Symbiotic stony and soft corals: Is their host-algae relationship really mutualistic at lower mesophotic reefs?

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Symbiotic stony and soft corals: Is their host-algae relationship really mutualistic at lower mesophotic reefs?

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Abstract

Mesophotic coral ecosystems (30–150 m depth) present a high oceanic biodiversity, but remain one of the most understudied reef habitats, especially below 60 m depth. Here, we have assessed the rates of photosynthesis and dissolved inorganic carbon (DIC) and nitrogen (DIN) assimilation by Symbiodiniaceae associated with four soft coral species of the genus *Sinularia* and two stony coral species of the genus *Leptoseris* collected respectively at 65 and 80–90 m depth in the Gulf of Eilat. Our study demonstrates that both *Leptoseris* and *Sinularia* species have limited autotrophic capacities at mid-lower mesophotic depths. DIC and DIN assimilation rates were overall ~ 10 times lower compared to shallow corals from 10 m depth in the same reef. While *Leptoseris* symbionts transferred at least 50% of the acquired nitrogen to their host after 8-h incubation, most of the nitrogen was retained in the symbionts of *Sinularia*. In addition, the host tissue of *Sinularia* species presented a very high structural carbon to nitrogen ratio (C : N) compared to *Leptoseris* or to the shallow coral species, suggesting nitrogen limitation in these mesophotic soft corals. The limited capacity of soft coral symbionts to acquire DIN and transfer it to the coral animal, as well as the high C : N ratios, might explain the scarcity of symbiotic soft corals at mid-lower mesophotic depths compared to their prevalence in the shallower reef. Overall, this study highlights the significance of DIN for the distribution of the Cnidarian- Symbiodiniaceae association at mesophotic depth.

Shallow tropical reefs are based on the mutualistic nutritional association between corals and symbiotic microorganisms such as dinoflagellates belonging to the Symbiodiniaceae (LaJeunesse et al. 2018). Dinoflagellates transform inorganic nutrients dissolved in seawater into organic compounds, which are then transferred in varying quantities to the animal host for its own metabolic requirements (Muscatine 1990). Recently, reef ecosystems featuring understudied diversity have been observed at mesophotic depths (30–150 m, Loya et al. 2016). Mesophotic coral ecosystems, characterized by the presence of symbiotic corals and associated communities, are often more protected from disturbances than shallow reefs (Eyal et al. 2019a). Specifically, compared with shallow reefs, mesophotic reefs experience more stable and lower temperatures and a different light spectrum, to which species such as symbiotic corals have to adapt (Tamir et al. 2019). They have thus been suggested as potential refuges for shallow water coral species, although this function remains controversial and needs further research (Bongaerts and Smith 2019; Kramer et al. 2019).

Recent studies have focused on understanding the morphological, biochemical, metabolic, and photophysiological adaptations of symbiotic corals to mesophotic depths (Smith et al. 2017; Kahng et al. 2019; Ben-Zvi et al. 2020). Although

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Additional Supporting Information may be found in the online version of this article.

Christine Ferrier-Pagès and Vanessa Bednarz contributed equally to this study.

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nutrient acquisition is one of the key parameters that influence animal growth, reproduction capacity, and overall distribution, the nutritional ecology of mesophotic corals has been much less investigated (Muscatine et al. 1989; Einbinder et al. 2009; Lesser et al. 2010). The relative contribution of autotrophy vs. heterotrophy has mainly been inferred from the interpretation of stable isotope values of coral tissue and symbionts or from dietary markers such as lipid composition (Alamaru et al. 2009; Crandall et al. 2016; Pupier et al. 2019). In addition, most studies focused on corals that live in the upper edge of mesophotic coral ecosystems (30–40 m), therefore, direct evidence for the contribution of autotrophy to the metabolism of deeper coral holobionts, which are often depth-specialists, remains sparse. Depth-specialist species such as *Leptoseris* spp., that are restricted almost exclusively to mesophotic environments exhibit horizontal plate-like morphologies, with a large coenosarc tissue, sparse corallites, and tiny tentacles (Englebert et al. 2017); such morphology and polyp arrangement may increase mass transfer rates of inorganic carbon and nitrogen and thus the autotrophic nutrient assimilation. It, however, appears inconsistent with passive suspension feeding, although uptake of sedimented organic material through pores and extended gastrovascular canals was observed in this species (Schlichter 1991). Not all symbiotic mesophotic corals uniformly exhibit plate-like morphologies. *Sinularia* species, for example, bear small and numerous polyps, which can be more suited for heterotrophic feeding via suspension feeding. Measurements of nutrient fluxes in corals with different morphologies and polyp sizes have therefore the potential to inform about the relevance of autotrophy for corals thriving at lower mesophotic depth.

In the northern Red Sea, upper mesophotic coral ecosystems are well developed and comprise a high diversity and abundance of scleractinian and octocoral species (Shoham and Benayahu 2017; Eyal et al. 2019a). On the contrary, the communities at mid to lower mesophotic depths (> 60 m) are less diverse and among their dominating elements are symbiotic depth specialists such as the stony corals *Leptoseris fragilis* and *Leptoseris glabra* and the soft coral species *Sinularia mesophotica* (Benayahu et al. 2017; Eyal et al. 2019a). In this study, we used a remotely operated vehicle (ROV) to sample representatives of these and related coral taxa at depths close to their maximum depth distribution limit (60–65 for *Sinularia* species and under 85 m for *Leptoseris* species). The aim of the study was to investigate the autotrophic capacity of these symbiotic associations with regard to the acquisition of dissolved inorganic carbon (DIC) and nitrogen (DIN). We hypothesize that the autotrophic nutrient acquisition is largely decreased in mid-lower mesophotic corals with heterotrophy becoming more important for their nutrition. In addition, *Sinularia* species might depend even more on passive suspension feeding/heterotrophy than *Leptoseris* species due to a different morphology and polyp arrangement. Such measurements will inform us on the strategies for energy acquisition in mesophotic corals. A better knowledge on the trophic ecology of habitat specialists is critical to understand their capacity to successfully establish, and compete in these light-limited environments and withstand future anthropogenic environmental changes.

