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Cover picture: A small fish *(Emblemariopsis pricei)* camouflages itself perfectly in *Diploria labyrinthiformis*.
Photograph taken in August 2015 in Roatán, Honduras (Photo: Angela Randazzo Eisemann).

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Preface

Research note

Collage

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Journal/Revista

The study of Mexican coral reefs under the threat of climate change: Contributions from XII CMAC–III CPAC

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In 2000, the first Mexican Coral Reef Conference (I CMAC, for its acronym in Spanish) was held in the city of Veracruz and offered 91 presentations. Eleven years later, VI CMAC took place in the city of Ensenada and grew to feature 126 presentations. Over the intervening years, the scope of this conference has been enhanced by the integration of colleagues from other countries in the Americas, giving rise to the Panamerican Coral Reef Conference (CPAC, for its acronym in Spanish), which was held concurrently with CMAC in 2022 and 2024. For the second time, Ensenada was selected to host this conference, with XII CMAC–III CPAC held from 22–26 April 2024.

Notably, XII CMAC–III CPAC, which featured a total of 299 presentations, talks, and posters, was by far the largest gathering to date of researchers, managers, government officials, and students involved in research, management actions, and conservation efforts in the reef ecosystems of Latin America. This important event was organized by the Mexican Society of Coral Reefs (SOMAC, for its acronym in Spanish), with support from the International Coral Reef Society and the local host institutions of *Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California* (CICESE) and *Universidad Autónoma de Baja California* (UABC).

During XII CMAC–III CPAC, the featured presentations covered multiple topics that were categorized into five thematic sessions: (1) genomic sciences and the physiology of reef organisms; (2) the population and community ecology of reef organisms; (3) social-ecological systems; (4) physics, chemistry, and innovation applied to coral reefs; and (5) temperate reefs. As such, the conference, which reflected a diverse array of research approaches and methodologies, covered a wide range of topics related to corals, reef ecosystems, and their associated species, with a strong emphasis on coral health and reef resilience, physiology, restoration, and the impacts of climate change in these ecosystems.

From the 299 presentations, 11 studies were selected for publication (3 research notes and 8 research articles) in a special issue of *Ciencias Marinas* (vol. 50 [1b]). These studies presented novel findings on issues related to coral reef health, growth, and physiology, as well as interactions with other marine organisms and the impacts of environmental stressors and human activities on the resilience of vital coral ecosystems in the seas and oceans of the Americas.

Within the special issue of *Ciencias Marinas*, you will find 2 studies focused on aspects of coral reef health and resilience and the importance of continued monitoring efforts. Correa et al. (2025) explored the value of using the Reef Health

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Index as a tool for regional monitoring and reef conservation under climate change. In this study, the authors assessed the status of 11 reefs in the southwestern Gulf of Mexico and Mexican Caribbean, finding that reefs in the southwestern Gulf of Mexico exhibited better health than those in the Mexican Caribbean. Carreño-Loaiza et al. (2025) noted the rapid recovery of scleractinian corals only 5 months after a bleaching event in the Veracruz Reef System. The long-term data set (2008–2021) revealed that the health of the coral community could be classified as "good" based on the coral index (CI ≈ 3.7), indicating resilience and reinforcing the importance of continuous monitoring.

Regarding the physiology of corals and associated species, Trejo-Estrada et al. (2025) studied the physiological acclimation of *Porites panamensis* under high-latitude marginal conditions. The authors found that *P. panamensis* acclimates to seasonal changes in temperature and turbidity by using mixotrophy as a key nutritional strategy to withstand fluctuating environmental conditions, thus allowing this species to distribute throughout the Eastern Tropical Pacific, even in seemingly suboptimal regions. In addition, Rodríguez-Jiménez et al. (2024) explored the immune response of the anemone *Exaiptasia diaphana* and found that immune activity peaked during the daytime and full moon, especially when *E. diaphana* lacked symbionts. The results of these authors provide relevant information on protective immune mechanisms, which is critical for understanding cnidarian resilience under climate change scenarios.

Two articles in the special issue focused on coral restoration and adaptation. Gutiérrez-Coral et al. (2025) found that colonies of *Orbicella faveolata* were nearly able to fully regenerate following the extraction of donor microfragments within 24 months, providing essential information that supports the sustainability of employing this technique in restoration efforts. Lorenzo-Jiménez et al. (2024) assessed the acclimation of *O. faveolata* to light changes resulting from the translocation of coral fragments between different depths and demonstrated the potential for assisted migration in restoration programs.

