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Exploring the bacterial assemblages of *Acropora cervicornis* in the Mexican Caribbean

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ABSTRACT. Coral-associated bacterial assemblages play vital roles in the nutrition, physiology, and health of hosts. Therefore, understanding this microbiota is essential to elucidate this symbiotic relationship. The present study characterized the bacterial assemblage of *Acropora cervicornis* in 2 Mexican Caribbean sites and analyzed the putative metabolic functions of the dominant bacterial genera in coral tissue, as well as the surrounding seawater and sediments. The bacterial assemblages were analyzed using next-generation sequencing from the hypervariable V4 region of 16S rRNA and compared with bioinformatic analyses. The bacterial microbiota associated with *A. cervicornis* tissue was similar between the 2 study sites but differed from the assemblages of seawater and sediment. The genera *Pseudomonas*, *Candidatus_Midichloria*, and *Acinetobater* prevailed in *A. cervicornis* tissue. *Enterobacter*, *Vibrio*, and *Synechococcus* dominated in seawater, whereas *Thioprofundum*, *Pleurocapsa*, and *Ilumatobacter* were the most abundant in sediments. Geographical distance notwithstanding, the bacterial assemblages associated with *A. cervicornis*, seawater, and sediments were similar between the sampling sites, indicating spatial stability was present. In addition, the substrates differed within each site; the genera favoring the main differences among studied substrates were *Pseudomonas*, *Synechococcus*, *Thioprofundum*, *Owenweeksia*, *Pleurocapsa*, *Candidatus_Puniceispirillum*, *Candidatus_Midichloria*, and *Rhodovibrio*. The most frequently occurring metabolic functions identified in the substrates were aerobic chemoheterotrophy, sulfur respiration, and nitrogen fixation. The present study enhances our understanding of acroporid coral-associated bacteria in the Mexican Caribbean.

Key words: coral, bacteria, *Acropora*, microbiome, 16S RNA gene.

INTRODUCTION

The coral metaorganism is an interspecific community (or holobiont) consisting of the host and associated microbiota (Rohwer et al. 2002, Voolstra and Ziegler 2020). Coral microbiota include microorganisms from the Eukarya, Bacteria, and Archaea domains, as well as viruses (Rohwer et al. 2002, Bosch and McFall-Ngai 2011). Bacteria play a vital role in coral reef functioning (Hernandez-Agreda et al. 2016, McDevitt-Irwin et al. 2017, Ostria-Hernández et al. 2022); they contribute to coral health and nutrition (Kushmaro and Kramarsky-Winter 2004, Leite et al. 2018, Epstein et al. 2019), secondary metabolite production (Sharma et al. 2019), and biogeochemical cycles (Vanwonterghem and Webster 2020). Bacteria can also perform commensal or pathogenic functions (Peixoto et al. 2017). Some members of the bacterial assemblage favor coral growth, survival, and protection against potential pathogens, increasing the resilience of the host to environmental stress (Zaneveld et al. 2016, Peixoto et al. 2017, Sweet et al. 2017, Rosado et al. 2019).

The coral-associated bacterial microbiota is dynamic, highly diverse, and abundant (Rodriguez-Lanetty et al. 2013, Shiu et al. 2017). Several factors influence the taxonomic composition and abundance of coral microbiota,

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including host specificity (Littman et al. 2009, Carlos et al. 2013), the type of niche association (surface mucopolysaccharide layer, tissue, or skeleton) (Sweet et al. 2011, Hernández-Zulueta et al. 2016), and the surrounding environmental conditions (e.g., seawater temperature, pH, and nutrient availability) (Bourne and Webster 2013, Dunphy et al. 2019). In addition, coral adaptation to environmental conditions is favored by the restructuring capacity of their associated microbiota bacterial assemblage (Reshef et al. 2006, Ainsworth et al. 2015, Bourne et al. 2016). Therefore, understanding coral-associated bacterial assemblages is essential to elucidate their role in holobiont health.

The coral *Acropora cervicornis* is one of the main shallow reef builders with bioengineering functions in the Caribbean region (Miller et al. 2002, Selwyn and Vollmer 2023) and is a critical contributor to the structure, function, and resilience of coral reefs (Lirman et al. 2014, García-Urueña and Garzón-Machado 2020). In the Caribbean Sea, a drastic decline in acroporid coral cover has been observed in the last 3 decades, which has mainly been due to the appearance of diseases of microbial origin (e.g., white-band disease and the white-pox epidemic) (Gignoux-Wolfsohn et al. 2012, Alvarez-Filip et al. 2022, Hernández-Zulueta et al. 2022). However, despite the emerging tissue loss disease of stony corals, the population structure of acroporid corals in the Caribbean has remained stable in recent years (Precht et al. 2016, Alvarez-Filip et al. 2022). Therefore, there is an urgent need to study the composition of bacterial assemblages in apparently healthy corals to elucidate the role of these microbiota in the adaptability and resistance of these holobionts and corals to stressful environmental changes.

Few studies have been conducted on the composition of the bacterial assemblages associated with *A. cervicornis*. Chu and Vollmer (2016) showed that the bacterial microbiota structure in *A. cervicornis* was influenced by seasonal variation and not by spatial variation in the coral reefs of Panama. Meanwhile, Godoy-Vitorino et al. (2017) found that the microbial assemblage of this species differed depending on the depth in which the samples were taken. Gignoux-Wolfsohn et al. (2017) also reported that the development of white band disease in *A. cervicornis* was influenced by the pre-existing healthy microbiome of the coral, which responds to the colonization of primary and secondary pathogens at different stages of disease progression. Miller et al. (2020) found that the microbial assemblages of *A. cervicornis* in ocean nurseries of the Cayman Islands varied among corals with different genotypes, showing the influence of coral population genetics on their microbiota, their relevance in nursery breeding, and their possible role in coral health, adaptability, and resilience. Recently, Klinges et al. (2023) observed high microbial diversity in disease-resistant *A. cervicornis* colonies, which contributed to their ability to resist nutrient enrichment.

These results suggest that a highly diverse microbiome favors the initial resistance of this coral. Given the importance of the bacterial microbiota in corals, this study aims to characterize the taxonomic composition of the bacterial assemblage associated with colonies of apparently healthy *A. cervicornis*, as well as the seawater and surrounding sediments in 2 sites in the Mexican Caribbean. In this work, we expected the bacterial microbiota to exhibit species-specificity among coral colonies at both sites and to differ from that of the surrounding substrates.

