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SHORT COMMUNICATIONS

Symbiont-coral relationship in the main reef building scleractinians of the Central Mexican Pacific

Violeta Martínez-Castillo[1] · Alma Paola Rodríguez-Troncoso [1] · Eric Bautista-Guerrero[1] · Amílcar Leví Cupul-Magaña[1]

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Abstract

Hermatypic corals maintain obligate symbiosis with symbiodiniacean dinoflagellates, forming either general or specific relationships with these microalgae. The differences in these associations can be attributed to local environmental conditions: different symbiont species are adapted to different ranges of environmental conditions, which directly influences the vitality of the mutualism in different environments. We identified the Symbiodiniaceae present in deep and shallow corals from the two most abundant reef-building coral genera in the Northeastern Tropical Pacific using two molecular markers, the complete ITS region and the chloroplast 23 S region. The molecular identification showed that *Pocillopora* corals harbor a symbiont belonging to the genus *Durusdinium*, while *Pavona* corals harbor *Cladocopium* sp. symbionts. No differences between deep and shallow coral colonies were observed, suggesting a stable association between coral and symbiont across the environmental gradient sampled. These unique associations appear to be thriving a region considered marginal for coral development and it appears that both kinds of symbionts endure a wide range of environmental conditions.

Keywords *Cladocopium* · *Durusdinium* · Endosymbiont · Microalgae · Northeastern Tropical Pacific · Symbiodiniaceae

1 Introduction

Stony corals are marine invertebrates that distribute globally from shallow waters to thousands of meters below the sea surface (Sheppard et al. 2009). Sallow water Scleractinian corals have an obligate symbiosis with photosynthetic dinoflagellates (microalgae) in the family Symbiodiniaceae (formerly known as the genus *Symbiodinium*; LaJeunesse et al. 2018). The coral-dinoflagellate relationship is essential as corals receive most of their metabolic daily requirements from their dinoflagellate symbionts as photosynthates (mainly carbohydrates; Morris et al. 2019) and in turn, the coral provides their symbionts with nitrogen metabolic wastes and respiratory CO_2 that the microalgae metabolize during their photosynthetic activity (Baker 2011). Stony corals depend on the photosynthesis of their symbiotic dinoflagellates to obtain nutrients used for growth and reproduction, which are energetically costly physiological processes; hence, they are restricted to the euphotic zone and are more abundant in shallow tropical waters (Sheppard et al. 2009) with high transparency and low nutrients across the globe (Venn et al. 2007; LaJeunesse et al. 2018).

Among the recently designated Symbiodiniaceae family, at least five of the current eleven valid genera are associated with stony corals: *Symbiodinium*, *Breviolum*, *Cladocopium*, *Durusdinium* and *Philozoon* (LaJeunesse et al. 2018, 2021; Nitschke et al. 2020; Pochon and LaJeunesse 2021), and species in each genus have different adaptations to light, depth, temperature, and nutrient ranges (LaJeneusse et al. 2004; Pochon et al. 2006; LaJeneusse et al. 2018; Goulet et al. 2019; LaJeunesse et al. 2021). Therefore, different types of symbionts present different optimal environmental conditions for their growth and maintenance. For example, some *Symbiodinium* dinoflagellates are more common in waters with high irradiancies, there are *Breviolum* species that can be found in high latitudes and at variable depths and light

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✉ Alma Paola Rodríguez-Troncoso
pao.rodriguezt@gmail.com

[1] Laboratorio de Ecología Marina, Centro Universitario de la Costa, Universidad de Guadalajara, Av. Universidad #203, Delegación Ixtapa, Puerto Vallarta, C.P. 48280 Jalisco, México

conditions, (Wham et al. 2017; LaJeunesse et al. 2018), while *Philozoon* are principally temperate species (LaJeunesse et al. 2021). Therefore, the stability of these mutualisms rely on the coral-symbiont ability to cope with annual, interannual, and seasonal environmental fluctuations (Done 2011; Lough and van Oppen 2018) and, as the ability of corals to cope with environmental changes depends on the identity of their dinoflagellate symbiont, different physiological responses to such changes are observed among coral hosts (Glynn et al. 2001; LaJeunesse et al. 2010a; McGinley et al. 2012a, b; Wall et al. 2020). Hence, the specific coral-dinoflagellate association influences coral distribution along environmental gradients while others create specific associations with one or a few host species (Baker 2011; Davies et al. 2019). These associations can be stable in different local, regional, and global scales through time (Pettay et al. 2011; McGinley et al. 2012b; Pettay and LaJeunesse 2013).