Five articles focused on biodiversity and ecosystem functions. López-Pérez et al. (2024a) characterized locations in the southern Mexican Pacific and found that up to 10 coral species were present at sites and depths where they had not been reported previously (e.g., at depths of 37 m) and highlighted the need to address local anthropogenic threats to promote species conservation. Focusing on fish communities, Torres-García et al. (2025) explored the taxonomic and functional richness of fishes in the Mexican Pacific, identifying biodiversity hotspots and a regional "backbone" (i.e., common functional groups throughout the study region) composed of 74 species, which likely maintains ecological functions and processes across biogeographic provinces. This fish diversity analysis aimed to provide information for the management and conservation of reef ecosystems. Jáquez-Domínguez et al. (2025) evaluated species richness and the abundance of cryptobenthic reef fishes, exploring the critical role of *P. panamensis* as a microhabitat and its influence on the benthic organization of this often-neglected fish group. Cabrera-Rivera et al. (2025) explored the erosive potential of urchins in Campeche Bank and found that it was likely underestimated due to the omission of adequate nighttime surveys in studies, highlighting the scarcity of information despite the important roles these echinoderms play in coral reefs. Lastly, reflecting the ongoing multidisciplinary development of coral reef research, Hernández-Zulueta et al. (2025) studied the bacterial assemblages of *Acropora cervicornis* and identified the associated bacterial genera responsible for vital metabolic functions linked to coral immunity, nutrition, and resilience, such as *Pseudomonas* and *Acinetobacter*, which may influence how *A. cervicornis* responds to environmental stressors that can increase coral vulnerability to bleaching. Such studies are essential for improving our understanding of coral resilience in the face of climate change.

The body of knowledge contained in the special issue of *Ciencias Marinas*, which arose from XII CMAC–III CPAC, attests to the commitment to advance our understanding of coral reef ecosystems and to generate high-quality scientific information that supports the management and conservation of coral reefs in Mexico and the Americas. This commitment is crucial given the recent negative impacts and dire predictions these ecosystems face under climate change (Hoegh-Guldberg et al. 2017, Fabricius et al. 2024).

The year 2023 was especially devastating for coral reef ecosystems worldwide, and the Americas was no exception. The effects of an El Niño event, combined with elevated temperatures due to climate change, resulted in the most intense and prolonged heat wave recorded in recent years (Goreau and Hayes 2024). Along the coasts of Mexico, water temperatures rose above normal causing stress that led to bleaching and massive mortality. This situation was observed in corals on the Pacific coast, as well as those in the Caribbean and the Gulf of Mexico, leading to the death of tens of millions of corals and extensive devastation to reef ecosystems (López-Pérez et al. 2024b; McField et al. 2024).

Members of SOMAC were surveyed regarding the effects of this heat wave on the reefs in their study regions, which were based on the regional definitions proposed by Spalding et al. (2007) and included the Gulf of California, Tropical Pacific, Caribbean, and Gulf of Mexico (Table 1). Based on the survey results, the most affected region was the Tropical Pacific, which lost an average of almost half of its coral cover, although some authors reported sites with coral mortality as high as 93% (López-Perez et al. 2024b). In contrast, the least affected region was the Gulf of Mexico (5%), followed closely by the Gulf of California (6%) (Table 1).

The current degradation of coral reefs forms part of an ongoing trend that has been documented over several decades. In the Caribbean, the loss of coral cover has been particularly notable and documented since the 1980s (Glynn 1991, Gardner et al. 2003). This loss has been mainly due to poor water quality and coastal development resulting from

Table 1. Average values of coral cover before and after the bleaching event of 2023, prevalence of bleaching, and loss of cover in the geographical ecoregions of Mexico described by Spalding et al. (2007). Data were obtained from an online survey distributed to key senior members of the Mexican Society of Coral Reefs (SOMAC, for its acronym in Spanish) who kindly contributed information. The number of completed surveys is indicated next to each region. Numbers in parentheses are the standard error.

Region	Coral cover before (%)	Coral cover after (%)	Coral cover change (%)	Bleaching prevalence (%)
Gulf of California (*n* = 3)	18 (6.7)	12 (6.7)	–6	58 (26.7)
Tropical Pacific (*n* = 5)	63 (9.7)	15 (3.2)	–48	65 (19.0)
Caribbean (*n* = 1)	15	5	–10	75
Gulf of Mexico (*n* = 4)	33 (14.4)	28 (13.1)	–5	55 (13.2)

deforestation, land use changes, excessive nutrient inputs, and contamination. In addition to local threats, the effects of climate change have also contributed to the loss of coral cover. Given this context, the current scenario surrounding the coral reefs of the Americas is very concerning.

