les milieux superficiels deviennent hostiles.

Chapitre 5. Ce chapitre présente des résultats montrant que des peuplements coralliens mésophotiques de Polynésie Française ont échappé à un épisode de blanchissement thermique. Au cours d'une vague de chaleur ayant causé une sévère mortalité des coraux superficiels, il a été observé que l'incidence du blanchissement corallien diminuait avec la profondeur : le blanchissement et la mortalité corallienne en résultant, passant de 35% à 6 m à moins de 5% à 20m, pour devenir inexistant au-delà de 40 m. Cette réduction dans le blanchissement avec la profondeur a été observée pour tous les genres dans toute l'étendue de leur intervalle de distribution bathymétrique. Je suggère de plus que la diminution dans l'incidence du blanchissement est plus fortement corrélée avec l'atténuation de la radiation lumineuse qu'avec la température. En conclusion, il apparaît que l'augmentation de la profondeur offrirait un certain niveau de protection, et il est proposé en conséquence que les ECM pourraient servir de refuge temporaire vis-à-vis des épisodes de blanchissement.

Chapitre 6. Dans le chapitre 6 sont rassemblées les discussions concernant les résultats exprimés dans les chapitres précédents. Quelques résultats préliminaires supplémentaires issus de « DEEPHOPE » y ont été rajoutés pour expliquer l'écologie et la physiologie des coraux scleractiniaires vivant dans les ECM de Polynésie Française. L'étude d'un échantillon le plus profondément jamais récolté à 172 m, a permis d'évaluer les capacités physiologiques extrêmes des scleractiniaires photosynthétiques. Si les

communautés symbiotiques se sont révélées les mêmes que pour les coraux peu profonds, une symbiose potentielle avec l'algue *Ostreobium* a été mise en évidence, témoignage de notre déficit de connaissances quant à la capacité des coraux à coloniser de plus grandes profondeurs. Par ailleurs j'ai souligné comment un effort de récolte soutenu a permis de repousser plus profondément les limites inférieures de distribution de multiples espèces. Je compare les différences spatiales observées en Polynésie Française avec d'autres localités, et attire l'attention sur le potentiel à l'échelle locale pour renfermer des ECM présentant un très fort taux de couverture par les scleractiniaires. La combinaison de résultats écologiques et physiologiques permet d'expliquer pourquoi certains aspects des recherches sur les ECM devraient être repensés, en prenant notamment en compte les abondances quantitatives plutôt que la seule zonation en fonction de la profondeur. De façon générale, j'explique l'importance jouée par les ECM dans la capacité de résilience des récifs coralliens et je discute la nécessité de prendre en compte les ECM dans les futurs projets de conservation des récifs en Polynésie Française, dans le contexte des changements climatiques. Finalement, je souligne les limites des recherches effectuées et esquisse des voies pour le futur, destinées à améliorer notre connaissance des ECM de façon à obtenir davantage de données, lesquelles pourraient avoir un impact positif sur les décisions de conservation.

Au travers de ses différents chapitres, les résultats de cette thèse contribuent à l'amélioration de nos connaissances de ECM de Polynésie Française, d'un point de vue écologie quantitative et physiologique. Ce travail fournit suffisamment d'arguments pour suggérer que la Polynésie Française est une région prometteuse au développement des ECM. De plus, il souligne d'une façon ou d'une autre dans chacun des chapitres que les profondeurs mésophotiques sont un environnement d'importance stratégique pour les lendemains difficiles auxquels les récifs coralliens auront à faire face en raison des changements climatiques. Il promeut également ces ECM comme étant des zones potentiellement dignes d'intérêt pour la conservation, renfermant des peuplements à forte diversité et taux de couverture, et étant moins susceptibles d'être affectés par les futurs changements globaux. Bien que ce travail présente des résultats nouveaux, en contribuant à l'amélioration de nos connaissances sur ces écosystèmes encore largement méconnus et fournisse une base pour de futures études en Polynésie Française, il convient de demeurer prudent. En effet il représente un instantané de la situation actuelle et ignore les trajectoires coralliennes passées et futures. Dans cette perspective je réitère et souligne le

besoin d'effectuer des recherches portant sur la zone mésophotique, afin d'améliorer notre capacité de prédiction et de mieux cerner les changements temporels.