The coral communities along the Eastern Pacific have suffered historical bleaching events associated with El Niño Southern Oscillation (ENSO) events Carriquiry et al. 2001; Guzmán and Cortés 2007; LaJeunesse et al. 2007; Glynn et al. 2015; Cruz-García et al. 2020; Romero Romero-Torres et al. 2020), with a slow but constant recovery. Therefore, these communities appear highly resilient to ENSO anomalies (Rodríguez-Troncoso et al. 2016; Martínez-Castillo et al. 2022). Indeed, the community structure has shown no differences in the physiological activity of corals despite the non-optimal conditions that characterize the area (Martínez-Castillo et al. 2020), and the identity of the symbionts inhabiting these coral communities can explain the performance of corals in this marginal region (LaJeunesse et al. 2008, 2010), an important topic of research given current rates of anthropogenic climate change. Moreover, this research may further characterize coral communities in areas that may

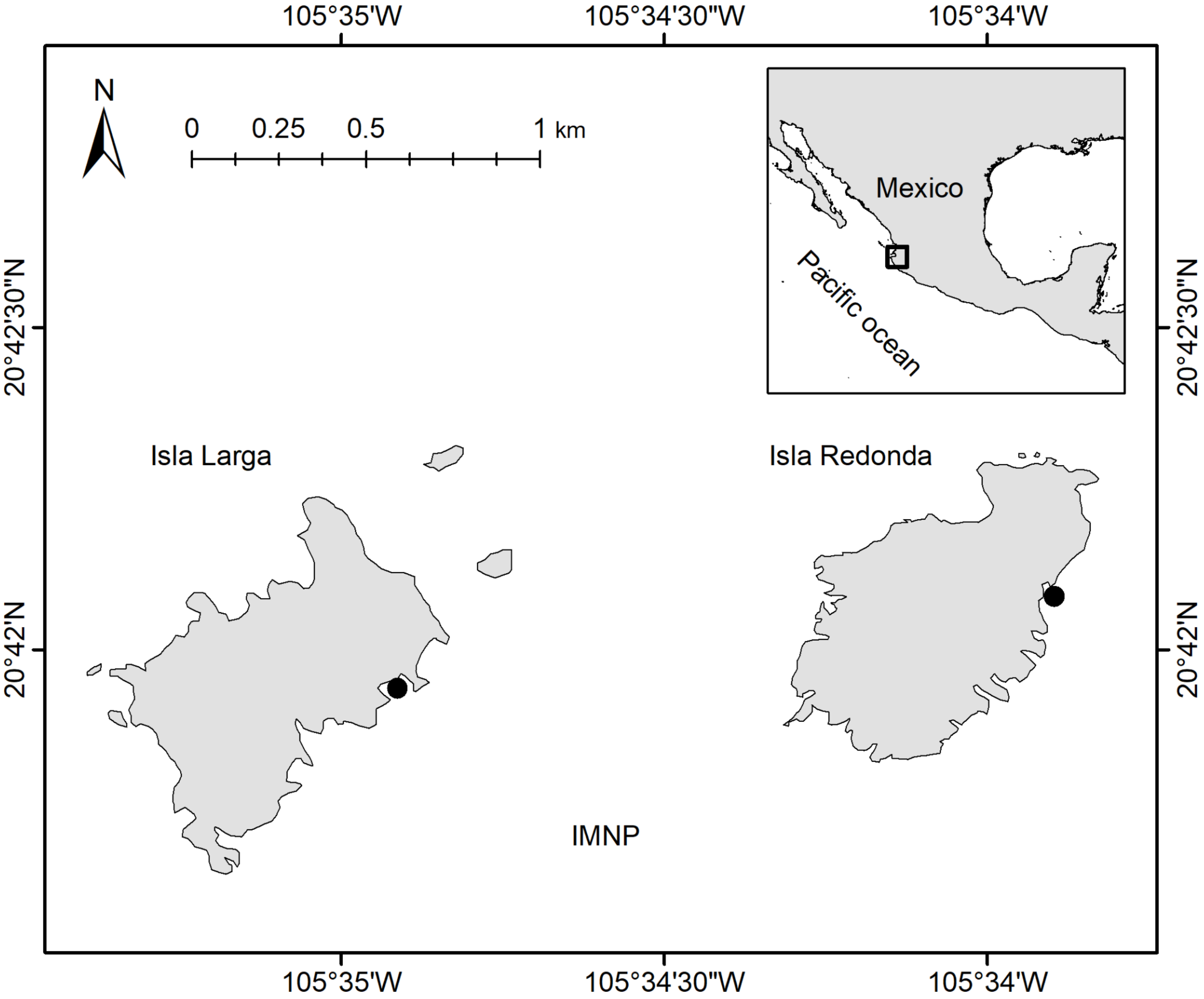

Fig. 1 Study site in the Central Mexican Pacific. Black dots mark the sampling sites at each island in the Islas Marietas National Park (IMNP)

represent future coral refugia in need of protection. In this study we evaluated.

Symniodiniaceae present in *Pavona* and *Pocillopora* (Cupul-Magaña and Rodríguez-Troncoso 2017) colonies, two of the main reef-building coral genera from the Central Mexican Pacific (CMP). We collected coral samples at two different depths in two nearby locations in a region characterized by widely fluctuating environmental conditions both at large (annual) or small (daily) time scales (e.g., annually, temperature ranges from 18 to > 25 °C, while daily fluctuations in sea surface temperature can be of 4 °C; Plata et al. 2006; Portela et al. 2016), variations associated with internal waves, seasonal upwellings, and the convergence of three water masses (Plata et al. 2006; Portela et al. 2016). Our goal is to determine if corals at different depths harbored different species of dinoflagellate symbiont and whether the identity of symbionts between *Pocillopora* and *Pavona* corals were different as was previously reported in higher latitude communities (LaJeunesse et al. 2008).

