

Comment

Comment on Lesser et al. Using Stable Isotope Analyses to Assess the Trophic Ecology of Scleractinian Corals. *Oceans* 2022, 3, 527–546

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Abstract: In warm oligotrophic waters, photosymbiotic coral can flourish across a wide depth range (0–170+ m), extending to depths where light attenuates to ~0.1% of surface values. Conventional wisdom has long assumed that mixotrophic corals must increasingly rely on heterotrophy as the ambient light available to drive photosynthesis decreases with depth. However, evidence challenging this traditional dogma has been accumulating in recent years. Although some evidence suggests that some depth-generalist coral species likely increase their reliance on heterotrophy with increasing depth, there is growing evidence that other species do not. Analysis of bulk stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) applied to photosymbiotic corals has been used in several ways to infer their trophic ecology and their relative dependence on symbiont photosynthesis versus heterotrophic feeding. However, metrics based on bulk tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are subject to considerable uncertainty due to the multiple factors that can affect their values independent of trophic ecology. These competing factors can be quite challenging to disentangle and have led to inconsistent results and conclusions regarding trends in coral heterotrophy with depth. The evidence to date suggests no uniform trophic pattern with increasing depth or decreasing light. Different corals appear to function differently, which is not surprising given their phylogenetic diversity.

Keywords: corals; mesophotic; trophic ecology; stable isotopes; heterotrophy; photosymbiotic



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In warm oligotrophic waters, photosymbiotic coral can flourish across a wide depth range (0–170+ m), extending to depths where light attenuates to ~0.1% of surface values [1,2]. However, there are limited scientific data on photosymbiotic corals below safe normoxic scuba diving depths (~60 m), including trophic ecology. Supported by early evidence [3,4], conventional wisdom has long assumed that mixotrophic corals must increasingly rely on heterotrophy as the ambient light available to drive photosynthesis decreases with depth. However, in recent years, evidence challenging this traditional dogma has been steadily accumulating (reviewed in [5]).

The article “Using stable isotope analyses to assess the trophic ecology of photosymbiotic scleractinian corals” by Lesser et al. [6] concludes that evidence to date “strongly” supports the generalization that photosymbiotic scleractinian corals transition from autotrophy to heterotrophy with increasing depth due to their declining photosynthetic productivity. To support their conclusion, Lesser et al. revisit their original study [7], selectively highlight supporting evidence, disregard conflicting evidence, dismiss factors which confound bulk stable isotopic analysis (SIA), and ignore fundamental tenets of isotope geochemistry and energetics. By focusing on partial subsets of data for select species from past studies [8–11], Lesser et al. also attempt to reverse the conclusions of the original authors and overlook their analyses.

A comprehensive and objective preponderance of the available evidence does not support the generalization that photosymbiotic corals transition to being predominately

heterotrophic at mesophotic depths. Lesser et al. rely on four lines of SIA evidence to support their conclusion:

1. Decreasing $\delta^{13}\text{C}_{\text{host}}$ with increasing depth;
2. Increasing $\Delta^{13}\text{C}_{\text{host-symbiont}}$ with increasing depth;
3. A lack of isotope niche overlap in bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between coral and symbiont using Stable Isotope Bayesian Ellipses in R (SIBER);
4. Decreasing $\delta^{13}\text{C}_{\text{skeleton}}$ -based proxy for P/R ratio with increasing depth.

As in their original study [7], Lesser et al. [6] concede that their $\delta^{15}\text{N}$ data do not support a conclusion of increasing heterotrophy with increasing depth due to several confounding factors affecting bulk $\delta^{15}\text{N}$ values.

For the first three lines of evidence, their conclusion relies on contrasting $\delta^{13}\text{C}$ source/diet values from symbiont photosynthesis versus heterotrophic resources (i.e., zooplankton and POM). When coral host carbon is mainly acquired through symbiotic dinoflagellate photosynthesis, the host tissue displays $\delta^{13}\text{C}$ values in the same range as the symbionts' values (i.e., -11‰ to -16‰) (reviewed in Ferrier-Pages and Leal [12]). Although heterotrophic resources (particulate organic matter or POM and zooplankton) can vary by location, their $\delta^{13}\text{C}$ values are significantly lower. Therefore, an increased reliance on heterotrophic resources can be expected to manifest itself in lower coral host $\delta^{13}\text{C}$ values approaching the value of zooplankton/POM and in a greater $\delta^{13}\text{C}$ difference (more negative) between host and symbiont (i.e., $\Delta^{13}\text{C}_{\text{symbiont-host}}$) in the absence of other influences (reviewed in Ferrier-Pages and Leal [12]).

Confounding factors affecting $\delta^{13}\text{C}$

Unfortunately, there are several other well-known factors (see list below) that can significantly affect $\delta^{13}\text{C}$ values of coral hosts and their symbionts independent of trophic ecology (reviewed in Kahng et al. [5]; Ferrier-Pages and Leal [12]). Despite unfounded claims to the contrary, the following factors can potentially affect $\delta^{13}\text{C}$ values in all photosymbiotic corals, regardless of location, depth, or physiological status:

- Light-dependent fractionation rates [13–16];
- Biomass composition (carbohydrate/protein/lipid ratio) [17];
- Symbiont type and density [18,19];
- Seawater DIC pool and pCO_2 [20,21];
- Host-symbiont recycling of carbon [8,9];
- Host carbon retention [22,23];
- Nitrate and phosphate availability [24];
- Interspecies differences [3,18,25,26].

These influences can cause bulk $\delta^{13}\text{C}$ values to vary substantially among coral colonies of the same species in response to spatial environmental heterogeneity, and thus affect the ability to detect trophic changes [25,27]. Several analogous confounding factors affect bulk $\delta^{15}\text{N}$ values in photosymbiotic corals (reviewed in Kahng et al. [5]; Ferrier-Pages and Leal [12]). Although there are numerous flaws in Lesser et al. [6], a few key factors are worth highlighting, and sufficient to reveal key misrepresentations and unambiguously invalidate their conclusion.