Materials and methods

Coral collection

Colonies of the stony corals *L. glabra* and *L. fragilis* and of the soft corals *Sinularia eilatensis*, *Sinularia leptoclados*, *S. mesophotica*, and *S. vrijmoethi* were sampled in October 2019 during a 5-d field trip, between 65 and 120 m depths (see Table 1) under the permits of the Israel Nature and Parks Authority. While *Leptoseris* species could be observed at high abundance at 85–90 m, *Sinularia* species could not be observed below 60–65 m. Colonies (ca. 15–25 cm^2 for *Leptoseris* and 25–30 cm^2 for *Sinularia*) were collected with an ROV (ECA H800), equipped with an HD video camera (VS300 Eca Robotics), and a manipulative arm for sampling. The ROV was operated from the R/V Sam Rothberg using a fiber-optics umbilical cable. Once on board, coral colonies were photographed for identification. Then, they were kept in black cooler boxes and brought back immediately (max. 2 h) to the Red Sea simulator aquaria system at the Inter University Institute for Marine Sciences at Eilat (IUI) (Bellworthy and Fine 2018) for subsequent measurements. All species were briefly maintained (between 3 h and 1 d) in six replicated aquaria (one per species) before being processed, to minimize changes in the oxygen fluxes due to the acclimation of the corals to the aquarium conditions through changes in symbiont numbers and pigment content. They were maintained under photon flux densities (PFD) that corresponded to those measured at 70 m depth at the month of collection (see below for the PFD determination). PFD was obtained by applying two layers of filters (Lee Filters, #172: Lagoon Blue) above and around the tanks, also blocking UV radiation. Temperature was kept constant at the in situ temperature of 23°C at 70 m depth. Dissolved inorganic nutrient concentrations between 50 and 100 m depth have been regularly measured and are comparable to those in shallow depths, < 0.5 μM nitrate, 0.1 μM ammonium, and 0.2 μM phosphate in September–November (Manasrah et al. 2020; Torfstein et al. 2020). To determine the mean irradiance received by corals at their corresponding depth (65 m depth for soft corals and 90 m depth for scleractinians), we considered the daily irradiance dose received in surface waters during October, and monitored by the National Monitoring Program of the Gulf of Eilat (http://www.iui-eilat.ac.il/NMP/Default.aspx). We then applied the light attenuation coefficient (Kd of 0.06 m^{-1}) estimated in previous studies (Stambler 2006; Overmans and Agusti 2019) to calculate the daily dose of irradiance received at each specific depth. Average irradiance of 19 μmol m^{-2} s^{-1} at 65 m depth and 9 μmol m^{-2} s^{-1} at 90 m depth were obtained. For matters

of consistency, all measurements were performed at 15 μmol m^{-2} s^{-1} for all coral species. While being notable, the difference between the mean irradiance of the two deep water habitats (19 and 9 μmol m^{-2} s^{-1}, respectively) is small compared to the mean irradiance (510 μmol m^{-2} s^{-1}) experienced by corals in the same reef system at 10 m depth. Physiological measurements were thus performed on three to six colonies per species (Table 1) at the temperature and light level mentioned above.

Rates of photosynthesis and respiration

Rates of net photosynthesis (Pn) and respiration (R) of three colonies per species were measured using optodes connected to an Oxy-4 oxygen meter (PreSense, Regensburg, Germany). Optodes were calibrated against air-saturated and di-sulfite treated water for the 100% and 0% oxygen, respectively. Coral colonies were individually placed in plexiglass chambers, filled with a known volume of 0.45 μM filtered seawater (FSW) and stirred using a magnetic stirrer. Temperature was maintained at 23°C. Changes in oxygen production were then monitored during the daylight period, and once polyps were expanded, for 60 min at 15 μmol quanta cm^{-2} s^{-1} and for subsequent 60 min in the dark to assess Pn and R, respectively. Gross photosynthesis (Pg) was assessed by adding R to Pn. Pg:R ratio was estimated considering that Pg was sustained over 10 h and that R was continuous over 24 h. At the end of each incubation, colonies were frozen at −20°C and freeze-dried prior to the subsequent determination of ash free dry weight (AFDW), natural isotopic abundance, and surface area (for stony corals) as described below. Rates of photosynthesis and respiration were therefore normalized either by skeletal surface area for stony corals and AFDW for all coral species. Such normalizations allow estimating the total amount of photosynthetically acquired carbon available for the energetic needs of each symbiotic association.

Table 1. Number of colonies of *Leptoseris* sp. and *Sinularia* sp. sampled using a remotely operated vehicle in the deep mesophotic reefs of Eilat.