MATERIALS AND METHODS

Study area and fieldwork

Fieldwork was carried out in 2 reef sites in the Mexican Caribbean in the summer of 2019 (Fig. 1): Cancún Reef (21°04′07″N, 86°45′53″W) and La Poza Reef, Xcalak (18°16′27″N, 87°49′42″W). The distance between both sites is ~325 km. Three apparently healthy *A. cervicornis* fragments were collected between 3 and 6 m depth. Fragments (~7 cm) were collected from different colonies and stored within sterile plastic bags. The coral fragments were processed following the criteria of Hernández-Zulueta et al. (2016). In addition, we collected 1 L of seawater from above the coral colony and filtered it through 0.22-µm pore size Sterivex filters (Millipore, Burlington, USA). Approximately 10 g of sediment was collected below the coral colony with sterile 50-mL Falcon tubes. Three replicates were obtained for each substrate (coral, seawater, and sediment) to obtain 9 samples per site (18 in total). Samples were preserved in 99% pure anhydrous ethanol (Avantor, Radnor, USA) and stored at –20 °C for DNA extraction.

DNA extraction and sequencing

The total DNA of the coral tissue, sediment, and seawater samples (18 total) was extracted using the MagMAX™ DNA Multi-Sample Ultra kit (ThermoFisher Scientific, Waltham, USA) and a KingFisher Duo Prime System (Thermo Fisher Scientific). A Genova Nano Micro-volume Spectrophotometer (Jenway, Gransmore Green, UK), and 1% agarose gels were used to evaluate DNA quality and quantity. The triplicate DNA samples collected from each substrate across the sites were pooled, resulting in 6 samples that were processed in the MiSeq flow cell lane.

The 16S rRNA gene amplification was performed at *Laboratorio Nacional de Apoyo a Ciencias Genómicas*, *Unidad Universitaria de Secuenciación Masiva at Instituto de Biotecnología*, *Universidad Nacional Autónoma de México* (UNAM). Samples were quantified with the Qubit dsDNA HS Assay Kit (Invitrogen, Waltham, USA) before sequencing analysis. The V4 region of the 16S rRNA gene was amplified using the Illumina protocol 16S Metagenomic Sequencing Library Preparation; the degenerate oligonucleotides 16S Amplicon PCR Forward Primer (5'-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCCTACGGGNGGCWGCAG-3') and 16S Amplicon PCR Reverse Primer

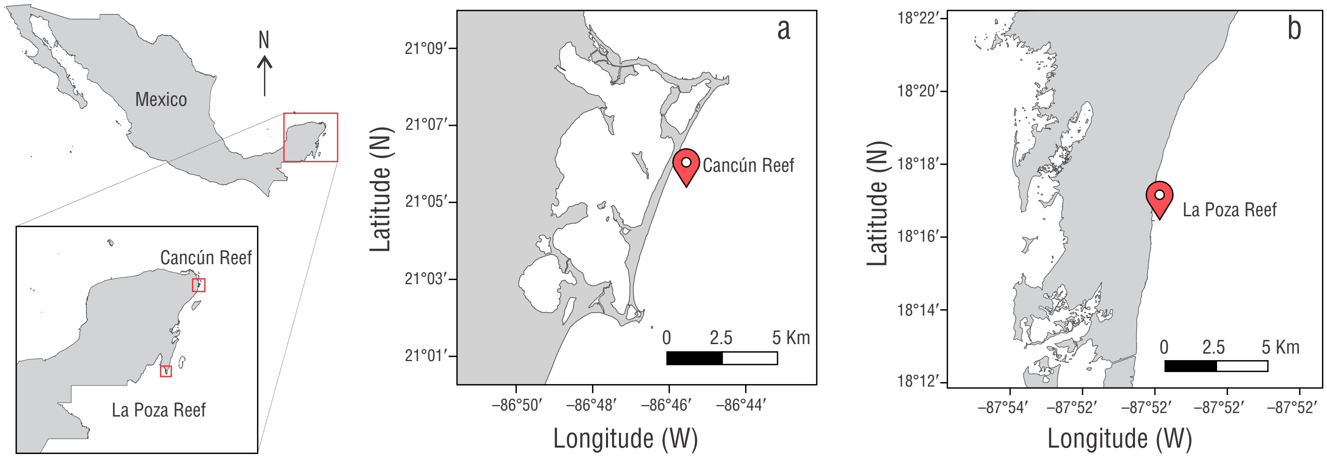

Figure 1. Study area in the Mexican Caribbean. Sampling sites: Cancún Reef in Cancún and La Poza Reef in Xcalak.

(5′-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGACTACHVGGGTATCTAATCC-3') were used to construct libraries. Sequencing was conducted in an MiSeq instrument (Illumina, San Diego, USA) with a V3 chemistry of 2 × 300 cycles. The clean reads were deposited in the Sequence Read Archive (SRA) of the National Center for Biotechnology Information (NCBI) under the accession number PRJNA749734.

Bioinformatics and statistical analyses

The assembly and reconstruction of the sequenced 16S fragment length were conducted with FLASH v. 1.2.11 (Magoc and Salzberg 2011). Operational taxonomic units (OTUs) were defined by clustering at 3% divergence (97% similarity). The taxonomic classification of the generated sequences was obtained with Parallel-META v. 2.4.1 (Su et al. 2014) and the Metaxa2 v. 2.1.1 (Bengtsson-Palme et al. 2018) database (Escobar-Zepeda et al. 2018). Subsequently, the taxonomic level tables were obtained using Perl and R scripts of *Instituto de Biotecnología*, UNAM. All methods and programs were performed following the criteria of Escobar-Zepeda et al. (2018).

The sampled-based rarefaction method assessed the sampling effort, contrasting the observed richness of the bacterial genera with expected richness, which was estimated with the Chao 1 non-parametric estimator and 10,000 permutations (Clarke and Gorley 2006, Hernández-Zulueta et al. 2022). This analysis positively impacted this study because it considered the taxonomic level of genus to be the most appropriate level of ecological analysis, which allowed it to estimate the representativeness of the observed richness of the bacterial genera despite having reduced replication due to pooled samples. In addition, rank abundance curves were built to analyze the evenness patterns of the bacterial microbiome of each studied substrate. These curves showed the dominant bacterial genera with the highest number of sequences.