Light-dependent fractionation

A major confounding factor with depth that impedes the simplistic trophic level interpretation of $\delta^{13}\text{C}$ values is the increase in $\delta^{13}\text{C}$ fractionation that occurs with lower rates of photosynthesis (due to decreasing light with depth), resulting in lighter $\delta^{13}\text{C}$ values [13–16]. By itself, a trend of declining $\delta^{13}\text{C}$ coral host values with increasing depth does not constitute conclusive evidence for increased heterotrophy, because it is inherently confounded by the co-occurring light fractionation effect. Unless these two effects are isolated, a definitive conclusion remains elusive. For example, Crandall et al. [10] reported that the $\delta^{13}\text{C}$ of sterols in *Montastraea cavernosa* declined with depth, while the relative proportion of sterols from photosymbiont translocation (phytosterols) versus feeding

(cholesterol) did not change, illustrating that the hypothetical heterotrophic signature of declining bulk $\delta^{13}\text{C}$ values with depth can be caused by light fractionation and other factors unrelated to heterotrophy.

$\Delta^{13}\text{C}_{\text{host-symbiont}}$ as a metric for autotrophy and heterotrophy

Although the metric $\Delta^{13}\text{C}_{\text{host-symbiont}}$, as pioneered by Muscatine et al. [3], may superficially appear to be an elegant way to avoid the aforementioned confounding factor with increasing depth (and decreasing light), subsequent studies have revealed a high degree of variability for this metric that cannot be explained by an isolated interplay between autotrophy and heterotrophy [8,10,15,18,19,25,28]. Among other factors, intraspecies differences in symbiont type and density appear to influence this metric [18,19], both of which change in *Montastraea cavernosa* with depth [7,29–31]. Expected differences in $\Delta^{13}\text{C}_{\text{host-symbiont}}$ between fed and unfed corals do not always materialize (e.g., [18]). When directly compared to other metrics of heterotrophy (i.e., $\Delta^{15}\text{N}_{\text{host-symbiont}}$, SIBER, and MixSIAR), the results can be contradictory, depending on the species [32]. Similarly, the ability to use $\Delta^{15}\text{N}_{\text{host-symbiont}}$ to delineate autotrophic versus more heterotrophic photosymbiotic corals can be confounded by a host of other dynamics (reviewed in Kahng et al. [5]) and has not always been consistently supported by available empirical data (e.g., [18,33]).

Biomass composition

Using mass balance calculations, Wall et al. [17] demonstrated the effect of biomass compositional change (i.e., protein/lipid/carbohydrate ratios) on bulk $\delta^{13}\text{C}$ values without any change in the $\delta^{13}\text{C}$ values of individual components. Variations in bulk $\delta^{13}\text{C}$ values can reflect small biomass compositional change independent of trophic ecology, and need to be considered in the interpretation of spatiotemporal variability in isotopic values in corals. For example, bleached *Montipora capitata* in Kaneohe Bay, Hawaii, exhibits a reduction in protein resulting in a lighter bulk $\delta^{13}\text{C}$ value compared to that of non-bleached conspecifics (due to the more positive $\delta^{13}\text{C}$ value for proteins) [17]. A lighter bulk $\delta^{13}\text{C}$ value for bleached (vs. unbleached) *M. capitata* at the same location has previously been interpreted as evidence for increased heterotrophy [34]. Given the known changes in physiological parameters of corals with increasing depth, to what extent can biomass composition be expected to remain constant? The claim of Lesser et al. [6] that this biomass composition factor is “contextually” irrelevant to the trophic analysis of mesophotic corals is unambiguously false.

Stable Isotope Bayesian Ellipses in R (SIBER)—Isotopic niche evidence

Given the inherent variability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in corals and their symbionts, the application of SIBER can aid in quantifying and integrating multi-dimensional variability and uncertainty [35]. Isotopic niche and trophic niche are expected to be tightly correlated, but should not be confused as being the same. SIBER does not eliminate underlying confounding factors and the low resolution inherently associated with bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements of photosymbiotic corals. Lesser et al. [6] state that the lack of host and symbiont overlap in the SIBER isotopic niche for *Montastraea cavernosa* at lower mesophotic depths (their Figure 3) and for *Stylophora pistillata* at mesophotic depths (their Figure 5) provide evidence of a transition from autotrophy to heterotrophy with increasing depth. However, upon closer inspection, the lack of isotope niche overlap for lower mesophotic *Montastraea cavernosa* was entirely due to $\delta^{15}\text{N}$ values ($\delta^{13}\text{C}$ values completely overlapped), which showed no significant depth effect. For *Stylophora pistillata*, the lack of host and symbiont overlap in the SIBER isotopic niche also occurs in shallow water with greater separation when compared to mesophotic depths. Therefore, for these specific cases highlighted in Lesser et al. [6], this metric does not support a unidirectional transition to increased heterotrophy with increasing depth.

$\delta^{18}\text{O}_{\text{skeleton}}$ -corrected $\delta^{13}\text{C}_{\text{skeleton}}$ proxy for photosynthesis/respiration (P/R) ratio

Lesser et al. [6] revisit the application of the theoretical $\delta^{18}\text{O}_{\text{skeleton}}$ -corrected $\delta^{13}\text{C}_{\text{skeleton}}$ proxy for the P/R ratio from their previous study [7] (reviewed in [5]). This isotope-based

proxy for the P/R ratio depends on the ability to use $\delta^{18}\text{O}_s$ to remove kinetic effects from $\delta^{13}\text{C}_s$ [20] and is based on McConnaughey's model of kinetic and metabolic isotope effects [36–38], which has been replaced by Adkin's model of biologically induced pH controls on $\delta^{18}\text{O}_s$ [39,40]. The original correction proposed by Heikoop et al. [20] relies on three key assumptions, that (1) the corals being compared are grown under the same environmental conditions, (2) the variability in $\delta^{18}\text{O}_s$ is only caused by kinetic isotope effects, and (3) the kinetic effects of $\delta^{18}\text{O}_s$ and $\delta^{13}\text{C}$ are constant relative to each other (however, see [41,42]). Variability in $\delta^{18}\text{O}_s$ can be caused by factors other than kinetic isotope effects, such as variations in seawater temperature, salinity, seawater $\delta^{18}\text{O}$ (reviewed in [43]), and endosymbiont type [41,44]. If temperature is not controlled, the temperature dependency of isotope fractionation against $\delta^{13}\text{C}_{\text{eq}}$ and $\delta^{18}\text{O}_{\text{eq}}$ also needs to be considered [45]. Comparing in situ corals across a large depth gradient can meet this assumption if the water column is well mixed (i.e., uniform water column properties) and the symbiont type remains constant; these conditions were not met for *Montastraea cavernosa* in Lesser et al. [7].