2 Materials and methods

2.1 Study area

The Central Mexican Pacific (CMP) region is a transition zone between tropical and temperate waters in the Northeastern Tropical Pacific that harbors important coral communities along the western Mexican coast (Carriquiry and Reyes-Bonilla 1997). Within the CMP, Islas Marietas National Park (IMNP) is a Marine Protected Area with two main islands (Isla Larga and Isla Redonda) and several islets located ~ 6 km off the coast (20.69 °N, 105.57 °W; CONANP 2007; Fig. 1). At Isla Larga, *Pocillopora* colonies are found within the first 7 m in a small shallow continental shelf with higher light conditions than at Isla Redonda (Cupul-Magaña et al. 2000), where *Pavona* colonies are distributed in a depth range from 6 to 16 m in a deep rocky slope where corals develop along its wall (Cupul-Magaña et al. 2000). Differences in the structure of these islands cause corals to develop at different depths and environments despite being at close sites (Cupul-Magaña and Rodríguez-Troncoso 2017), with corals developing from 1 to 20 m depth (Hernández-Zulueta et al. 2017).

2.2 Sample collection and processing

Coral sampling was performed in November 2018 (federal Mexican permit PPF/DGOPA-224/18) at two different depths using a hammer and a chisel to obtain coral fragments of 1 cm^2 from both shallow and deep coral colonies from the main reef building coral genera: *Pocillopora* and *Pavona*. From each genus 10 adult colonies were sampled at each depth ($N = 40$): at Isla Larga, 20 *Pocillopora* spp. colonies were sampled (10 at 2 m and 10 at 7 m), while at Isla Redonda 20 *Pavona gigantea* adult colonies (10 at 6 m and 10 at 15–16 m) were sampled. After sample collection, coral fragments were immediately preserved in 90% ethanol, translated to the laboratory, and stored at 4 °C until DNA extraction was performed.