Bacterial alpha diversity was analyzed for each substrate (i.e., coral tissue, seawater, and sediment), and the richness (*S*), Shannon diversity (*H*′, decits), and total abundance (*N*) that corresponded to the total number of sequences per substrate of the bacterial genera were estimated. The variation in these community metrics was evaluated with a no-replication two-way experimental design with fixed factors:

$$Y = SU_i + SI_j + \varepsilon_{ij}\,, \tag{1}$$

where Y is the community metric matrix, SU_i is the substrate factor with 3 levels (coral tissue, seawater, and sediment), SI_j is the sampling site factor with 2 levels (Cancún and Xcalak), and ε_{ij} is the accumulated error. Community attributes were assessed using this experimental design with a two-way permutational multidimensional analysis of variance (PERMANOVA) with cross-factors without replication (i.e., additive model without interaction) that was performed using normalized data (i.e., Z-values) and Euclidean distances. The PERMANOVA overall test was evaluated with 10,000 residual permutations with a reduced model and type III sum of squares. In contrast, given the low replication, a Monte-Carlo (MC) test was used to analyze the significance of the pairwise comparisons.

A principal coordinates analysis (PCO) was conducted to elucidate the relationships between alpha bacterial diversity and substrate type and sampling site. The PCO ordination was performed based on the same resemblance coefficient and data pretreatment from the first PERMANOVA. The contribution of the community attributes (*S*, *H*′, and *N*) was calculated using multiple correlations and represented as vectors.

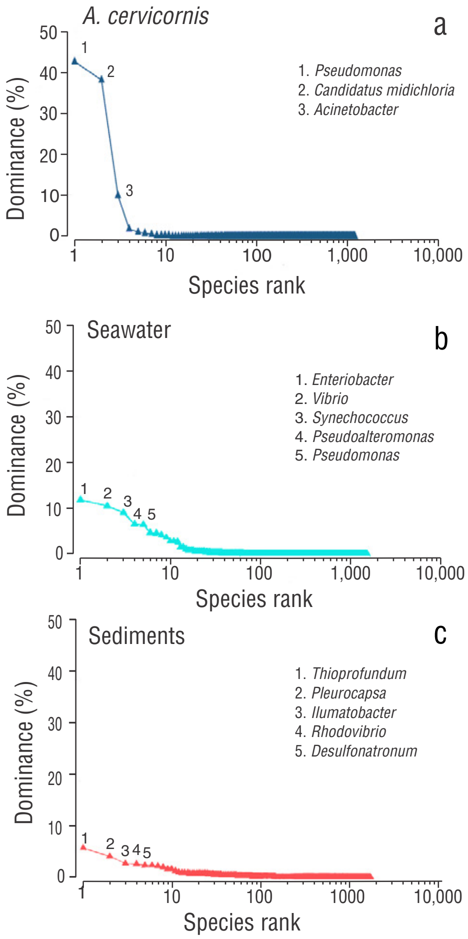

Figure 2. Rank abundance curves for the bacterial assemblages by analyzed substrate. The blue, turquoise, and coral triangles represents the bacterial genera present in *Acropora cervicornis*, seawater, and sediments, respectively.

Beta diversity (i.e., the composition and abundance of bacterial genera) was also evaluated with another two-way PERMANOVA without replication. This PERMANOVA was performed based on a Bray–Curtis similarity matrix and employed a fourth root data pretreatment and the same statistical significance procedure as the first PERMANOVA. A second PCO ordination was built to assess bacterial similarities among substrates in the same sampling site. The contribution of bacterial genera to the average dissimilarity among the studied substrates was calculated using a similarity percentage (SIMPER) analysis routine. The SIMPER results were analyzed following the proposed methodology of Cáceres et al. (2020); bacterial genera that most favored dissimilarities between substrates in terms of their frequency and contribution to the differences were identified. The PCO ordination and SIMPER routine were performed based on the resemblance coefficient, data pretreatment, and results from the second PERMANOVA. The rank abundance curves, community metrics (S, H', and N), PERMANOVA, PCO ordinations, and SIMPER routine were conducted in PRIMER v7 + PERMANOVA v. 1.01 (Anderson et al. 2008, Clarke and Gorley 2015).

Bacterial metabolic functions

The putative bacterial metabolic functions were identified from the Functional Annotation of Prokaryotic Taxa (FAPROTAX) database v. 1.2.4 (Louca et al. 2016, Louca et al. 2017), which has information on ~4,600 taxa based on data from cultured taxa and the published literature with verified functions for several taxonomic groups. This study related putative metabolic functions only for the most dominant bacterial genera by substrate (coral, sediment, and surrounding seawater) based on the SIMPER results. For this, we used a binary data matrix that recorded the metabolic function of each bacterial genera. A shade plot was built using the most dominant bacterial genera and metabolic functions. Dendrograms were constructed with Sørensen similarity and UPGMA linking to associate bacterial genera (R mode) with metabolic functions (Q mode). A similarity profile routine (SIMPROF) with 10,000 permutations was also used to identify clusters within the dendrograms.

RESULTS

Illumina sequencing yielded 3,209,260 high-quality sequences from the coral *A. cervicornis* and the surrounding seawater and sediment. These sequences corresponded to 51 phyla, 132 classes, 298 orders, 575 families, and 1,790 genera. The sample-based rarefaction results indicated an average representativity of 98.8% of the sampling effort (i.e., bacterial genera observed richness vs. expected richness [Chao 1 = 1,811.5 genera]). The most abundant families in the 3 substrates were Pseudomonadaceae, Midichloriaceae, Enterobacteriaceae, Moraxellaceae, Vibrionaceae, Synechococcaceae, Pseudoalteromonadaceae, Thioalkalispiraceae, and Xanthomonadaceae (Supplementary material 1, Fig. S1).

The ordinary dominance curves revealed differences in dominance and evenness patterns of the different genera between substrates. In this sense, *A. cervicornis* tissue showed a greater dominance of only 2 bacterial genera (Fig. 2). In contrast, seawater and sediments showed higher evenness among bacterial taxa (Fig. 2). In *A. cervicornis* tissue, *Pseudomonas* contributed the highest relative abundance (45.2%), followed by *Candidatus_Midichloria* (40.4%), *Acinetobacter* (10.7%), *Enterobacter* (2.1%), and *Stenotrophomonas* (1.1%) (Fig. 2 and 3). In seawater, the most dominant bacterial genera were *Enterobacter* (16.9%), *Vibrio* (14.9%), *Synechococcus* (12.9%), *Pseudoalteromonas* (9.3%), and *Pseudomonas* (9.1%), while *Thioprofundum* (24.9%), *Pleurocapsa* (17.9%), *Ilumatobacter* (11.9%), and *Rhodovibrio* (11.6%) were most dominant in sediments (Fig. 2 and 3).

