Mesophotic depths hide high coral cover communities in French Polynesia

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HIGHLIGHTS

- We evaluated 2880 quadrats from 6 to 120 m to identify high coral cover communities.
- 20 out of 64 mesophotic studied sites exhibited higher coral cover than expected.
- Coral hotspots reached 81 % at 40 m, 74.5 % at 60 m, 53 % at 90 m or 42 % at 120 m.
- Hotspots are more likely in hard benthos with steep-moderate slopes.
- Hotspots are unlikely on gentle slopes with sediments and rubble or vertical slopes.

GRAPHICAL ABSTRACT
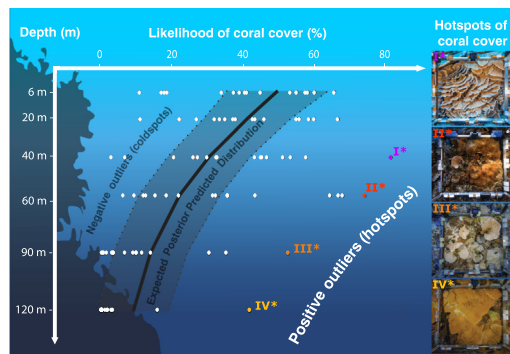
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ABSTRACT

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 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 influence such high scleractinian cover. Using Bayesian modelling, we found that 20 out of 64 of studied deep sites exhibited a coral cover higher than expected in the mesophotic range (e.g. as high as 81.8 % at 40 m, 74.5 % at 60 m, 53 % at 90 m and 42 % at 120 m vs the average expected values based on the model of 31.2 % at 40 m, 22.8 % at 60 m, 14.6 % at 90 m and 9.8 % 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 at 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.

1. 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 (Beyer et al., 2018; Cinner et al., 2016). 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 et al., 2019). As a continuation of shallow coral reefs, Mesophotic Coral Ecosystems (MCEs) occur between 30 and 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 >90 % between 60 and 120 m) has been described in a few reef locations since the early 1970s (Bridge et al., 2012; Eyal et al., 2016; Hoeksema et al., 2017; Hopley et al., 2007; Kahng et al., 2010, 2012, 2014; Kinzie and Robert, 1973; Sánchez, 1999; Zlatarski, 2007, 2018; Zlatarski and Estalella, 1982), 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 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 (Beaman et al., 2016; Benayahu et al., 2019; Bo et al., 2019; Bridge et al., 2012; 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 scleractinian corals to thrive in MCEs (Appeldoorn et al., 2016; Bridge et al., 2011; Englebert et al., 2017; Liddell et al., 1997; Liddell and Ohlhorst, 1988; Sherman et al., 2010, 2019). 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 largely unexplored.

While MCEs are considered biodiversity hotspots (Muir et al., 2018; Pérez-Rosales et al., 2022) with a potential role as short-term thermal refuges (Baird et al., 2018; Frade et al., 2018; Giraldo-Ospina et al., 2020; Muir et al., 2017; Pérez-Rosales et al., 2021) and/or larval sources for damaged shallow reef areas (Bongaerts and Smith, 2019; Montgomery et al., 2021), they have been traditionally overlooked in conservation management efforts due to logistical and cost challenges. Instead, these are mainly focused on shallow reefs (Beyer et al., 2018; Cinner et al., 2016; 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.

2. Material 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. 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 2880 quadrats and a total area of 1620 m^2. 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 videolights. The relative cover of each benthic group was quantified and identified to the maximum taxonomic resolution possible in 75 stratified random points per quadrat (Roelfsema et al., 2021; Van Rein et al., 2011) 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. as calcifying macroalgae, (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 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 to scleractinian corals. Soft corals and other sessile invertebrates were not separated into higher taxonomic groups for the current analysis (Sup. Table 2). Points falling on abiotic categories (except for turf) were classified into hard-fixed, soft sediment and rubble. The total percentage of coral cover was calculated as the relative abundance of the sum of all scleractinian-coral points.