Coral species	Number of colonies	Depth range (m)
Leptoseris fragilis (depth specialist)	9	85–90
Leptoseris glabra (depth specialist)	9	82–90
Sinularia eilatensis (depth generalist)	7	60–66
Sinularia leptoclados (depth generalist)	6	64–65
Sinularia mesophotica (depth specialist)	9	60–65
Sinularia vrijmoethi (depth generalist)	7	58–63

Assimilation of dissolved inorganic carbon and nitrogen

Assimilation rates of DIC (bicarbonate, HCO_3^-) and DIN (ammonium, NH_4^+) were measured on three to six colonies per species. Ammonium was chosen because it is the preferred DIN source in corals (Taguchi and Kinzie 2001). Each colony was incubated, the day after being collected, and during 8 h in an individual beaker filled with 200 mL FSW enriched with 0.6 mM $NaH^{13}CO_3$ (98 atom %^{13}C; Sigma-Aldrich, St-Louis, MO) and 3 μM $^{15}NH_4Cl$ (98 atom %^{15}N; Sigma-Aldrich). Considering 2 mM DIC and 0.5 μM DIN in seawater, the percent seawater enrichment was 30% and 16%, respectively. At the end of the incubation, nubbins were rinsed for 15 min in non-enriched seawater and then frozen at −20°C before subsequent analysis. The percentage of ^{13}C and the percentage of ^{15}N enrichment, as well as the carbon (C) and nitrogen (N) in the algal and animal compartments, were obtained with a Delta plus Mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) coupled to a C/N analyzer (Flash EA; Thermo Fisher Scientific).

The DIC and DIN assimilation rates were calculated according to the equations presented in Tremblay et al. (2012) and Grover et al. (2002), respectively. Rates were normalized to the AFDW and surface area (only for stony corals) as described below. DIC assimilation rates in symbionts correspond to the C that has been fixed minus the C that has been respired or translocated to the host. DIC assimilation rates in the host tissue correspond to the amount of C that has been translocated from the symbiont to the host minus the carbon that has been respired. Ammonium uptake rates reflect mostly the assimilation by symbionts, and a subsequent, partial translocation of organic N to the host. Indeed, Pernice et al. (2012) demonstrated that symbionts can fix 14–23 times more N than their coral host cells and that the fixation occurs within 30 min after a nitrogen pulse. Therefore, for ammonium, N assimilation rates also correspond to the rates of N translocation by the symbionts.

Sample treatment

For stony coral samples, coral tissue was removed from the skeleton in 10 mL FSW with an air-brush, and homogenized with a potter tissue grinder. Host tissue and dinoflagellate symbionts were separated by centrifugation at 8000 × *g* for 10 min at 4°C to pellet the symbionts. The pellet was rinsed three times with FSW and each fraction was then freeze-dried, and weighed to measure the total dry weight (DW). A fraction of powder (i.e., ca. 30 mg) was used for the determination of the AFDW, while the remaining powder was used for the measurements of the DIC and DIN assimilation rates. The subsample used for the determination of the AFDW was first weighed, and then combusted at 450°C for 4 h in a muffle furnace (Thermolyne 62700; Thermo Fischer Scientific, Waltham, MA). AFDW was determined as the difference between the total DW and ash weight of the subsample and extrapolated to the total weight of the nubbin. The surface area of the skeleton was measured using the wax-dipping technique (Veal et al. 2010).

The soft corals were directly freeze-dried and processed according to Pupier et al. (2019). Briefly, each sample was weighed to determine the total DW and then crushed into powder. A fraction of the powder was used for the determination of the AFDW as described above, and the remaining tissue was homogenized in 10 mL distilled water with a Potter tissue grinder. The host and symbiont fractions of each sample were separated through a series of centrifugations (8000 × *g* for 5 min). Each fraction of the host and symbionts were subsequently freeze-dried and weighed, before being processed for the measurements of the DIC and DIN assimilation rates.

Statistical analyses

All statistical tests were conducted separately for the different *Leptoseris* and *Sinularia* species, since they were collected at two different depths and could not be compared. Differences in Pg, Pn, and R rates between the two mesophotic *Leptoseris* coral species were analyzed using individual Student's *t*-tests. Data were beforehand checked to meet *t*-test assumptions (normal distribution, homogeneity of variances). Differences in Pg, Pn, and R rates (normalized to AFDW) between the different mesophotic *Sinularia* species were analyzed with a one-factor permutational multivariate analyses of variance (PERMANOVA) using Primer-E version 6 software (Clarke and Gorley 2006) with the PERMANOVA+ add on (Anderson 2001). Euclidean distance of square-root transformed data and type III partial sums of squares were used with unrestricted permutation of the raw data (9999 permutations). Differences in DIC and DIN assimilation rates, C and N content, and in C : N ratio were analyzed with a two-factor PERMANOVA with either *Leptoseris* or *Sinularia* species and coral compartment (host tissue and symbiont) as fixed effects. Analysis was based on Euclidean distance of square-root transformed data and type III partial sums of squares were used with permutation of residuals under a reduced model (9999 permutations). The significance for all main tests and the pair-wise comparisons was based on Monte Carlo tests (significance level, $p < 0.05$).

