



Juvenile octocorals acquire similar algal symbiont assemblages across depths

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Abstract Establishment of the coral–algal symbiosis begins during early ontogeny when juveniles acquire a mix of algae from their environment that often differs from the adults’ algal assemblages. Despite the importance of the type of Symbiodiniaceae to this symbiosis, it is largely unknown how coral host identity and environment affect symbiosis establishment and is affected by the genetic composition of the symbionts. Here, we reciprocally transplanted planulae of the octocoral *Rhytisma fulvum* (Forskål, 1775) across depths and monitored the algal assemblages in the developing juveniles for 11 months. We then compared these to adult assemblages using ITS2 metabarcoding. Juveniles were consistently dominated by *Symbiodinium*, in addition to multiple *Cladocopium* species, which shifted in dominance with the juvenile age but maintained high similarity across depths. The type of Symbiodiniaceae environmentally available thus likely contributes to the algal symbionts that are initially acquired, while host identity may play a significant role in selecting for symbionts that are maintained during juvenile development.

Keywords Coral-algal symbiosis · Development · *Rhytisma fulvum* · Mesophotic coral ecosystems · Symbiodiniaceae · Red Sea

Introduction

Octocorals are highly abundant on many reef ecosystems, providing essential habitat and nutrition services to a variety of reef dwellers, as well as filtering nutrients and maintaining water quality (Fabricius 2005; Fabricius and Klumpp 1995). Most shallow Indo-Pacific octocorals establish mutualistic endosymbioses with intracellular photosynthetic dinoflagellates of the family Symbiodiniaceae (Fabricius and Klumpp 1995; LaJeunesse et al. 2018; Goulet et al. 2008). Previous studies have shown that genetically different Symbiodiniaceae assemblages can lead to distinct responses of their hosts under diverse environmental conditions (DeSalvo et al. 2010; Sampayo et al. 2008). In most coral species, the algal symbionts must be acquired anew from the environment each generation (i.e., horizontal transmission: Baird et al. 2009). This implies a potential for environmental adaptation by means of flexibility in algal symbiont uptake, even though the high genetic diversity of algal communities during the initial acquisition stage is eventually winnowed in favor of relatively stable and less diverse assemblages in adult corals (Abrego et al. 2009; Poland and Coffroth 2017). Examining the effects of prevailing environmental conditions on the symbiont acquisition process and their winnowing during the highly dynamic stage of juvenile development is critical to our understanding of the possible effects of external cues on this symbiosis and its trajectory under climate change (Coffroth et al. 2022; Cumbo et al. 2013; Poland and Coffroth 2017; Quigley et al. 2017).

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Mesophotic coral ecosystems (MCEs, 30–150 m depth) extend the shallow-water coral reefs down to the lower edge of the photic zone (Hinderstein et al. 2010). MCEs are subjected to light attenuation, thus affecting coral community structure and reliance on photoautotrophic carbon production (Kahng et al. 2019). While most coral species have a limited vertical distribution, some species are able to thrive across a wide depth range (i.e., “depth-generalists”: Bongaerts et al. 2015). Certain coral species may host different Symbiodiniaceae assemblages across depth that is considered to be more acclimatized to the deeper water environment (Andras et al. 2011; Bongaerts et al. 2015; Cooper et al. 2011; Kirk et al. 2009; Pochon et al. 2015; Prada et al. 2014), whereas others maintain similar algal assemblages across depth (Ziegler et al. 2015; Liberman et al. 2022a, b). In contrast with studies on symbiont assemblages in adult colonies, there are very few studies on algal symbiont acquisition and identity in MCE juvenile corals.