2.3 DNA extraction and sequencing

In the laboratory, individual coral polyps from each fragment were removed from the coral skeleton using a needle and a surgical blade; DNA was then extracted from the polyps using a Wizard® Genomic DNA Purification kit (Promega, Madison, WI, USA) following the manufacturer's instructions. To genetically identify the symbionts present in corals, two ribosomal regions were amplified: the first comprises the entire ITS region and partial sequences from both the large and small ribosomal subunits (further referred in this manuscript as ITS), and the second comprises the ribosomal region of the chloroplast (further referred as 23S). The ITS region was amplified using primers S_DINO (5'-CGCTCCTACCGATTGAGTGA-3') and L_O (5'-GCTATCCTGAG(AG)GAAACTTCG-3') to generate fragments of ~ 1500 bp (Pochon et al. 2001); the 23 S region of the chloroplast was amplified using primers 23S4F (5'-GACGGCTGTAACTATAACGG-3') and 23S7R (5'-CCATCGTATTGAACCCAGC-3') to generate fragments of ~ 600 bp (Pochon et al. 2005). PCR mix reactions included 7.23 µl of nuclease-free H_2O, 0.75 µl of $MgCl_2$, 0.66 µl of dNTPs, 2.5 µl of 10x buffer, 0.13 µl of each primer, 0.10 µl of Taq polymerase (Promega), and 2 µl of DNA. PCRs were performed with the following program: one initial denaturation step at 94 °C for 30 s, 40 cycles comprising of 1 min at 94 °C, 30 s at 58 °C (ITS) or 54 °C (23 S), 2 min at 72 °C, and a final extension step at 72 °C for 5 min. To confirm the presence of PCR products, samples were visualized in a TAE (Tris-acetate-EDTA) 2% agarose gel. Positive PCR products were cleaned and purified using a Wizard® SV Gel and PCR Clean-Up System kit (Promega, Madison, WI, USA) following the manufacturer's protocol and sent to Macrogen, Inc. (Seoul, Korea) to obtain the symbiont sequences.

2.4 Bioninformatic analyses

The sequences were manually edited using ®Geneious v.2021.1.1. software (https://www.geneious.com) and aligned (forward and reverse) to obtain a consensus sequence of each ribosomal marker from each coral sample. To verify that the sequences belonged to the Symbiodiniaceae family, they were first analyzed in the Basic Local Alignment Search tool (BLAST) of the National Center for Biotechnology Information (https://blast.ncbi.nlm.nih.gov). The identity of the dinoflagellate symbionts present in both *Pocillopora* and *Pavona* corals from IMNP were determined by the nucleotide relationship among sequences obtained in this study and all available sequences from each gene from Symbiodiniaceae genera obtained from the GenBank database (ITS N = 38, 23 S N = 40; Benson et al. 2013). All sequences were aligned in Mega-X software using the Clustal W alignment tool (Kumar et al. 2018). ITS sequences were trimmed when conducting the alignment since available GenBank sequences are shorter than the ones obtained in this study (500–600 bp), after which maximum likelihood (ML) and Bayesian Information (BI) analyses were performed with the resulting molecular datasets. ML analyses were performed in Mega-X software (Kumar et al. 2018) with 1000 bootstraps using the Kimura 2-parameter model (*Pavona* and *Pocillopora* ITS and *Pocillopora* 23 S analyses) and the Tamura 3-parameter model (*Pavona* 23 S analysis) since they were the best-fitting nucleotide substitution models. BI analyses were performed in Mr.Bayes v.3.2.7a (Ronquist et al. 2012) with appropriate substitution models for each marker and 100 000 Markov chain Monte Carlo generations. Both ML and BI analyses were conducted using *Alexandrium tamarense* (Dinophyceae: Gonyaulacales) as the outgroup. All consensus sequences were submitted to NCBI with the following accession numbers: MZ147809-15 and MZ147852-57 for ITS complete sequences, and MZ158686-91 and MZ158693-96 for 23 S sequences.