Results

All data were normalized to both surface area and AFDW for *Leptoseris* species, whereas they were normalized to AFDW only for *Sinularia* species. Surface area allows comparing with

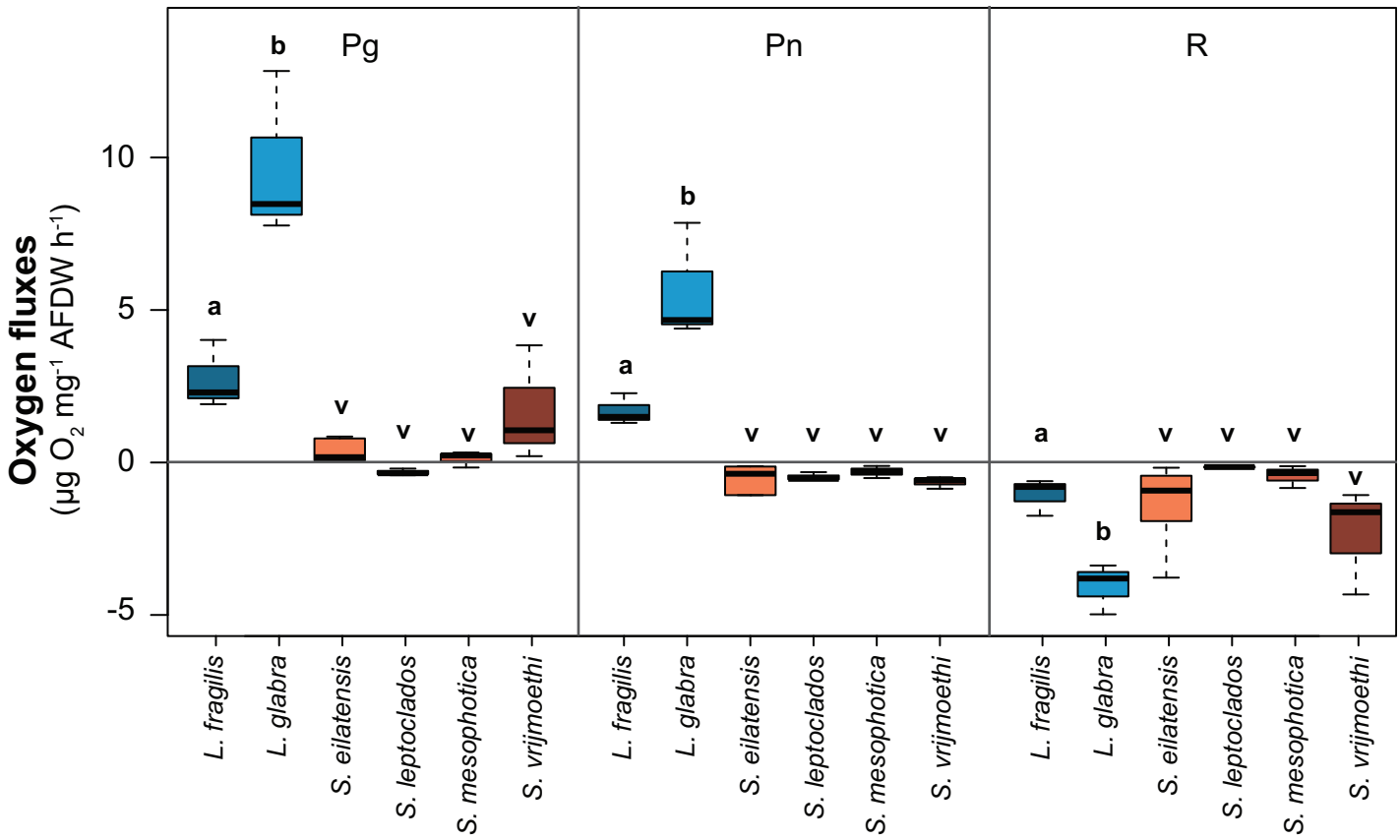

Fig. 1. Rates of gross (Pg) and net (Pn) photosynthesis, and respiration (R) measured for the different mesophotic *Leptoseris* and *Sinularia* coral species investigated. Different lettering above bars indicate significant differences between coral species tested for Pg, Pn, and R rates tested separately for the hard (a-b) and soft (v-w) corals with one-factor permutational ANOVAs and pairwise Monte Carlo tests (significance level, $p < 0.05$).

studies in shallow hard corals while AFDW can highlight differences between hard and soft corals.

Data normalized to AFDW show significantly lower rates of Pg and Pn in *L. fragilis* compared to *L. glabra* (Fig. 1, Supporting Information Table S1). Pn rates were however positive for both species, meaning that the oxygen production was higher than the oxygen consumption in the light. Nevertheless, daily Pg:R ratios, calculated with 10 h irradiance at 15 μmol photons m^{-2} s^{-1}, were below 1, suggesting that photosynthesis could not sustain respiration over a day. All four *Sinularia* species exhibited comparable but negative Pn rates (Fig. 1, Supporting Information Table S2), suggesting that high rates of oxygen consumption in the light masked any oxygen production by the symbiotic algae, and thus Pg could not sustain R over the daytime. Only *S. eilatensis* and *S. vrijmoethi* presented slightly positive rates of Pg. In *Leptoseris* species, DIC assimilation rates were not different between the two species (Fig. 2). However, significantly more DIC was assimilated in the symbionts (3000–4000 ng C h^{-1} mg^{-1}AFDW) compared to the host compartment (300–400 ng C h^{-1} mg^{-1}AFDW) during the 8-h incubation (Fig. 2, Suppl. Table S3). Similarily, DIC assimilation rates in *Sinularia* were not different between the four species, while the symbionts (between 26 and 41 ng C h^{-1} mg^{-1}AFDW) assimilated approximately twice as much DIC compared to the host compartment (between 10 and 15 ng C h^{-1} mg^{-1}AFDW) among all species (Fig. 2, Suppl. Table S4). Overall, total DIC assimilation (in host and symbionts combined) was comparable between all *Sinularia* species. For both *Leptoseris* and *Sinularia* species, total DIC assimilation rates were two orders of magnitude lower than the oxygen production, suggesting that most of the photosynthetically acquired C was quickly respired in the light.