The octocoral *Rhytisma fulvum* (Forskål, 1775) is a surface-brooder that releases azooxanthellate planula larvae whose algal symbionts are acquired during early metamorphosis (Benayahu and Loya 1983). In the Gulf of Aqaba (GoA), *R. fulvum* hosts similar *Cladocopium* sp. symbionts across its entire depth of occurrence (0–50 m: Liberman et al. 2022a, b). The previous studies have shown the critical role of the environment in shaping octocoral-Symbiodiniaceae associations during early life stages of the host (Abrego et al. 2012; Coffroth et al. 2001; McIlroy et al. 2019). However, other findings on scleractinians have revealed that host genetics may have a role in determining symbiont associations (McIlroy and Coffroth 2017; Quigley et al. 2017; Yamashita et al. 2014). Despite rather extensive research on symbiont acquisition across spatial scales, comparisons across depth ranges, such as between shallow reefs and MCEs, are lacking. To address this gap, we examined the symbiont associations in *R. fulvum* juveniles from shallow waters to MCEs in the GoA. We addressed the question of whether depth affects the identity of algal symbionts present in the juveniles over time. We further assessed whether depth affects the winnowing process during the 1st year of the juveniles’ development. The findings from examining symbiont dynamics from shallow to mesophotic depths are expected to provide an ecological context concerning the role played by the host and its environment during early establishment of the octocoral–algal partnership across depth gradients.

Materials and methods

Study site and sampling

Collection of *R. fulvum* planulae took place at the reef across from the Interuniversity Institute for Marine Sciences (IUI)

in Eilat (Israel), from both the shallow reef (5–10 m) and an upper mesophotic reef (40–42 m), at a short horizontal distance from one another (see Supplementary Information). Upon sampling, the planulae were cleansed of mucus by washing them in filtered seawater. They were then introduced into 50-ml transparent PVC chambers (40 planulae per chamber, 80 chambers) (see also Liberman et al., 2020). Each chamber contained two preconditioned terracotta tiles (2 × 2 cm each) and was sealed with a 100 µm mesh. The terracotta tiles had been preconditioned on the Eilat reef for 7–8 months at the shallow (8 m) and the upper mesophotic (40 m) depth prior to the experiment (November 2018). The tiles were then placed into the chambers according to their preconditioning history (i.e., shallow-conditioned tiles in all chambers deployed in shallow and MCE-conditioned tiles in all chambers deployed in MCE). The chambers were transferred to the reef and placed on artificial structures at both shallow (8 m) and upper MCE (40 m) locations (20 chambers from each sampling depth at each depth). The planulae successfully settled on the tiles, metamorphosed into primary polyps, and subsequently developed into juvenile colonies (hereafter “juveniles”) that were later retrieved at five time points: 1 week and 2, 5, 7, and 11 months after placement on the reef, in order to determine any changes in Symbiodiniaceae identity as the coral development progressed. To ensure sufficient DNA quantities from *R. fulvum* juveniles, samples comprised of primary polyps with 1–4 polyps were pooled together into individual samples (between 2 and 8 juveniles per sample), while larger juveniles, comprised of more than 4 polyps, were sampled individually (see Table S1).

ITS2- and psbA-based algal symbiont typing

DNA isolation was performed on a total of 49 samples using the Qiagen DNeasy Blood and Tissue kit, with minor adjustments. Briefly, the ethanol used to preserve the samples was removed, and the samples were left to air-dry to remove any residual ethanol. Following this, 180 µl of ATL buffer was added, and each sample was ground with a pestle to rupture the algal cells. Next, 20 µl of proteinase K was added, and the samples were incubated at 56 °C for 1.5 h. DNA extractions were then performed according to the manufacturer’s instructions, with a final elution volume of 40 µl in molecular-grade water. DNA concentrations were quantified by Qubit (Invitrogen). Amplification of the ITS2 region was done using the primers SYM_VAR_5.8S2 and SYM_VAR_REV, according to Hume et al. (2018), with unique 8-mer barcodes at their 5’ ends. To confirm successful amplification, 1 µl of each PCR product was run on a 1% agarose gel. Samples were cleaned using ExoProStar (GE Healthcare) and normalized using the SequalPrep Normalization Plate Kit (Thermo Fisher Scientific). Samples were paired-end

sequenced (2 × 250 bp) on the NovaSeq 6000 platform at the Novogene Sequencing Centre (Cambridge, England).

Samples were further analyzed by amplifying the non-coding region of the plastid *psbA* minicircle, following Lajeunesse and Thornhill (2011). To accommodate for samples comprising more than one algal symbiont community, PCR products were run on a 2% TBE gel for 2 h. Samples comprising more than one band were then extracted directly from the gel (QIAquick Gel Extraction Kit). For samples featuring a single band, the DNA was sequenced directly from the PCR product. Samples were Sanger-sequenced at Eurofins Genomics with internal primer, following Hume et al. (2015).