No easy or simple solutions exist to mitigate these growing threats to corals or to reverse severe reef deterioration. Restoration, given its nature, is costly and has very limited local impacts. More efficient solutions with ecosystem-level effects require proposals that address not only the consequences of reef deterioration, but also its causes. The studies published in the special issue of *Ciencias Marinas* address some of the problems affecting reef resilience, restoration efforts, biodiversity patterns, and microbial communities and offer actionable insights and future research avenues for the coral reef research community of the Americas to foster coral reef conservation in the face of climate change.

DECLARATIONS

Supplementary Material

This work includes no supplementary material.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: LMC, HPE, GRO, JAZD; Data curation: LMC, HPE, GRO, JAZD; Formal analysis: HPE;

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Data availability

The data for this study are available from the corresponding author by reasonable request.

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The authors employed DeepSeek V3.2 to translate and improve the grammar of the text. After any portion of text was prossesed by DeepSeek V3.2, the authors revised and proofread the outputs to ensure accuracy. The authors are fully responsible for the content of this work.

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Comparing richness and abundance of cryptobenthic reef fishes in coral and rocky microhabitats in Bahía de los Ángeles, Gulf of California

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ABSTRACT. Rocky-coral ecosystems host highly heterogeneous habitats and functionally diverse fish communities. Within these systems, coral microhabitats play a pivotal role by offering a subset of the available resources to cryptofauna, particularly cryptobenthic reef fishes (CRF), which are notable for their abundance and diversity. This group of fishes, with adult lengths of less than 5 cm, shows highly specialized visual and behavioral camouflage, which often leads to their underrepresentation in studies. Due to the scarcity of research and the significant taxonomic complexity of CRF, this study investigated the association between CRF and the massive coral *Porites panamensis* in Bahía de los Ángeles, Gulf of California, and rocky substrate. We hypothesized that CRF densities would be higher in coral microhabitats because of their superior three-dimensional complexity. Two extractive sampling efforts were conducted in March and October 2022 ($N = 16$). A total of 238 individuals were collected, representing 14 species from 5 fish families. Five species accounted for 76.62% of the total abundance, with the families Gobiidae, Tripterygiidae, and Chaenopsidae being the most represented. The average density of CRF in *P. panamensis* microhabitats was twice that observed in rocky microhabitats ($W = 46.5$, $P = 0.036$). Moreover, CRF assemblage structure and composition differed significantly between microhabitats (Pseudo-$F = 4.41$, $P = 0.004$). These findings highlight the critical role of *P. panamensis* as a microhabitat and its influence on the benthic organization of CRF. Given the ongoing degradation of coral cover and the decline in structural habitat complexity, these results are essential to understand long-term shifts in cryptofaunal communities.

Key words: microhabitat, endemism, habitat complexity, cryptofauna, cryptobenthic reef fishes, Gobiidae, Tripterygiidae, Chaenopsidae.

INTRODUCTION

Coral reef ecosystems and their complex ecological interactions are home to a great diversity of marine species, including fishes. The relationship between reef fishes and coral cover has been widely documented (Muruga et al. 2024), highlighting the importance of coral colonies as refuge areas that facilitate the convergence of diverse ecological processes (Komyakova et al. 2013). These processes and interactions, along with the use and distribution of resources, play a key role in structuring benthic communities. Worldwide, studies have identified more than 320 fish species that use live corals as their main habitat and refuge, representing approximately 8% of the total diversity of reef fishes (Coker et al. 2014). These interactions could be related to refuge search or establishment (i.e., Cirrhitidae), feeding (i.e., Stegastes), and predation (i.e., Scaridae), among other ecological processes (Depczynski and Bellwood 2003). However, a large number of reef fish species are not obligately dependent on live corals and make extensive use of the ecosystem, influencing reef trophodynamics (Depczynski and Bellwood 2003, Coker et al. 2014).