At the site level, *Pseudomonas* (69.3%) and *Enterobacter* (4.1%) were dominant in *A. cervicornis* in Cancún Reef. In seawater, these same genera showed relative abundance values of 31.1% (*Enterobacter*) and 14.9% (*Pseudomonas*). Another dominant genus in *A. cervicornis* was *Acinetobacter* (19.9%).

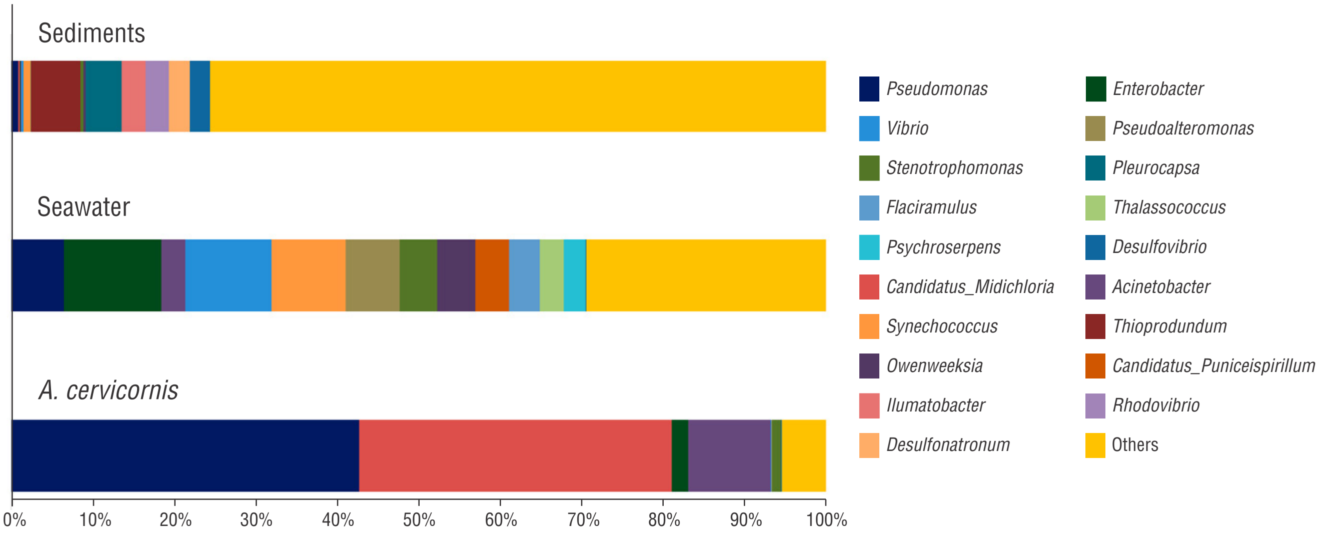

Figure 3. Dominant bacterial genera associated with *Acropora cervicornis*, seawater, and sediments in the entire study area. Each color represents a different bacterial genus in each substrate.

Synechococcus (22.7%) and *Stenotrophomonas* (11.9%) were dominant in seawater samples, while *Thioprofundum* (7.9%), *Ilumatobacter* (4.3%), and *Pleurocapsa* (3.6%) were dominant in sediments (Fig. 4). In La Poza Reef, *Candidatus_Midichloria* (72.7%) and *Pseudomonas* (18.2%) presented high levels of abundance in *A. cervicornis*. The sediments presented large quantities of *Pleurocapsa* (6.5%), *Thioprofundum* (6.2%), and *Rhodovibrio* (4.9%). *Vibrio* (22.4%), *Pseudoalteromonas* (14.0%), and *Flaviramulus* (7.5%) were dominant in seawater samples (Fig. 4).

In the alpha diversity analysis, the PERMANOVA outputs showed that the average community metrics (*S*, *N*, and *H*′) were similar at the site and substrate levels (Table 1). The highest *S* values were observed in sediments and seawater. A similar pattern was found with *H*′, which was higher in sediments (5.40) than in seawater (3.41) or *A. cervicornis* tissue (1.10). The highest *N* value was observed in sediments (536,476), followed by seawater (533,756) and *A. cervicornis* tissue (521,445) (Table 1). The PCO ordination showed that the highest values of *S* and *H*′ were correlated with sediments. In contrast, the lowest *S* and *H*′ values and intermediate *N* values were observed in *A. cervicornis*. However, the community attributes of *S*, *H*′, and *N* exhibited intermediate values in seawater (Fig. 5).

Regarding beta diversity, the PERMANOVA model indicated that the composition and abundance of bacterial genera exhibited significant differences with only the substrate factor, which explained 60.7% of the total variation (Table 1). However, pairwise comparisons could not identify differences between substrates due to the poor replication of our analysis. The results also showed no spatial variation of bacterial microbiota. The PCO ordination showed that coral tissue and sediment were more dissimilar in terms of bacterial assemblage (Fig. 6). Seawater and *A. cervicornis* tissue also exhibited different assemblages. The SIMPER outputs identified that *Pseudomonas*, *Synechococcus*, *Thioprofundum*, *Owenweeksia*, *Pleurocapsa*, *Candidatus_Puniceispirillum*, *Candidatus_Midichloria*, and *Rhodovibrio* were the bacterial genera that primarily contributed to the average dissimilarities between substrates (Supplementary material 1, Table S1).

Twenty-five putative bacterial functional categories were assigned to the 19 genera selected by the dominance and SIMPER analyses. The putative metabolic functions with the highest proportions were aerobic chemoheterotrophy (AeCh) (84%), sulfur respiration (SuRe) (42%), nitrogen fixation (NiFi) (42%), invertebrate parasites (InvP) (37%), ureolysis (Ureo) (32%), nitrate reduction (NiRed) (32%), cellulolysis (Cell) (32%), fermentation (Ferm) (26%), and animal parasites or symbionts (APoS) (26%); the other 16 categories occurred less (Supplementary material 2, Table S2). Conversely, the genera with more putative functions were *Pseudomonas* (11), followed by *Enterobacter*, *Desulfovibrio*, and *Synechococcus* (10); *Vibrio* (8) and *Desulfonatronum* (7); *Candidatus_Midichloria* (6); *Acinetobacter*, *Thioprofundum*, *Stenotrophomonas*, and *Psychroserpens* (5); and *Candidatus_Puniceispirillum*, *Owenweeksia*, and *Pseudoalteromonas* (4). The remaining 5 genera (*Pleurocapsa*, *Flaviramulus*, *Ilumatobacter*, *Thalassococcus*, and *Rhodovibrio*) had less than 4 functions (Fig. 7; Supplementary material 2, Table S2). The putative metabolic functions identified in only one bacterial genus were hydrocarbon degradation (HyDe) and intracellular parasites (IncP) in *Candidatus_Midichloria* and iron respiration (IrRe) in *Synechococcus* (Fig. 7; Supplementary material 2, Table S2).