Data analysis

Demultiplexed ITS2 paired reads from each sample were analyzed using the SymPortal framework (Hume et al. 2019). The prediction of Symbiodiniaceae ITS2 profiles (putative symbiont genotypes) was based on the presence and abundance of the ITS2 sequences within the SymPortal database. Additionally, we merged ITS2 profiles by using a clustering approach to consider highly similar profiles as the same distinct entity. For example, all profiles featuring A1-A1bw-A1bf were clustered into “A1-A1bw-A1bf,” while other profiles from this genus were named “Other *Symbiodinium*.”

To resolve cases in which more than a single Symbiodiniaceae genus was present in an individual coral sample, *psbA* marker sequences were used (Davies et al. 2023). Sequence chromatograms for the *psbA* region were visually inspected for accuracy in base calling using Geneious, and the edited sequences were aligned together with sequences from Hume et al. (2015) and Lajeunesse and Thornhill (2011). Phylogenetic relationships were reconstructed under the maximum-likelihood (ML) criterion, as implemented in the program IQ-TREE version 2.1.3 (Nguyen et al. 2015).

Results and discussion

To assess algal symbiosis establishment and their assemblage dynamics, also in relation to the host environment, *R. fulvum* planulae were removed from their shallow-water and mesophotic environments and reciprocally transplanted into each other’s collection depth (Fig. 1). Overall, the algal symbiont profiles observed across the first 11 months of development in *R. fulvum* juveniles differed across time, but remained similar across depth, although some exceptions did occur (Fig. 1).

Three profiles corresponding to *Cladocopium* were detected in *R. fulvum* juveniles at both transplanted depths (8 and 40 m). The clustered profile “C1-C. *thermophilum*

mix” accounted for 4–31% and 21–31% of the relative abundance in 1-week and 2-month-old juveniles, respectively (Table S2). One exception was detected in the 2-month-old juveniles that had been collected and developed in the MCE, and which mostly hosted *Cladocopium* symbionts of the clustered profile “C64a/C64b” (30% of relative abundance, Table S2). While the clustered *Cladocopium* profile “C64a/C64b” dominated the symbiont community of 5-month and 7-month-old juveniles (30–59% and 29–59% of the relative abundance, respectively), this profile was absent from juveniles that had been collected from the MCE environment and developed in the shallow transplanted environment (Fig. 1 and Table S2). Later in the experiment, the relative abundance of the clustered *Cladocopium* profile C64a/C64b in 11-month-old juveniles remained high (45% and 30% of juveniles that had been collected and transplanted in the shallow and MCE depths, respectively). In addition, the clustered *Cladocopium* profile “C1-C1dw” dominated the shallow symbiont community of 11-month-old juveniles, whereas its relative abundance in juveniles that were collected and transplanted in the MCE was considerably lower (47% and 12%, respectively). Surprisingly, the latter profile also dominated the symbiont composition of 1-week-old juveniles that had been collected from the MCE and transplanted to the shallow environment (61% of the relative abundance).

Clustered profiles corresponding to genera that had not been previously detected in adult colonies of *R. fulvum* dominated the juveniles across depth (Fig. 1). For example, *Symbiodinium* algal symbionts of the clustered profile “A1-A1bw-A1bf” were detected in all sampled juveniles. Their relative abundance remained high throughout the experiment, ranging from 30 to 74%, with the exception of two time points (9% in 1-week-old juveniles collected from the MCE and developed in shallow-water; and 5% in 11-month-old juveniles collected from shallow-water and developed in a similar (shallow) transplanted environment (Table S2)). Notably, *Symbiodinium* is commonly found in the early ontogeny of some coral recruits and has been previously shown to be one of their first colonizers, although its presence may disappear in the adult stage (Coffroth et al. 2001, 2022; Gómez-Cabrera et al., 2008; Yamashita et al. 2013). Shallow *Stylophora pistillata* adult colonies may release algal symbionts into the surrounding seawater and could potentially serve as a source of *Symbiodinium* spp. in the reef environment (Mass et al. 2007). It is also noteworthy that in the northern Red Sea, *Symbiodinium* have also been detected in vertically-transmitting octocoral species (Barneah et al. 2004; Liberman et al. 2022a, b). Moreover, other profiles of the genus *Symbiodinium* were acquired by *R. fulvum* juveniles during the first 2 months of ontogeny (Fig. 1). A low incidence of *Durudinium* algal symbionts

