



Differential strategies developed by two light-dependent scleractinian corals to extend their vertical range to mesophotic depths

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Abstract Mesophotic coral ecosystems are characterised by the presence of photosynthetic scleractinian corals despite the decreasing amounts of light available with depth. To better understand physiological strategies across a broad depth gradient, we studied the biological trait responses of *Pocillopora* cf. *verrucosa* from 6 to 60 m depth and *Pachyseris* “*speciosa*” spp. from 20 to 90 m depth at four islands of French Polynesia. Specifically, we characterised associated Symbiodiniaceae communities, photophysiological traits (Symbiodiniaceae density and chlorophyll concentrations), micro-morphology and trophic plasticity (autotrophy vs heterotrophy inferred from stable isotopes). Our results showed that both taxa can live at mesophotic depths without significant genetic structuring in their generic Symbiodiniaceae communities, mainly composed of *Cladocopium* and *Durusdinium*. Yet, the prevalence of Symbiodiniaceae ITS2 profiles revealed location-based variations that sometimes

interact with depth and highlight putative shallow- or depth-tolerant taxa. For both taxa, symbiont density and chlorophyll pigment concentrations increased with increasing depth. We also found a change in their skeletal micro-morphology with an increase in the inter-corallite distance for *Pocillopora* cf. *verrucosa* and a decrease in the height of septa for *Pachyseris* “*speciosa*” spp. with depth. Finally, we found no isotopic evidence of switching to a more heterotrophic diet as their primary energy source, although host-tissue $\delta^{13}\text{C}$ ratios became more negative with depth in both corals. Overall, our findings show similarity (across the two species) and species-specific strategies (biological trait patterns with increasing depth) underlying the capacity of symbiotic scleractinian corals to live in low-light environments.

Keywords *Scleractinia* · Mesophotic · Physiology · Acclimation · Adaptation

Héloïse Rouzé and Laetitia Hédouin have equal contribution in supervision.

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Introduction

Reef-building scleractinian corals are the foundation for the invaluable biodiversity of coral reef ecosystems. However,

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most scleractinian corals rely on an obligate symbiosis with single-cell dinoflagellate algae (Symbiodiniaceae) that require sunlight to photosynthesise. The photosynthetic output provides the coral host with up to 95% of the necessary energy (Falkowski et al. 1984; Blackall et al. 2015) to fuel metabolic activities, such as growth, reproduction and bio-calcification of the skeleton that constructs and sustains coral reefs (Muscatine 1990; Allemand et al. 2011). Due to their light dependency, light availability was perceived as a limiting resource for coral communities, shaping the ecological niches of species and driving vertical community structure changes with depth (Laverick et al. 2017). Although exhaustive research on corals' adaptation and acclimation to distinct light regimes is available spatially for shallow depths, the integrative response of the coral holobiont from species across wide depth ranges remains little known, restricted to specific locations and rarely considering the whole depth gradient of species (Bongaerts et al. 2015a; Ziegler et al. 2015; Eckert et al. 2020).

Although scleractinian corals are usually associated with shallow depths, the exploration of mesophotic coral ecosystems (MCEs) from 30 to 150 m depth (Puglise et al. 2009) has shed light on the capacity of photosynthetic scleractinian corals to live at depth in low-light environments (Pyle and Copus 2019). The environmental conditions change along the depth gradient, especially the amount and composition of light, photosynthetically active radiation (PAR), decreasing on average to less than 5% of surface PAR at 100 m (Kahng et al. 2019; Laverick et al. 2020). Thus, for light-dependent organisms like symbiotic scleractinian corals, the exponential decrease in light irradiance with depth should be a limiting factor for their physiological performances and subsequent ecological niches (Fricke and Schuhmacher 1983).

Likewise, other environmental conditions, e.g. potential anomalies in seawater temperatures, extreme concentrations in nutrient levels and low or high hydrodynamic flow, are likely to influence scleractinian development (Huston 1985; Kahng et al. 2010, 2019; Rooney et al. 2010). Yet, light appears to be the primary determinant in the vertical distribution of symbiotic scleractinian corals (Kahng et al. 2019; Tamir et al. 2019). A recent discovery reported the presence of the deepest symbiotic scleractinian coral collected at 172 m, towards the lower limit of the photic zone (less than 1% of surface PAR) (Rouzé et al. 2021). According to our present knowledge of MCEs (Bongaerts et al. 2019; Kahng et al. 2019), species-specific depth distributions respond to two distinct strategies. On the one hand, some species have specific acclimations/adaptations to a narrow depth range (either at shallow or deep depths), constrained by their ecophysiological performances that limit their capacities to live outside these narrow ranges (e.g. *Acropora nasuta* and *Lobophyllia agaricia*, 1–38 m: Muir and Pichon 2019; *Agaricia humilis*, 2–10 m; or *Madracis*

formosa, 40–60 m: Bongaerts et al. 2013). On the other hand, other species are more plastic in their ecophysiological properties and, therefore, can live in broader depth ranges (e.g. *Leptoseris hawaiiensis*, 3–172 m; or *Leptoseris scabra*, 5–127 m: Muir and Pichon 2019; Rouzé et al. 2021).

Results of a growing number of studies conducted to understand how corals cope with low-light environments indicate that corals may indeed use genetically determined adaptations or phenotypically plastic responses. For example, they may (i) shift endosymbiotic (Symbiodiniaceae) composition to more low-light-adapted communities (Bongaerts et al. 2015b); (ii) increase the symbiont density or the photosynthetic pigments for photosynthesis (Wyman et al. 1987; Maritorena et al. 2002; Stambler et al. 2008; Mass et al. 2010; Smith et al. 2017; Padilla-Gamiño et al. 2019); (iii) adopt a flattened skeletal morphology to increase light exposure (Muir et al. 2015; Soto et al. 2018; Malik et al. 2021); (iv) reduce the number of polyps per surface area to limit energy needs (Soto et al. 2018); (v) decrease tissue thickness to reduce the energy required for calcification (Kaniewska et al. 2011); (vi) increase active feeding (heterotrophy) (Williams et al. 2018; Watanabe et al. 2019); or even (vii) decrease growth and reproductive efforts to conserve the energy for other vital requirements such as surviving (Mass et al. 2007; Shlesinger and Loya 2019).

There are two hypothesised biological strategies by which coral species may live in low-light environments: (1) maintaining metabolic and physiological rates similar to those of shallower specimens (Cooper et al. 2011; Shlesinger and Loya 2019) and or (2) reducing the energetic needs at deeper depths (Barnes 1990; Grigg 2006; Mass et al. 2007; Bongaerts et al. 2015b). Additionally, the high inter- and even intra-specific variability, with contrasting trends reported across locations in ecophysiological performances along the depth gradient (Soto et al. 2018; Padilla-Gamiño et al. 2019), makes the acclimation and adaptation mechanisms to low-light environments still not fully understood (Ziegler et al. 2015; Kahng et al. 2019; Slattery et al. 2024). Therefore, despite valuable knowledge from a handful of species and locations, robust conclusions on their ability to optimise and or maintain their performances in low-light mesophotic depths are still lacking (Kahng et al. 2019). Furthermore, the understanding may have been hindered by the fact that coral species are usually investigated through limited (1) species and depth zones and (2) biological traits examined. In the end, works focusing on broad depth ranges and overall strategies (i.e. simultaneously studying individual biological traits to combine results and assess overall response) remain relatively scarce (Lesser et al. 2010; Padilla-Gamiño et al. 2019). Nevertheless, we hypothesise that different coral species' responses to low light are likely driven by specific biological traits acting simultaneously and leading

to overall strategies, *e.g.* photophysiology, morphology and heterotrophy.

Here, we used two widely (*i.e.* geographically and vertically) distributed and abundant corals, *Pocillopora* cf. *verrucosa* and *Pachyseris* “*speciosa*” spp., collected from 6 to 60 m and 20 to 90 m, respectively, in four islands of two archipelagos in French Polynesia (Fig. 1 table) as model organisms to test the ecophysiological changes along the outer reef slope depth gradients. In particular, we investigated individually and through a multi-disciplinary approach (with a Bayesian multivariate model) the (1) qualitative composition of coral-associated Symbiodiniaceae communities; (2) multiple biological traits involved in the coral holobiont photophysiology (symbiont density, photosynthetic pigments and morphology); and (3) nutritional pathways to better apprehend the importance that each individual trait plays in the overall strategy (*i.e.* response) to increasing depth.

Material and methods

Coral species model

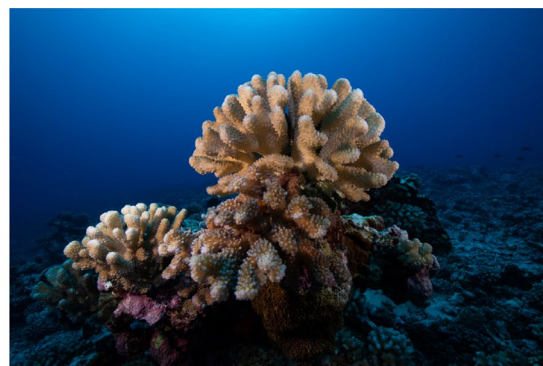
We selected two widely geographically occurring species or complex of species in the Indo-Pacific (Veron and Pichon 1979; De Vantier and Turak 2017; Bongaerts et al. 2021): *Pocillopora* cf. *verrucosa* (Ellis and Solander 1786) and the complex of species *Pachyseris* “*speciosa*” spp. (Dana 1846).

These are ideal model species/taxa for studying physiological responses to depth because (a) of their broad vertical depth range distribution with different dominance at particular depths, shallow vs mesophotic, respectively (Muir and Pichon 2019); (b) they belong to different families and exhibit contrasted morphologies, branching vs laminar, respectively (Schmidt-Roach et al. 2014; Soto et al. 2018; Bongaerts et al. 2021); and (c) they play a significant role in the overall community structure of coral reefs in French Polynesia from shallow to mesophotic depths (Pérez-Rosales et al. 2021; Pérez-Rosales et al. 2022). *Pocillopora* cf. *verrucosa* (Ellis and Solander 1786) is a common branching coral living in lagoons and fore reefs. Its depth distribution is primarily in shallow waters, but it is also found down to 60 m on the outer reef slopes in French Polynesia. The complex of species *Pachyseris* “*speciosa*” spp., known as *Pachyseris* “*speciosa*” (Dana 1846), are ubiquitous laminar corals found on the reef slopes. Recently described as a complex of at least four distinct species (Bongaerts et al. 2021), the complex has not yet been studied in French Polynesia and, therefore, will be referred to as *P. “speciosa”* spp. in this study. Their depth distribution in French Polynesia ranges from approximately 20 m to 90 m, and they are a dominant taxa at mesophotic depths. We identified both complex species/taxa according to the available literature (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 taxa, we studied each species separately to ensure the robustness of our statistical

Fig. 1 Coral species model and table with the number of replicates used in this study. **a** *Pocillopora* cf. *verrucosa* and **b** *Pachyseris* “*speciosa*” spp. Copyright images: Franck GAZZOLA / UNDER THE POLE / Zeppelin Network

(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



analyses due to the weight of inter- and intra-specific variation, the different depth zonations (*i.e.* specific depths for particular species) and the species-specific biological traits (*e.g.* micro-morphological metrics) investigated.