More importantly, this theoretical $\delta^{13}\text{C}_s$ isotope proxy for the P/R ratio has been consistently refuted by all empirical data measuring corresponding P/R ratios to date [14,46,47]. Despite the lack of empirical validation, Lesser et al. [6] assume the validity of this metric and by highlighting evidence supporting its general theoretical foundation. Lesser et al. [6] dismiss results in Swart et al. [14] due to the lack of dark-adapted respiration data. However, whether such minor adjustments could reverse the original conclusion is questionable, given the extensive nature of the study (monthly samples and high-resolution diel incubations) and the large-scale seasonal pattern revealed. Lesser et al. also attempt to dismiss Schoepf et al. [47] under the guise that bleached corals were included in their study, when in fact an equivalent number of unbleached/unstressed corals were measured for P/R via respirometry and compared to the $\delta^{18}\text{O}_{\text{skeleton}}$ -corrected $\delta^{13}\text{C}_s$ isotope proxy. Schoepf et al.'s [47] data for healthy corals are self-evident, and the data correction proposed by Heikoop et al. [20] to remove kinetic isotope effects is generally not effective, even under controlled laboratory conditions. Thus, isotope-based P/R ratios are not reliable, quantitative proxies for measured P/R ratios [47].

Stylophora pistillata

With respect to trophic ecology, arguably the most thoroughly studied coral taxon to date is *Stylophora pistillata* from Eilat in the Red Sea (e.g., [8,9,11,48–51]). Based on a select subset of misinterpreted data, Lesser et al. [6] conclude that this coral transitions from autotrophy to heterotrophy with depth, contradicting the original conclusions of authors of multiple detailed studies [8,9,11]. For *S. pistillata*, the $\delta^{13}\text{C}$ coral host values decline with increasing depth and reach -22.7‰ at the deepest depth (50–65 m), exceeding the values of local zooplankton (-19.6 to -20.9‰) [9]. These data are not consistent with POM and zooplankton, especially given the trophic enrichment associated with $\delta^{13}\text{C}$ (0.4‰ to 1‰ between each trophic level) (reviewed in [12]). As previously mentioned, there is no increase in the separation of host and symbiont SIBER isotopic niches (for carbon and nitrogen) from shallow water to mesophotic depths [6].

Calculating trophic position (TP) from $\Delta^{15}\text{N}_{(\text{glu-phe})}$, the difference between the $\delta^{15}\text{N}$ of trophic amino acid glutamic acid and source amino acid phenylalanine [52,53], Martinez et al. [11] reported no difference between shallow (5 m) and mesophotic (60 m) colonies for both host and symbiont, indicating that heterotrophy as a percentage of total input remains constant between these depths (i.e., heterotrophic input decreases at depth proportionately with photosynthesis) [11]. Lesser et al. [6] argue that this result is anomalous based on a hypothetical increase in the availability of heterotrophic resources due to a deep mixed layer in the winter (when primary productivity is lowest) [54]. Lesser et al. further imply that the conclusion of Martinez et al. [11] can be reversed by the fact that two of five essential amino acids (valine and isoleucine) exhibit a lighter $\delta^{13}\text{C}$ signature at depth, which they interpret as a signature of heterotrophy (their Figure 7). This interpretation is contradicted by experimental evidence that suggests that the $\delta^{13}\text{C}$ of valine and isoleucine are independent of trophic ecology [55]. Without decoding the biosynthesis pathway for

the $\delta^{13}\text{C}$ in each essential amino acid with their corresponding fractionation dynamics, no inference on potential heterotrophic influence can be ascertained. Of the essential amino acids (AA_{ess}), the most informative for carbon source is probably the aromatic AA_{ess} phenylalanine, which shows no significant change in $\delta^{13}\text{C}$ with depth (their Figure 7). Across multiple organisms, phenylalanine is known as a “source” AA_{ess} with no significant fractionation and near zero $\Delta^{13}\text{C}$ (and $\Delta^{15}\text{N}$) between consumer and diet ([56] and references therein). If there was a shift in carbon source (i.e., original primary production source) between depths, the $\delta^{13}\text{C}$ in phenylalanine would arguably be a more reliable indicator than the four branch-chained AA_{ess} , which as a set do not show a consistent pattern with depth. Although the TP metric from $\Delta^{15}\text{N}_{(\text{glu}-\text{phe})}$ can be influenced by both diet quality (diet–consumer AA imbalances) and metabolic flux (e.g., mode of nitrogen excretion) (Ohkouchi et al., 2017) [57], the purported evidence presented in Lesser et al. [6] does not weaken the original conclusion of Martinez et al. [11] or provide any relevant geochemical evidence that *S. pistillata* transitions from autotrophy to heterotrophy with depth.

Energetic balance

The logic that Lesser et al. [6] use to support their generalized conclusion of a transition from autotrophy to heterotrophy in photosymbiotic corals is predicated on the assumption that the energetic balance for coral holobionts is dictated by inputs (i.e., exponentially declining photosynthetic production with depth), which must require heterotrophic subsidies to remain positive at increasing depths. All organisms require energy to fuel metabolic activity (typically, in the form of organic C for aerobic organisms) and elemental resources to build organic molecules and biomass. For all forms of life, including photosymbiotic corals across a depth gradient, energetic balance depends on both inputs and outputs (metabolic demands). Although trophic ecology focuses on the former, the latter is of equal importance and cannot be expected to be constant with depth. For example, the growth rate of *Porites lobata* in Hawaii decreases exponentially with depth in a similar manner to the attenuation of downwelling light [58]. Corals can exhibit declining rates of calcification with depth and much slower growth rates in their lower depth range [9,43,59].