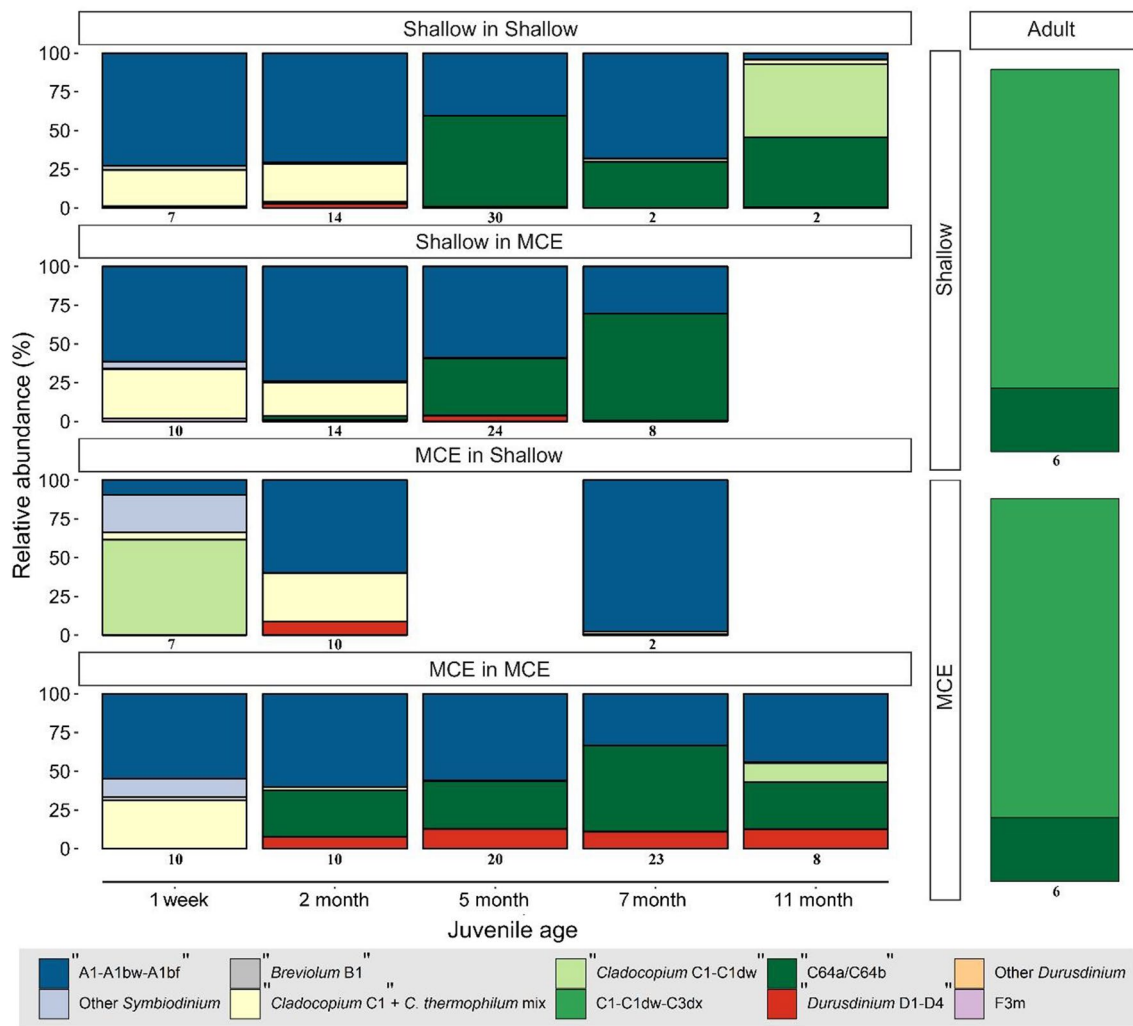


Fig. 1 Algal symbiont assemblage dynamics in octocorals collected from shallow and mesophotic reefs and transplanted to reciprocal depths. Normalized relative abundance of ITS2-type profiles in *Rhytisma fulvum* juveniles and adult colonies in shallow and meso-

photoc depth environments. The different squares represent different parental and transplanted depth environments. N indicates the total number of primary polyps, juveniles, and colonies sampled and analyzed at each time point at a given depth

of the clustered profile “D1–D4” (1–12%) was occasionally detected in juveniles of *R. fulvum* from week 1 to month 11.