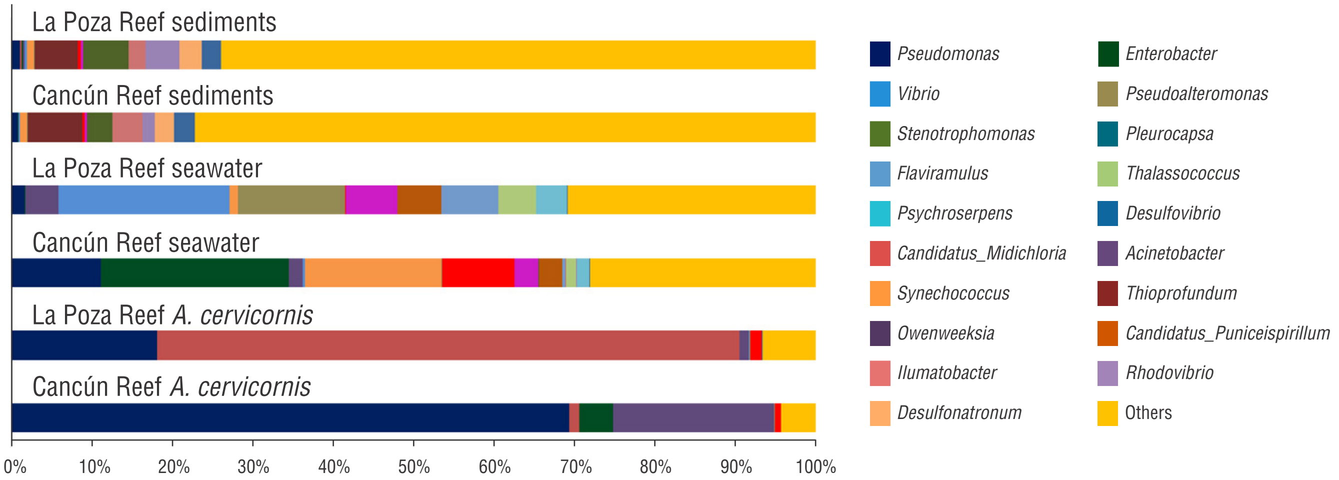

Figure 4. Dominant bacterial genera associated with *Acropora cervicornis*, seawater, and sediments per site. Each color represents a different bacterial genus in each substrate.

Discussion

Despite the geographic distance between the 2 Mexican Caribbean sampling sites (~325 km), the corals exhibited similar compositions of bacterial genera, indicating bacteria-coral specificity. Previous studies have reported similarities in the bacterial assemblages of distantly located coral colonies (Rohwer et al. 2001; Carlos et al. 2013; Hernández-Zulueta et al. 2016, 2022, 2023). Regarding seawater and sediments, bacteria-coral specificity was observed in the prevalence of specific bacterial genera (*Pseudomonas*, *Candidatus_Midichloria*, and *Acinetobacter*) in the corals. Although *Pseudomonas* was the most abundant in *A. cervicornis* (45.2%), it was observed to have higher values in Cancún Reef (69.3%) than in La Poza Reef in Xcalak (18.2%). We believe that the differences in the relative abundance of this genus between corals at both sites could be attributed to local characteristics, which may include physicochemical variables that, unfortunately, were not evaluated in this study.

However, there is information that supports the idea that both reef sites could have different seawater conditions. For example, Rodríguez-Muñoz (2020), in an assessment of the impact of Sargassum arrival and decomposition on water quality in Xcalak between July and October 2019, reported a decrease in dissolved oxygen (0.17 mg·L^{-1}) and pH (7.84), along with an increase in ammonium (1.27 µM) and phosphate (0.33 µM) concentrations. These findings suggest that the influx of Sargassum has contributed to the eutrophication of coastal marine ecosystems, such as coral reefs, as the recorded physicochemical values fall outside the reference ranges previously established for this reef site in the absence of Sargassum (Rodríguez-Martínez et al. 2019). However, Xcalak is sparsely populated by humans, as well as being a protected reef site with low wastewater discharge and vessel activity (CONANP 2004). On the other hand, Cejudo et al. (2021) analyzed variations in water quality parameters in Cancún between the rainy season (October 2018) and the dry season (June 2019). Their study reported fluctuations in phosphate (0.4–19.8 µM), silicate (139–427 µM), chlorophyll *a* (0.8–6.6 mg·m^{-3}), and dissolved inorganic nitrogen (32–106 µM) concentrations. The results indicated that phosphate and dissolved inorganic nitrogen concentrations exceeded the permissible limits for the protection of aquatic life in coastal areas (CE-CCA-001/89). This disturbance may be attributed to the proximity of urban zones and the intense tourism activity in the region, which could affect seawater quality in adjacent protected natural areas. Therefore, these studies show that the seawater conditions of each studied reef site could be different, which supports our hypothesis in that the composition and abundance of the microbiota of *A. cervicornis* are also influenced by local environmental effects. However, these interpretations should be taken cautiously, as we did not have replicates for each substrate nor a detailed analysis of seawater conditions.

The *Pseudomonas* genus showed lower abundance in seawater and sediments. The differences observed among substrates might be related to its function in the substrate; in corals, some members of this genus can produce compounds with antibacterial activity against coral pathogens (Sabdono et al. 2015) and sulfur cycling (Raina et al. 2010). Hernández-Zulueta et al. (2022) observed the dominance of *Pseudomonas* in the coral *Acropora palmata*, in both apparently healthy colonies and colonies with white band disease type I (WBD-1). These authors also showed that *Pseudomonas*

Table 1. Results of the ecological diversity indices of the substrates and sampling sites.

Substrate	Site	Genera richness (*S*)	Abundance (*N*, or total number of sequences)	Shannon diversity (*H*′, nats)
Acropora cervicornis	Cancún	821	480,814	1.1036
Acropora cervicornis	Xcalak	1,103	521,445	1.1534
Seawater	Cancún	1,420	533,756	3.2812
Seawater	Xcalak	1,277	514,756	3.4101
Sediments	Cancún	1,673	536,476	5.2995
Sediments	Xcalak	1,667	523,478	5.4017

abundance increased in diseased colonies, suggesting a possible coral response mechanism against the disease.