The pivotal assumption of Lesser et al. [6] that the compensation point for autotrophy is surpassed at lower mesophotic depths is refuted by examining the benthic algae that co-occurs at these depths and deeper (reviewed in [2,5,60,61]). Given the superior light-harvesting efficiency of corals vs. non-calcified plants [62–64], there is no a priori reason to expect corals to be less capable of sustaining a positive energetic balance from autotrophy in the lower photic zone. The regression model for GPP with depth in Lesser et al. is based on limited coral parameters (e.g., Φ_m , maximum quantum yield for photosynthesis) collected at 1–50 m and extrapolated to deeper depths [7,65]. Some coral conspecifics can significantly enhance their photosynthetic capabilities due to changes in bio-optical properties at depth (e.g., the nine-fold higher light-use efficiency of *Stylophora pistillata* [48]). Likewise, a decrease in respiration rates can cause P/R ratios to increase with depth for some species [66]. Any model attempting to represent the energetics of the lower photic zone must account for both actual photosynthetic performance and for any changes in metabolic demand (i.e., energetic output) with depth.

Several factors may cause metabolic costs to differ between deep- and shallow-water habitats. In high light, photosynthetic organisms must invest in photoprotective pigments, repairing photo-damage, heat shock proteins, and antioxidants (reviewed in [67,68]). Likewise, physical stress and damage from corallivores, wave stress, and sedimentation, and episodic disturbance from storms and thermal events are more frequent in shallow water and can attenuate with depth [69,70]. By inhabiting deeper waters further offshore, corals can be less metabolically impacted by these potential stressors. A lower average temperature (within their aerobic thermal range) may facilitate lower rates of respiration, and, therefore, higher growth efficiencies in ectothermal organisms [71]. The evidence provided by Lesser et al. to support their implicit conclusion about energetics in the lower photic zone is tenuous and cannot support a generalization for all photosymbiotic corals.

Interestingly, with the exception of some temperate zooxanthellate corals (reviewed in [2]), photosymbiotic reef-building corals appear to be obligate autotrophs, which cannot persist indefinitely in darkness regardless of heterotrophic resources. This dependency may be associated with the coral host lacking critical biosynthesis pathways for essential biomolecules originating from their photosymbiont and not assimilated via their heterotrophic diet (e.g., certain essential amino acids [27,55]). Therefore, light energy as the limiting factor for the depth distribution of photosymbiotic corals in warm water may not necessarily be just for their metabolic requirements, but also for biosynthetic pathways within their phototrophic symbionts. Evolutionary streamlining in obligate photosymbiotic holobionts may have resulted in the loss of redundant biosynthetic pathways in the coral host.

Facultative heterotrophy

Finally, the other major implication of the generalized conclusion of Lesser et al. [6] is that photosymbiotic corals are facultatively heterotrophic and can compensate for lower rates of photosynthesis at depth. If true, three possible scenarios exist.

1. **Heterotrophic capabilities are constant** with depth, but photosynthesis declines with increasing depth as available light decreases. Therefore, a coral species becomes increasingly reliant on heterotrophy.
2. **Heterotrophic feeding within a species is simply a function of food availability** (passive feeding rate = food concentration $\times$ flow rate). Coral colonies feed when they can, which is location and time specific, but depth per se is not the causal factor.
3. **Corals have the ability to upregulate heterotrophic feeding** to increase energetic input when photosynthesis declines with lower light availability at increasing depths.

The first two scenarios are not mutually exclusive. The second scenario is increasingly supported by accumulating evidence (reviewed in [5,72,73]). Interestingly, there is some evidence for physiological changes with depth (both within and between species) which may actually reduce heterotrophic capabilities at depth (e.g., lower profiles, lower density of polyps, smaller corallites, polyps lacking tentacles, etc.) (reviewed in [2,5,61]).

Although seemingly logical, the third scenario advocated by Lesser et al. [6] has an implicit corollary: in shallow water, corals down-regulate heterotrophic feeding in favor of utilizing organic C from photosynthesis. Energy and organic C are commonly available in excess in clear oligotrophic shallow water (e.g., [74,75]), but macronutrients (bioavailable nitrogen and soluble reactive phosphorus) are often limiting (e.g., [75–78]). Given the nutrient limitation common in shallow-water coral habitat, this hypothesis is not consistent with optimal foraging. Short of satiation, why would any coral down-regulate heterotrophic feeding and their acquisition of limiting elemental resources?

Concluding thoughts on SIA and trophic analysis

Although there is certainly evidence to suggest that some depth-generalist coral species likely increase their reliance on heterotrophy with increasing depth (e.g., [3,4,73,79]), there is growing evidence that other species do not [8–11,73,80,81]. Given the diversity of photosymbiotic corals with their deeply divergent evolutionary lineages [82] and the diversity of physical environments supporting coral reef habitats, there is no a priori reason to expect a uniform trophic strategy across all coral species in their adaptations to depth. The collective evidence to date suggests that different colonies function differently, both between and within species (reviewed in [5,25,72,73]).

A comprehensive review of the relevant literature indicates that available empirical and experimental SIA data from photosymbiotic corals are quite variable. The bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of photosymbiotic corals represent the integration of multiple concurrent processes and factors, which can be quite challenging to disentangle. Although sometimes correlated, different methodological approaches for using bulk tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopic data to infer trophic ecology (i.e., $\Delta\delta^{13}\text{C}_{\text{host-symbiont}}$, $\Delta\delta^{15}\text{N}_{\text{host-symbiont}}$, SIBER, and MixSIAR) can also produce conflicting results for the same individual corals [32]. When bias is applied to selectively highlight subsets of data, there can appear to be sufficient

evidence to support a dubious conclusion, especially for readers who are not directly familiar with the extensive literature on isotope geochemistry. Despite the economic and logistical challenges associated with higher resolution techniques (i.e., dietary biomarkers and compound-specific stable isotopic analysis), they appear to be the most promising way to clarify the complex trophic interactions of photosymbiotic organisms [32]. To date, these higher resolution techniques have not been applied to corals at depths > 60 m. Therefore, direct evidence for the trophic ecology of photosymbiotic corals in the lower half of the photic zone, including depth-specialist species (*Leptoseris* spp.), which dominate the photosymbiotic community at the deepest depth, is essentially nonexistent.