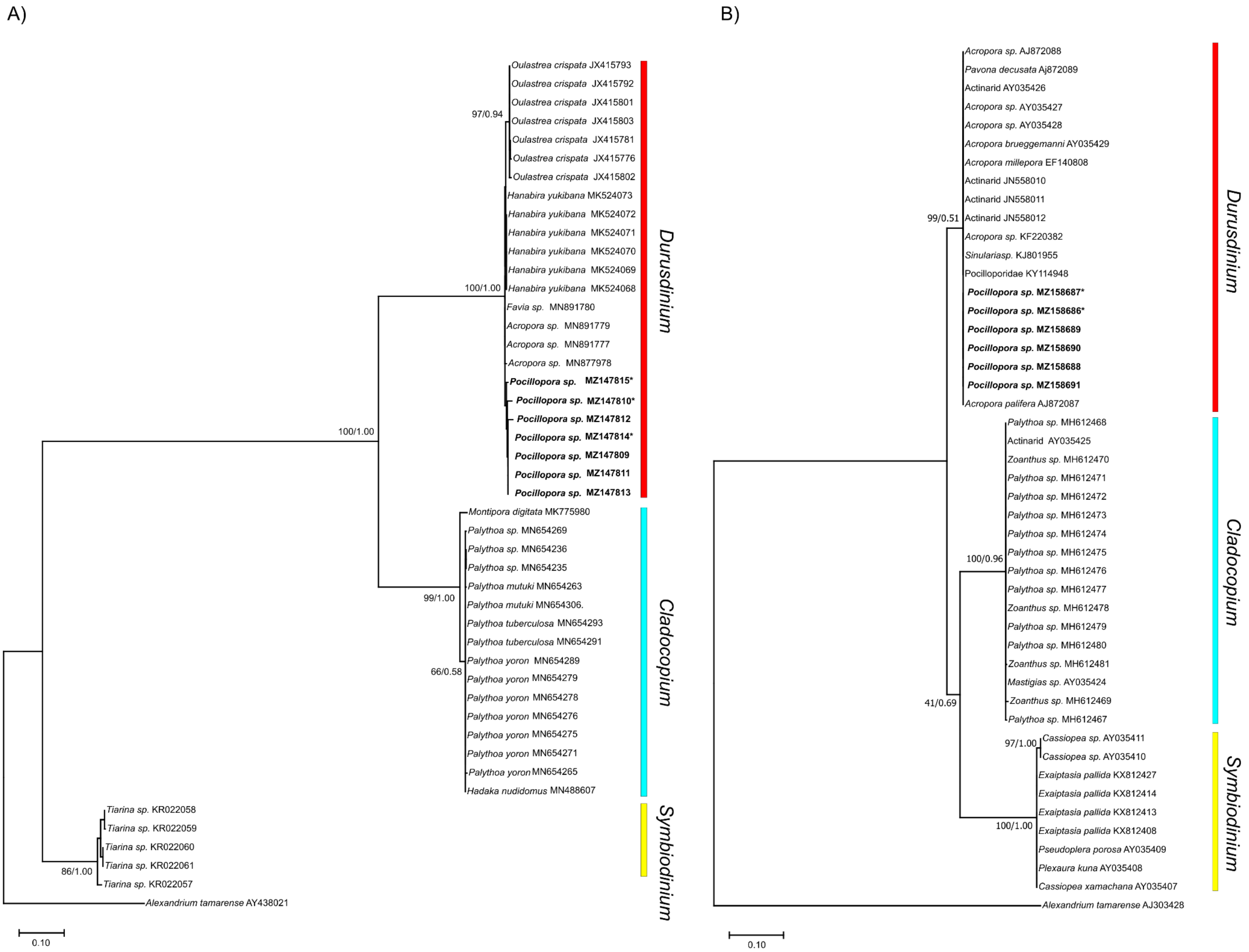

Fig. 2 Consensus trees of the Symbiodiniaceae family including available GenBank sequences and the dinoflagellates sampled from *Pocillopora* corals of the CMP (this study). (A) Consensus tree for the ITS region. (B) Consensus tree for the 23S region. The trees show the name of the dinoflagellate's host from which Symbiodiniaceae were obtained, sequences from this study are shown in bold. Sequences with a (*) were obtained from deep corals. Boostrap values and posterior probabilities are indicated in the nodes (ML/BI)

3 Results

The dinoflagellate symbionts' ITS sequences obtained in the present study from both *Pocillopora* and *Pavona* corals were 1560–1570 bp long, which include the complete ITS-1, 5.8 S, and ITS-2 regions and partial sequences from the 18 and 28 S regions; the resulting 23 S sequences were 524–525 bp long. A BLAST analyses confirmed that all sequences obtained and used in this study were similar to those of other Symbiodiniaceae organisms found not only in corals, but in other marine invertebrate hosts as well. From the 40 coral colonies sampled, good-quality ITS sequences from 7 *Pocillopora* and 6 *Pavona* samples, and 23 S sequences from 6 *Pocillopora* and 4 *Pavona* samples were retrieved and used in the MI and BI analyses along with the available GenBank sequences obtained from other Symbiodiniaceae. Alignments showed that there were 396 variable sites in all the ITS sequences analyzed, from which 347 were informative. As for the 23 S region there were 330 variable sites in the alignments built with the *Pocillopora* symbionts, from which 107 were informative; while in the *Pavona* dinoflagellate alignment, there were 358 variable sites, from which 126 were informative.