Most studies on fish-coral associations have focused on regions of high diversity and large areas of coral cover, such as the Caribbean (Olán-González et al. 2020) or the Indo-Pacific (Holbrook et al. 2008, Coker et al. 2014, Moynihan et

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al. 2022). In both regions, fish diversity increases with coral presence and cover (Coker et al. 2014). In that respect, several studies have evaluated the influence of benthic characteristics on the structuring of fish fauna in the Eastern Tropical Pacific (ETP) (Dominici-Arosemena and Wolff 2006, Galván-Villa et al. 2011, Ricart et al. 2016, Salas-Moya et al. 2021); however, the effect of habitat on the ichthyofauna in the ETP is not entirely clear, with some authors suggesting that fish diversity increases with greater habitat complexity (Benfield et al. 2008), whereas others indicate that fish diversity decreases as coral cover increases (Olán-González et al. 2020). In addition, ETP reefs are considered isolated coral patches, called rocky-coral fringing reefs, mainly due to the narrow continental shelf that prevents the development of large reef areas (Reyes-Bonilla 2003), since the majority of the coral reef-forming species (i.e., *Pocillopora*) do not develop beyond 8-m depths (López-Pérez et al. 2024).

There is a group of reef fishes called cryptobenthic reef fishes (CRF), which are small fishes with total lengths that do not exceed 5 cm in their adult stage (Depczynski and Bellwood 2003, Brandl et al. 2018). CRF show limited dispersal, low longevity, quick generational turnover, and high specialization in their habitat preferences (Hastings and Galland 2010, Brandl et al. 2018). Furthermore, on tropical reefs, CRF can represent more than 40% of the diversity of fish species (Ackerman and Bellwood 2000) and up to 85% of the total abundance (Galland et al. 2017). However, evaluating CRF assemblages is not easy because they are difficult to obtain, show extremely miniaturized anatomical structures that complicate their identification, and vary greatly in color in different growth stages (Brandl et al. 2018). Thus, CRF are highly dependent on the availability of specific microhabitats due to their specialized habitat preferences. Microhabitats are small areas within a larger habitat that are differentiated from the surrounding environment by structural, faunal, ecological, or climatic characteristics (Morrison et al. 2012, Shi et al. 2016). Therefore, when studying CRF, microhabitats are usually classified based on the characteristics of benthic structures (i.e., cracks, coral debris, or boulders) or the type of coral morphology (Depczynski and Bellwood 2004, Brooks et al. 2007, Troyer et al. 2018).

In the north-central region of the Gulf of California, rocky reefs are mainly made up of the species *Porites panamensis* that forms colonies and isolated patches (Reyes-Bonilla and López-Pérez 2009), with average percentage of cover values of around 1% (Glynn et al. 2017), although in some regions of the Gulf of California, such as Bahía de los Ángeles, this value increases until reaching 3.5% (Norzagaray-López et al. 2015). This coral species could be key in the creation of coral microhabitats, contributing notably to the biodiversity of the Gulf of California, an ecosystem that hosts approximately 4,852 species of invertebrates and 911 species of fish (Brusca 2010), and 16–20 species of scleractinian corals, with the genera *Pocillopora* and *Porites* being the most abundant (Reyes-Bonilla et al. 2005, Glynn et al. 2017). Therefore, studying fish associated with coral microhabitats is essential to understand their ecological role.

In recent years, the use of 3D modeling and photogrammetry tools has revolutionized the study of coral structures. These technologies allow us to obtain precise data on the three-dimensionality and complexity of seabed structures, which has transformed coral reef research (Storlazzi et al. 2016, Urbina-Barreto et al. 2022). In addition, they allow us to overcome the small-scale limitations of traditional methods by enabling 3D reconstructions of individual coral colonies and microhabitats (Urbina-Barreto et al. 2021), which facilitates the study of associated cryptofauna (Curtis et al. 2023). Considering this, we used 3D modeling tools to evaluate the complexity and importance of the massive coral *P. panamensis* and its influence on the structuring of CRF. To do this, fish were collected in microhabitats made up of coral and rock to later evaluate their association with these structures. Therefore, the objective of this study was to compare the density, structure, and composition of the CRF community between coral microhabitats, made up of the *P. panamensis*, and rocky microhabitats. We hypothesize that CRF richness and density will be greater in coral microhabitats because these microhabitats are three-dimensionally more complex. This study provides empirical evidence to better understand the association of CRF with the microhabitats in the Gulf of California.