Study locations and sampling

Between September and November 2018, we sampled four reefs in four islands from 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 Archipelago. We used technical Trimix Closed Circuit Rebreather diving to collect fragments of *Pocillopora cf. verrucosa* and *Pachyseris "speciosa"* spp. from their local shallower to deeper distribution range. In total, we collected 118 samples of *P. cf. verrucosa* from 6 to 60 m and 116 samples of *P. "speciosa"* spp. from 10 to 90 m (Fig. 1 table). During the collection of each coral sample, we immediately subsampled 3–5 micro-fragments that we preserved in 96% ethanol for further genetic analyses and one ~5 cm fragment that we flash-froze in liquid nitrogen (−80°C) for physiological analyses and later morphometric measurements. At the same time, we measured in situ light—photosynthetically active radiation (PAR)—at the sampling depths and sites (DEFI2-L JFE Advantech) (Sup.Fig. 1). We estimated the few missing data using the Beer–Lambert equation (Gordon 1989). All values were normalised according to the shallowest depth available measure (6 m) to avoid weather variation and, to a certain extent, the seasonality when the light was recorded across locations.

Genetic identification of Symbiodiniaceae communities

We extracted the total genomic DNA of the coral samples (averaging 1 cm²). We used the MOBIO PowerSoil DNA Isolation Kit (Qiagen, Hilden, Germany) for DNA extraction following standard protocols (Sunagawa et al. 2010; Saad et al. 2020) and the slight modifications by Rouzé et al. (2021). Specifically, we added a pre-step with three cryo-shock cycles (5 min in liquid nitrogen, 5 min at 65 °C and 2 min of vortex), followed by mechanical treatments using lysing matrix A (MP Biomedicals, Strasbourg, France) and the FastPrep Cell Disruptor system (3 cycles: speed 6 m s^{−1} during 30 s with pause time of 60 s) (MP Biomedicals). We retrieved Symbiodiniaceae communities amplifying the ITS2 gene with the following specific primers: SYM_VAR_5.8 S and SYM_VAR_REV (Hume et al. 2015). We sequenced the PCR products using the MiSeq Illumina (Comeau et al. 2017). All amplifications and sequencings were carried out at the Integrated Microbiome Resource (www.imr.bio, Canada). We submitted the demultiplexed

paired forward and reverse ITS2 fastq.gz to SymPortal for analysis. This analysis involved using the platform analytical framework and database (Hume et al. 2019) to predict ITS2 type profiles (access date of the SymPortal database: 2020-12-03_DBV). 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 analyses

We removed the tissue from the frozen (preserved at −80°C) coral fragment from each sample using the air-pick technique with filtered (GF-F 47 mm—Whatman) seawater (FSW). We mixed and homogenised the tissue in falcon tubes with the used FSW and then centrifuged (20 min, 12,000 rpm and 4 °C) for at least four cycles to completely separate the two fractions: the pellet (*i.e.* Symbiodiniaceae fraction) and the supernatant (*i.e.* host fraction). With the Symbiodiniaceae fraction, we resuspended with 5 ml FSW. To estimate Symbiodiniaceae density, we used 0.5 ml of the solution. While we acknowledge that these centrifugations were higher than usually used in the literature (2000 g-force around 5 min; Nahon et al. 2013), we validated the purity of the symbionts' fraction at this stage and set a higher centrifugation speed (consistent among all our samples) to account for large amounts of mucus encountered in our samples (high viscosity). For analysing chlorophyll pigment concentration, we used 1.5 ml with the use of pure acetone, which allows the breaking of cell walls to liberate the photosynthetic pigments. To do so, we centrifuged the 1.5 ml of chlorophyll pigment concentration (20 min, 12,000 rpm and 4°C), dried and redissolved with 1 ml acetone for 24 h. Finally, we stored the remaining volume of both Symbiodiniaceae and host fractions for further isotopic analyses, and we kept the coral fragments (without tissue) to measure the surface area and the morphometric traits analysis.

We estimated the Symbiodiniaceae density (i) by manually counting (≥ 6 times) the cells present in the fraction using a hemocytometer and a light 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 dissolved Symbiodiniaceae fraction with acetone. Before the reading, we centrifuged (5 min, 12,000 rpm and 4°C), and we measured pigments concentration with a spectrometer at 630, 663 and 750 nm wavelengths (Thermo Scientific Evolution 60 S UV–Visible). Again, we dried the pellet, dissolved it again with 1 ml acetone and repeated this process 24 h later to ensure we completely extracted chlorophyll pigments, obtaining reading values equal to

the blank. With the spectrometer readings, we used Jeffrey & Humphrey (Jeffrey and Humphrey 1975) equations (Eq. 1–2) to measure chlorophyll *a* and *c*₂. We computed concentrations of chlorophyll *a* and *c*₂ according to (1) the three-dimensional surface area (Einscan Sp Software) of the coral fragment (Kramer et al. 2021, 2022) to take into account the morphological differences with depth and (2) the number of Symbiodiniaceae cells. Finally, we calculated the ratio between chlorophyll *c*₂ per symbionts divided by chlorophyll *a* per symbionts. At all stages, we kept samples at 4 °C and in dark conditions. Finally, we stored the same coral fragment samples for micro-morphometric analyses.

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

$$\text{Chl}c_2 [\mu\text{g}/\text{mL}] = 27.09 \times (A_{630} - A_{750}) - 3.63 \times (A_{663} - A_{750}) \quad (2)$$

Micro-morphometric traits

We measured multiple morphological features (iii) according to classic morphometric traits used in taxonomy (pers. obs. 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 Leica Application Suite EZ software. For *P. cf. verrucosa*, we measured the corallite size diameter (CS) and the intercorallite distance (CD). We performed the measures in two zones of the colony because of the existence of different micro-environments of light exposure due to the branching morphology. We realised the measures in the apical (*i.e.* which was the top axial part of the branch) and basal (*i.e.* which was the bottom part of the branch next to the main body) zones of the colony (Sup. Fig. 2). For *P. “speciosa”* spp., we measured the height of septa (HS) from the valley floor to the top of the ridge, the distance between septa (DS) and valley width (VW) (Sup. Fig. 3).

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 host (coral animal) and the Symbiodiniaceae (coral symbionts) fraction, we filtered with a vacuum system between 1.5 and 2 ml on previously burned (4 h, 460°C) filters (GF-F 47 mm diameter). For the Symbiodiniaceae fraction, we applied 1N 0.5 mL of HCl on the filter to remove any remaining residual carbonate and rinsed them with Milli-Q water (Nahon et al. 2013; protocol published by Price et al. 2020). Between samples, we cleaned the filtering system with HCl, acetone, Milli-Q water and FSW and sterilised the material with an autoclave. We dried the filters in a laboratory stove at 60°C

and stored them in sterilised conditions until further isotopic analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which were analysed on ThermoFisher Isotope Radio Mass Spectrometer at Cornell University Stable Isotope Laboratory (Cornell University, Supplementary Method). With the available $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data for symbionts (later called *symbionts*) and host (later called *host*) fraction, we measured the following variables: the ratio of $\delta^{13}\text{C}/\delta^{15}\text{N}$ for the host, the ratio of $\delta^{13}\text{C} / \delta^{15}\text{N}$ for the symbionts, the delta $\delta^{13}\text{C}$ (host–symbionts) and the delta of $\delta^{15}\text{N}$ (host–symbionts).

Light penetration as a function of 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 < 0.05; Sup. Fig. 1). With this assumption and running our tests according to depth independently for each location, we omitted the potential light variability that could influence our outcomes (*i.e.* possible seasonal differences because the light loggers registered measures at different times of the year (not simultaneously) or even atmospheric weather sky conditions, clear vs overcast cloudy days). Another reason to use depth instead of the irradiance of light and to test separately for each location is to consider site variability while reducing inter-site data deviations (*i.e.* based on seasonal and sky conditions) and increasing the robustness of our results. This approach means we considered spatial variability but omitted spatial comparisons because the study was aimed at coral physiology along the depth gradient. In other words, the model will test the same question of how it changes with depth for each location separately but provide an overall output. Despite the fact that ignoring spatial variability would have meant a higher number of replicates (*i.e.* considering all sites as one), we preferred to treat each site individually to be statistically more robust and compensate for the few replicates by running Bayesian models with more iterations. Finally, we considered each sample as individual entries for our multivariate model. However, we had to separately analyse the associated Symbiodiniaceae ITS2 type profiles and the trophic (isotope) niche plasticity along the depth gradient because of the minimum number of replicates required for statistical tests.

Associated Symbiodiniaceae ITS2 type profile analysis

Statistical analyses were conducted on ITS2 type profile data inputs produced by Symportal (Hume et al. 2019) using Eckert’s et al. (2020) R pipeline (Kenkel’s script) to test for Symbiodiniaceae community differences across depths and sites. The *betadisper* function from the *vegan* package 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 sampling design and to overcome 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 were obtained, pairwise PERMANOVA tests were conducted with the package *pairwiseAdonis* (Martinez Arbizu 2019) using false discovery rate (FDR) corrected *p*-values. Finally, similarity percentage (SIMPER) analyses were performed to determine ITS2 type profiles that best characterised the symbiotic community of each sample across depths and sites.

Biological traits of coral symbiont analysis (photophysiology)

Considering now all available variables, we tested them individually with increasing depth and together to ascertain the differences between variables (biological traits). First, we standardised the data by subtracting the mean and dividing it 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 (within collinearity, we kept the variable with the most robust correlation with depth, yet these correlated variables were commented on in the results; Fig. 3, Sup. Figs. 4 and 5). Third, we performed a principal component analysis (PCA) to test the correlations and influence of all quantitative variables (excluding depth as the unique environmental variable) with the packages *FactoMinerR* and *Factoshiny* (Lê et al. 2008; Vaissie et al. 2021). Here, depth was used to group samples with ellipses with a significance level of 0.5 to allow visualisation (i.e. acting only as a supplementary categorical variable not to influence the coordinate system). Fourth, we ran a multivariate Bayesian model to test how the different measures responded to increasing depth using the package *brms* (Bürkner 2017). 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 small number of replicates by increasing the number of iterations to 4,000. To ascertain the effect of increasing depth on each measured variable and comparing between variables, we studied the slopes using their confidence intervals (CI) of 95% from the converged model. Fifth, we computed a dissimilarity

matrix and tested a permutational multivariate analysis of variance (PERMANOVA) according to the individual biological traits acting simultaneously. At this stage, we also tested whether depth significantly separated these variables in different groups and ran pairwise comparisons (Pairwise PERMANOVA) between depths. All individual values and comparisons between sites and depths are available in supplementary data.