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) and temperature were recorded for at least 48 h with a 5 min interval 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. Although these relative values decreased the variations between deployment times, these were still subjected to unavoidable seasonality and daily differences between the registered times across locations. 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 Englebert et al. (2017) and Sherman et al. (2019), reef slopes were categorised as (a) 'Gentle', from subhorizontal shelves to up to 30°; (b) 'Moderate' ~ from 30° to 50°; (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 4000 iterations after 1000 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. 1). Based on similar studies applying this approach (Cinner et al., 2016; Edmunds, 2021; Parravicini et al., 2014), positive outliers were named as 'hotspots' of coral cover in the mesophotic zone (Sup. Box 1), whereas negative outliers as 'coldspots' (Sup. Box 2).
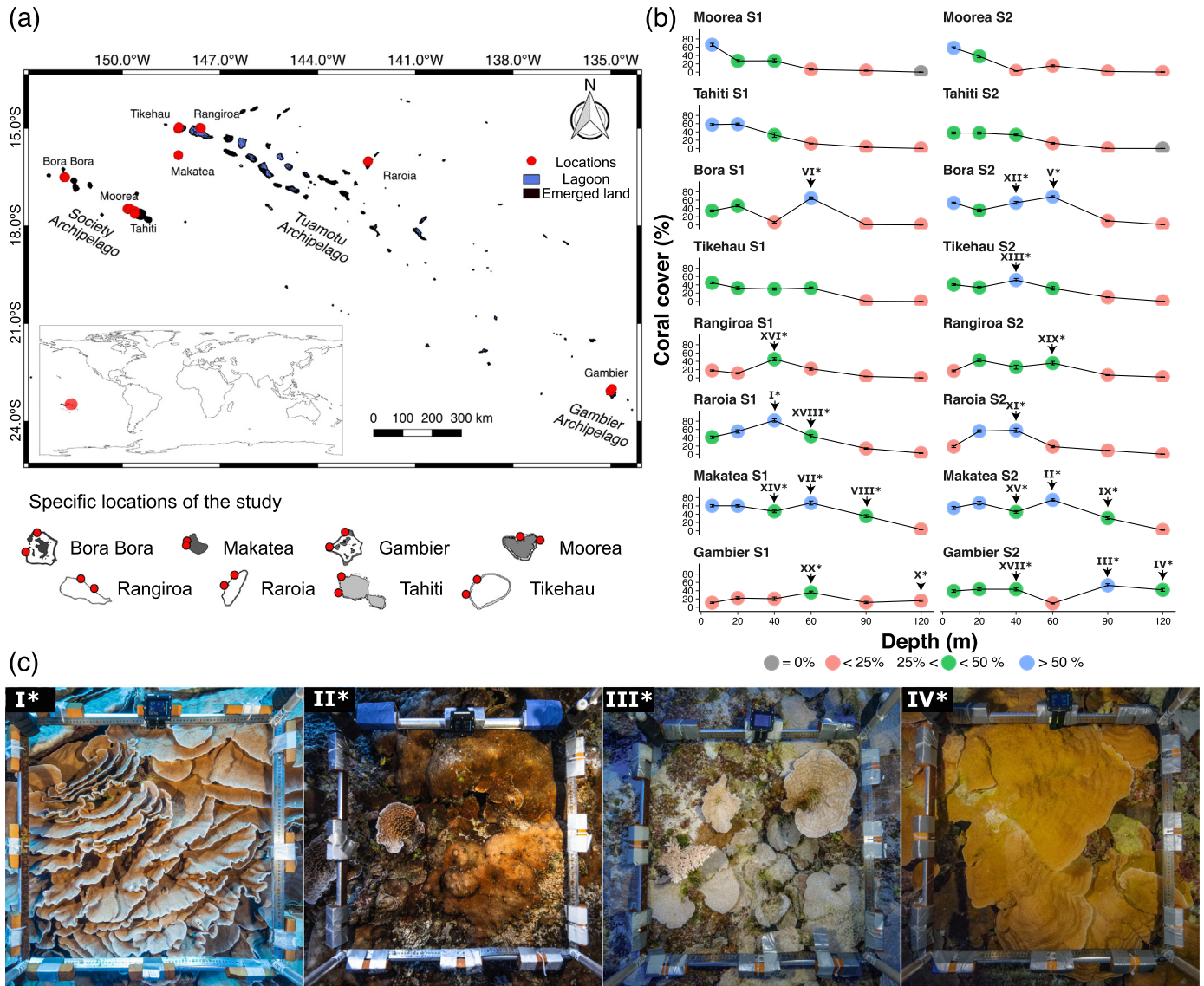
Fig. 1. High scleractinian coral cover 'hotspots' (positive outliers). (a) Map of French Polynesia detailing the study locations by islands. (b) Scleractinian coral cover profiles over depth across locations. 'Hotspots' outliers from the null expected distribution are indicated with arrowheads, roman numbers and asterisks (see model in Sup. Fig. 1 and correlations over depth in Sup. Fig. 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 Sup. Box 1.