The genus *Candidatus_Midichloria*, which belongs to the family Midichloriaceae, was also dominant in *A. cervicornis*. Several studies of Midichloriaceae have reported high abundances in apparently healthy *A. cervicornis* colonies (Casas et al. 2004, Miller et al. 2014, Godoy-Vitorino et al. 2017, Rosado et al. 2019). However, the role of this family from the order Rickettsiales in the coral is difficult to elucidate because it has been associated with diseases (Casas et al. 2004, Godoy-Vitorino et al. 2017, Shaver et al. 2017, Rosales et al. 2019, Gignoux-Wolfsohn et al. 2020).

The genus *Acinetobacter* has been previously reported in *A. cervicornis* (Kalimutho et al. 2007, Godoy-Vitorino et al. 2017). In apparently healthy corals, other studies have also detected a high abundance of this genus (Chen et al. 2011, Carlos et al. 2013, Cai et al. 2018). There is little information on the role of this genus in the coral holobiont, but some studies have suggested that these microorganisms are involved in coral nutrient metabolism (i.e., carbon, nitrogen, and sulfur) and host detoxification (Raina et al. 2010, Cai et al. 2018).

The genus *Stenotrophomonas* was also dominant in *A. cervicornis*; this coincides with the results of Hernández-Zulueta et al. (2022), who reported its dominance in apparently healthy colonies of *A. palmata* in the Gulf of Mexico and Mexican Caribbean. However, this genus has also been detected in diseased corals (Cárdenas et al. 2012, Meyer et al. 2014) and corals that inhabit relatively disturbed sites with high nutrient concentrations (Lee et al. 2012). Likewise, it has been reported that some marine strains of *Stenotrophomonas* spp. can produce antimicrobial compounds (Romanenko et al. 2007) and degrade chitin (Salas-Ovilla et al. 2019).

This study showed that the genus *Enterobacter* was more abundant in seawater samples than in corals. Members of the *Enterobacter*iaceae family have been reported to be responsible for various diseases in tropical corals (Daniels et al. 2015, Peixoto et al. 2017). Moreover, strains of this genus have been isolated with the ability to exhibit antibacterial activity against clinical and aquacultural bacterial pathogens (Gopi et al. 2012, Nursyirwani et al. 2018). In our study, the most dominant bacterial genera have been previously associated with coral diseases. This could be because these microorganisms are part of the coral bacterial microbiota, which, under conditions of severe and persistent environmental stress, undergoes dysbiosis, favoring an increase in the

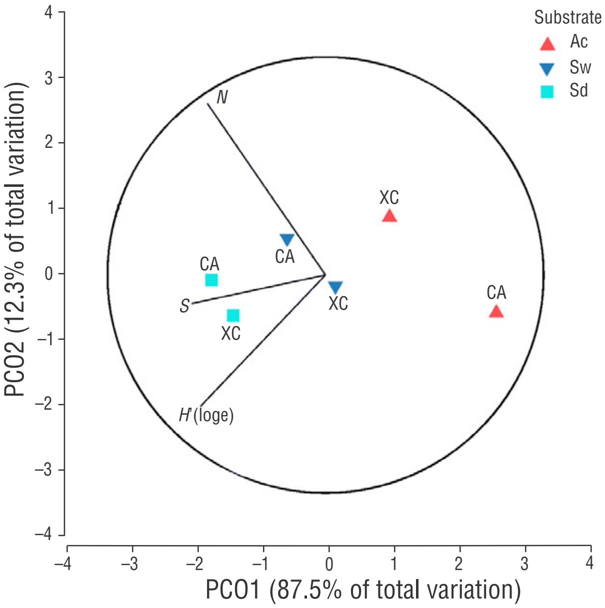

Figure 5. Principal coordinates analysis (PCO) ordination of the variation in community attributes (genera richness [*S*], abundance [*N*], and Shannon diversity [*H*′]) by substrate type and sampling site. The vectors were generated based on a multiple correlation analysis. The correlation circle represents the Pearson correlation range (−1 to 1). Codes: Cancún (CA); Xcalak (XC); *Acropora cervicornis* (Ac); sediments (Sd); seawater (Sw).

Table 2. Two-way crossed un-replicated PERMANOVA outputs of the community attributes (genera richness [*S*], abundance [*N*], Shannon diversity [*H'*]) and the bacterial genera composition and abundance among substrates through sampling sites. Codes: CV(%) is the component of variation percentage; *P* is the *P*-value. *P*-values ≤ 0.05 are shown in bold.

	Community attributes (alpha diversity)			Bacterial genera composition and abundance (beta diversity)		
Source of variation	Pseudo-*F*	*P*	CV (%)	Pseudo-*F*	*P*	CV (%)
Substrates	3.835	0.1562	54.4	5.7513	**0.0466**	60.7
Sites	0.039	0.8887	0.0	0.7926	0.5068	0.0
Residuals			45.6			39.3

abundance and metabolic activity of specific bacterial groups due to the immunocompromised state of the coral (Cárdenas et al. 2012, Certner and Vollmer 2015, Pollock et al. 2016, Ziegler et al. 2016). The above has been found to induce significant changes in the coral microbiome, directly affecting its physiology and triggering diseases, syndromes, and coral bleaching (Zhou et al. 2020, Mohamed et al. 2023).

Our study found that the structure of the bacterial assemblage differed between *A. cervicornis* tissue and the surrounding seawater and sediments. These observations agree with those made by Carlos et al. (2013), Beltrán et al. (2016), and Hernández-Zulueta et al. (2016), who also showed significant differences in the bacterial microbiome between corals and their surrounding environment. This could be an indication that the site exhibits good conservation status. For instance, Hernández-Zulueta et al. (2016) found that the sites with the highest conservation status and lowest human disturbance were responsible for the main differences between studied substrates. However, in the present work, physicochemical variables were not evaluated in the sampled locations; we suggest future studies evaluate these variables and the relationship between the spatial specificity of corals and the conservation status of sites. On the other hand, in the present study, we considered that the specific bacterial assemblages observed in the corals might ensure their ability to acclimate or adapt to environmental changes and transient stress (Ziegler et al. 2017, Bang et al. 2018). Likewise, this microbiota may play a key role in coral health because it supports immunity (Reshef et al. 2006) and actively participates in nutrient cycling (Gates and Ainsworth 2011). However, Klinges et al. (2023) found that the bacteriome resists some changes in bacterial assemblage structure in disease-resistant *A. cervicornis*, although this could be considerably altered following strong environmental pressure.