Both *Leptoseris* species exhibited similar DIN assimilation rates, but the assimilation was significantly higher in the host compared to the symbiont compartment when normalized to AFDW (Fig. 2). Rates of N translocation from symbionts to host was equal to 65%. In all *Sinularia* species, DIN assimilation was 10–20 times higher in the symbionts (between 4 and 23 ng N h^{-1} mg^{-1}AFDW depending on the species) than in the host (between 0.25 and 0.74 ng N h^{-1} mg^{-1}AFDW, Fig. 2). Translocation rates of N from symbionts to host therefore ranged between 1% and 5% for all four *Sinularia* species. DIN assimilation was species specific, with *S. leptoclados* showing the lowest assimilation rates. In *Leptoseris* sp., symbionts contained a significant higher cellular C (500 μg mg^{-1} AFDW) and N (100 μg mg^{-1} AFDW) content compared to the host tissue (range, 300 μg C mg^{-1} AFDW and 50–70 μg N mg^{-1} AFDW, Fig. 3, Suppl. Table S3), although the difference in N content was not as pronounced compared to the differences in C content. No difference was observed between *Leptoseris* species in the C and N content of both host and symbionts. In *Sinularia* sp., symbionts contained more C (800 μg mg^{-1} AFDW) and N (100–200 μg mg^{-1} AFDW) than the host tissue (350 μg C mg^{-1} AFDW; 10 μg N mg^{-1} AFDW, Fig. 3). No difference was observed between *Sinularia* species in the C and N content of both host and symbionts (Fig. 3, Suppl. Table S4). The C : N ratio was higher in symbionts (8–10) than in the host (5–6) of *Leptoseris* sp., while the contrary was observed for *Sinularia* sp (C : N = 10 in symbionts and 50 in the host). Overall, the C : N ratios of *Sinularia* hosts were significantly higher than the one of *Leptoseris* species.

The normalization of *Leptoseris* parameters to skeletal surface area highlights some differences with the normalization to AFDW. Pg and Pn rates, as well as DIC assimilation in

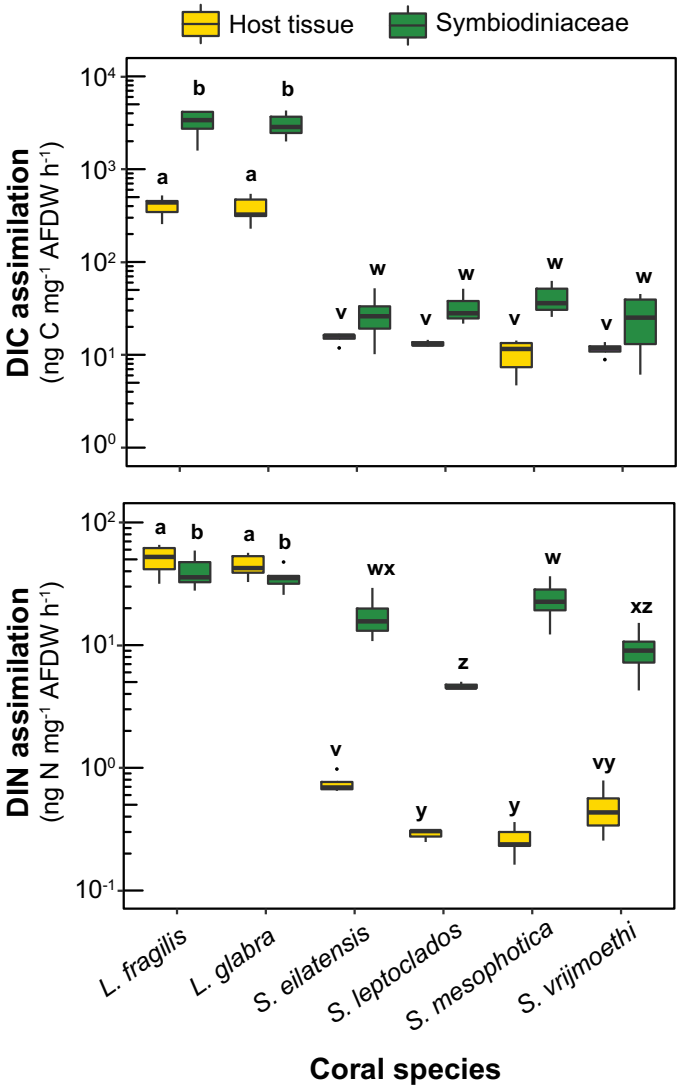

Fig. 2. **(a)** Rates of dissolved inorganic carbon (DIC) and **(b)** nitrogen (DIN) assimilation into the two compartments (host and symbionts) of the different mesophotic *Leptoseris* and *Sinularia* coral species investigated. The *Y* axis is in log scale. Different lettering above bars indicate significant differences of DIC and DIN assimilation tested separately for the hard (a-b) and soft (v-z) corals with two-factor permutational ANOVAs and pairwise Monte Carlo tests (significance level, $p < 0.05$).