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References

1. Pérez-Castro, M.Á.; Schubert, N.; De Oca, G.A.-M.; Leyte-Morales, G.E.; Eyal, G.; Hinojosa-Arango, G. Mesophotic Coral Ecosystems in the Eastern Tropical Pacific: The current state of knowledge and the spatial variability of their depth boundaries. *Sci. Total Environ.* **2022**, *806*, 150576. [CrossRef] [PubMed]
2. Kahng, S.E.; Garcia-Sais, J.R.; Spalding, H.L.; Brokovich, E.; Wagner, D.; Weil, E.; Hinderstein, L.; Toonen, R.J. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* **2010**, *29*, 255–275. [CrossRef]
3. Muscatine, L.; Porter, J.; Kaplan, I. Resource partitioning by reef corals as determined from stable isotope composition. *Mar. Biol.* **1989**, *100*, 185–193. [CrossRef]
4. Fricke, H.W.; Vareschi, E.; Schlichter, D. Photoecology of the coral *Leptoseris fragilis* in the Red Sea twilight zone (an experimental study by submersible). *Oecologia* **1987**, *73*, 371–381. [CrossRef] [PubMed]
5. Kahng, S.E.; Akkaynak, D.; Shlesinger, T.; Hochberg, E.J.; Wiedenmann, J.; Tamir, R.; Tchernov, D. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. In *Mesophotic Coral Ecosystems*; Loya, Y., Puglise, K., Bridge, T., Eds.; Springer: Cham, Switzerland, 2019; pp. 801–828.
6. Lesser, M.P.; Slaterry, M.; Macartney, K.J. Using Stable Isotope Analyses to Assess the Trophic Ecology of Scleractinian Corals. *Oceans* **2022**, *3*, 527–546. [CrossRef]
7. Lesser, M.P.; Slaterry, M.; Stat, M.; Ojimi, M.; Gates, R.D.; Grottoli, A. Photoacclimatization by the coral *Montastraea cavernosa* in the mesophotic zone: Light, food, and genetics. *Ecology* **2010**, *91*, 990–1003. [CrossRef]
8. Alamaru, A.; Loya, Y.; Brokovich, E.; Yam, R.; Shemesh, A. Carbon and nitrogen utilization in two species of Red Sea corals along a depth gradient: Insights from stable isotope analysis of total organic material and lipids. *Geochim. Cosmochim. Acta* **2009**, *73*, 5333–5342. [CrossRef]
9. Einbinder, S.; Mass, T.; Brokovich, E.; Dubinsky, Z.; Erez, J.; Tchernov, D. Changes in morphology and diet of the coral *Stylophora pistillata* along a depth gradient. *Mar. Ecol. Prog. Ser.* **2009**, *381*, 167–174. [CrossRef]
10. Crandall, J.; Teece, M.; Estes, B.; Manfrino, C.; Ciesla, J. Nutrient acquisition strategies in mesophotic hard corals using compound specific stable isotope analysis of sterols. *J. Exp. Mar. Biol. Ecol.* **2016**, *474*, 133–141. [CrossRef]
11. Martinez, S.; Kolodny, Y.; Shemesh, E.; Scucchia, F.; Nevo, R.; Levin-Zaidman, S.; Paltiel, Y.; Keren, N.; Tchernov, D.; Mass, T. Energy sources of the depth-generalist mixotrophic coral *Stylophora pistillata*. *Front. Mar. Sci.* **2020**, *7*, 566663. [CrossRef]
12. Ferrier-Pagès, C.; Leal, M.C. Stable isotopes as tracers of trophic interactions in marine mutualistic symbioses. *Ecol. Evol.* **2019**, *9*, 723–740. [CrossRef] [PubMed]
13. Williams, D.F.; Röttger, R.; Schmaljohann, R.; Keigwin, L. Oxygen and carbon isotopic fractionation and algal symbiosis in the benthic foraminiferan *Heterostegina depressa*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **1981**, *33*, 231–251. [CrossRef]
14. Swart, P.K.; Szmant, A.; Porter, J.W.; Dodge, R.E.; Tougas, J.I.; Southam, J.R. The isotopic composition of respired carbon dioxide in scleractinian corals: Implications for cycling of organic carbon in corals. *Geochim. Cosmochim. Acta* **2005**, *69*, 1495–1509. [CrossRef]
15. Nahon, S.; Richoux, N.B.; Kolasinski, J.; Desmalades, M.; Ferrier Pages, C.; Lecellier, G.; Planes, S.; Berteaux Lecellier, V. 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* **2013**, *8*, e81247. [CrossRef] [PubMed]
16. Swart, P.K. Carbon and oxygen isotope fractionation in scleractinian corals: A review. *Earth-Sci. Rev.* **1983**, *19*, 51–80. [CrossRef]
17. Wall, C.B.; Ritson-Williams, R.; Popp, B.N.; Gates, R.D. Spatial variation in the biochemical and isotopic composition of corals during bleaching and recovery. *Limnol. Oceanogr.* **2019**, *64*, 2011–2028. [CrossRef]
18. Hoogenboom, M.; Rottier, C.; Sikorski, S.; Ferrier-Pagès, C. Among-species variation in the energy budgets of reef-building corals: Scaling from coral polyps to communities. *J. Exp. Biol.* **2015**, *218*, 3866–3877. [CrossRef]
19. Wall, C.B.; Kaluhiokalani, M.; Popp, B.N.; Donahue, M.J.; Gates, R.D. Divergent symbiont communities determine the physiology and nutrition of a reef coral across a light-availability gradient. *ISME J.* **2020**, *14*, 945–958. [CrossRef]
20. Heikoop, J.M.; Dunn, J.J.; Risk, M.J.; Schwarcz, H.P.; McConnaughey, T.A.; Sandeman, I.M. Separation of kinetic and metabolic isotope effects in carbon-13 records preserved in reef coral skeletons. *Geochim. Cosmochim. Acta* **2000**, *64*, 975–987. [CrossRef]