Trophic (isotope) niche plasticity

To evaluate trophic niches and nutritional plasticity, we used HOTELLING tests from the package *Hotelling* to measure the distances between the host and symbiont fractions of both isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) with all available samples at each depth and site (>3). If the distances of centroids are distinct between the two fractions and the *p*-values are significant, it means the coral host is decoupling from the symbiont and trending towards greater heterotrophy (Conti-Jerpe et al. 2020; Thibault et al. 2021). Therefore, we tested how these distances interacted with increasing depth. Finally, we measured the relative degree of heterotrophy (RDH) as an indicator of potential nutritional shifts (RDH, $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{Host}} - \delta^{13}\text{C}_{\text{Symbiont}}$) (Williams et al. 2018).

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

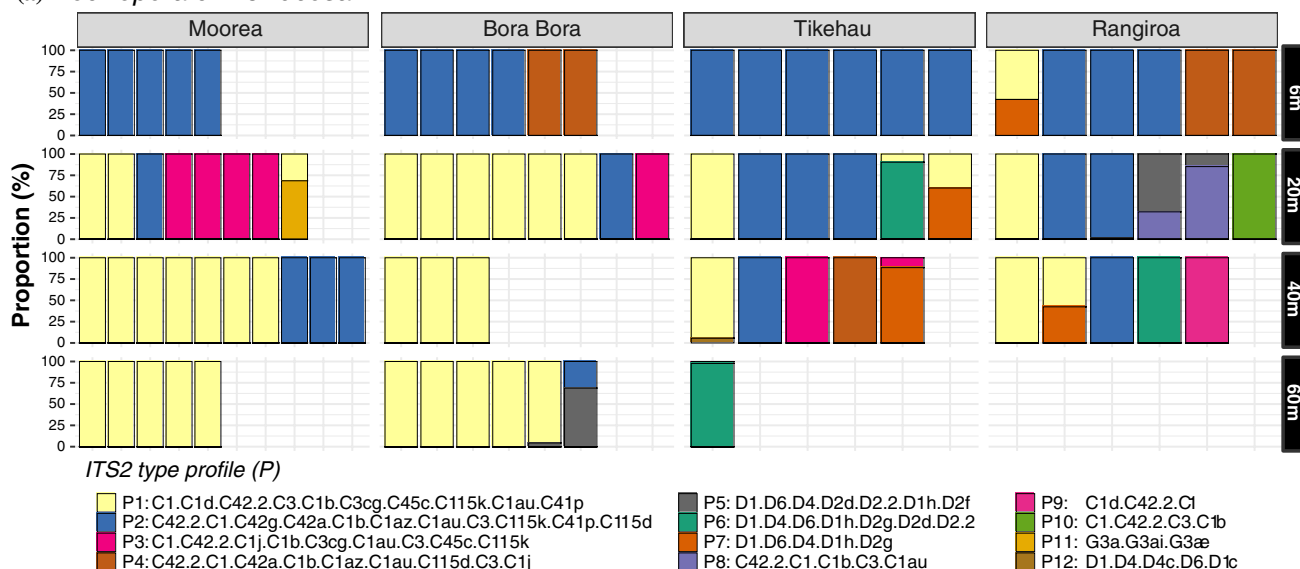
Results

Pocillopora cf. verrucosa

Associated Symbiodiniaceae ITS2 type profiles along the depth gradient

Across all *P. cf. verrucosa* samples, we identified 12 unique ITS2 type profiles. Seven composed of *Cladocypium* (formerly clade C), four of *Durusdinium* (formerly clade D) and for one single colony *Gerakladium* (formerly clade G) (Fig. 2a). The Symbiodiniaceae communities at the generic level were statistically constant with depth. Yet their respective ITS2 type profile prevalence varied significantly with depth, sites and the interaction between depth and sites (PERMANOVA $p < 0.05$, Table 1). While non-exclusive to the 6 m depth, ITS2 type profiles C42-related like *P2* and *P4* were largely predominant in the shallowest depth (6 m), accounting for over 38–42% and 9–12% of the dissimilarity with deeper depths (SIMPER tests) (Fig. 2). However, a closer analysis per archipelago showed that only in the Society Islands the Symbiodiniaceae communities differed significantly between 6 m and

(a) *Pocillopora cf. verrucosa*



(b) *Pachyseris "speciosa" spp.*

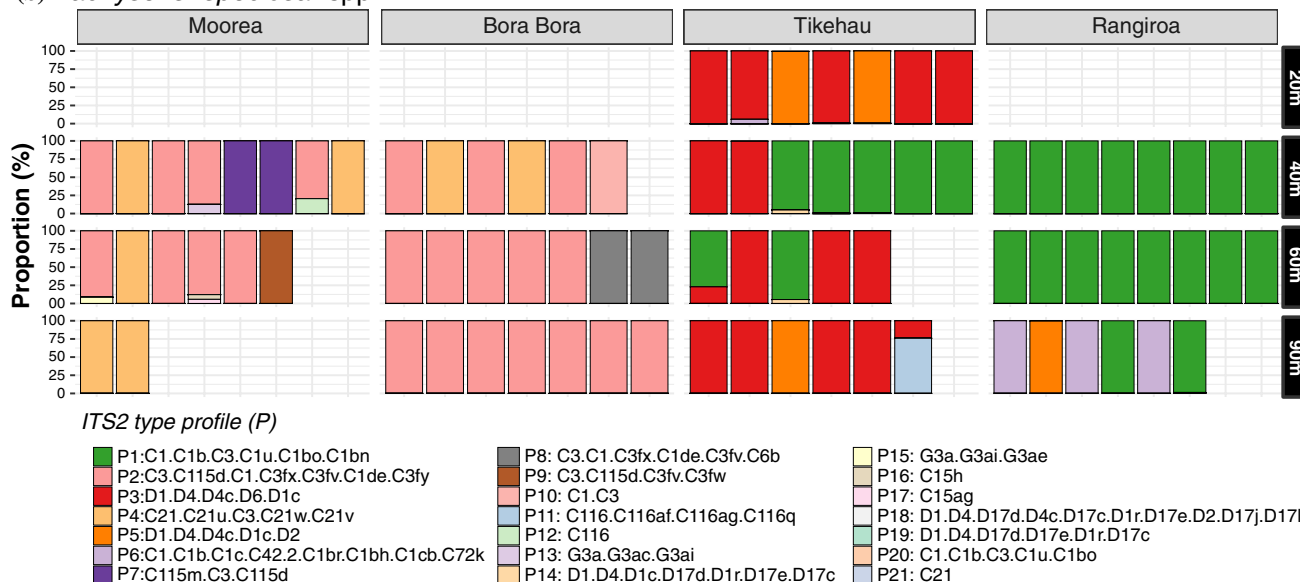


Fig. 2 Normalised relative proportion of ITS2 type profiles from **a** *Pocillopora cf. verrucosa* and **b** *Pachyseris "speciosa" spp.* at different depths and islands. ITS2 type profiles are listed in order of overall decreasing abundance

all other depths (PERMANOVA results; Table 1). From 20 m to mesophotic depths, we observed two geographical patterns but no significant depth effect. In the Society Islands, 85% of the associated Symbiodiniaceae communities were characterised with predicted ITS2 type profiles belonging to the C1 radiation (Fig. 2a). In the Tuamotu, associated Symbiodiniaceae communities along the depth gradient were more diverse and overlapped with ITS2 type profiles dominated by C42 (profiles P2 and P4) and or C1-related (profiles P1 and P3) at ≥80% and in some cases with D1-related (~ 17%; profiles P6, P7 and P5).

Biological coral symbiont traits along the depth gradient

For *P. cf. verrucosa*, the measured photophysiological variables clustered by depths and locations (PERMANOVA = 16.85, $p < 0.05$, $R^2 = 0.16$ and PERMANOVA = 6.96, $p < 0.05$, $R^2 = 0.13$; respectively, residual $R^2 = 0.67$) (Fig. 3a) because some variables had clear patterns with increasing depth, aligning with the principal component Dimension (Dim) 1 contribution (23.7% of data). In order of importance, the variables that increased with depth were the distance between corallites in the basal parts

Table 1 Test results from permutational multivariate analysis of variance (black bold) (PERMANOVA; 9,999 permutations) of Symbiodiniaceae ITS2 type profiles from *P. cf. verrucosa* and *P. “speciosa”* spp. colonies and pairwise comparisons (grey italic) between

all depth zones (FDR corrected). Islands are (Society Islands: MOO=Moorea, BOR=Bora Bora; and Tuamotu Archipelago: TIK=Tikehau and RAN=Rangiroa)

Species	Test	Comparison	R^2	F	P adjusted
<i>Pocillopora cf. verrucosa</i>	Overall	<i>depths</i>	0.22	8.59	<0.05
		<i>6–20</i>	0.18	10.60	<0.05
		<i>6–40</i>	0.24	13.79	<0.05
		<i>6–60</i>	0.45	26.74	<0.05
		<i>20–40</i>	0.02	0.93	0.41
		<i>20–60</i>	0.08	3.44	<0.05
		<i>40–60</i>	0.05	1.70	0.15
		<i>islands</i>	0.06	2.27	<0.05
		<i>MOO–BOR</i>	0.01	0.69	0.52
		<i>MOO–TIK</i>	0.07	3.53	0.07
		<i>MOO–RAN</i>	0.05	2.27	0.11
		<i>BOR–TIK</i>	0.11	5.02	<0.05
		<i>BOR–RAN</i>	0.06	2.56	0.11
		<i>TIK–RAN</i>	0.03	0.90	0.51
		<i>depths:islands</i>	0.12	1.74	<0.05
	Society	<i>depths</i>	0.36	9.45	<0.05
		<i>6–20</i>	0.32	11.772	<0.05
		<i>6–40</i>	0.42	16.12	<0.05
		<i>6–60</i>	0.61	31.54	<0.05
		<i>20–40</i>	0.08	2.21	0.18
		<i>20–60</i>	0.12	3.54	0.06
		<i>40–60</i>	0.05	1.21	0.33
		<i>islands</i>	0.02	1.91	0.13
		<i>depths:islands</i>	0.06	1.46	0.19
	Tuamotu	<i>depths</i>	0.11	1.99	0.05
		<i>islands</i>	0.03	1.09	0.33
<i>depths:islands</i>		0.07	1.24	0.25	
<i>Pachyseris “speciosa”</i> spp. (20 m excluded)	Overall	<i>depths</i>	0.05	3.6421	<0.05
		<i>40–60</i>	0.01	0.802	0.501
		<i>40–90</i>	0.06	2.972	0.057
		<i>60–90</i>	0.04	1.881	0.153
		<i>islands</i>	0.41	20.6661	<0.05
		<i>MOO–BOR</i>	0.06	2.34	0.072
		<i>MOO–TIK</i>	0.27	11.69	<0.05
		<i>MOO–RAN</i>	0.37	20.72	<0.05
		<i>BOR–TIK</i>	0.36	20.57	<0.05
		<i>BOR–RAN</i>	0.47	35.45	<0.05
		<i>TIK–RAN</i>	0.25	12.48	<0.05
		<i>depths:islands</i>	0.11	2.8504	<0.05
	Society	<i>depths</i>	0.06	1.29	0.252
	Tikehau	<i>depths</i>	0.29	3.01	0.06
	Rangiroa	<i>depths</i>	0.46	8.14	<0.05
		<i>40–90</i>	0.40	8.09	<0.05
		<i>60–90</i>	0.40	8.09	<0.05