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 4000 iterations after a 1000 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 and coral morphologies were evaluated using tests of homogeneity of variances (*BETADISPER*), permutational analysis of variance (*PERMANOVA*, blocked by quadrat)

and pairwise analyses (*PERMUTEST*) 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 et al., 2008). All analyses are conducted with R Studio (Version 1.3.959; R Core Development team 2013) and the necessary data and scripts to replicate our analyses are available at: www.github.com/gonzaloprb/Cover_with_Depth.

3. Results

Thirty-one 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. 1b and Sup. Fig. 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 ± 7.7 %, s.e.), Bora Bora sites at 60 m (64.7 to 68 %), Makatea S2 at 60 m (74.5 ± 3.1 %) and Gambier S2 at 90 and 120 m (52.8 ± 5.1 % and 42 ± 4.2 %, respectively) (Fig. 1 and Sup. Fig. 1). While Moorea and Tahiti presented a sharp decrease in coral cover below 40 m (from ~30 % to ~10 % at 60 m to <3 % at 90 m), other islands, such as Tikehau, Rangiroa and Raroia, exhibited a relatively 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. 1b; Sup. Fig. 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 ~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: $p < 0.001$, average distance to centroids 0.36 at 40 m vs 0.29 at 6 m, 0.31 at 20 and 60 m, 0.3 at 90 m and 0.29 at 120 m) despite 40 m showing similar scleractinian coral cover (20–50 % coverage across sites, Fig. 1b). In general, we found that coral cover tended to decrease along the depth gradient (Sup. Fig. 