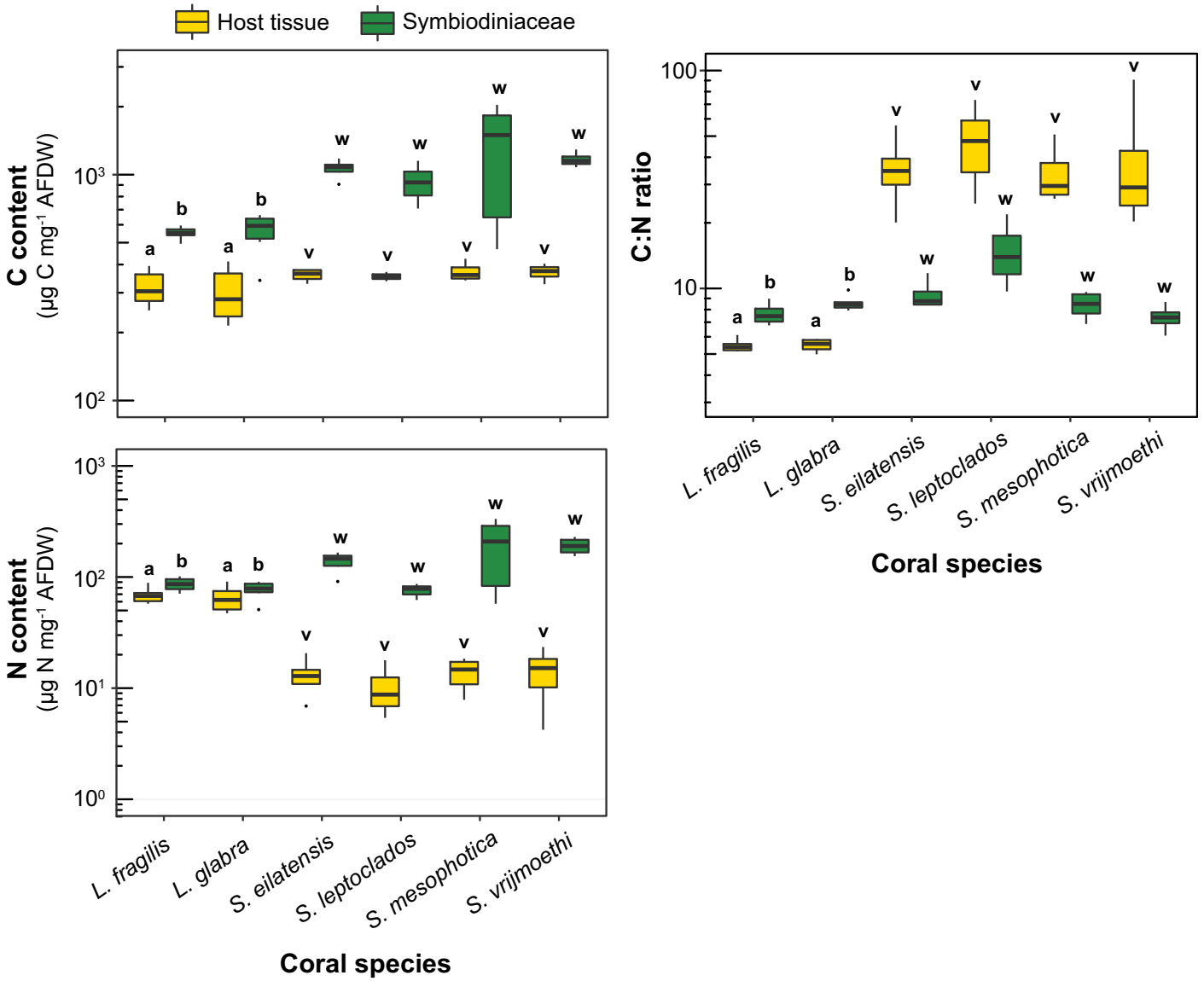

Fig. 3. **(a)** Carbon (C) and **(b)** nitrogen (N) content, as well as the C : N ratios (**c**) in the two compartments (host and symbionts) of the different *Leptoseris* and *Sinularia* mesophotic coral species investigated. The *Y* axis is in log scale. Different lettering above bars indicate significant differences of C and N content and of C : N ratios tested separately for the hard (a-b) and soft (v-w) corals with two-factor permutational ANOVAs and pairwise Monte Carlo tests (significance level, $p < 0.05$).

symbionts, were not different between *L. glabra* and *L. fragilis* ($p > 0.05$, Table 2, Suppl. Table S1). DIN assimilation rates were also not different between the two *Leptoseris* species for the symbiont compartment, but they were lower in the host of *L. glabra* compared to *L. fragilis* (Table 2). For both species, more N was assimilated in the host than in the symbionts (Table 2). Therefore, rates of N translocation from symbionts to host ranged between 65% and 90%.

Discussion

The use of an ROV to sample corals at mesophotic depth at sites in proximity to a laboratory allowed examination of trophic interactions within a short time between collection and analyses, thereby minimizing changes in coral physiology due to acclimation to the ex situ environment. In addition, the application of C and N isotopic tracers has highlighted key nutritional aspects of stony and soft coral-dinoflagellate symbioses living at mid-lower mesophotic depths. The rates of autotrophic assimilation of DIC and DIN were several orders lower for mesophotic corals compared to shallow water counterparts, suggesting that corals rely more on hetero- than autotrophy at mesophotic depths. In addition, the significant lower DIC assimilation rates compared to the oxygen production rates suggest that most of the C produced was instantly respired by the host and/or the symbionts to gain energy.

Leptoseris symbionts transferred at least 50% of the acquired N to their host after 8-h incubation, while most of the N was assimilated in the symbionts of *Sinularia*. In addition, the host tissue of *Sinularia* species presented a very high structural C : N ratio compared to *Leptoseris* or shallow coral species, suggesting N limitation in these mesophotic soft corals. A similar N limitation was observed in mesophotic colonies of *Stylophora pistillata*, compared to shallow ones (Ezzat et al. 2017), suggesting that N availability may drive the abundance of both scleractinian and soft corals along the depth gradient.