In this study, bacterial diversity was higher in sediments than in coral tissue and seawater. Schöttner et al. (2012) and Carlos et al. (2013) found that the sediments also exhibited higher bacterial diversity than other substrates (e.g., corals and seawater) in Brazilian reefs. They proposed that the sediments represent a bacterial reservoir that can colonize coral surfaces. Bernasconi et al. (2019) stated that seawater and sediments are the main coral bacteria suppliers due to the location of corals in the benthos.

From a metabolic perspective, it was observed that various metabolic functions were repeated across different genera (*Pseudomonas*, *Synechococcus*, *Thioprofundum*, *Owenweeksia*, *Pleurocapsa*, *Candidatus_Puniceispirillum*, *Candidatus_Midichloria*, and *Rhodovibrio*), which were present in all 3 substrates but showed variations in relative

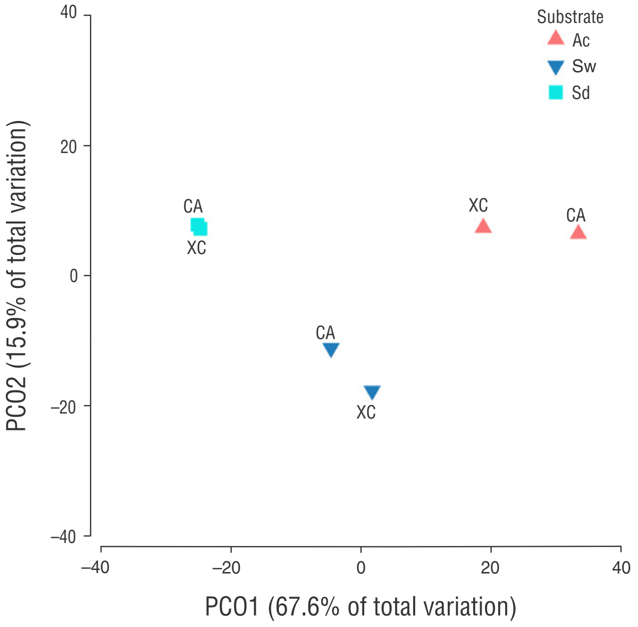

Figure 6. Principal coordinates analysis (PCO) ordination of the changes in the composition and abundance of bacterial genera by substrate type and sampling site. Codes: Cancún (CA); Xcalak (XC); Acropora cervicornis (Ac); sediments (Sd); seawater (Sw).

abundance. We believe this is due to high functional diversity and redundancy (i.e., the ability of one species to functionally compensate for the loss of another) (Eisenhauer et al. 2023), which are critical for ecosystem functioning and resilience (Nyström 2006, Mori et al. 2013, Cárdenas et al. 2022). This could suggest that this redundancy allows the coral to capture microorganisms from the surrounding substrates to meet the needs of the holobiont. For example, the prevalence of the genus *Thioprofundum* has been previously reported in sediments from the southeastern Gulf of Mexico (Suárez-Moo et al. 2020). This genus, known for its sulfur-oxidizing capability (Takai et al. 2009), could play a key role in the sulfur cycle within coral reef sediments. The genus *Owenweeksia* has been reported as a novel bacteria for the bioremediation of organic matter in seawater (Lau et al. 2005). The genera *Synechococcus* and *Pleurocapsa* play fundamental functional roles in nitrogen fixation in coral reef ecosystems (Charpy et al. 2012). Meunier et al. (2019) found that corals exposed to thermal stress increased their consumption of bacteria from this genus (*Synechococcus*) present in picoplankton, which could be due to these microorganisms being a rich nitrogen source (Berthelot et al. 2016). Choi et al. (2015) reported a strain of the genus *Candidatus_Puniceispirillum* with the ability to produce dimethyl sulfide from dimethylsulfoniopropionate, which is relevant to the sulfur cycle in coral reefs (Guibert et al. 2020). The presence of *Rhodovibrio* has been previously reported in the shallow subsurface sediments of the Bonneville Salt Flats (McGonigle et al. 2019). Similarly, Hernández Zulueta et al. (2022) identified *Rhodovibrio* in the surrounding sediments of *A. palmata* in the Mexican Caribbean. However, the role played by *Rhodovibrio* in this type of substrate remains unknown.

Aerobic chemoheterotrophy and SuRe were the predominant putative metabolic functions among the 8 bacterial genera that contributed the most to substrate dissimilarity. The prevalence of the chemoheterotrophic bacteria in corals has also been reported previously (Ostria-Hernández et al. 2022, Hernández-Zulueta et al. 2023); heterotrophic bacteria support coral health and drive the carbon cycle (Hu et al. 2022). As discussed previously, it has also been reported that some members of the bacterial assemblages in coral tissues participate in sulfur metabolism through the degradation