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. 1b and Sup. Figs. 1 and 2). Thus, within sites, the coral cover at a particular depth seems to be independent of the remaining depths along the depth gradient (Fig. 2b and 3, and Sup. Fig. 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 with increasing depth (Fig. 2). Based on the second (full) model ($R^2 = 0.62$), the likelihood of coral cover was 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 were more likely to harbour scleractinian coral cover at deeper depths than other substrates and slopes. Moderate and steep slopes
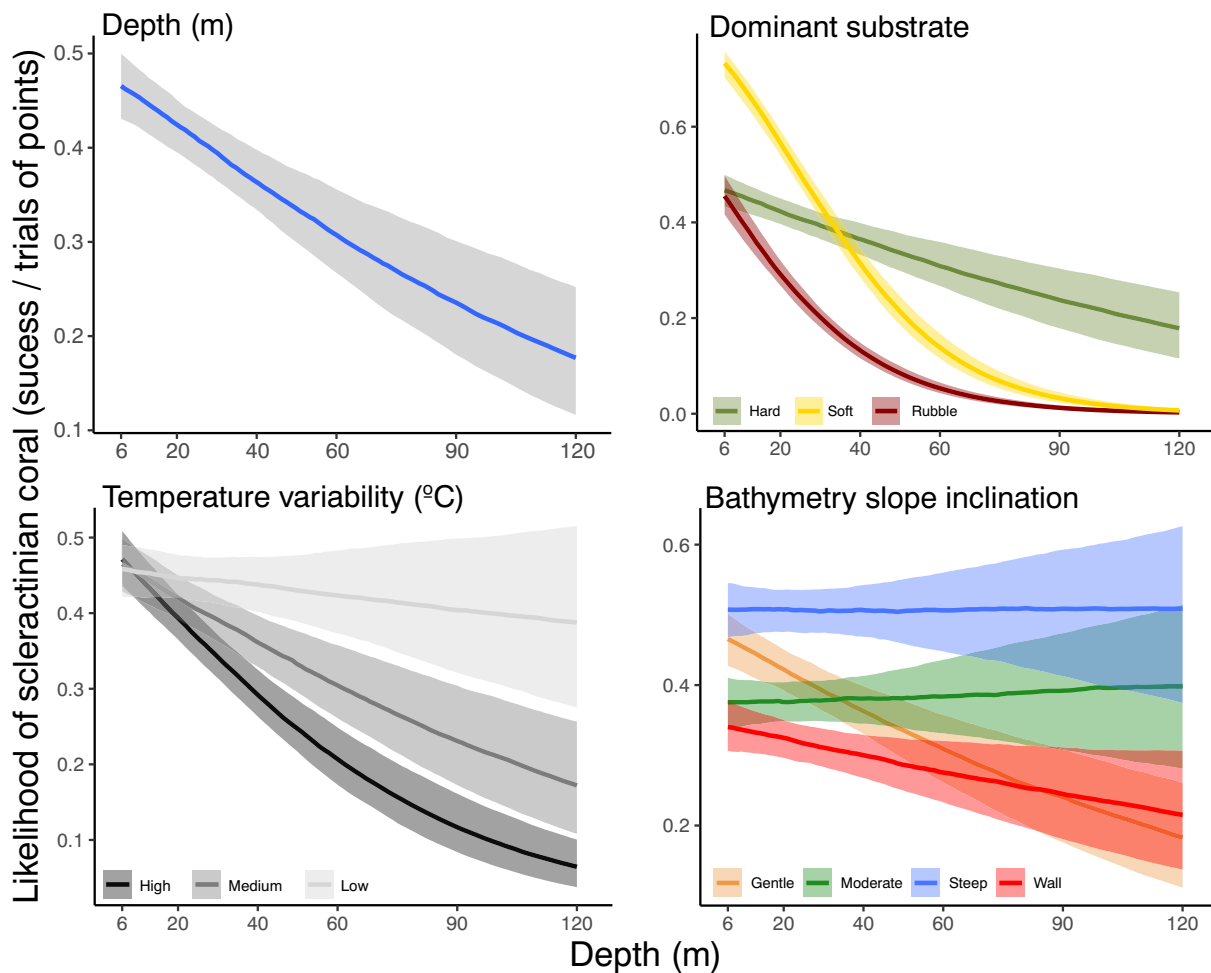
Fig. 2. Bayesian prediction probability of the likelihood of scleractinian corals (success/trials of total number of points) according to environmental variables co-varying with increasing depth. Depth and the light relative index are collinear (negatively correlated; cor. test, −0.85, $p < 0.05$) and equally determined the likelihood of scleractinian coral cover.
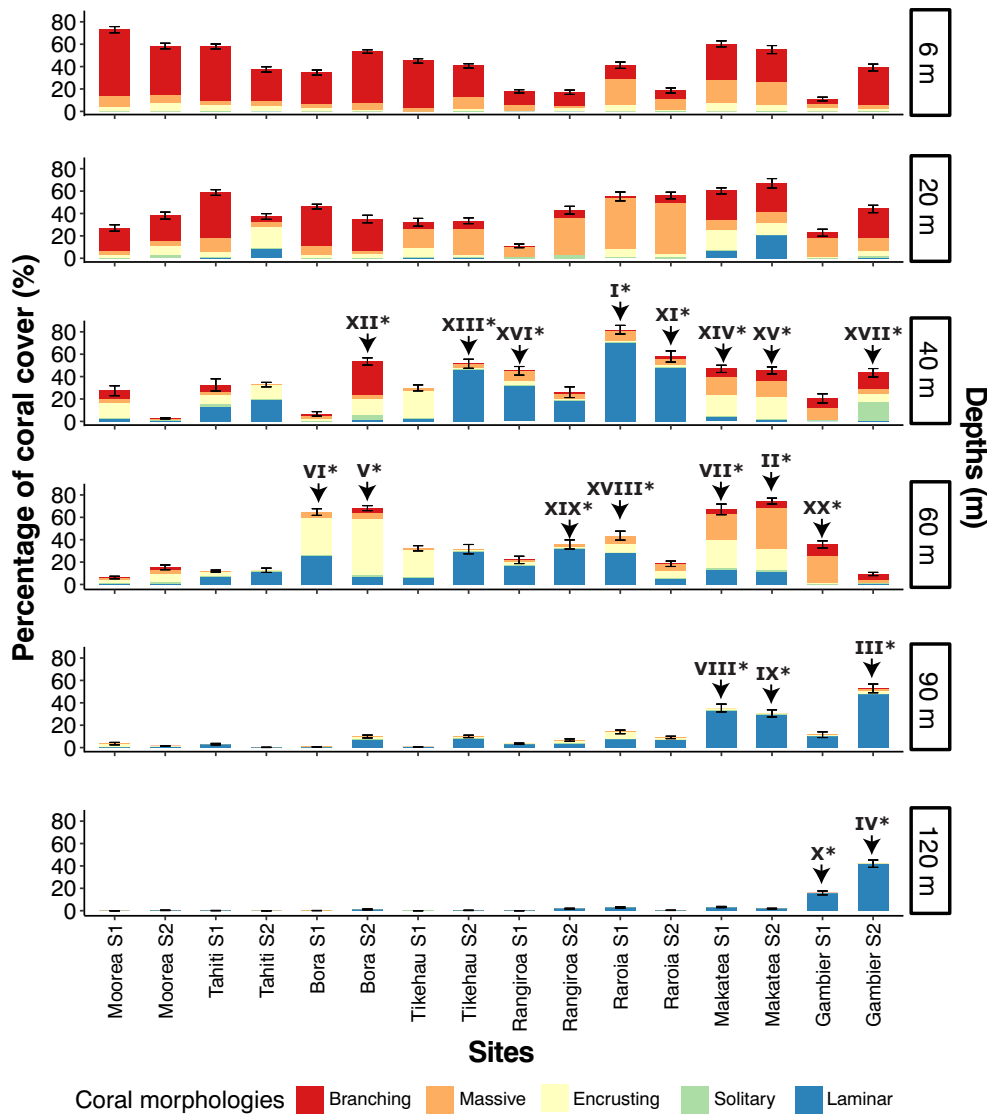
Fig. 3. Scleractinian coral cover composition by morphologies. 'Hotspots' outliers of coral cover are indicated with arrowheads, roman numbers and asterisks (see model in Sup. Fig. 1).