Mesophotic reefs thriving at more than 60 m depth are characterized by a specific light spectrum (Tamir et al. 2019), to which symbiotic corals need to adapt. The depth specialist species *Leptoseris* spp. benefit from structural and physiological adaptations of the coral host to improve the photosynthesis of its symbionts, in addition to symbiont photoadaptation and photoacclimatization (Padilla-Gamiño et al. 2019). For example, host pigments and chromatophore systems both allow lower light reflectance compared to shallow scleractinian species and transform short wavelengths into longer ones, which fit into the absorption maxima of the light harvesting pigments of the symbionts (Schlichter and Fricke 1991; Kahng et al. 2012). In addition, incident light travels through the tissue of *Leptoseris* spp. several times due to the presence and structure of the skeleton, thereby increasing photon-pigment interactions without increasing pigment concentrations (Khang et al. 2012). Such adaptations allow *Leptoseris* spp. to present positive rates of net photosynthesis at 15 μmol photons m^{-2} s^{-1}, comparable to the rates of photosynthesis measured for some corals at upper mesophotic depth (Table 3). These results ssuggest that the photosynthates produced were sufficient to cover the immediate respiratory needs of the colonies during the daylight period. On the contrary, the negative rates of net photosynthesis in *Sinularia* spp. indicate that rates of oxygen consumption in the light were much higher than the rates of oxygen production. A low dependency of soft corals on autotrophy is already a feature of these animals in shallow reefs (Baker et al. 2015; Rossi et al. 2018; Pupier et al. 2019). Explanations for a low autotrophic capacity of soft corals include the lack of light amplification and dispersion by the skeleton (Wangpraseurt et al. 2014), a thick coenenchyme which does not favor gas and nutrient exchanges through the epidermal tissue and the fact that soft corals can contract their tissue, preventing symbionts to be fully exposed to light and nutrients. This low autotrophic efficiency may be one of the factors that explain the very low abundance of symbiotic soft coral species below 60–65 m depth in the Gulf of Eilat (Shoham and Benayahu 2017; Benayahu et al. 2019).

For both *Leptoseris* and *Sinularia* species, the Pg:R ratios calculated on a 24 h basis were below 1, indicating that autotrophic carbon acquisition could not sustain the corals' daily respiratory needs. The low photosynthetic production was also quickly respired to cover immediate metabolic needs, as demonstrated by the very low rates of DIC assimilation (in both host and symbionts) compared to oxygen production. This explains the low coral growth or reproduction rates at mesophotic depth (Shlesinger and Loya 2019; Watanabe et al. 2019; Eyal et al. 2019b). Overall, the rates of oxygen production (photosynthesis rates) and DIC assimilation by Symbiodiniaceae associated with both *Leptoseris* and mesophotic *Sinularia* species were ca. 10 times lower than the rates measured for most shallow coral-dinoflagellate associations (Tables 3 and 4). Such difference can be due to the Symbiodiniaceae species associated to mesophotic corals (Pochon et al. 2015; Padilla-Gamiño et al. 2019), to lower symbiont densities (Kaiser et al. 1993), to a light limitation of symbiont activity, or to different physiological state and/or nutritional behavior of the symbiotic associations at mid to lower mesophotic depths. Although C translocation rates from symbionts to host could not be estimated in this study, the higher C content (per mg AFDW) of Symbiodiniaceae compared to the host tissue in both *Leptoseris* or *Sinularia* further suggests a higher retention of C in symbionts for their own needs, and a limited nutritional mutualism in mesophotic symbioses. Mesophotic corals should therefore rely more on heterotrophy than autotrophy, as previously suggested using stable isotope analyses (Ezzat et al. 2017; Kahng et al. 2019; Martinez et al. 2020). Considering the total DIC assimilation rates in host tissue and symbionts over the 8-h incubation, the C content per mg AFDW, as well as 3–6 mg AFDW per cm^{-2} of skeleton, *Leptoseris* species will need between 75 and 150 d to build tissue over 1 cm^2 skeleton if only autotrophy is considered. For comparison, shallow stony corals such as *S. pistillata* can cover 1-cm^2 skeleton with tissue in 3–5 d (considering the carbon assimilation rates of Table 2, 8 h of assimilation and the carbon content in Grover et al. 2002).

As for carbon, DIN assimilation rates by Symbiodiniaceae were several orders of magnitude lower in *Leptoseris* (0.05–

Table 2. Rates of net (Pn) and gross (Pg) photosynthesis, respiration (R), dissolved inorganic carbon (DIC), and nitrogen (DIN) assimilation in *Leptoseris glabra* and *Leptoseris fragilis* normalized to skeletal surface area.

Parameter	*L. fragilis*	*L. glabra*
($\mu g\ O_2\ cm^{-2}\ h^{-1}$)		
Pn	8.089 ± 0.032	7.799 ±0.001
R	−5.343 ± 0.010	−6.054 ± 0.010
Pg	13.432 ± 0.031	13.853 ± 0.011
($ng\ C\ cm^{-2}\ h^{-1}$)		
DIC assimilation in host	0.640 ± 0.221	0.376 ± 0.184
DIC assimilation in symbionts	2.368 ± 1.375	1.674 ± 0.322
($ng\ N\ cm^{-2}\ h^{-1}$)		
DIN assimilation in host	0.096 ± 0.015	0.0457 ± 0.015
DIN assimilation in symbionts	0.036 ± 0.024	0.0140 ± 0.005