In general, three monophyletic clades in both the ML and BI analyses of the ITS and 23 S regions were formed: one comprising *Symbiodinium* dinoflagellates, a second one formed by *Cladocopium* organisms, and a third one consisting of *Durusdinium* symbionts; all clades were supported by high posterior probabilities and bootstraping (Figs. 2 and 3). In all the resulting phylogenetic trees, the *Pocillopora* dinoflagellates analyzed in this study were grouped within the genus *Durusdinium* (Fig. 2), while *Pavona* dinoflagellates were clustered within the genus *Cladocopium* (Fig. 3). For both the ITS and 23 S markers, the ML and BI topologies generated for the Symbiodiniaceae found in *Pocillopora* and *Pavona* corals agreed (Figs. 2 and 3). Finally, each genus exhibited one type of dinoflagellate regardless of the depth at which each coral colony was sampled, i.e., each coral genus exhibited only one type of endosymbiont along its depth distribution range.

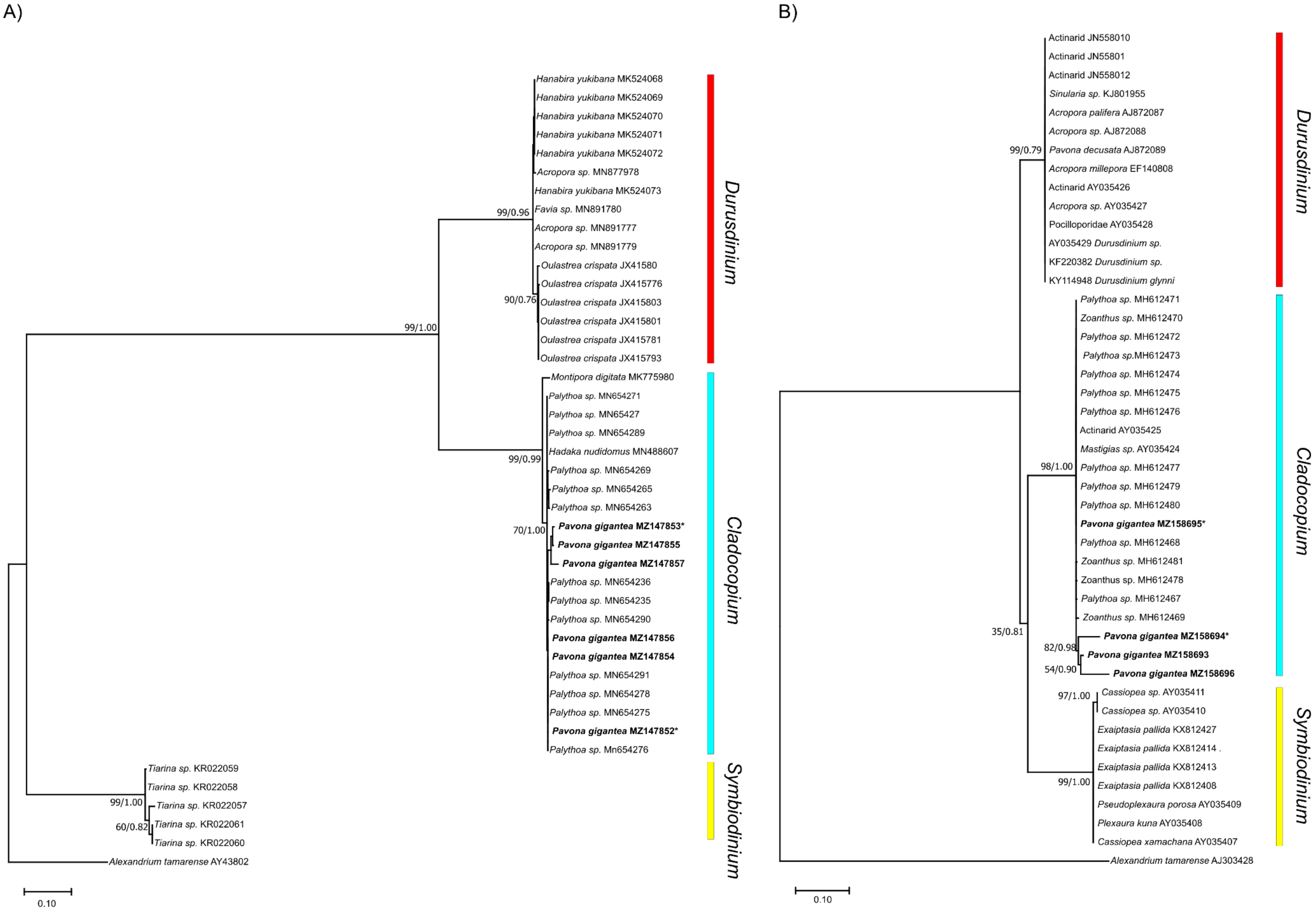

Fig. 3 Consensus trees of the Symbiodiniaceae family including available GenBank sequences and the dinoflagellates sampled from *Pavona* corals of the CMP (this study). (A) Consensus tree for the ITS region. (B) Consensus tree for the 23S region. The trees show the name of the dinoflagellate's host from which Symbiodiniaceae were obtained, sequences from this study are shown in bold. Sequences with a (*) were obtained from deep corals. Boostrap values and posterior probabilities are indicated in the nodes (ML/BI)/

4 Discussion

Coral associations with different types of symbionts change over different latitudinal, longitudinal, and environmental gradients (LaJeunesse et al. 2004, 2008, 2010b), thus, coral colonies belonging to the same species may associate with different symbionts depending on the surrounding environment, even at local scales (Wall et al. 2020). Within the Eastern Tropical Pacific (ETP), shallow coral communities (above 6 m) are dominated by corals from the genus *Pocillopora*, while in deeper coral reef zones (below 10 m) colonies of *Pavona* are common (Iglesias-Prieto et al. 2004). While there are differences in depth zonation among coral species, both occur in deep and shallow habitats, and therefore, variations in the dinoflagellate