A considerable number of studies have assessed the effect of light intensity and symbiont availability on symbiont composition in horizontally-transmitting corals at the planula and juvenile stages (Coffroth et al. 2022; Cumbo et al. 2013; Howells et al. 2013; Quigley et al. 2017). Although it is commonly assumed that a well-lit environment significantly affects algal symbiont assemblages (Rowan et al. 1997; Rowan and Knowlton 1995), our findings may suggest that light environment (depth) had only a minor effect on the symbiont composition in juveniles of *R. fulvum*. It has also been posited that it is not fully clear whether Symbiodiniaceae associations during larval stages already represent mutualistic interactions, which would further explain the here-observed pattern (Mies et al. 2017). In addition, the

previous studies have suggested that if the symbionts in the environment are similar, then that pool that is likely where the similarities originate from (Andras et al. 2011; Coffroth et al. 2022). By preconditioning the settlement tiles used here at similar depths to those of the transplanted depths, we sought to simulate the symbiont composition that is found at the respective environmental depth. Thus, the observed similarity in symbiont composition between most juveniles at the early time points across depth (Fig. 1) may be a reflection of comparable Symbiodiniaceae populations in their adjacent environment (i.e., on the settlement tiles or in the water). Moreover, the similarity of algal compositions across depth at the later stages of some juveniles is likely due to host selection during the winnowing process. However, in the future studies, juveniles would need to be followed for a longer time period to unequivocally confirm this. Further

studies elucidating the relative effect of environmental symbiont availability and selection by host identity may provide insights into the intriguing question of how these drivers interact to shape host-symbiont early life stage associations from shallow to mesophotic depths.

Our current findings indicate that 5- and 7-month-old juveniles were dominated by algal symbionts (C64a/C64b) that are rarely found in adult colonies and were absent from most of the juveniles sampled at earlier time points. In addition to this profile, 11-month-old juveniles were also found to harbor two distinct *Cladocopium* profiles; C64a/C64b and an additional profile not found in adults (“C1-C1dw”; Figs. 2 and 3). Thus, the findings indicate a marked disparity between the composition of *Cladocopium* algal symbionts in *R. fulvum* juveniles at various ages and those found in the respective adult colonies, which is likely a combination of the locally predominant algal symbiont pool and symbiont competition. Such disparity challenges the prediction of identity of algal symbionts by means of exclusively identifying those of adult colonies or those of juveniles from a single time point in their 1st year of development.

Little is known regarding the duration of the winnowing process in corals, in particular with regard to the time required for juveniles to establish a stable-state symbiosis with those complementary symbionts that are eventually present in the adult colonies. The previous studies have indicated that such a process in juvenile corals can be extensive and may differ among species (3–4 yrs.: Abrego et al. 2009; Poland and Coffroth 2017). The current results indicate that, at 11 months, *R. fulvum* juveniles still host a different *Cladocopium* algal community from that found in adult colonies, while also hosting *Symbiodinium* and *Durusdinium* D1–D4 symbionts. These findings are in line with the previous studies (Gómez-Cabrera et al., 2008), also reinforcing the notion that the duration of the winnowing process in *R. fulvum* juveniles is extensive. Thus, it is likely that the period of our experiment was not sufficiently long to capture the entire winnowing process until host adulthood.