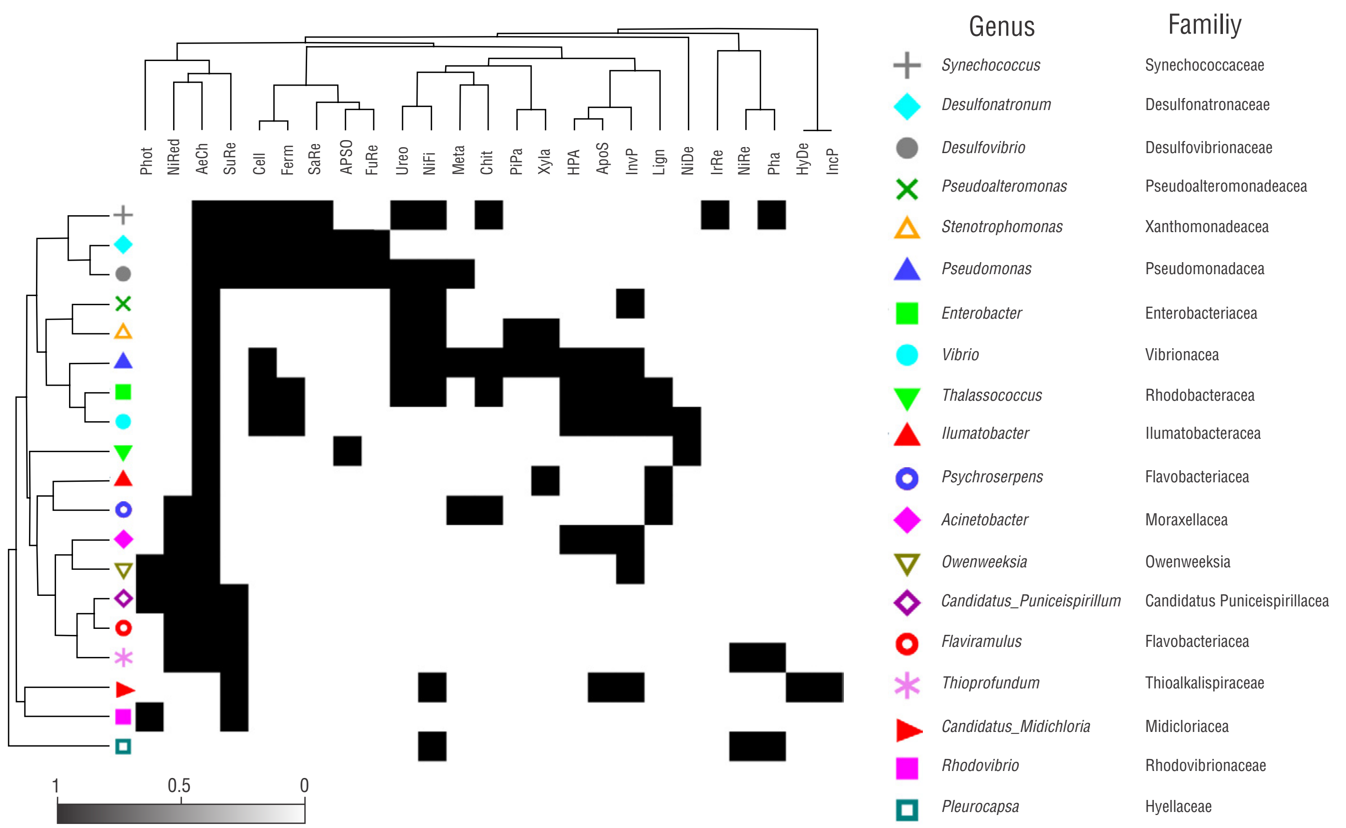

Figure 7. Shade plot of the dominant bacterial genera and respective putative metabolic functions. Codes: Photoheterotrophy (Phot); Nitrate reduction (NiRed); Aerobic chemoheterotrophy (AeCh); Sulfur respiration (SuRe); Cellulose (Cell); Fermentation (Ferm); Sulfate respiration (SaRe); Anoxygenic photoautotrophy S oxidizing (APSO); Fumarate Respiration (FuRe); Ureolysis (Ureo); Nitrogen fixation (NiFi); Methanotrophy (Meta); Chitinolysis (Chit); Plant pathogen (PlPa); Xylanolysis (Xyla); Human pathogens all (HPA); Animal parasites or symbionts (APoS); Invertebrate parasites (InvP); Ligninolysis (Lign); Nitrate denitrification (NiDe); Iron respiration (IrRe); Nitrate respiration (NiRe); Photoautotrophy (Pha); Hydrocarbon degradation (HyDe); Intracellular parasites (IncP).

of dimethylsulfoniopropionate (DMSP) into dimethyl sulfide (DMS), suggesting that these compounds represent a key nutrient source with a relevant role in coral health (Raina et al. 2009, Tandon et al. 2020). Nitrogen fixation, NiRed, and NiRe were other relevant metabolic functions reported in this study. Nitrogen supply through microbial metabolism, facilitated by cyanobacteria and diazotrophic bacteria, constitutes an additional nitrogen source for coral systems (Sohm et al. 2011). This process can cover up to 10% of the nitrogen requirements of symbiotic algae (Cardini et al. 2015, Bednarz et al. 2019) and is crucial for the survival and growth of autotrophic corals (Pogoreutz et al. 2017, Li et al. 2023). Likewise, as previously mentioned, some of the reported genera (*Pseudomonas*, *Enterobacter*, and *Stenotrophomonas*) have been associated with coral diseases (Meyer et al. 2014, Peixoto et al. 2017, Gignoux-Wolfsohn et al. 2020), which supports the prevalence of the putative metabolic function InvP in the present study.

CONCLUSIONS

This study constitutes a first approach to explore the coral-associated bacterial assemblage in *A. cervicornis* in the Mexican Caribbean, where the geographic distance between sampling sites was not a significant factor because the bacterial assemblage associated with *A. cervicornis* tissue, seawater, and sediments revealed the specificity of dominant bacterial genera that indicated spatial stability. These dominant bacterial genera were *Pseudomonas*, *Synechococcus*, *Thioprofundum*, *Owenweeksia*, *Pleurocapsa*, *Candidatus_Puniceispirillum*, *Candidatus_Midichloria*, and *Rhodovibrio*. Likewise, the most important metabolic functions in the dominant bacterial genera in all substrates were AeCh, SuRe, and Nifi. Although this study produced relevant results, it is important to mention that one of the limitations of this work was the loss of replication due to the pooling of substrate samples. In future studies, it will be important to increase the number of replicates to evaluate the existing variation within each site and, thus, strengthen data analysis. It is also essential to consider intra- and inter-annual temporal variation to evaluate if the dominant bacterial genera significantly change. In addition, it will be necessary to increase the number of substrate samples and measure additional environmental and habitat structure variables to provide better statistical support to understand the distribution and spatial patterns of coral bacterial assemblages. Finally, culture-based approaches may provide a more comprehensive view of the functional roles of coral-associated bacteria.

FINAL DECLARATIONS

Supplementary materials

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3487/420421191 and https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3487/420421192.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Conceptualization: FARZ, JHZ; Data curation: JHZ; Formal analysis: FARZ; Funding acquisition: GGNM, MÁGS, FARZ, JHZ; Investigation: FARZ, JHZ; Methodology: FARZ, JHZ, GGNM, MÁGS; Project administration: GGNM, MÁGS, FARZ, JHZ; Resources: FARZ, JHZ, GGNM, MÁGS; Software: FARZ, JHZ; Supervision: FARZ, JHZ; Validation: FARZ, JHZ; Visualization: FARZ, JHZ, GGNM, MÁGS; Writing – original draft: FARZ, JHZ, GGNM, MÁGS; Writing – review & editing: FARZ, JHZ. All authors read and agreed to the final version of the manuscript.

Data availability

The data generated and analyzed in the present study are included in the article. Clean reads were deposited in the SRA of the NCBI (accession number PRJNA749734): https://www.ncbi.nlm.nih.gov/bioproject/?term=749734.

Use of AI tools

The authors did not employ any AI tools in this work.

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