MATERIALS AND METHODS

Study area

The study was carried out on a shallow rocky-coral reef located in the southern part of La Llave Island (Fig. 1a). This island is located within Bahía de los Ángeles, *Zona marina Bahía de los Ángeles, canales de Ballenas y de Salsipuedes* Biosphere Reserve, in the north-central region of the Gulf of California. This region is characterized by an arid climate and high seasonal climate variability. Between February and April, sea surface temperatures can drop to less than 16 °C; in the months of August and September, they can exceed 27 °C (Martínez-Fuentes et al. 2022).

Field work

To compare CRF assemblages in coral and rock microhabitats, 2 field trips were carried out, the first in March 2022 and the second in October 2022. We obtained 8 sample units in each season (Table S1). We defined coral microhabitats as 1-m wide by 1-m long areas, with a percentage of *P. panamensis* coral cover greater than 10% (Fig. 1b). Conversely, rocky microhabitats were classified as those areas with coral cover equal to or less than 10%, and a predominance of rock. It should be noted that *P. panamensis* is the only species of scleractinian coral observed in the study area.

We analyzed 16 microhabitats at average depths of ~5.7 m with scuba diving equipment: 5 coral microhabitats

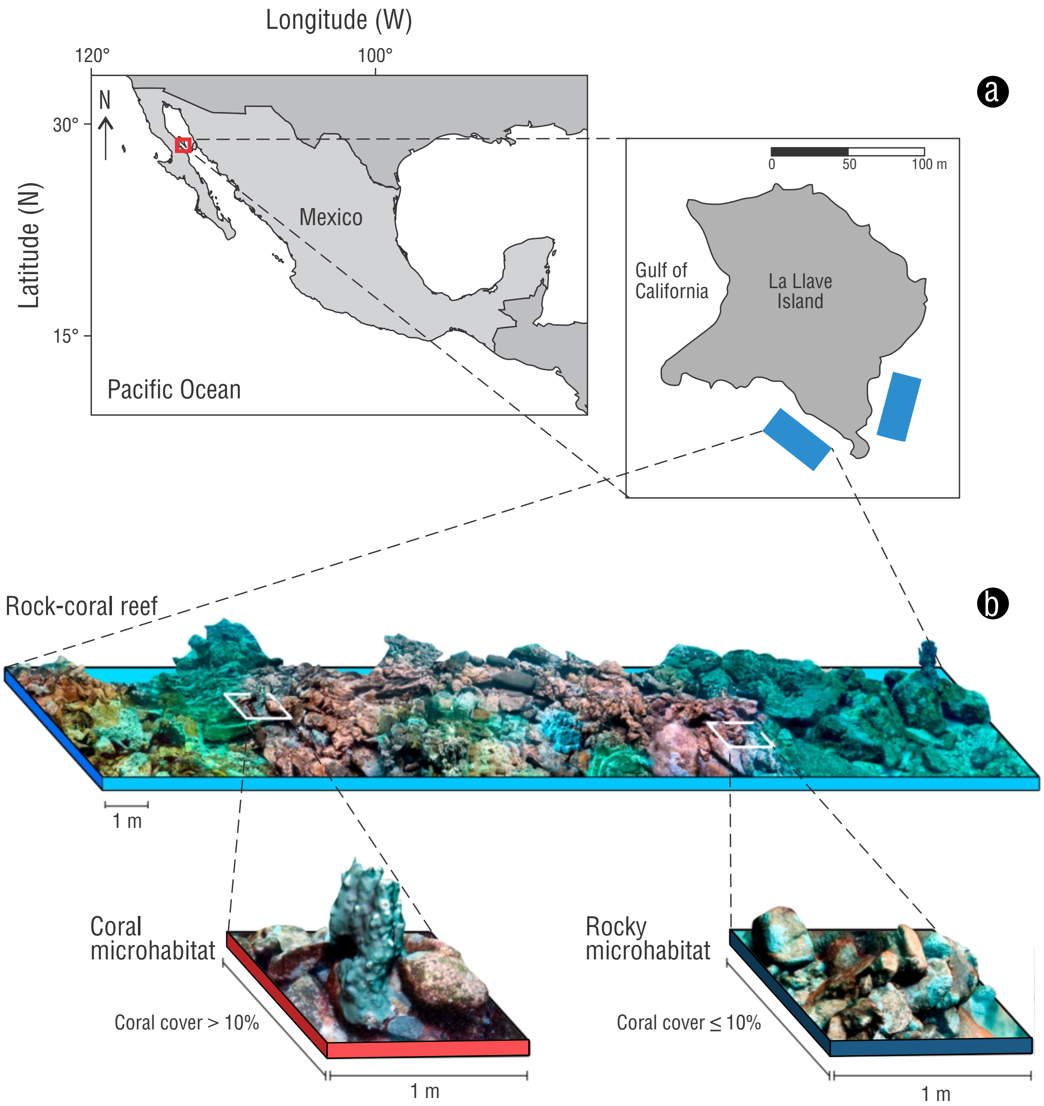

Figure 1. Study area. The blue polygons indicate the areas where sampling was carried out on La Llave Island, *Zona marina Bahía de los Ángeles, canales de Ballenas y de Salsipuedes* Biosphere Reserve (**a**). Schematic drawing of a rocky-coral reef composed of coral microhabitats (*Porites panamensis*) and rocky microhabitats (**b**).

and 11 rocky microhabitats (Table S1). First, a 12-cm diameter metric reference was placed and 1-min recordings were made using a circular scan to capture the three-dimensional structure of each microhabitat. Recordings were made with a GoPro Hero 10 camera (GoPro, San Mateo, USA) set at a resolution of 2,704 × 1,520 pixels (2K) and a speed of 60 photographs per second. Subsequently, fish were extracted from each microhabitat using a conical net with an opening area of 0.42 m^2 and mesh size of 0.5 mm (Fig. S1) and a solution composed of 100 mL of concentrated clove oil (eugenol) and 900 mL of 96% ethanol as an anesthetic (Depczynski and Bellwood 2004). We waited ~1 min for the anesthetic to take effect and collected all the fish inside the net. In the laboratory, each individual was identified to the species level based on Ginsburg (1938), Rosenblatt and Taylor (1971), Bussing (1990), and Robertson et al. (2024). To prepare the final list, the name of each species was corroborated and validated using the Eschmeyer catalog (Fricke et al. 2023).