Using both data from the ITS2 marker and the psbA non-coding region, the current results indicate an unexpected presence of *C. thermophilum* in 1-week and 2-month old juveniles (Figs. 1 and 3). This is the first

Fig. 2 Principal coordinate analysis (PCoA) based on Bray–Curtis distances of ITS2-type profiles. The PCoA shows the grouping of *Rhytisma fulvum* juveniles/adults based on associated algal symbiont ITS2 sequences for the three most dominant genera throughout the study: **A** *Cladocopium*, **B** *Symbiodinium*, and **C** *Durusdinium*. Color indicates juvenile age at the time of collection, and shape indicates their transplanted depth. The percentage variation explained by each PC1 and PC2 is indicated

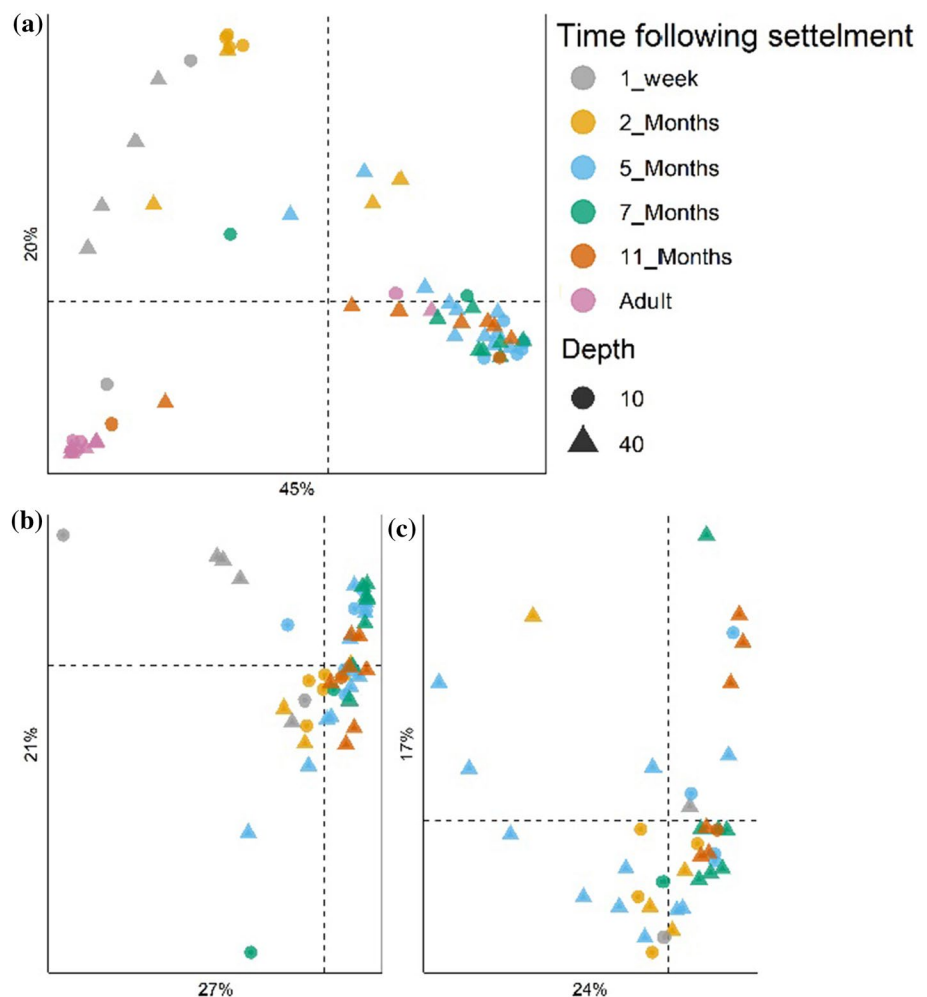
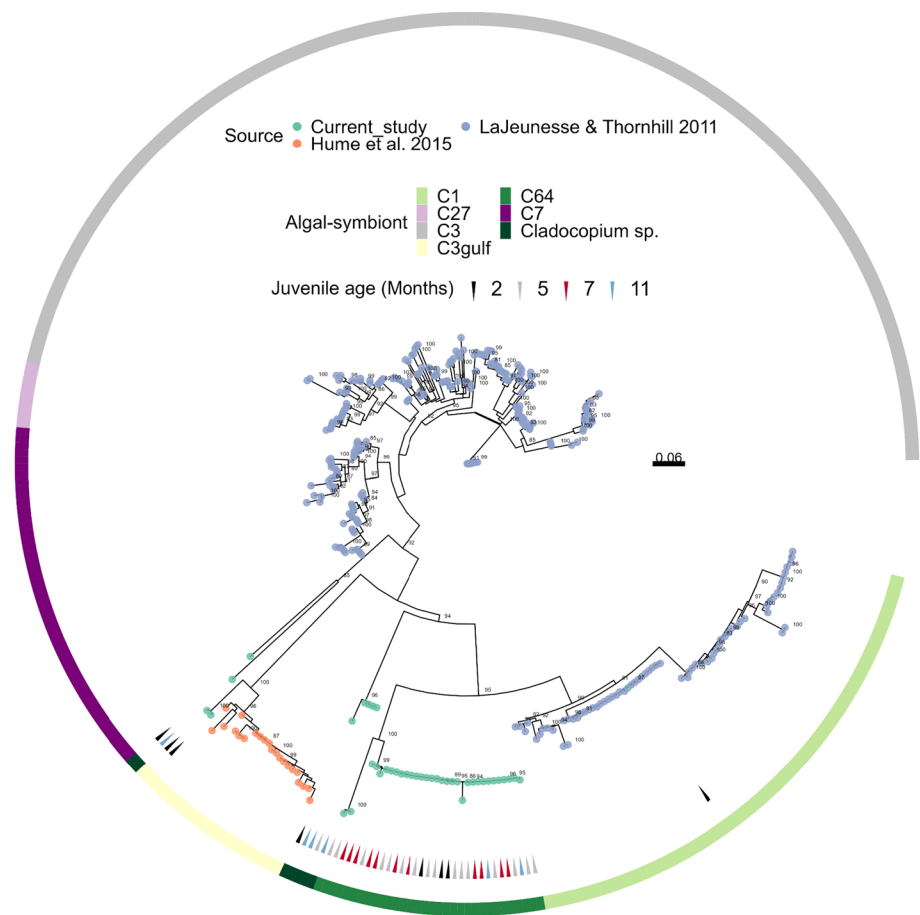