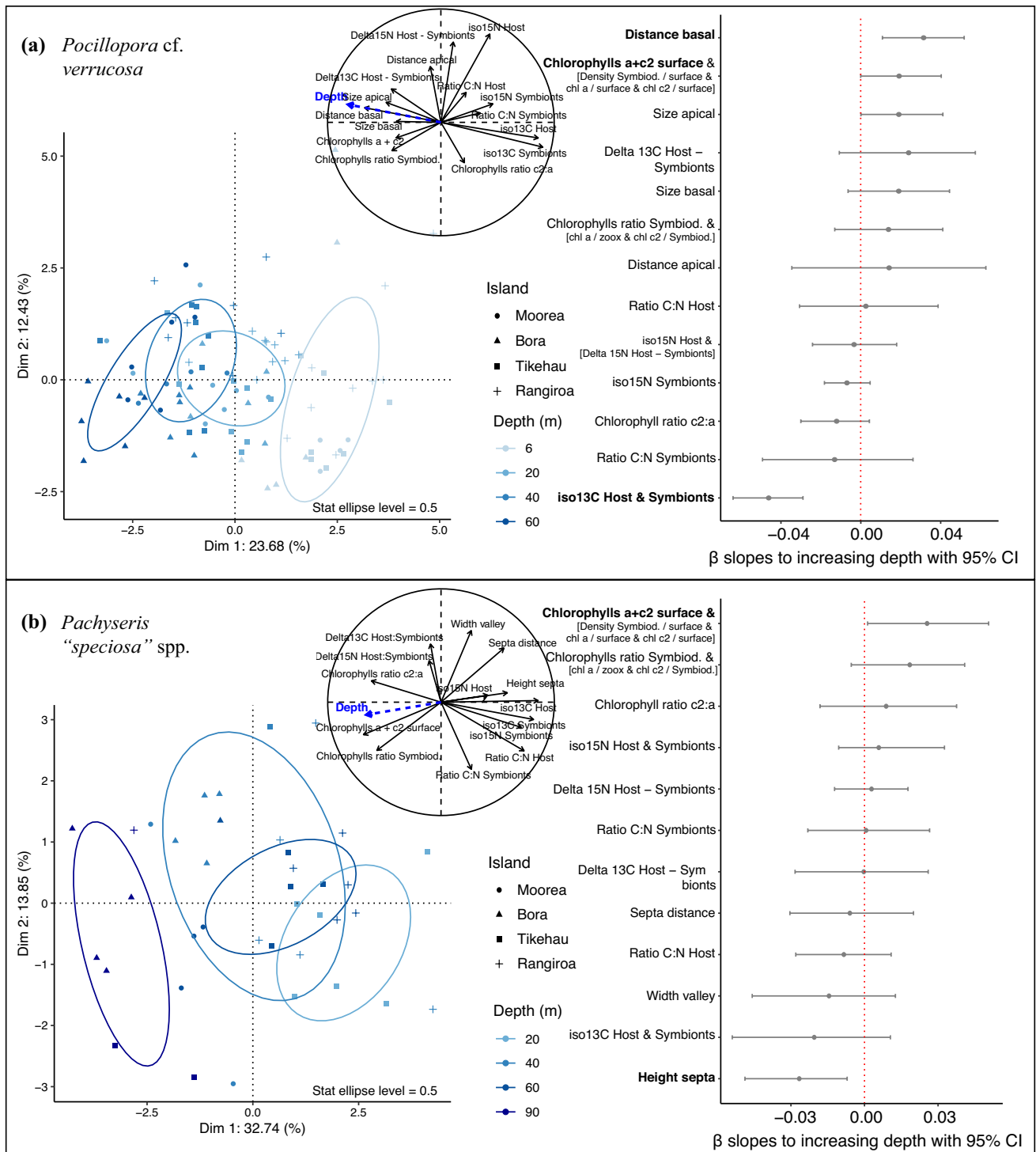


Fig. 3 a *Pocillopora cf. verrucosa* and **b** *Pachyseris "speciosa" spp.* (Left) Principal component analysis grouping by depths. Ellipses represent significance level=0.5. (Right) Slopes represent responding to increasing depth from the multivariate Bayesian model. The model considered spatial variability with a random intercept and

slope for each location. The variables (in bold) are the ones whose interval confidence of 95% (IQ 2.5 and IQ 07.5) does not go across 0.0. Between brackets and lower size show variables correlated with the represented variable Sup. Figs. 4 and 5

($\beta > 0$ with 95% CI > 0), the total chlorophyll concentration ($a + c_2$) per surface area and the size of corallites in the apical part ($\beta > 0$ with 95% CI > 0) (Fig. 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 chlorophyll concentration increased from *ca.* $13 \mu\text{g cm}^{-2}$ at 6 m to *ca.* $25 \mu\text{g cm}^{-2}$ at 60 m. Lastly, the size of corallites in the apical parts increased from *ca.* 0.79 cm at 6 m to 0.87 cm at 60 m (Sup. Table 1). These findings were also reflected in the positive correlations with depth (Sup. Fig. 4a). Conversely, the $\delta^{13}\text{C}$ in the host and symbionts fraction decreased with increasing depth ($\beta < 0$ with 95% CI < 0), from -15% $\delta^{13}\text{C}$ at 6 m to -19% $\delta^{13}\text{C}$ at 60 m (Fig. 3b and Sup. Table 2).

The other variables were less affected by depth. They included, for instance, the ratio of c_2/a of chlorophyll types [Chl $c_2/\text{Chl } a$], the $\delta^{15}\text{N}$ in its symbionts and host fraction, the ratio of $\delta^{13}\text{C}/\delta^{15}\text{N}$ in its host and symbionts fraction and the $\delta^{13}\text{C}$ hosts–symbionts. Hence, these variables did not significantly contribute to separating the different depth groups. They had positive and negative slopes in their 95% CI, aligned with Dim 2 (12.43% of data), and had neutral correlations [abs 0.5] (Fig. 3 and Sup. Fig. 4).

The effect of depth in this differentiation (significance level for the ellipses of 0.5; Fig. 3a left) was statistically significant (PERMANOVA $F = 18.8$, $p < 0.05$, $R^2 = 0.15$, residual $R^2 = 0.67$), notably between the 6 m and the other 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; $p > 0.05$). Finally, the remaining variables described in the methods but missing in Fig. 3 were omitted because they were correlated (PEARSON > 0.75) to at least one of the presented ones (Sup. Fig. 4). 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.

Morphological analysis of the branching zones Besides the increasing inter-corallite distance in the basal zone and increasing corallite size in the apical zone with depth, we found that when comparing the two zones of the branch (*i.e.* apical vs basal zone) for any given depth, the distance between the corallites was significantly shorter in the apical than the basal zone of the colony (ANOVA $F = 99.53$, $p < 0.05$ for the zone of the colony alone; and ANOVA $F = 20.84$, $p < 0.05$ for the interaction of zone and depth; being non-significant ANOVA $F = 0.673$, $p > 0.05$ for depth alone). However, the sizes of the corallites were larger in

the apical part than in the basal part (ANOVA $F = 20.98$, $p < 0.05$ for the zone alone, ANOVA $F = 11.41$, $p < 0.05$ for the depth alone and ANOVA $F = 0.46$, $p > 0.05$ for the interaction of zone and depth). In the more light-exposed areas of the colonies' "apical zone," the corallites have a larger size, and therefore, the distance between corallites decreases (Sup. Fig. 2 and Sup. Table 1).

Trophic (isotope) niche plasticity along the depth gradient

We found no significant isotopic evidence of a switch to heterotrophy with depth for any islands (HOTELLING $p > 0.05$). The distances between the hosts and the symbionts communities (HOTELLING test stat values were independent of depth) did not follow a particular pattern with increasing depth. Yet, the distances changed across locations with considerable spatial variability between depths. Although individual fractions of $\delta^{13}\text{C}$ in both host and symbionts decreased with depth, the relative degree of heterotrophy (expressed as $\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{Host}} - \delta^{13}\text{C}_{\text{Symbiont}}$) did not increase nor decrease significantly with depth. Overall, these results suggest that this species conserved an autotrophic strategy along the depth gradients (Fig. 4a).

Pachyseris "speciosa" spp.

Associated Symbiodiniaceae ITS2 type profiles along the depth gradient

We identified 21 unique ITS2 profiles across all *P. "speciosa" spp.* samples between 20 and 90 m. Fourteen profiles were composed of *Cladocopium* and the remaining of *Durusdinium* and *Gerakladium* (Fig. 2b). Although the shallowest samples studied were at 10 and 20 m, these were only specific to one site (Tikehau). Thus, we performed dissimilarity analyses from 40 to 90 m for statistical reasons and consistency across sites. The community composition of Symbiodiniaceae (also at generic level) varied significantly with depth, sites and the interaction with depth and sites (PERMANOVA $p < 0.05$, Table 1). Yet, pairwise analyses across depths (with all islands included) revealed non-significant differences in Symbiodiniaceae communities between corals from 40, 60 and 90 m (results of pairwise comparisons in Table 1: $p > 0.05$). Reducing the spatial variation by looking within the two archipelagos Society (Moorea and Bora Bora) vs. Tuamotu (Tikehau and Rangiroa), the Symbiodiniaceae ITS2 profiles did not differ along the depth gradient (Fig. 2b). In general, the Symbiodiniaceae communities from the Society Islands were mainly represented with the two ITS2 profiles *P2*, belonging to the C3 radiation