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 non-existent. 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 <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).

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

and Sup. Fig. 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 or by multiple coral forms (Sup. Box 1 and 2). Monotypic stands at 40 m mainly consisted of *Pachyseris* "*speciosa*"; deeper at 60–90 m, of *Leptoseris solida* showing diverse sizes across locations (e.g. in Makatea, sizes could reach up to 2000 cm^2); and at 90 and 120 m, of large thin plates of *Montipora* spp. (e.g. in Gambier, sizes could reach 2500 cm^2). When mesophotic reefscapes 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 and 26 % in upper mesophotic depths (40–60 m). At the deepest depths (>100 m), only small and thin laminar coral colonies (≤20 cm^2) of *Leptoseris hawaiiensis*, *Leptoseris scabra*, *Leptoseris fragilis*, *Echinophyllia aspera* and *Oxypora echinata* were found. Contrary to the 'hotspots' of coral cover, 'coldspots' were mainly dominated by CCA and sponges (average cover across sites of 7.23 ± 1.8 % and 9.09 ± 1.7 % at 90 m and 3.83 ± 0.9 % and 11.8 ± 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 ± 1.3 %, 3.51 ± 0.6 %, and 0.76 ± 0.5 % at 90 m and 7.02 ± 1.6 %, 5.6 ± 1.3 % and 2.44 ± 0.7 % at 120 m, respectively (maximum cover across sites, see Sup. Fig. 5, Sup. Tables 1, 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. 4 and Sup. Figs. 6 and 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 latter 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. 6b). Overall, we found that each coral form benefited from different environmental conditions and laminar corals dominated at lower mesophotic depths (Sup. Fig. 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. 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.

4. 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'). Conversely, 'coldspots' or low-cover sites were associated with vertical/negative slopes and gentle slopes with substrates mostly characterised by soft sediment and rubble favouring the presence of gorgonians, hydroids and sponges. 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 (Appeldoorn et al., 2016; Bridge et al., 2011; Hubbard, 1986; Perry, 2007; 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 part of the South Pacific represents a promising bioregion for the identification and research of high scleractinian cover in MCEs (as in Pichon, 2019; Rouzé et al., 2021).

The positive outliers reflected the morphological 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 glance these could appear to be monotypic stands, laminar-dominated outliers were diverse, comprising between 8 and 22 scleractinian species (SBox 1 and 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"* 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 (Bouchon, 1983; Faure and Laboute, 1984; Hoeksema et al., 2017; Hopley et al., 2007; Kahng et al., 2014, 2010; Kahng and Kelley, 2007; Kühlmann and Chevalier, 1986; Pyle et al., 2016; Rooney et al., 2010; Zlatarski and Estalella, 1982), and hypothesised to be related to potential physiological adaptations inherent to the host (Kahng et al., 2020), or acquired through symbiosis (Gonzalez-Zapata et al., 2018). For example, the observed skeletal geometry in laminar *Leptoseris* and *Montipora* species confers a higher