Image processing

To generate 3D models of the microhabitats in the Agisoft Metashape software (Agisoft LLC, Saint Petersburg, Russia), frames were extracted from each microhabitat video following the methodologies of Burns et al. (2015) and Fukunaga et al. (2019). Coral cover was estimated with the 3D model orthomosaics using the Coral Point Count with Excel extensions software (Kohler and Gill 2006) by overlaying 30 random points in each microhabitat (Tabugo et al. 2016). The 3D rugosity was estimated from the 3D models using the methodology of Ventura et al. (2020), with the following formula:

$$R_{3D} = \frac{SA_{3D}}{A_{2D}} \quad , \tag{1}$$

where R_{3D} is the 3D rugosity as a proxy for habitat complexity, SA_{3D} is the three-dimensional area of the microhabitat model, and A_{2D} is the planar area or base area occupied by the microhabitat model.

Data analysis

To compare 3D rugosity and CRF richness and density between coral and rock microhabitats, we performed a Mann–Whitney–Wilcoxon analysis with the 'stats' package. On the other hand, to compare the composition and structure of CRF assemblages between microhabitats, we performed a one-way permutational multivariate analysis of variance (PERMANOVA) using a Bray–Curtis dissimilarity matrix based on the transformed CRF density data ($\sqrt[4]{x}$); P and Pseudo-F values were calculated by performing 9,999 permutations. The microhabitat factor was included as an independent variable with 2 levels (coral and rocky). On the other hand, we graphically complemented the evaluation of the composition of CRF between microhabitats (coral and rocky) with non-metric multidimensional scaling (NMDS), based on the Bray–Curtis dissimilarity matrix (Wisconsin double standardization) with the 'metaMDS()' function of the 'vegan' package (Oksanen et al. 2019). All statistical analyses were performed with a value of α = 0.05 in the RStudio software and plotted with the 'ggplot2' package (Wickham 2016, R Core Team 2022).

Finally, we evaluated the preference of species for coral and rocky microhabitats with a similarity percentage analysis (SIMPER) and made an alluvial diagram to graphically illustrate it. The SIMPER analysis allows us to discriminate between 2 groups of species based on Bray–Curtis dissimilarities and provides the average contribution per species (Oksanen et al. 2019):

$$\delta_{jk}i = 100\frac{\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}\left(y_{ij} - y_{ik}\right)} \quad , \tag{2}$$

where $\delta_{jk}i$ is the dissimilarity associated with the ith species between samples j and k. We obtained the average contribution per species ($\overline{\delta_i}$) by averaging $\delta_{jk}i$.