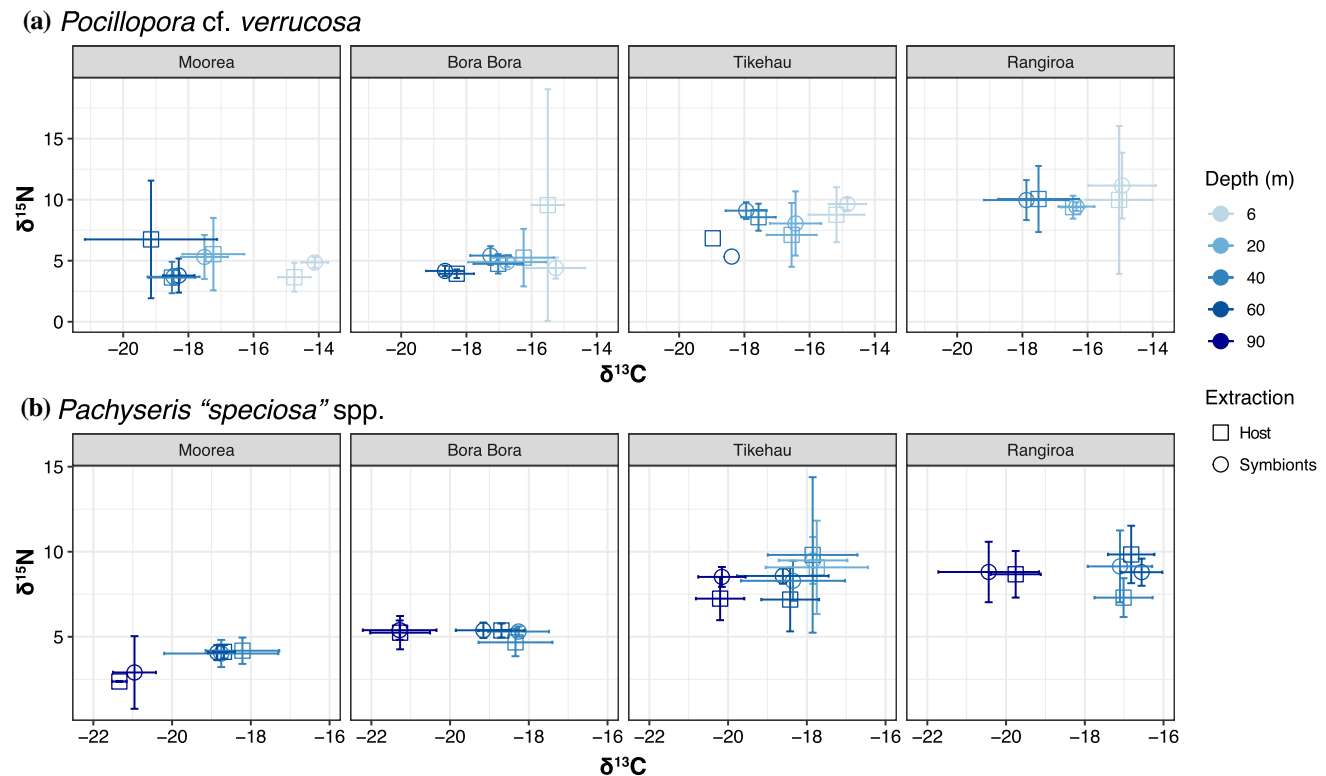


Fig. 4 Coral host and algal symbiont stable isotope $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios for the different depths across locations. Trophic (isotope) niche plasticity analysis was assessed with HOTELLING tests measuring the distance ratios between the host and the symbionts

at 63.9% and *P4*, belonging to the C21 radiation at 16.7%. Conversely, the Symbiodiniaceae communities from the Tuamotu belonged to (i) C1 radiation at both islands and all depths (95.4% with profiles *P1* and *P6* on Rangiroa and 28% with profile *P1* on Tikehau) or (ii) D1 radiation exclusively on Tikehau (68% profiles *P3* and *P5*) at all depths. Only on Rangiroa, we observed a significant shift in prevalence of the ITS2 profile *P1* between 40 and 60 m 100% and 90 m 33% (pairwise comparisons: $p < 0.05$ for 40 vs. 90 m and 60 vs. 90 m). Finally, we found rare and exclusive ITS2 type profiles, such as *P6* dominated with C1 radiation on Rangiroa.

Biological traits of coral symbiont measures along the depth gradient

Considering the variables of the model (see above), *P. “speciosa”* spp. clustered by depths (PERMANOVA $F = 4.28$, $p < 0.05$, $R^2 = 0.08$), especially between the 90 m and the other depths, and by locations (PERMANOVA $F = 5.64$, $p < 0.05$, $R^2 = 0.32$, residual $R^2 = 0.56$) (Fig. 3b left). This differentiation was because some variables aligned with Dim 1 (32.7% of data) increasing or decreasing with depth. The total chlorophyll concentration ($a + c_2$) per surface area increased with depth ($\beta > 0$ with 95% CI > 0) (Fig. 3b). For example, this increase was

from *ca.* $30 \mu\text{g cm}^{-2}$ at 20 m to *ca.* $80 \mu\text{g cm}^{-2}$ at 90 m (Sup. Table 3). This increase of chlorophyll per unit surface area also indicates the increase in Symbiodiniaceae density and/or chlorophyll *a* and *c*₂ because the variables were highly correlated (> 0.9 , Sup. Fig. 5). Conversely, the height of septa decreased 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. 3b (right) and Sup. Table 3).

The remaining variables were less affected by depth and aligned more with Dim 2 (13.8% of data). For example, the delta (Host—Symbionts) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the distance between septa or the ratio $\delta^{13}\text{C}/\delta^{15}\text{N}$ did not vary or correlate with increasing depth (Fig. 3b (right) and Sup. Fig. 5).

Trophic (isotope) niche plasticity along the depth gradient

The HOTELLING test for *P. “speciosa”* spp. revealed no significant isotopic switch to heterotrophy along the depth gradient across islands (HOTELLING p -values > 0.05 between the host and symbiont), except for 90 m at Tikehau (HOTELLING p -values < 0.05). Although these values had considerable spatial and depth variability, the distance between host and symbiont communities seems not to increase with depth (three out of four sites), reinforcing our conclusion (HOTELLING stat, e.g. Bora Bora at 40 m = 4.5,

60 m = 1.8 and 90 m = 0.2; but see Tikehau HOTELLING stat at 10 m = 0.31, 20 m = 0.34, 40 m = 1.1, 60 m = 5.6 and 90 m = 9.5). We also found that increasing depth did not affect the dispersion of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in neither the host fraction (ANOVA linear model on the distance to the centroids, p -values = 0.5) nor the symbiont fraction (p -values = 0.09) validating the HOTELLING tests. Finally, even if the amount of $\delta^{13}\text{C}$ visually decreased with increasing depth in both fractions (Fig. 4b), the decrease was not significant according to the 95% CI of the model (Fig. 3b). The relative degree of heterotrophy ($\Delta\delta^{13}\text{C} = \delta^{13}\text{C}_{\text{Host}} - \delta^{13}\text{C}_{\text{Symbiont}}$) was stable with depth at all locations, even on Tikehau, reinforcing the fact that specimens conserved an autotrophic strategy at all depths.

Discussion

Although the amount of light available to photosynthesis becomes a limiting factor for scleractinian corals with depth, several species exhibit wider depth ranges that extend into the deeper (mesophotic) parts of the reef. Despite the growing physiological studies on MCEs (mainly concentrated in, e.g. Red Sea, Hawaii and some Caribbean islands) (from mesophotic.org, filtering scleractinian physiology studies; Bongaerts et al., 2019), we still have a poor understanding of how different coral species can thrive in such low-light environments. Here, we assess two mesophotic species from French Polynesia along an exceptional but highly valuable broad depth gradient, considering their ample depth zonation. Our findings revealed photophysiological adjustments where both taxa increased chlorophyll pigment concentrations and the symbiont density with depth, likely contributing to maintaining photosynthesis levels 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 present morphological skeletal differences, with an increase in corallite size (*P. cf. verrucosa*) and in the height of septa (*P. "speciosa"* spp.), most likely to increase the light-harvesting capacity (Kramer et al. 2021). Conversely, we found, in most islands, no evidence for a transition to specialised Symbiodiniaceae communities or nutritional plasticity as previously observed for some scleractinian corals in other locations (Bongaerts et al. 2015a; Williams et al. 2018; Sturaro et al. 2021); perhaps, due to the relatively high light available to MCEs in French Polynesia versus other locations (Pichon 2019; Rouzé et al. 2021). Our multi-biological traits model studying the coral holobiont with depth suggests that scleractinian corals' acclimation or adaptation to decreasing light can exhibit phenotypic variation involving multiple biological trait strategies (e.g. photophysiology, morpho-acclimation and, in some cases,

trophic nutritional plasticity) rather than a single unique trait strategy (Kahng et al. 2019). Part of these strategies are sometimes shared among scleractinian species and other times species-specific (e.g. increasing the height of septa) yet not exempt from considerable variability with and within species and locations (Apprill et al. 2007; Nir et al. 2011). Such contrasting results and variability across the literature and our study highlight the need for further studies on the plasticity of scleractinian corals' physiology to decreasing light with depth.

Photoacclimation strategies have been extensively studied down to 40 m depth, yet studies below 60 m are scarce. Some species exhibited significant structuring of Symbiodiniaceae communities to low light at specific locations (Ziegler et al. 2015; Sturm et al. 2022; Terraneo et al. 2023). However, other studies on different target species, regions and habitats reported no change in symbiont composition with depth (Polinski and Voss 2018). Here, we demonstrate that in French Polynesia, both *P. cf. verrucosa* and *P. "speciosa"* spp. can live at mesophotic depths without hosting a distinct Symbiodiniaceae community. However, we found location-based variation in the magnitude of the prevalence of ITS2 profiles (e.g. Society vs Tuamotu Archipelagos) or occasionally (e.g. Tikehau) in genetic structuring that possibly interacts with extreme depths. As previously reported for different coral species or spatial contexts, including shallow versus deep environments (Ziegler et al. 2015; Sturm et al. 2022), and acknowledging that a more extensive sampling size at individual depths and locations could have exposed a more subtle depth partitioning and ITS2 profile diversity, we also found *Cladocopium* as the dominant genus involved in associated Symbiodiniaceae communities for both coral taxa. For *P. cf. verrucosa*, ITS2 profiles belonging to C1 and C42 radiations were the dominant profiles across different depths (6–60 m), corroborating evidence previously obtained from shallow reefs in French Polynesia with congeners (e.g. Putnam et al. 2012) or in other regions (De Palmas et al. 2021). In addition, the Symbiodiniaceae communities were characterised by a significant decrease in the prevalence of P2 profile, belonging to C42 radiation with depth, that may represent a key putative shallow-tolerant ITS2 profile. Such a decrease could also relate to the separation of ellipses (acknowledging the 0.5 significance) by depths in the PCA coral holobiont phenotype (Fig. 3a). Similarly, *P. "speciosa"* spp. displayed generally no differences in its Symbiodiniaceae community composition as a function of depth. However, we observed contrasting spatial patterns in the Symbiodiniaceae communities between islands, suggesting contrasted thermal regimes or specific environmental conditions. Symbiodiniaceae communities from the Society Islands were mostly represented by ITS2 type profiles belonging to C3 radiation, as observed for host congeners adapted to warm conditions in the Central Red Sea (Ziegler

et al. 2015; Terraneo et al. 2023). In contrast, communities from the Tuamotu Archipelago were dominated by C1 radiation or, exclusively on Tikehau, by D1 radiation, generally known for its high tolerance to thermal stress or other stressors (Stat and Gates 2011; Rouzé et al. 2016; Silverstein et al. 2017). On Rangiroa, the Symbiodiniaceae communities exhibited a significant shift between 40–60 m (*i.e.* strictly represented by ITS2 P1 profile belonging to C1 radiation: C1-C1b-C3-C1u-C1bo-C1bn) and 90 m (*i.e.* characterised by diverse ITS2 profiles including one unique ITS2 P6 profile belonging to C1 radiation: C1-C1b-C1c-C42.2-C1br-C1bh-C1cb-C72k). The ITS2 P6 profile observed in Rangiroa likely represents a distinct and putative depth-specialist *Cladocopium* taxa.