Fig. 3 Phylogenetic tree of the genus *Cladocopium* based on psbA non-coding region sequences from Indo-Pacific anthozoans. The maximum-likelihood tree was reconstructed using IQ-TREE. ML bootstrap support of over 80% (based on 1000 replicates) is indicated on the nodes



evidence of this thermally-tolerant algal species in the GoA, confirming that it has a wider geographic distribution than previously described (Hume et al. 2016). In addition, it is the first observation of the heat-stress-tolerant *D. trenchii* (Silverstein et al. 2014; Stat and Gates 2010), in the very northern tip of GoA, although it has been previously recorded in the Arabian Peninsula (Hume et al. 2016; Osman et al. 2020; Ziegler et al. 2017). Accelerated warming in the northern Red Sea, compared to global averages (Chaidez et al. 2017; Fine et al. 2013), coupled with the Symbiodiniaceae potential for rapid, long-distance dispersal (LaJeunesse et al. 2014), may facilitate the establishment of these heat stress-tolerant symbiont species in the GoA reef environment. By sampling the octocoral juveniles, however, we uncovered the regional Symbiodiniaceae diversity, including the presence of cryptic and previously overlooked taxa. To verify whether these findings represent a true range expansion of the different symbionts, further analyses of both juveniles and adults across their host species are required. As ocean warming accelerates globally (IPCC 2021), insights into the flexibility of coral juveniles to acquire and maintain diverse photosymbionts, including potential stress-tolerant taxa,

are critical for predicting and mitigating climate change impacts.

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Data availability The Illumina sequences of the ITS2 marker are available under NCBI BioProject PRJNA953952 (<https://www.ncbi.nlm.nih.gov/bioproject/PRJNA953952>). SymPortal ITS2 abundance files and scripts used in this work can be found on GitHub (<https://github.com/ronenliberman/Symbiodiniaceae-in-juvenile-octocoral>).

Declarations

Conflict of interest The authors declare that they have no financial or personal interests that may have influenced the research work or its outcome. They have no conflict of interest to disclose and have pro-

vided an unbiased analysis and interpretation of the data presented in this study.

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