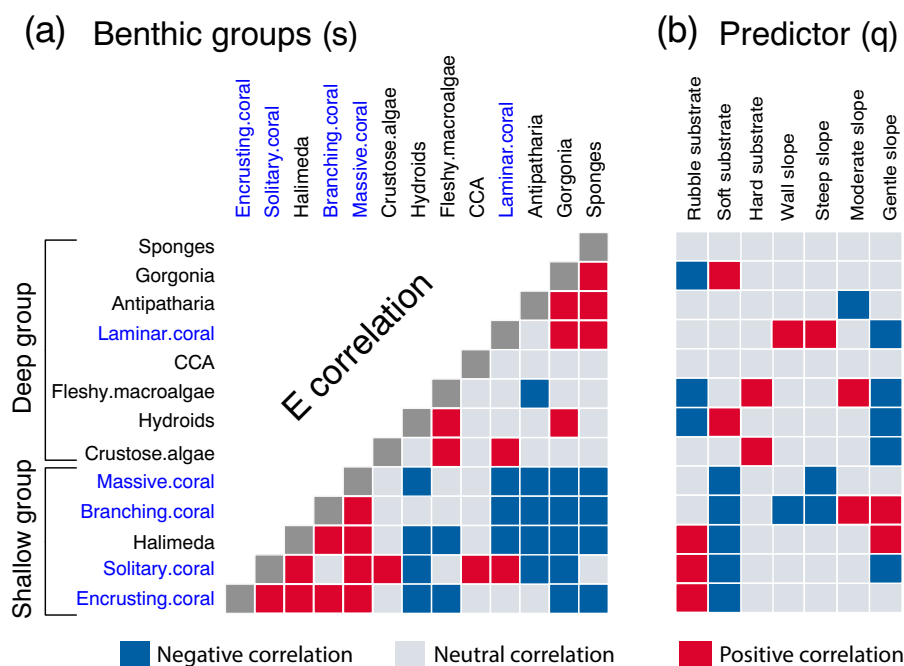**Fig. 4.** Correlation between the different benthic groups (*s*) and the most important environmental predictors (*q*). Correlations were simplified into negative (< -0.4), neutral ($-0.4 < 0.4$) and positive (>0.4). Neutral correlations are interpreted as neither positive nor negative influence, or the absence of supporting data. Shallow and deep groups were clustered based on E correlation (Sup. Figs. 6 and 7).

efficiency in light harvesting (Kahng et al., 2012), promoting moderate growth rates of these genera (Kahng et al., 2020), which could result in advantage while recruiting at mesophotic depths. Further, potential symbiosis with the endolithic green algae *Ostreobium*, observed as part of the benthic 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 and negative outliers highlight the unique and heterogeneous characteristics of MCEs and advances in elucidating some factors that could favour high coral cover at mesophotic depths. Studying the 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 be critical in advancing our understanding of MCEs, and in particular the potential role (s) of MCEs in overall coral reef resilience. Further consideration of negative outliers will contribute to predicting habitats unlikely to harbour mesophotic coral communities as well as to explain the heterogeneity observed in MCEs across spatial scales. Improving our predictive 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 and the diverse life histories across coral species. While coral reefs continue to be threatened by climate change (Bellwood et al., 2019; Hughes et al., 2018; Souter et al., 2021), comprehensive characterisation and monitoring efforts in MCEs are crucial for their incorporation in the conservation planning of tropical coral reefs (Bridge et al., 2013; Hernandez-Agreda et al., 2022; Rocha et al., 2018). By establishing a baseline for the geographical and temporal monitoring of MCEs in French Polynesia, we hope to provide a robust foundation for studying these ecosystems and ultimately enable their effective incorporation into conservation mangement efforts.

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Data availability

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

CRediT authorship contribution statement

Author Contributions. Gonzalo Pérez-Rosales: Conceptualization, Data curation, Formal analysis, Writing- Original draft preparation. **Alejandra Hernández-Agreda:** Formal analysis, Writing- Reviewing and Editing. **Pim Bongaerts:** Conceptualization, Writing- Reviewing and Editing. **Héloïse Rouzé:** Data curation, Writing- Reviewing and Editing. **Michel Pichon:** Writing- Reviewing and Editing. **Jérémy Carlot:** Writing- Reviewing and Editing, **Gergely Torda:** Writing- Reviewing and Editing. **Under The Pole consortium:** Data curation. **Valeriano Parravicini:** Conceptualization, Formal analysis, Supervision, Writing-Reviewing and Editing. **Laetitia Hédouin:** Funding acquisition, Supervision, Writing- Reviewing and Editing.

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Declaration of competing interest

The authors declare that there are no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.157049.

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