Instead of an exclusive adaptive genetic structuring in the Symbiodiniaceae communities to cope with the decreasing light with depth, the two scleractinian taxa studied are able to use other photoacclimation strategies (*i.e.* phenotypic variation) that could also respond to host-specific genetics. The strategies may vary from macroskeletal morphological changes to cell-scale changes inside the coral tissue to adapt to low-light environments. The morphological plasticity of corals with a tendency to adopt flattened morphologies is well reported in the literature (Fricke and Schuhmacher 1983; Kramer et al. 2021; Lesser et al. 2021; Scucchia et al. 2023). Indeed, we also found that the laminar *P. “speciosa”* spp. was deeper (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 6–20 m and rarer at 40 and 60 m). Likewise, we noticed changes in skeletal micro-morphology aimed at increasing light harvesting towards the coral polyps (Kramer et al. 2021). Specifically, *P. cf. verrucosa* increased the size and inter-corallite distance with depth 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 (apical zone) or lower (basal zone) light levels, suggesting that corallites disperse with low light while they aggregate with high light (Sup. Fig. 2). *P. “speciosa”* spp. also changed its micro-morphology with depth by decreasing the height of septa, which is likely to be a way to reduce shading at a polyp scale. However, morphological changes are 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. The literature indicates that once light penetrates inside the coral polyps (*i.e.* in the gastrovascular cavity), corals might increase photosynthetic efficiency via a higher concentration of chlorophyll pigments and Symbiodiniaceae density, a micro-morphological strategy found in our results and shared among most scleractinian corals with depth (Fig. 3) (Wyman et al. 1987; Maritorea et al. 2002; Apprill et al. 2007; Mass et al. 2007, 2010; Stambler et al. 2008; Lesser

et al. 2010; Smith et al. 2017; Kahng et al. 2019; Kramer et al. 2021). Despite other studies finding that different proportions of chlorophyll ratio a/c_2 might be more depth-specific than others (Nir et al. 2011), we did not observe a similar pattern. Yet, we found high spatial and specific inter- and intra-specific variability with increasing depth, making the understanding of corals’ photophysiological capacities more complex. Our acclimation findings imply that our two species could compensate for the lack of light even at their deepest depths, where only 10–12% of the 6 m light was available at 60 m and 3–4% at 90 m. However, how depth modifies the metabolism of scleractinian corals, and their subsequent growth, calcification and reproduction deserves future research.

Our results suggest that the combined photophysiological and morphological changes could compensate for the lack of light and energy with depth for the two species in this study because we did not find isotopic evidence of a nutritional shift towards heterotrophy. These findings differ from some previous studies reporting a nutritional shift strategy with depth (Lesser et al. 2010, 2022; Williams et al. 2018) but agree with others inferring that such shifts from bulk isotopes can be problematic without necessarily indicating a move towards heterotrophy (Price et al. 2021; Sturaro et al. 2021; Carmignani et al. 2023; Kahng 2024). Albeit our method to separate host and symbiont fractions might have caused some contamination of the latter with the former (using a higher speed and time centrifugation than usually utilised in the literature, *e.g.* Nahon et al. 2013), we still observed a more negative $\delta^{13}\text{C}$ in both the symbionts and host fraction with increasing depth. At some depths, we observed differences in the host–symbiont fractions (Tikehau at 90 m for *P. “speciosa”* spp.), indicating that any contamination was insufficient to obscure isotope differences between fractions. Additionally, although some studies interpreted an increased separation of $\delta^{13}\text{C}$ between host and symbionts as an indication of heterotrophy (Muscatine et al. 1989b; Williams et al. 2018; Padilla-Gamiño et al. 2019; Radice 2019; Watanabe et al. 2019), our HOTELLING tests did not confirm transition from autotrophy to heterotrophy. Likewise, 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) did not increase enough with depth to support a higher reliance on heterotrophy (*i.e.* with $\delta^{13}\text{C}$ more similar to that of zooplankton as a food source) (Muscatine et al. 1989a; Palardy et al. 2008). Nevertheless, the interpretation of stable isotopes results remains very complex and, accordingly, still very much discussed in the literature, with different interpretations leading to different conclusions (Kahng et al. 2019). These changes in trophic plasticity seem to be very variable, specific to species and conditions and with significant spatial differences (Fox et al. 2019; Watanabe et al. 2019). For instance, a switch to heterotrophy has been

reported for certain species during bleaching (Wall et al. 2019; Conti-Jerpe et al. 2020; Radice et al. 2020). Therefore, there is still evidence that some degree of heterotrophy may help some scleractinian corals compensate for the lack of light during certain conditions. Comparing our two taxa and despite both taxa still depend on their photophysiology (*i.e.* autotrophy as a primary energy source) at their deepest occurrences, it seems that *P. cf. verrucosa* might increase heterotrophy more than *P. "speciosa" spp.*, which could also be explained by the increase of the corallites size (polyp mouth) in *P. cf. verrucosa*. In contrast, *P. "speciosa" spp.* decreased the height of septa to facilitate light harvesting at deeper depths.

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 conclusions in this field highlight how little we still know about coral's capacity to deal with low-light environments at depth. Given that the outcomes of this study derive from rigorous statistical analysis (Bayesian) (Bürkner 2017), considering spatial variability albeit reducing the number of replicates, we are confident that our findings are valid for the four different study locations. Nevertheless, we acknowledge the need to better understand the intra- and inter-specific variability, likely influenced by the coral physiology and environment (*e.g.* temperature, nutrients), taking into account a better understanding of coral biology and the local oceanographic and atmospheric conditions. Since we cannot holistically replicate "mesophotic" conditions in aquariums to control external factors, more transplants and long-term experimental studies are necessary. Also, future investigations are necessary on scleractinian interactions with the other micro-organisms (*e.g.* bacteria, endolithic green algae *Ostreobium*) likely to contribute to the adaptation to low-light conditions (Halldal 1968; Peixoto et al. 2017; Rouzé et al. 2021). Finally, our findings indicate that the two taxa studied can compensate for the lack of light thanks to multiple individual biological traits acting simultaneously, including the increase of the density of symbionts and chlorophyll concentration and skeleton modifications, suggesting that these taxa may not need to rely that much on active feeding (*i.e.* heterotrophy), in the clear waters of French Polynesia (Pichon 2019). However, whether such physiological changes are enough to maintain growth, calcification and reproduction at similar rates as corals living in the shallows or whether new trade-offs will arise from corals living in low-light environments remain to be investigated. Future efforts should target the metabolism (*e.g.* photosynthesis, reactive oxygen species, respiration, calcification, reproduction) along the depth gradient. Then, comparing results with other deeper scleractinian species

(*e.g.* *Leptoseris* spp.; Kahng et al. 2019; Padilla-Gamiño et al. 2019) will be crucial to predicting better the sensibility of lower mesophotic corals to depths and low-light conditions. In conclusion, the findings of this study show the potential ability of light-dependent scleractinian corals to combine multiple biological strategies to live in low-light conditions.

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Author contributions GP-R, HR and LH conceived the study. GP-R, HR, MP, UTPC and LH organised and planned the field expedition. GP-R, HR, MP and UTPC carried out the fieldwork. GP-R and HR did the laboratory work. GP-R and HR conducted the data analysis and generated figures. LH and UTPC secured funding for this research. All authors reviewed and contributed to the final manuscript.

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

Declarations

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

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References

- Allemand D, Tambutté É, Zoccola D, Tambutté S (2011) Coral Calcification, Cells to Reefs. *Coral Reefs: An Ecosystem in Transition* 119–150. https://doi.org/10.1007/978-94-007-0114-4_9.
- Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecol Monogr* 83:557–574. <https://doi.org/10.1890/12-2010.1>