21. Horwitz, R.; Borell, E.M.; Yam, R.; Shemesh, A.; Fine, M. Natural high pCO₂ increases autotrophy in *Anemonia viridis* (Anthozoa) as revealed from stable isotope (C, N) analysis. *Sci. Rep.* **2015**, *5*, 8779. [\[CrossRef\]](#)
22. Tremblay, P.; Grover, R.; Maguer, J.-F.; Hoogenboom, M.; Ferrier-Pagès, C. Carbon translocation from symbiont to host depends on irradiance and food availability in the tropical coral *Stylophora pistillata*. *Coral Reefs* **2014**, *33*, 1–13. [\[CrossRef\]](#)
23. Tremblay, P.; Gori, A.; Maguer, J.F.; Hoogenboom, M.; Ferrier-Pagès, C. Heterotrophy promotes the re-establishment of photosynthetic translocation in a symbiotic coral after heat stress. *Sci. Rep.* **2016**, *6*, 38112. [\[CrossRef\]](#)
24. Tanaka, Y.; Grottoli, A.G.; Matsui, Y.; Suzuki, A.; Sakai, K. Effects of nitrate and phosphate availability on the tissues and carbonate skeleton of scleractinian corals. *Mar. Ecol. Prog. Ser.* **2017**, *570*, 101–112. [\[CrossRef\]](#)
25. Fox, M.D.; Elliott Smith, E.A.; Smith, J.E.; Newsome, S.D. Trophic plasticity in a common reef-building coral: Insights from $\delta^{13}\text{C}$ analysis of essential amino acids. *Funct. Ecol.* **2019**, *33*, 2203–2214. [\[CrossRef\]](#)
26. Conti-Jerpe, I.E.; Thompson, P.D.; Wong, C.W.M.; Oliveira, N.L.; Duprey, N.N.; Moynihan, M.A.; Baker, D.M. Trophic strategy and bleaching resistance in reef-building corals. *Sci. Adv.* **2020**, *6*, eaaz5443. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Wall, C.B.; Wallsgrove, N.J.; Gates, R.D.; Popp, B.N. Amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses reveal distinct species-specific patterns of trophic plasticity in a marine symbiosis. *Limnol. Oceanogr.* **2021**, *66*, 2033–2050. [\[CrossRef\]](#) [\[PubMed\]](#)
28. Maier, C.; Weinbauer, M.G.; Pätzold, J. Stable isotopes reveal limitations in C and N assimilation in the Caribbean reef corals *Madraca auretenra*, *M. carmabi* and *M. formosa*. *Mar. Ecol. Prog. Ser.* **2010**, *412*, 103–112. [\[CrossRef\]](#)
29. Bongaerts, P.; Carmichael, M.; Hay, K.B.; Tonk, L.; Frade, P.R.; Hoegh-Guldberg, O. Prevalent endosymbiont zonation shapes the depth distributions of scleractinian coral species. *R. Soc. Open Sci.* **2015**, *2*, 140297. [\[CrossRef\]](#) [\[PubMed\]](#)
30. Polinski, J.M.; Voss, J.D. Evidence of photoacclimatization at mesophotic depths in the coral-Symbiodinium symbiosis at Flower Garden Banks National Marine Sanctuary and McGrail Bank. *Coral Reefs* **2018**, *37*, 779–789. [\[CrossRef\]](#)
31. Eckert, R.J.; Reaume, A.M.; Sturm, A.B.; Studivan, M.S.; Voss, J.D. Depth influences Symbiodiniaceae associations among *Montastraea cavernosa* corals on the Belize Barrier Reef. *Front. Microbiol.* **2020**, *11*, 518. [\[CrossRef\]](#)
32. Price, J.T.; McLachlan, R.H.; Jury, C.P.; Toonen, R.J.; Grottoli, A.G. Isotopic approaches to estimating the contribution of heterotrophic sources to Hawaiian corals. *Limnol. Oceanogr.* **2021**, *66*, 2393–2407. [\[CrossRef\]](#)
33. Reynaud, S.; Martinez, P.; Houllbrèque, F.; Billy, I.; Allemand, D.; Ferrier-Pagès, C. Effect of light and feeding on the nitrogen isotopic composition of a zooxanthellate coral: Role of nitrogen recycling. *Mar. Ecol. Prog. Ser.* **2009**, *392*, 103–110. [\[CrossRef\]](#)
34. Rodrigues, L.J.; Grottoli, A.G. Calcification rate and the stable carbon, oxygen, and nitrogen isotopes in the skeleton, host tissue, and zooxanthellae of bleached and recovering Hawaiian corals. *Geochim. Cosmochim. Acta* **2006**, *70*, 2781–2789. [\[CrossRef\]](#)
35. Jackson, A.L.; Inger, R.; Parnell, A.C.; Bearhop, S. Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *J. Anim. Ecol.* **2011**, *80*, 595–602. [\[CrossRef\]](#) [\[PubMed\]](#)
36. McConnaughey, T. ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates: I. Patterns. *Geochim. Cosmochim. Acta* **1989**, *53*, 151–162. [\[CrossRef\]](#)
37. McConnaughey, T. ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates: II. In vitro simulation of kinetic isotope effects. *Geochim. Cosmochim. Acta* **1989**, *53*, 163–171. [\[CrossRef\]](#)
38. McConnaughey, T.A.; Burdett, J.; Whelan, J.F.; Paull, C.K. Carbon isotopes in biological carbonates: Respiration and photosynthesis. *Geochim. Cosmochim. Acta* **1997**, *61*, 611–622. [\[CrossRef\]](#)
39. Adkins, J.F.; Boyle, E.A.; Curry, W.; Lutringer, A. Stable isotopes in deep-sea corals and a new mechanism for “vital effects”. *Geochim. Cosmochim. Acta* **2003**, *67*, 1129–1143. [\[CrossRef\]](#)
40. Rollion-Bard, C.; Chaussidon, M.; France-Lanord, C. pH control on oxygen isotopic composition of symbiotic corals. *Earth Planet. Sci. Lett.* **2003**, *215*, 275–288. [\[CrossRef\]](#)
41. Felis, T.; Pätzold, J.; Loya, Y. Mean oxygen-isotope signatures in *Porites* spp. corals: Inter-colony variability and correction for extension-rate effects. *Coral Reefs* **2003**, *22*, 328–336. [\[CrossRef\]](#)
42. McConnaughey, T. Sub-equilibrium oxygen-18 and carbon-13 levels in biological carbonates: Carbonate and kinetic models. *Coral Reefs* **2003**, *22*, 316–327. [\[CrossRef\]](#)
43. Watanabe, T.; Watanabe, T.K.; Yamazaki, A.; Yoneta, S.; Sowa, K.; Sinniger, F.; Eyal, G.; Loya, Y.; Harii, S. Coral sclerochronology: Similarities and differences in the coral isotopic signatures between mesophotic and shallow-water reefs. In *Mesophotic Coral Ecosystems*; Springer: Cham, Switzerland, 2019; pp. 667–681.
44. Maier, C.; Felis, T.; Pätzold, J.; Bak, R.P. Effect of skeletal growth and lack of species effects in the skeletal oxygen isotope climate signal within the coral genus *Porites*. *Mar. Geol.* **2004**, *207*, 193–208. [\[CrossRef\]](#)
45. Omata, T.; Suzuki, A.; Sato, T.; Minoshima, K.; Nomaru, E.; Murakami, A.; Murayama, S.; Kawahata, H.; Maruyama, T. Effect of photosynthetic light dosage on carbon isotope composition in the coral skeleton: Long-term culture of *Porites* spp. *J. Geophys. Res. Biogeosci.* **2008**, *113*. [\[CrossRef\]](#)
46. Swart, P.K.; Dodge, R.E.; Hudson, H.J. A 240-year stable oxygen and carbon isotopic record in a coral from South Florida: Implications for the prediction of precipitation in southern Florida. *Palaios* **1996**, *11*, 362–375. [\[CrossRef\]](#)
47. Schoepf, V.; Levas, S.J.; Rodrigues, L.J.; McBride, M.O.; Aschaffenburg, M.D.; Matsui, Y.; Warner, M.E.; Hughes, A.D.; Grottoli, A.G. Kinetic and metabolic isotope effects in coral skeletal carbon isotopes: A re-evaluation using experimental coral bleaching as a case study. *Geochim. Cosmochim. Acta* **2014**, *146*, 164–178. [\[CrossRef\]](#)
48. Kramer, N.; Tamir, R.; Ben-Zvi, O.; Jacques, S.L.; Loya, Y.; Wangpraseurt, D. Efficient light-harvesting of mesophotic corals is facilitated by coral optical traits. *Funct. Ecol.* **2022**, *36*, 406–418. [\[CrossRef\]](#)