composition might be expected across this vertical distribution even in colonies belonging to the same coral species. Our results found different symbionts in each species; however, symbiont identity was homogeneous across colonies over a range of depths. *Pocillopora* colonies were symbiotic with *Durusdinium glynnii* dinoflagellates; in contrast, distinct species of *Cladocopium* populated individual colonies of *Pavona*. Therefore, specificity between species of host and symbiont is greater than the influence of environmental factors as previously observed along the Eastern Pacific (Iglesias-Prieto et al. 2004; LaJeunesse et al. 2008; Pettay and LaJeunesse 2013; Walther-Mendoza et al. 2016).

However, along the ETP, *Pocillopora* colonies are known to harbor both *Cladocopium* and *Durusdinium* dinoflagellates, and in some cases, mixtures of both (e.g., colonies distributed along the southern Gulf of California; Pettay et al. 2011). In places where both symbionts occurred, different partner combinations were not explained by external physical factors (depth, light, among others) like in the Pocilloporidae found in the Western Pacific (Sampayo et al. 2007), where differences in the symbiotic community correspond to different environmental conditions (Glynn et al. 2001; LaJeunesse et al. 2007, 2008; Sampayo et al. 2007). In the Central Mexican Pacific (CMP) as well as in the ETP, *D. glynnii* seems to be the most prevalent symbiont species in *Pocillopora* colonies and is therefore the most abundant endosymbiont in the Eastern Pacific (LaJeunesse et al. 2008, 2010; Pettay and LaJeunesse 2013). Symbionts in the genus *Durusdinium* are often associated with animals living in shallow warm, often turbid waters in environments with wide changes in temperature from season to season and from upwelling (LaJeunesse et al. 2014); it remains unknown why they can physiologically tolerate stress caused by thermal extremes and high irradiances (Baker et al. 2017; Hoadley et al. 2019). Given the environmental oceanographic conditions of the Eastern Pacific and history of severe bleaching and mortality (Cupul-Magaña et al. 2000; LaJeunesse et al. 2010a; Portela et al. 2016), it is surprising that *Pocillopora* across the region commonly has *D. glynni*.