En conclusion, cette thèse change notre vision d'une simple image des récifs coralliens superficiels en la remplaçant par un concept panoramique dans lequel les récifs de surface sont seulement la partie émergée d'un iceberg englobant la totalité des peuplements coralliens et dans lequel les ECM jouent vraisemblablement un rôle important. Ce travail souligne l'importance que les ECM peuvent avoir dans la résilience globale de l'écosystème récifal et suggère que la zone mésophotique est potentiellement une zone critique à prendre en compte dans le développement des stratégies de conservation des récifs coralliens, dans une perspective de changement global. Les résultats présentés dans cette thèse ont été établis à l'échelle géographique de la Polynésie Française, et des études quantitatives semblables en d'autres localités seraient nécessaires pour confirmer le caractère général et global de nos conclusions.

Extended summary

Climate change and other disturbances are causing the loss of scleractinian coral reefs. Underneath shallow coral reefs and despite light decreases with depth, Mesophotic Coral Ecosystems (MCEs) are characterised by photosynthetically active scleractinian corals, and associated reef communities, at depths ranging between 30 and 150 m in tropical and subtropical oceans worldwide. Although the interest in studying MCEs lies in increasing their little knowledge and potential as shallow reef refugia, most MCEs remain understudied or even unexplored due to the logistical constraints of studying beyond the limits of traditional scuba diving. However, along with advances in diving technologies, such interest triggered research into these extreme and marginal ecosystems to increase sharply in recent years. Yet, the body of literature has grown disproportionately around the world. While locations such as the Gulf of Eilat (Israel), the Great Barrier Reef (Australia), Curaçao (Dutch Caribbean), or American islands (Puerto Rico, US Virgin Islands and Hawaii) produced a large amount of research, locations like French Polynesia remain poorly studied.

Being part of the DEEPHOPE project (a collaboration between scientists and technical divers from Under The Pole), the present thesis addresses the knowledge gap in the Mesophotic Coral Ecosystems of French Polynesia shedding light on the ecology and physiology of these ecosystems. This thesis focuses on scleractinian corals to evaluate the MCEs' importance in the overall coral reef resilience. To do so, I tested if the diversity patterns and coral cover increased with depth to find key depths for conservation. I characterised the physiological acclimation and adaptation responses to depth to understand how scleractinian corals live in such low light environments. Finally, I tested whether mesophotic corals were equally impacted as shallow corals by the main threat of coral reefs today, a thermal bleaching event.

To answer my hypotheses, I realised and profited from the 10-month expedition across 11 islands from 5 archipelagos [1,600,000 km²] of French Polynesia and the ~800 TRIMIX rebreather dives below 100 m of DEEPHOPE. The expedition allowed me to gather (a) an unprecedented quantitative database (>3,500 photo-quadrats) along a wide depth range (6, 20, 40, 60, 90 and 120 m); (b) a physiological database (118 replicates of *P. cf. verrucosa* from 6 to 60 m depths, and 116 replicates of *P. "speciosa" spp.* from

10 or 20 to 90 m); and (c) an environmental database (*e.g.* light, temperature, bathymetry, CTD profiles and nutrients) along all working depths. At last, the expedition also collected (d) a comprehensive taxonomic database (>1,800 scleractinian specimens), which reinforced some of my data.

Chapter 1 introduces the generalities of coral reefs and Mesophotic Coral Ecosystems (MCEs) worldwide and the context for French Polynesia. I present the environment and community structure of MCEs and the current physiological knowledge of scleractinian corals living in low-light conditions. Although some studies are available, the reality is that there is not much knowledge from the MCEs of French Polynesia. According to the current shallow coral reef conditions and the previous knowledge of MCEs, I set the departing hypotheses of the different chapters.