49. Martinez, S.; Grover, R.; Baker, D.M.; Ferrier-Pagès, C. Symbiodiniaceae Are the First Site of Heterotrophic Nitrogen Assimilation in Reef-Building Corals. *mBio* **2022**, *13*, e01601–e01622. [[CrossRef](#)] [[PubMed](#)]
50. Ezzat, L.; Fine, M.; Maguer, J.-F.; Grover, R.; Ferrier-Pages, C. Carbon and nitrogen acquisition in shallow and deep holobionts of the scleractinian coral *S. pistillata*. *Front. Mar. Sci.* **2017**, *4*, 102. [[CrossRef](#)]
51. Blanckaert, A.C.; Grover, R.; Marcus, M.-I.; Ferrier-Pagès, C. Nutrient starvation and nitrate pollution impairs the assimilation of dissolved organic phosphorus in coral-Symbiodiniaceae symbiosis. *Sci. Total Environ.* **2023**, *858*, 159944. [[CrossRef](#)]
52. Chikaraishi, Y.; Ogawa, N.O.; Kashiya, Y.; Takano, Y.; Suga, H.; Tomitani, A.; Miyashita, H.; Kitazato, H.; Ohkouchi, N. Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnol. Oceanogr. Methods* **2009**, *7*, 740–750. [[CrossRef](#)]
53. Chikaraishi, Y.; Ogawa, N.O.; Ohkouchi, N. Further evaluation of the trophic level estimation based on nitrogen isotopic composition of amino acids. *Earth Life Isot.* **2010**, *415*, 37–51.
54. Qurban, M.A.B.; Wafar, M.; Heinle, M. Phytoplankton and primary production in the Red Sea. In *Oceanographic and Biological Aspects of the Red Sea*; Springer: Cham, Switzerland, 2019; pp. 491–506.
55. Ferrier-Pagès, C.; Martinez, S.; Grover, R.; Cybulski, J.; Shemesh, E.; Tchernov, D. Tracing the Trophic Plasticity of the Coral–Dinoflagellate Symbiosis Using Amino Acid Compound-Specific Stable Isotope Analysis. *Microorganisms* **2021**, *9*, 182. [[CrossRef](#)] [[PubMed](#)]
56. Takizawa, Y.; Takano, Y.; Choi, B.; Dharampal, P.S.; Steffan, S.A.; Ogawa, N.O.; Ohkouchi, N.; Chikaraishi, Y. A new insight into isotopic fractionation associated with decarboxylation in organisms: Implications for amino acid isotope approaches in biogeoscience. *Prog. Earth Planet. Sci.* **2020**, *7*, 50. [[CrossRef](#)]
57. Ohkouchi, N.; Chikaraishi, Y.; Close, H.G.; Fry, B.; Larsen, T.; Madigan, D.J.; McCarthy, M.D.; McMahon, K.W.; Nagata, T.; Naito, Y.I.; et al. Advances in the application of amino acid nitrogen isotopic analysis in ecological and biogeochemical studies. *Org. Geochem.* **2017**, *113*, 150–174. [[CrossRef](#)]
58. Grigg, R.W. Depth limit for reef building corals in the Au‘au Channel, S.E. Hawaii. *Coral Reefs* **2006**, *25*, 77–84. [[CrossRef](#)]
59. Gattuso, J.; Jaubert, J. Features of depth effects on *Stylophora pistillata*, an hermatypic coral in the Gulf of Aqaba (Jordan, Red Sea). In Proceedings of the Fifth International Coral Reef Congress, Tahiti, French Polynesia, 27 May–1 June 1985; pp. 95–100.
60. Kahng, S.E.; Copus, J.M.; Wagner, D. Mesophotic Coral Ecosystems. In *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*; Rossi, S., Bramanti, L., Gori, A., Orejas, C., Eds.; Springer International Publishing: Cham, Switzerland, 2017; pp. 185–206.
61. Kahng, S.E.; Copus, J.; Wagner, D. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Curr. Opin. Environ. Sustain.* **2014**, *7*, 72–81. [[CrossRef](#)]
62. Wangpraseurt, D.; Larkum, A.W.; Franklin, J.; Szabó, M.; Ralph, P.J.; Kühl, M. Lateral light transfer ensures efficient resource distribution in symbiont-bearing corals. *J. Exp. Biol.* **2014**, *217*, 489–498. [[CrossRef](#)] [[PubMed](#)]
63. Enriquez, S.; Méndez, E.R.; Iglesias-Prieto, R. Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnol. Oceanogr.* **2005**, *50*, 1025–1032. [[CrossRef](#)]
64. Enriquez, S.; Méndez, E.R.; Hoegh-Guldberg, O.; Iglesias-Prieto, R. Key functional role of the optical properties of coral skeletons in coral ecology and evolution. *Proc. R. Soc. B Biol. Sci.* **2017**, *284*, 20161667. [[CrossRef](#)]
65. Wyman, K.D.; Dubinsky, Z.; Porter, J.W.; Falkowski, P.G. Light absorption and utilization among hermatypic corals: A study in Jamaica, West Indies. *Mar. Biol.* **1987**, *96*, 283–292. [[CrossRef](#)]
66. Cooper, T.F.; Ulstrup, K.E.; Dandan, S.S.; Heyward, A.J.; Kühl, M.; Muirhead, A.; O’Leary, R.A.; Ziersen, B.E.; Van Oppen, M.J. Niche specialization of reef-building corals in the mesophotic zone: Metabolic trade-offs between divergent *Symbiodinium* types. *Proc. R. Soc. B Biol. Sci.* **2011**, *278*, 1840–1850. [[CrossRef](#)] [[PubMed](#)]
67. Dubinsky, Z.; Falkowski, P. Light as a source of information and energy in zooxanthellate corals. In *Coral Reefs: An Ecosystem in Transition*; Dubinsky, Z., Stambler, N., Eds.; Springer: Cham, Switzerland, 2011; pp. 107–118.
68. Lesser, M.P. Coral bleaching: Causes and mechanisms. In *Coral Reefs: An Ecosystem in Transition*; Springer: Dordrecht, The Netherlands, 2011; pp. 405–419.
69. Bongaerts, P.; Ridgway, T.; Sampayo, E.M.; Hoegh-Guldberg, O. Assessing the deep reef refugia hypothesis: Focus on Caribbean reefs. *Coral Reefs* **2010**, *29*, 309–327. [[CrossRef](#)]
70. Pérez-Rosales, G.; Rouzé, H.; Torda, G.; Bongaerts, P.; Pichon, M.; Consortium, U.T.P.; Parravicini, V.; Hédouin, L. Mesophotic coral communities escape thermal coral bleaching in French Polynesia. *R. Soc. Open Sci.* **2021**, *8*, 210139. [[CrossRef](#)] [[PubMed](#)]
71. Pörtner, H.O.; Bennett, A.F.; Bozinovic, F.; Clarke, A.; Lardies, M.A.; Lucassen, M.; Pelster, B.; Schiemer, F.; Stillman, J.H. Trade-Offs in Thermal Adaptation: The Need for a Molecular to Ecological Integration. *Physiol. Biochem. Zool.* **2006**, *79*, 295–313. [[CrossRef](#)] [[PubMed](#)]
72. Houlbrèque, F.; Ferrier-Pagès, C. Heterotrophy in tropical scleractinian corals. *Biol. Rev.* **2009**, *84*, 1–17. [[CrossRef](#)] [[PubMed](#)]
73. Sturaro, N.; Hsieh, Y.E.; Chen, Q.; Wang, P.L.; Denis, V. Trophic plasticity of mixotrophic corals under contrasting environments. *Funct. Ecol.* **2021**, *35*, 2841–2855. [[CrossRef](#)]
74. Muscatine, L.; R. McCloskey, L.; E. Marian, R. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration 1. *Limnol. Oceanogr.* **1981**, *26*, 601–611. [[CrossRef](#)]
75. Falkowski, P.G.; Dubinsky, Z.; Muscatine, L.; McCloskey, L. Population control in symbiotic corals. *BioScience* **1993**, *43*, 606–611. [[CrossRef](#)]