0.13 ng N h^{-1} cm^{-2}) than in shallow or upper mesophotic stony corals (between 900 and 100 ng N h^{-1} cm^{-2}, at similar DIN concentrations in seawater, Grover et al. 2002; Tanaka et al. 2015; Ezzat et al. 2017). A similar conclusion can be drawn for *Sinularia* species, with assimilation rates at least 10 times lower than shallow corals (Pupier et al. 2021). As for carbon, the lower DIN assimilation rates at mesophotic depth can be due to the Symbiodiniaceae species associated to mesophotic corals, to lower symbiont densities, or to a light limitation of symbiont activity, since DIN assimilation is linked to photosynthesis in corals (Grover et al. 2002). As a consequence, and despite retaining most of the acquired nitrogen, symbionts of mesophotic *Sinularia* and *Leptoseris* were nitrogen limited, with a higher C : N ratio (8–10) than the one of most other coral symbionts (C : N = 4–5, Blanckaert et al. 2020). In addition, almost no translocation of nitrogen was recorded in *Sinularia* species (2–5%) against more than 50% in *Leptoseris* species. *Sinularia* host tissues therefore appear to be seriously nitrogen limited, as highlighted by the four times higher C : N ratios compared to the tissue of

Table 3. Examples of gross photosynthesis (μmol O_2 cm^{-2} h^{-1}) and dissolved inorganic carbon (DIC) assimilation rates (μmol C cm^{-2} h^{-1}) in shallow and mesophotic scleractinian coral species.

Species	Photosynthesis	DIC assimilation	Reference
Shallow corals			
Stylophora pistillata	0.7–1.5	0.9–1.0	Hall et al. (2018); Krueger et al. (2017); Ezzat et al. (2017)
Porites astreoides	1.7		Tansik et al. (2017)
Siderastrea radians	1.2		Tansik et al. (2017)
Orbicella faveolata	0.7		Tansik et al. (2017)
Porites cylindrica	0.7–3		Jurriaans and Hoogenboom (2019)
Acropora spp	1.2		Jurriaans and Hoogenboom (2019)
Pachyseris speciosa	1.1		Cooper et al. (2011)
Seriatopora hystrix	0.6–0.8		Cooper et al. (2011)
Upper mesophotic (30–50 m)			
Stylophora pistillata		0.1–0.2	Ezzat et al. (2017)
Pachyseris speciosa	0.3		Cooper et al. (2011)
Seriatopora hystrix	0.2–0.4		Cooper et al. (2011)
Lower mesophotic (> 60 m)			
Leptoseris glabra	0.4	0.15×10^{-3}	This study
Leptoseris fragilis	0.1–0.4	$0.17–0.35 \times 10^{-3}$	Schlichter and Fricke (1991); This study
Montastrea cavernosa	0.5		Lesser et al. (2010)

Table 4. Examples of gross photosynthesis (μmol O_2 g^{-1} AFDW h^{-1}) and dissolved inorganic carbon (DIC) assimilation rates (μmol C g^{-1} AFDW h^{-1}) in shallow and mesophotic octocoral species.

Species	Photosynthesis	DIC assimilation	Reference
Shallow corals			
Lithophyton sp		65–80	Pupier et al. (2019)
Sarcophyton sp		42–62	Pupier et al. (2019)
Plexaurella nutans		30–200	Rossi et al. (2020)
Pterogorgia anceps		50–250	Rossi et al. (2020)
Different gorgonian species	28–300		Rossi et al. (2018)
Different soft corals	30–90		Fabricius and Klumpp (1995)
Upper mesophotic (< 60 m)			
Lithophyton sp.		65–80	Pupier et al. (2019)
Sarcophyton sp.		42–62	Pupier et al. (2019)
Lower mesophotic (> 60 m)			
Several species of *Sinularia*	0.1–0.3	4	This study

Leptoseris and other corals (Blanckaert et al. 2020). The difference in C : N ratios between *Leptoseris* and *Sinularia* host tissue can be explained not only by different DIN assimilation rates, but also by a different heterotrophic capacity, which however needs to be further investigated. In deep waters, plankton abundance is reduced compared to the first 30 m depth (Schmidt 1973; Radopor 1983; Farstey et al. 2002) and organic matter is rather in the form of detrital material available to corals (Torfstein et al. 2020). Therefore, the flat shape of *Leptoseris* species, and their position facing upward, perfect to collect sinking particles, can enhance the heterotrophic acquisition of food, compared to the finger shape of *Sinularia* species. In addition, the heterotrophic feeding of *Leptoseris* species can be enhanced through its capacity to take up sedimented organic material through pores and gastrovascular canals (Schlichter 1991). Experimental studies comparing the grazing rates of *Leptoseris* and *Sinularia* species on zooplankton and detrital organic matter are needed to confirm such hypothesis. Overall, high C : N ratios in host and symbionts of mesophotic *Sinularia* species further suggest that soft corals living in mesophotic reefs are unable to acquire sufficient nitrogen, either through autotrophy or heterotrophy, which can also explain their very low abundance at mesophotic depths.

Our study demonstrates that symbionts of both stony and soft corals thriving in mid to lower mesophotic reefs have limited autotrophic capacities. The results suggest that heterotrophy is likely a main nutrient source for mesophotic corals, but further studies are needed to specify the main available nutrient sources at such depths. In addition, the nitrogen limitation of soft corals at mesophotic depth suggests that nutrient acquisition via autotrophy or heterotrophy is reduced at such depth. Symbiotic soft corals in the Gulf of Eilat seem to have a distinct optimal depth range and their lack of nutritional capacity might limit their abundance beyond this range. Overall, mid and lower mesophotic reefs of the Red Sea can thus be considered rather marginal reefs than refugia for shallow symbiotic species.

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Conflict of Interest

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