Chapter 2 shows that MCEs are hotspots of scleractinian generic diversity in French Polynesia despite coral cover decreasing with depth. I found that the maximum genus richness (alpha, α -diversity) is between 20 and 60 m because genus richness followed a mid-domain effect. At around the peak of the mid-domain (40 m), it is the zone of maximum richness where you can simultaneously find the shallow and deep coral genus assemblages at the same time (*i.e.*, because dissimilarity and turnover increase with vertical distance between depths). I showed that the spatial (beta) β -diversity increased with depth, and it means that while shallow waters are similar across studied locations, mesophotic depths are different and unique. Therefore, requiring different conservation strategies to preserve regional diversity.

Chapter 3 shows that despite the general trend of coral cover decreasing with depth, MCEs are also home to unexpectedly high coral cover communities. Within the mesophotic range, 20 out of 64 studied deep sites exhibited a higher coral cover than expected (by models) for the depth. These outliers (named 'hotspots' of coral cover) were in some cases more highly-coral-covered than shallow reefs. I demonstrated that aside from depth and the amount of relative light according to the surface (co-variables), a moderate to steep slope and low sedimentation promote high coral cover with increasing depths, despite important differences among coral morphologies. I found that while laminar corals tend to associate with steeper slopes to dominate lower depths, a mix of encrusting and laminar corals are associated with more moderate slopes. At last, I laid the

foundations for predictive environmental modelling of coral cover in mesophotic depths while recognising the need to improve our prediction capacity and the need for future vulnerability assessments.

Chapter 4 shows the multidisciplinary trait strategies that two complex scleractinian species (*Pocillopora cf. verrucosa* and the complex of genetic diversity of *Pachyseris "speciosa" spp.*) use to cope with low-light environments, suggesting the capacity of corals to live along with broader depth ranges. With results deriving from studying the coral host and symbionts from a branching and shallow associated species and a laminar and mesophotic associated species, I found that despite symbiotic communities changing with depth, the dominant IST2 profiles (*Cladocopium*, *Durusdinium* and *Gerakladium*) remained the same with depth. I revealed that increasing chlorophylls pigments concentration, symbionts density, and modifying morphological skeleton (to increase light-harvesting capacity) were the most significant photophysiological strategies to keep up with photosynthesis. I found no evidence of nutritional plasticity (switching from autotrophy to heterotrophy as their primary energy source) even if both species reduced the $\delta^{13}\text{C}$ with increasing depth. However, I also showed evidence of the need of still future studies with standardised techniques to draw more robust conclusions on acclimation and adaptations strategies, which are currently unclear due to the natural and spatial variability. Such variability and multiple responses might suggest the corals' capacity to colonise deeper depths as shallow waters become hostile.

Chapter 5 demonstrates that mesophotic coral communities escaped a thermal coral bleaching event in French Polynesia. During a heatwave that caused severe shallow coral mortality, I found that the incidence of coral bleaching reduced with depth, with bleaching and subsequent mortality decreasing from 35% at 6 m to less than 5% at 20 m to non-existent after 40 m. This bleaching reduction was observed among all genera from their upper to their lower depth distribution range. Additionally, I suggested that the reduced prevalence of bleaching had a stronger relationship with the light-irradiance attenuation than temperature. In conclusion, I found that increasing depth may offer a level of protection, and therefore, the study suggested that MCEs might act as short term refugia from bleaching events.

Chapter 6 discusses the different outcomes of my chapters, with some additional preliminary results of DEEPHOPE, to explain the ecology and physiology of the scleractinian corals living in MCEs of French Polynesia. The physiological capacities were brought to the extreme by collecting and studying the deepest recorded photosynthetic scleractinian coral at 172 m. The finding came with similar symbiotic communities to shallow corals but with a potential symbiosis with the alga *Ostreobium*, which evidence our little knowledge of the corals' capacity to colonise deeper depths. I explain how a significant sampling effort confirmed the previous statement pushing the depth limits of multiple scleractinian species. I compare spatial differences in French Polynesia within and with other worldwide locations to describe the most highly scleractinian covered MCEs and suggest the potential of this region. According to the combination of physiological and ecological results, I explain why some “terms” of MCEs research should be rethought, considering quantitative abundances rather than depth zonation alone. Overall, I explain the potential ecological importance of MCEs to the overall coral reef resilience, and I discuss the potential need to consider MCEs for future systematic conservation planning of coral reefs in French Polynesia with climate change. Finally, I explain the limitations and how future directions can improve MCEs' research to have more data that will translate into a better understanding and impact on coral reef conservation decisions.