76. Muscatine, L.; Porter, J.W. Reef corals: Mutualistic symbioses adapted to nutrient-poor environments. *BioScience* **1977**, *27*, 454–460. [[CrossRef](#)]
77. Tanaka, Y.; Miyajima, T.; Koike, I.; Hayashibara, T.; Ogawa, H. Translocation and conservation of organic nitrogen within the coral-zooxanthella symbiotic system of *Acropora pulchra*, as demonstrated by dual isotope-labeling techniques. *J. Exp. Mar. Biol. Ecol.* **2006**, *336*, 110–119. [[CrossRef](#)]
78. Atkinson, M.J. Biogeochemistry of nutrients. In *Coral Reefs: An Ecosystem in Transition*; Dubinsky, Z., Stambler, N., Eds.; Springer: Dordrecht, The Netherlands, 2011; pp. 199–206.
79. Ferrier-Pagès, C.; Bednarz, V.; Grover, R.; Benayahu, Y.; Maguer, J.F.; Rottier, C.; Wiedenmann, J.; Fine, M. Symbiotic stony and soft corals: Is their host-algae relationship really mutualistic at lower mesophotic reefs? *Limnol. Oceanogr.* **2022**, *67*, 261–271. [[CrossRef](#)]
80. Radice, V.Z.; Hoegh-Guldberg, O.; Fry, B.; Fox, M.D.; Dove, S.G. Upwelling as the major source of nitrogen for shallow and deep reef-building corals across an oceanic atoll system. *Funct. Ecol.* **2019**, *33*, 1120–1134. [[CrossRef](#)]
81. Carmignani, A.; Radice, V.Z.; McMahon, K.M.; Holman, A.I.; Miller, K.; Grice, K.; Richards, Z. Levels of autotrophy and heterotrophy in mesophotic corals near the end photic zone. *Front. Mar. Sci.* **2023**, *10*, 1089746. [[CrossRef](#)]
82. McFadden, C.S.; Quattrini, A.M.; Brugler, M.R.; Cowman, P.F.; Dueñas, L.F.; Kitahara, M.V.; Paz-García, D.A.; Reimer, J.D.; Rodríguez, E. Phylogenomics, origin, and diversification of Anthozoans (Phylum Cnidaria). *Syst. Biol.* **2021**, *70*, 635–647. [[CrossRef](#)] [[PubMed](#)]

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