The presence of one symbiont species servicing the needs of *Pocillopora* populations from this region may be the result of colonies with more resistant symbionts dominating the community after stress events (Iglesias-Prieto et al. 2004; LaJeunesse et al. 2010a). Previous observations in ETP coral communities show host-symbiont stability and also specificity between the coral host and its dinoflagellate taxon/taxa (Iglesias-Prieto et al. 2004; LaJeunesse et al. 2008, 2010a), even though corals in this region have been affected by severe ENSO events (Hughes et al. 2018). The association of *Pocillopora* with *Durusdinium* allows them to be highly resistant to abnormal or fluctuating temperatures and to turbid environments (Wham et al. 2017; LaJeunesse et al. 2018); therefore, the permanence, resistance, and stability to recover from stress events can be attributed to the tolerance of the symbionts to such conditions (LaJeunesse et al. 2008, 2010a; Rodríguez-Troncoso et al. 2014, 2016; Romero-Torres et al. 2020), including both warm and cold bleaching episodes (Reyes-Bonilla et al. 2002; Romero-Torres et al. 2020). Corals in this region were particularly affected by the 1997–1998 El Niño event, but 20 years later, this negative effect was not evident during the last and most severe 2015–2016 El Niño event to date. Our results add evidence to demonstrate that not only the physiological traits and acclimatization capacity of Pocilloporidae is a major characteristic thriving resilience in ETP coral communities (Rodríguez-Troncoso et al. 2014, 2016; Tortolero-Langarica et al. 2017; Martínez-Castillo et al. 2020; Romero-Torres et al. 2020), but also the identity of their symbionts.

In the *Pavona* genus, specificity is lower given that this genus can present *Symbiodinium*, *Breviolum*, *Cladocopium*, or *Durusdinium* endosymbionts along the ETP (Baker et al. 2017). In the Mexican coast, *Pavona* corals only present *Cladocopium* sp. symbionts (LaJeunesse et al. 2008; Walther-Mendoza et al. 2016; this study). Therefore, at least in the Northeastern Pacific, this particular association can be considered a stable one. *Cladocopium* species are adapted to a wide range of irradiances (LaJeneusse et al. 2018) and can inhabit warm and turbid zones (i.e., fluctuating environments; Lee et al. 2020); hence, their inherent capacity to cope with different environmental gradients may explain their specificity with Mexican Pacific *Pavona* corals, along their vertical distribution range (Iglesias-Prieto et al. 2004; LaJeunesse et al. 2008; Walther-Mendoza et al. 2016).

Coral development hence does not only depend on the host's ability to acclimatize to environmental changes, it may also primarily depend on the algae-host association that enables the holobiont to survive in a region historically considered as marginal for coral development (Glynn

2017). Moreover, the fact that we could only identify *Pavona's* symbionts up to the genus level supports *prior* investigations that highlight the relevance to the fact that this genus acquires their symbionts from the environment rather than inheriting them from the parent colony (LaJeunesse et al. 2008), explaining the diversity of *Pavona-Cladocopium* symbioses (Walter et al. 2016; Turnham et al. 2021). Further research is needed to fully clarify specific associations in *Pavona* not only in the CMP, but in the ETP as well.

Coral ecosystems from the ETP represent natural laboratories to explore holobiont stability and resilience given the environmental variation within this region at both large and micro-scales, and their capacity to withstand disturbances should be furthermore explored given the current climate change scenario and the more frequent and severe thermal anomalies caused by ENSO events (Hughes et al. 2018). Our study confirms stability in the symbiotic associations found in Northeastern Pacific corals and that these symbioses depend in the identity of the coral host and its dinoflagellate, as well as their ability to cope with fluctuating environments and their acclimatization response to stress. Instead of adjusting their symbiotic relationship during environmental disturbances (e.g., adaptive bleaching hypothesis; Buddemeier et al. 2004), corals appear to maintain a stable and resistant symbiotic association. This, along with the sub-optimal conditions for coral development previously discussed, evidence the resilience nature of coral communities in the region which highlights the necessity for their conservation, maintenance, and long-term monitoring.

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Author contributions All authors conceived and designed the research. VMC, APRT, and ALCM performed field.

Declarations

Disclosure of potential conflicts of interest: The authors have no relevant financial or non-fionancial interests to disclose.

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