Across the different chapters, this thesis increases the knowledge of MCEs in French Polynesia from a quantitative ecological and physiological perspective. The thesis provides enough pieces of evidence to suggest French Polynesia as a promising location for the development of MCEs. Also, to support MCEs' importance because, in some way or the other, every chapter demonstrates that mesophotic depths are key depths for the difficult future of coral reefs with climate change. It presents MCEs as potential areas of conservation with highly diverse and covered reefs. It provides evidence that these MCEs might be less affected by future global changes. While the thesis presents new results, increasing knowledge about the still largely unknown MCEs and setting the basis for future studies in French Polynesia, it also calls for caution because it is a snapshot of the present state and ignores past and future coral trajectories. I emphasise the need for future research on the mesophotic range to improve our prediction capacity and to assess temporary changes.

In conclusion, this thesis changes the vision from a pure image of shallow corals to a vision where shallow coral reefs are just the tip of an iceberg from the overall ensemble of coral reefs, where MCEs are likely playing an important role. The thesis highlights the importance that MCEs might have in the overall coral reef resilience because these depths are potentially key areas to consider in future conservation planning for coral reefs with climate change. Although our outcomes are at the scale of French Polynesia, similar quantitative studies to this thesis are necessary for other locations to substantiate the global character of my findings.

RÉSUMÉ

La dégradation des récifs coralliens, causée par les changements climatiques, a attiré l'attention sur les Écosystèmes Coralliens Mésophotiques (ECM, 30-150 m), jusqu'à maintenant peu étudiés. Malgré la diminution de la lumière avec la profondeur, les ECM pourraient servir de refuge aux espèces des récifs superficiels, du fait de la diminution des perturbations avec la profondeur. Ce travail, basé sur les coraux scléactiniaires ayant fait l'objet d'un échantillonnage sur une large échelle de profondeur (6-120 m) et spatiale en Polynésie Française, montre que la zone 40-60 m est un point chaud de biodiversité et d'abondance et renferme simultanément des peuplements peu profonds et de type mésophotique. Cette zone peut également échapper aux effets de blanchissement. La multiplicité des stratégies développées pour s'adapter à des profondeurs différentes suggère que les coraux pourraient éventuellement se réfugier plus profondément si les couches de surface deviennent inhabitables. Il est donc suggéré que les ECM jouent un rôle critique dans la résilience de l'écosystème et leur prise en compte dans les stratégies de conservation est recommandée.

MOTS-CLÉS

Écosystèmes Coralliens Mésophotiques, scléactiniaires, écologie quantitative, patrons de diversité, points focaux, refuge spatial, blanchissement corallien, changement climatique, Polynésie Française.

ABSTRACT

Disappearing coral reefs under climate change increased attention to understudied Mesophotic Coral Ecosystems (30-150m; MCEs). Despite decreasing light, MCEs could act as refugia for shallow reefs because disturbances might reduce effects with depth. Focusing on scleractinian corals and using unprecedented data (with equal sampling effort along the reef slope) across a broad depth range (6-120m) and wide spatial scale, this thesis aims at shedding light on the MCEs in French Polynesia. The thesis suggests the potential of MCEs in the region and raises the ecological importance of MCEs, quantitatively showing that the 40-60m zone hosts: hotspots of biodiversity and cover, simultaneously shallow and deep-mesophotic communities, the most spatially variable communities, and the potential to escape a thermal bleaching event. The multidisciplinary strategies to live along different depths suggest corals might find refuge deeper if shallow waters become uninhabitable. Thus, it suggests MCEs are likely to play a critical role in the overall resilience and recommends their consideration in conservation planning.

KEYWORDS

Mesophotic Coral Ecosystems, Scleractinian, diversity patterns, quantitative ecology, hotspots, spatial refuge, coral bleaching, climate change, French Polynesia.