RESULTS

We collected 238 CRF from 14 species. However, 5 species represented 76.62%: *Elacatinus puncticulatus*, *Crocodilichthys gracilis*, *Lythrypnus pulchellus*, *Lythrypnus dalli*, and *Barbulifer pantherinus* (Fig. 2). Average CRF richness was slightly higher in coral microhabitats than in rocky microhabitats, with values of 5.6 ± 1.3 ($\bar{x}$ ± SE) and 4.7 ± 1.7 species, respectively. However, differences in richness were not significant (Fig. 3a; Mann–Whitney–Wilcoxon, $W = 35.5$, $P = 0.385$). In contrast, CRF density in coral microhabitats was 55.71 ± 14.88 ind·m^{-2}, which was significantly higher than that in rocky microhabitats 24.68 ± 4.06 ind·m^{-2} (Fig. 3b; Mann–Whitney–Wilcoxon, $W = 46.5$, $P = 0.036$). The highest CRF density was recorded in a coral microhabitat, with values of 102.38 ind·m^{-2}, whereas density never exceeded 50 ind·m^{-2} in rocky microhabitats (Table S1).

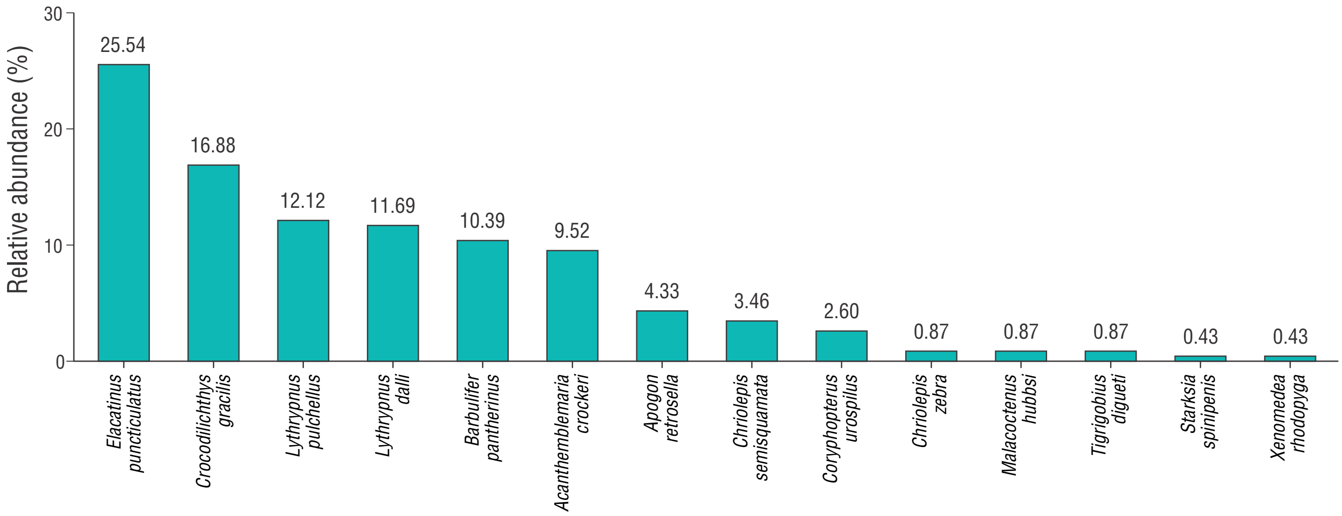

Figure 2. Relative abundance (%) of the total cryptobenthic reef fish (CRF) analyzed in this study.