- Apprill AM, Bidigare RR, Gates RD (2007) Visibly healthy corals exhibit variable pigment concentrations and symbiont phenotypes. *Coral Reefs* 26:387–397. <https://doi.org/10.1007/s00338-007-0209-y>
- Barnes C, Chalker B (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (ed). *Ecosystems of the World* 25:109–131
- Blackall LL, Wilson B, Van Oppen MJH (2015) Coral—the world’s most diverse symbiotic ecosystem. *Mol Ecol* 24:5330–5347. <https://doi.org/10.1111/MEC.13400>
- Bongaerts P, Carmichael M, Hay KB, Tonk L, Frade PR, Hoegh-Guldberg O (2015a) Prevalent endosymbiont zonation shapes the depth distributions of scleractinian coral species. *R Soc Open Sci* 2:140297–140297. <https://doi.org/10.1098/rsos.140297>
- Bongaerts P, Frade PR, Hay KB, Englebert N, Latijnhouwers KR, Bak RP, Vermeij MJ, Hoegh-Guldberg O (2015b) Deep down on a Caribbean reef: Lower mesophotic depths harbor a specialized coral-endosymbiont community. *Sci Rep* 5:1–9. <https://doi.org/10.1038/srep07652>
- Bongaerts P, Cooke IR, Ying H, Wels D, den Haan S, Hernandez-Agreda A, Brunner CA, Dove S, Englebert N, Eyal G, Forêt S, Grinblat M, Hay KB, Harii S, Hayward DC, Lin Y, Mihaljević M, Moya A, Muir P, Sinniger F, Smallhorn-West P, Torda G, Ragan MA, van Oppen MJH, Hoegh-Guldberg O (2021) Morphological stasis masks ecologically divergent coral species on tropical reefs. *Curr Biol* 31:2286–2298.e8. <https://doi.org/10.1016/j.cub.2021.03.028>
- Bosserelle P, Berteaux-Lecellier V, Chancerelle Y, Hédouin L, Nugues MM, Wallace C, Pichon M (2014) Guide d’identification des coraux de Moorea. CRILOBE, Polynésie française
- Bürkner P (2017) Advanced Bayesian Multilevel Modeling with the R Package brms. *R Journal* 10:395–411. <https://doi.org/10.32614/RJ-2018-017>
- Carmignani A, Radice VZ, McMahon KM, Holman AI, Miller K, Grice K, Richards Z (2023) Levels of autotrophy and heterotrophy in mesophotic corals near the end photic zone. *Front Mar Sci* 10:1089746. <https://doi.org/10.3389/fmars.2023.1089746>
- Comeau AM, Douglas GM, Langille MGI (2017) Microbiome Helper: a Custom and Streamlined Workflow for Microbiome Research. *Msystems*. <https://doi.org/10.1128/msystems.00127-16>
- Conti-Jerpe IE, Thompson PD, Wong CWM, Oliveira NL, Duprey NN, Moynihan MA, Baker DM (2020) Trophic strategy and bleaching resistance in reef-building corals. *Sci Adv* 6:5443–5453. <https://doi.org/10.1126/sciadv.aaz5443>
- Cooper TF, Ulstrup KE, Dandan SS, Heyward AJ, Kühl M, Muirhead A, O’Leary RA, Ziersen BEF, van Oppen MJH (2011) Niche specialization of reef-building corals in the mesophotic zone: Metabolic trade-offs between divergent Symbiodinium types. *Proceedings of the Royal Society B: Biological Sciences* 278:1840–1850. <https://doi.org/10.1098/RSPB.2010.2321>
- Dana JD (1846) United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes. Edited by P. Lea & Blanchard. Sherman
- De Vantier L, Turak E (2017) Species Richness and Relative Abundance of Reef-Building Corals in the Indo-West Pacific. *Diversity* 25(9):25. <https://doi.org/10.3390/D9030025>
- De Palmas S, Soto D, Ho MJ, Denis V, Chen CA (2021) Strong horizontal and vertical connectivity in the coral *Pocillopora verrucosa* from Ludao, Taiwan, a small oceanic island. *PLoS ONE* 16:e0258181. <https://doi.org/10.1371/JOURNAL.PONE.0258181>
- Eckert RJ, Reaume AM, Sturm AB, Studivan MS, Voss JD (2020) Depth Influences Symbiodiniaceae Associations Among *Montastrea cavernosa* Corals on the Belize Barrier Reef. *Front Microbiol* 11:518. <https://doi.org/10.3389/FMICB.2020.00518/BIBTEX>
- Ellis J, Solander D (1786) The natural history of many curious and uncommon zoophytes: collected from various parts of the globe
- Falkowski PG, Dubinsky Z, Muscatine L, Porter JW (1984) Light and the Bioenergetics of a Symbiotic Coral. *Bioscience* 34:705–709. <https://doi.org/10.2307/1309663>
- Fox MD, Elliott Smith EA, Smith JE, Newsome SD (2019) Trophic plasticity in a common reef-building coral: Insights from $\delta^{13}\text{C}$ analysis of essential amino acids. *Funct Ecol* 33:2203–2214. <https://doi.org/10.1111/1365-2435.13441>
- Fricke HW, Schuhmacher H (1983) The Depth Limits of Red Sea Stony Corals: An Ecophysiological Problem (A Deep Diving Survey by Submersible). *Mar Ecol* 4:163–194. <https://doi.org/10.1111/J.1439-0485.1983.TB00294.X>
- Grigg RW (2006) Depth limit for reef building corals in the Au’au Channel, S.E. Hawaii *Coral Reefs* 25:77–84. <https://doi.org/10.1007/S00338-005-0073-6>
- Halldal P (1968) Photosynthetic capacities and photosynthetic action spectra of endozoic algae of the massive coral *Favia*. *Biol Bull* 134:411–424. <https://doi.org/10.2307/1539860>
- Hume BCC, D’Angelo C, Smith EG, Stevens JR, Burt J, Wiedenmann J (2015) Symbiodinium thermophilum sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world’s hottest sea, the Persian/Arabian Gulf. *Sci Rep* 5:1–8. <https://doi.org/10.1038/srep08562>
- Hume BCC, Smith EG, Ziegler M, Warrington HJM, Burt JA, LaJeunesse TC, Wiedenmann J, Woolstra CR (2019) SymPortal: A novel analytical framework and platform for coral algal symbiont next-generation sequencing *ITS2* profiling. *Mol Ecol Resour* 19:1063–1080. <https://doi.org/10.1111/1755-0998.13004>
- Huston MA (1985) Patterns of Species Diversity on Coral Reefs. *Annu Rev Ecol Syst* 16:149–177. <https://doi.org/10.1146/annurev.es.16.110185.001053>
- Jeffrey S, Humphrey G (1975) New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem Physiol Pflanz* 167:191–194. [https://doi.org/10.1016/s0015-3796\(17\)30778-3](https://doi.org/10.1016/s0015-3796(17)30778-3)
- Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, Toonen RJ (2010) Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29:255–275. <https://doi.org/10.1007/s00338-010-0593-6>
- Kahng SE, Akkaynak D, Shlesinger T, Hochberg EJ, Wiedenmann J, Tamir R, Tchernov D (2019) Light, Temperature, Photosynthesis, Heterotrophy, and the Lower Depth Limits of Mesophotic Coral Ecosystems. Springer, Cham, pp 801–828. https://doi.org/10.1007/978-3-319-92735-0_42
- Kahng SE (2024) Comment on Lesser et al. Using Stable Isotope Analyses to Assess the Trophic Ecology of Scleractinian Corals. *Oceans* 2022, 3, 527–546. *Oceans* 5(3): 476–490. <https://doi.org/10.3390/oceans5030027>
- Kaniewska P, Magnusson SH, Anthony KRN, Reef R, Kühl M, Hoegh-Guldberg O (2011) Importance of macro- versus micro-structure in modulating light levels inside coral colonies. *J Phycol* 47:846–860. <https://doi.org/10.1111/J.1529-8817.2011.01021.X>
- Kassambara A, Kassambara M (2019) Package “ggcorrplot.” R package version 0133 cloud.r-project.org
- Kramer N, Tamir R, Ben-Zvi O, Jacques SL, Loya Y, Wangpraseurt D (2021) Efficient light-harvesting of mesophotic corals is facilitated by coral optical traits. *Funct Ecol* 36:406–418. <https://doi.org/10.1111/1365-2435.13948>
- Kramer N, Guan J, Chen S, Wangpraseurt D, Loya Y (2022) Morphofunctional traits of the coral *Stylophora pistillata* enhance light capture for photosynthesis at mesophotic depths. *Commun Biol* 5:861. <https://doi.org/10.1038/s42003-022-03829-4>
- Laverick JH, Andradi-Brown DA, Rogers AD (2017) Using light-dependent scleractinia to define the upper boundary of mesophotic coral ecosystems on the reefs of Utila, Honduras 12:e0183075. <https://doi.org/10.1371/journal.pone.0183075>

- Laverick JH, Tamir R, Eyal G, Loya Y (2020) A generalized light-driven model of community transitions along coral reef depth gradients. *Glob Ecol Biogeogr* 29:1554–1564. <https://doi.org/10.1111/geb.13140>
- Lê S, Josse J, Husson F (2008) FactoMineR: An R Package for Multivariate Analysis. *J Stat Softw* 25:1–18. <https://doi.org/10.18637/JSS.V025.I01>
- Lesser MP, Marc S, Michael S, Michiko O, Gates RD, Andrea G (2010) Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: Light, food, and genetics. *Ecology* 91:990–1003. <https://doi.org/10.1890/09-0313.1>
- Lesser MP, Mobley CD, Hedley JD, Slattery M (2021) Incident light on mesophotic corals is constrained by reef topography and colony morphology. *Mar Ecol Prog Ser* 670:49–60. <https://doi.org/10.3354/MEPS13756>
- Lesser MP, Slattery M, Macartney KJ (2022) Using Stable Isotope Analyses to Assess the Trophic Ecology of Scleractinian Corals. *Oceans* 3:527–546. <https://doi.org/10.3390/oceans3040035>
- Malik A, Einbinder S, Martinez S, Tchernov D, Haviv S, Almuly R, Zaslansky P, Polishchuk I, Pokroy B, Stolarski J, Mass T (2021) Molecular and skeletal fingerprints of scleractinian coral biomineralization: From the sea surface to mesophotic depths. *Acta Biomater* 120:263–276. <https://doi.org/10.1016/j.actbio.2020.01.010>
- Maritorena S, Payri C, Babin M, Claustre H, Bonnafoous L, Morel A, Rodière M (2002) Photoacclimatization in the zooxanthellae of *Pocillopora verrucosa* and comparison with a pelagic algal community. *Oceanol Acta* 25:125–134. [https://doi.org/10.1016/S0399-1784\(02\)01189-1](https://doi.org/10.1016/S0399-1784(02)01189-1)
- Martinez Arbizu P (2019) pairwise Adonis: pairwise multilevel comparison using Adonis. <https://github.com/pmartinezarbizu/pairwiseAdonis>
- Mass T, Einbinder S, Brokovich E, Shashar N, Vago R, Erez J, Dubinsky Z (2007) Photoacclimation of *Stylophora pistillata* to light extremes: metabolism and calcification. *Mar Ecol Prog Ser* 334:93–102. <https://doi.org/10.3354/meps334093>
- Mass T, Kine DI, Roopin M, Veal CJ, Cohen S, Iluz D, Levy O (2010) The spectral quality of light is a key driver of photosynthesis and photoadaptation in *Stylophora pistillata* colonies from different depths in the Red Sea. *J Exp Biol* 213:4084–4091. <https://doi.org/10.1242/jeb.039891>
- Muir P, Wallace C, Bridge TCL, Bongaerts P (2015) Diverse Staghorn Coral Fauna on the Mesophotic Reefs of North-East Australia. *PLoS ONE* 10:e0117933. <https://doi.org/10.1371/JOURNAL.PONE.0117933>
- Muir PR, Pichon M (2019) Biodiversity of Reef-Building, Scleractinian Corals. Springer, Cham, pp 589–620. https://doi.org/10.1007/978-3-319-92735-0_33
- Muscantine L, Falkowski PG, Dubinsky Z, Cook PA, McCloskey LR (1989a) The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proceedings of the Royal Society of London B Biological Sciences* 236:311–324. <https://doi.org/10.1098/RSPB.1989.0025>
- Muscantine L, Porter JW, Kaplan IR (1989b) Resource partitioning by reef corals as determined from stable isotope composition: I. $\delta^{13}\text{C}$ of zooxanthellae and animal tissue vs depth. *Mar Biol* 100:185–193. <https://doi.org/10.1007/BF00391957>
- Muscantine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. *Ecosystems of the world Coral Reefs* 77–87. <https://doi.org/10.2517/PRPSJ.10.359>
- Nahon S, Richoux NB, Kolasinski J, Desmalades M, Pages FF (2013) Spatial and Temporal Variations in Stable Carbon ($\delta^{13}\text{C}$) and Nitrogen ($\delta^{15}\text{N}$) Isotopic Composition of Symbiotic Scleractinian Corals. *PLoS ONE* 8:81247. <https://doi.org/10.1371/journal.pone.0081247>
- Nir O, Gruber DF, Einbinder S, Kark S, Tchernov D (2011) Changes in scleractinian coral *Seriatopora hystrix* morphology and its endocellular Symbiodinium characteristics along a bathymetric gradient from shallow to mesophotic reef. *Coral Reefs* 30:1089–1100. <https://doi.org/10.1007/s00338-011-0801-z>
- Oksanen J, Blanchet F, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens M (2019) vegan: Community Ecology Package. 2019. R package version 2.5–7. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Padilla-Gamiño JL, Roth MS, Rodrigues LJ, Bradley CJ, Bidigare RR, Gates RD, Smith CM, Spalding HL (2019) Ecophysiology of mesophotic reef-building corals in Hawai'i is influenced by symbiont–host associations, photoacclimatization, trophic plasticity, and adaptation. *Limnol Oceanogr* 64:1980–1995. <https://doi.org/10.1002/lno.11164>
- Palardy JE, Rodrigues LJ, Grottoli AG (2008) The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. *J Exp Mar Biol Ecol* 367:180–188. <https://doi.org/10.1016/J.JEMBE.2008.09.015>
- Peixoto RS, Rosado PM, de Leite DCA, Rosado AS, Bourne DG (2017) Beneficial microorganisms for corals (BMC): Proposed mechanisms for coral health and resilience. *Front Microbiol* 8:341. <https://doi.org/10.3389/FMICB.2017.00341/BIBTEX>
- Pérez-Rosales G, Pichon M, Rouzé H, Villeger S, Torda G, Bongaerts P, Carlot J, Parravicini V, Hédouin L, Under The Pole Consortium (2022) Mesophotic coral ecosystems of French Polynesia are hotspots of alpha and beta generic diversity for scleractinian assemblages. *Divers Distrib* 00:1–13. <https://doi.org/10.1111/ddi.13549>
- 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. *Mar Pollut Bull* 170:112659. <https://doi.org/10.1016/j.marpolbul.2021.112659>
- Pichon M (2019) French Polynesia. Springer, Cham, pp 425–443. https://doi.org/10.1007/978-3-319-92735-0_24
- Polinski JM, Voss JD (2018) Evidence of photoacclimatization at mesophotic depths in the coral-Symbiodinium symbiosis at Flower Garden Banks National Marine Sanctuary and McGrail Bank. *Coral Reefs* 37:779–789. <https://doi.org/10.1007/s00338-018-1701-2>
- Price JT, McLachlan RH, Jury CP, Toonen RJ, Grottoli AG (2021) Isotopic approaches to estimating the contribution of heterotrophic sources to Hawaiian corals. *Limnol Oceanogr* 66:2393–2407. <https://doi.org/10.1002/lno.11760>
- Price J, Smith A, Dobson K, Grottoli AG (2020) Airbrushed Coral Sample Preparation for Organic Stable Carbon and Nitrogen Isotope Analyses. <https://www.protocols.io/view/airbrushed-coral-sample-preparation-for-organic-st-n92ldy6q815b/v1> (Accessed 14 May 2024)
- Puglise KA, Hinderstein LM, Marr JCA, Dowgiallo MJ, Martinez FA, 1961- (2009) Mesophotic coral ecosystem research strategy International Workshop to Prioritize Research and Management Needs for Mesophotic Coral Ecosystems, Jupiter, Florida, 12–15 July, 2009
- Putnam HM, Stat M, Pochon X, Gates RD (2012) Endosymbiotic flexibility associates with environmental sensitivity in scleractinian corals. *Proceedings of the Royal Society B: Biological Sciences* 279:4352–4361. <https://doi.org/10.1098/RSPB.2012.1454>
- Pyle RL, Copus JM (2019) Mesophotic Coral Ecosystems: Introduction and Overview. Springer, Cham, pp 3–27. https://doi.org/10.1007/978-3-319-92735-0_1
- Radice VZ, Hoegh-Guldberg O, Fry B, Fox MD, Dove SG (2019) Upwelling as the major source of nitrogen for shallow and deep reef-building corals across an oceanic atoll system. *Funct Ecol* 33:1120–1134. <https://doi.org/10.1111/1365-2435.13314>

- Radice VZ, Fry B, Dove SG, Hoegh-Guldberg O (2020) Biogeochemical variability and trophic status of reef water column following a coral bleaching event. *Coral Reefs* 40:1–7. <https://doi.org/10.1007/S00338-020-02021-6>
- Radice V (2019) Trophic ecology of shallow and deep reef-building corals. The University of Queensland
- Rooney J, Donham E, Montgomery A, Spalding H, Parrish F, Boland R, Fenner D, Gove J, Vetter O (2010) Mesophotic coral ecosystems in the Hawaiian Archipelago. *Coral Reefs* 29:29:361–367. <https://doi.org/10.1007/s00338-010-0596-3>
- Rouzé H, Lecellier G, Saulnier D, Berteaux-Lecellier V (2016) Symbiodinium clades A and D differentially predispose *Acropora cytherea* to disease and *Vibrio* spp. colonization. *Ecol Evol* 6:560–572. <https://doi.org/10.1002/ECE3.1895>
- Rouzé H, Galand PE, Medina M, Bongaerts P, Pichon M, Pérez-Rosales G, Torda G, Moya A, Under The Pole Consortium, Herrmann P, Raina JB, Hédouin L (2021) Symbiotic associations of the deepest recorded photosynthetic scleractinian coral (172 m depth). *ISME Journal* 1–5. <https://doi.org/10.1038/s41396-020-00857-y>
- Saad OS, Lin X, Ng TY, Li L, Ang P, Lin S (2020) Genome Size, rDNA Copy, and qPCR Assays for Symbiodiniaceae. *Front Microbiol* 11:528552. <https://doi.org/10.3389/fmicb.2020.00847>
- Schmidt-Roach S, Miller KJ, Lundgren P, Andreakis N (2014) With eyes wide open: a revision of species within and closely related to the *Pocillopora damicornis* species complex (Scleractinia; Pocilloporidae) using morphology and genetics. *Zool J Linn Soc* 170:1–33. <https://doi.org/10.1111/ZOJ12092>
- Scucchia F, Wong K, Zaslansky P, Putnam HM, Goodbody-Gringley G, Mass T (2023) Morphological and genetic mechanisms underlying the plasticity of the coral *Porites astreoides* across depths in Bermuda. *J Struct Biol* 215:108036. <https://doi.org/10.1016/j.jsb.2023.108036>
- Shlesinger T, Loya Y (2019) Sexual Reproduction of Scleractinian Corals in Mesophotic Coral Ecosystems vs. Shallow Reefs. 653–666. https://doi.org/10.1007/978-3-319-92735-0_35
- Silverstein RN, Cuning R, Baker AC (2017) Tenacious D: Symbiodinium in clade D remain in reef corals at both high and low temperature extremes despite impairment. *J Exp Biol* 220:1192–1196. <https://doi.org/10.1242/JEB.148239>
- Slattery M, Lesser MP, Rocha LA, Spalding HL, Smith TB (2024) Function and stability of mesophotic coral reefs. *Trends Ecol Evol* 26:S0169–5347. <https://doi.org/10.1016/j.tree.2024.01.011>
- Smith EG, D’Angelo C, Sharon Y, Tchernov D, Wiedenmann J (2017) Acclimatization of symbiotic corals to mesophotic light environments through wavelength transformation by fluorescent protein pigments. *Proceedings of the Royal Society B: Biological Sciences* 284:20170320. <https://doi.org/10.1098/rspb.2017.0320>
- Soto D, De Palmas S, Ho MJ, Denis V, Chen CA (2018) Spatial variation in the morphological traits of *Pocillopora verrucosa* along a depth gradient in Taiwan. *PLoS ONE* 13:8. <https://doi.org/10.1371/JOURNAL.PONE.0202586>
- Stambler N, Levy O, Vaki L (2008) Photosynthesis and respiration of hermatypic zooxanthellate Red Sea corals from 5–75-m depth. *Isr J Plant Sci* 56:45–53. <https://doi.org/10.1560/IJPS.56.1-2.45>
- Stat M, Gates RD (2011) Clade D Symbiodinium in Scleractinian Corals: A “Nugget” of Hope, a Selfish Opportunist, an Ominous Sign, or All of the Above? *J Mar Biol* 2011:1–9. <https://doi.org/10.1155/2011/730715>
- Sturaro N, Hsieh YE, Chen Q, Wang PL, Denis V (2021) Trophic plasticity of mixotrophic corals under contrasting environments. *Funct Ecol* 35:2841–2855. <https://doi.org/10.1111/1365-2435.13924>
- Sturm AB, Eckert RJ, Carreiro AM, Simões N, Voss JD (2022) Depth-Dependent Genetic Structuring of a Depth-Generalist Coral and Its Symbiodiniaceae Algal Communities at Campeche Bank, Mexico *Front Mar Sci* 9:835789. <https://doi.org/10.3389/fmars.2022.835789>
- Sunagawa S, Woodley CM, Medina M (2010) Threatened corals provide underexplored microbial habitats. *PLoS ONE* 5:3. <https://doi.org/10.1371/JOURNAL.PONE.0009554>
- Tamir R, Eyal G, Kramer N, Laverick JH, Loya Y (2019) Light environment drives the shallow-to-mesophotic coral community transition. *Ecosphere* 10:e02839. <https://doi.org/10.1002/ECS2.2839>
- Terraneo TI, Ouhssain M, Castano CB, Aranda M, Hume BCC, Marchese F, Vimercati S, Chimienti G, Eweida AA, Voolstra CR, Jones BH, Purkis SJ, Rodrigue M, Benzoni F (2023) From the shallow to the mesophotic: a characterization of Symbiodiniaceae diversity in the Red Sea NEOM region. *Front Mar Sci* 10:1077805. <https://doi.org/10.3389/fmars.2023.1077805>
- Thibault M, Lorrain A, Houlbrèque F (2021) Comment on Trophic strategy and bleaching resistance in reef-building corals. *Sci Adv* 7(23):eabd9453. <https://doi.org/10.1126/sciadv.abd9453>
- Todd PA (2008) Morphological plasticity in scleractinian corals. *Biol Rev* 83:315–337. <https://doi.org/10.1111/J.1469-185X.2008.00045.X>
- Vaissie P, Monge A, Husson F (2021) Package “Factoshiny.” <https://cran.r-project.org/web/packages/Factoshiny/Factoshiny.pdf>
- Veron J, Pichon M (1979) Scleractinia of Eastern Australia, Part III Families Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae, Caryophylliidae, Dendrophylliidae
- Wall CB, Ritson-Williams R, Popp BN, Gates RD (2019) Spatial variation in the biochemical and isotopic composition of corals during bleaching and recovery. *Limnol Oceanogr* 64:2011–2028. <https://doi.org/10.1002/lno.11166>
- Watanabe T, Watanabe TK, Yamazaki A, Yoneta S, Sowa K, Sinniger F, Eyal G, Loya Y, Harii S (2019) Coral Sclerochronology: Similarities and Differences in the Coral Isotopic Signatures Between Mesophotic and Shallow-Water Reefs. 667–681. https://doi.org/10.1007/978-3-319-92735-0_36
- Williams GJ, Sandin SA, Zgliczynski BJ, Fox MD, Gove JM, Rogers JS, Furby KA, Hartmann AC, Caldwell ZR, Price NN, Smith JE (2018) Biophysical drivers of coral trophic depth zonation. *Mar Biol* 165:1–15. <https://doi.org/10.1007/S00227-018-3314-2>
- Wyman KD, Dubinsky Z, Porter JW, Falkowski PG (1987) Light absorption and utilization among hermatypic corals: a study in Jamaica, West Indies. *Mar Biol* 96:283–292. <https://doi.org/10.1007/BF00427028>
- Ziegler M, Roder CM, Büchel C, Voolstra CR (2015) Mesophotic coral depth acclimatization is a function of host-specific symbiont physiology. *Front Mar Sci* 2:4. <https://doi.org/10.3389/fmars.2015.00004>

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