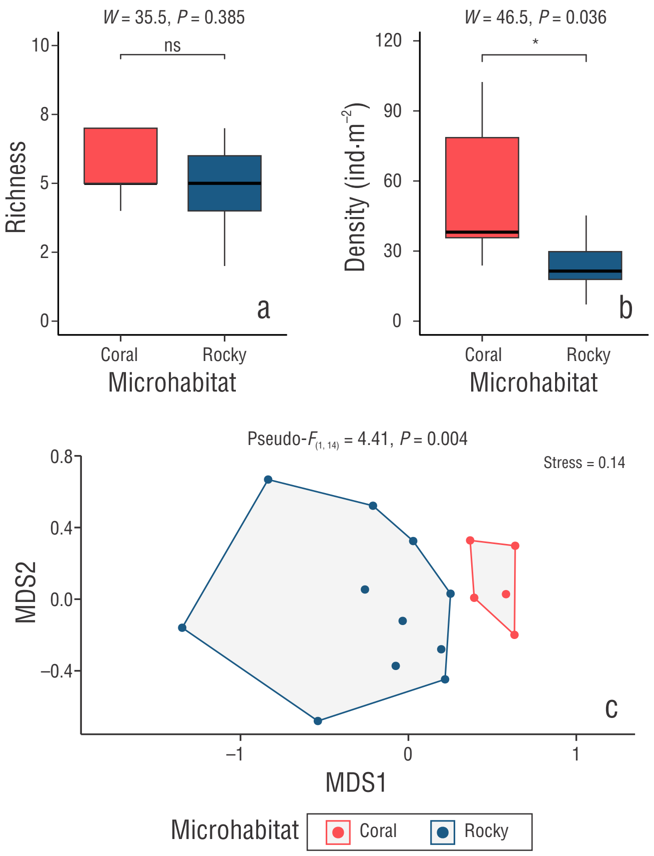

Figura 3. Comparison of richness (**a**) and density (**b**) of cryptobenthic reef fish (CRF) in coral microhabitats (*Porites panamensis*) and rocky microhabitats. Assemblage composition analysis using non-metric multidimensional scaling (NMDS) of the density of the 14 CRF species in the 16 analyzed microhabitats (**c**). The results of the Mann–Whitney–Wilcoxon analyses and permutational multivariate analysis of variance (PERMANOVA) are shown at the top of the graph.

The PERMANOVA analysis showed significant differences in the structure and composition of CRF assemblages between coral and rock microhabitats (Pseudo-F = 4.4, P = 0.004). Similarly, the NMDS revealed a differential ordering of 2 clearly defined groups, graphically evidencing the dissimilarity in the structure and composition of CRF assemblages for each microhabitat (Fig. 3c). The SIMPER analysis allowed us to identify the CRF species that contributed the most to this dissimilarity between microhabitats (Table 1). The species *E. puncticulatus*, *Acanthemblemaria crockeri*, and *L. dalli* contributed the most to the differences between microhabitats. Concurrently, these species had the highest density values in coral microhabitats, whereas other species, such as *C. gracilis*, *Apogon retrosella*, *Chriolepis semisquamata*, and *Coryphopterus urospilus*, had highest values in rocky microhabitats (Table 1, Table S2). In addition, the alluvial diagram allowed us to graphically represent the typical structure of CRF assemblages in coral and rocky microhabitats (Fig. 4).

Regarding habitat complexity, 3D rugosity reached an average value of 2.03 ± 0.56 in coral microhabitats, whereas rugosity was 1.69 ± 0.40 in rocky microhabitats. Nevertheless, differences between microhabitats were not significant (Mann–Whitney–Wilcoxon, W = 38, P = 0.257).

DISCUSSION

In the Mexican Pacific, numerous studies have explored the influence of habitat complexity on the structuring of fish assemblages (i.e., Aburto-Oropeza and Balart 2001, López-Pérez et al. 2013). However, these studies have commonly involved conspicuous species and evaluated relatively general characteristics of the reefs, such as coral cover, bottom rugosity, or variables derived from functional diversity analyses (Olán-González et al. 2020, Dubuc et al. 2023). Few studies in the TEP have analyzed, at a very fine spatial scale (i.e., 1 × 1 m), the influence of microhabitats (i.e., soft corals, hard corals, rock, and rubble) on the structure of cryptic fish assemblages (Alzate et al. 2014, Galland et al. 2017, González-Murcia et al. 2023). This study analyzes the importance of the coral *P. panamensis* in structuring the CRF of the north-central Gulf of California. The results of this study offer a window to explore the importance of this under-evaluated group of fish and how they could be influenced by microhabitat characteristics, particularly in reef-building corals.

Corals of the genus *Porites* can develop highly complex habitats, measuring more than 6 m in diameter and housing a notable abundance and diversity of reef fishes (Nanami and Nishihira 2004). *Porites* colonies with branching columnar morphology have been documented to host even greater functional richness of fish compared to corals of the genus *Pocillopora* (Richardson et al. 2017). The present study showed no differences in CRF richness between rocky and coral microhabitats, which differs from what was reported in the Pacific of Panama by Dominici-Arosemena and Wolff (2006), who observed differences in fish diversity between microhabitats of massive corals, branching corals, and coral rubble. However, in this study, we probably did not observe significant differences between microhabitats due to the low number of species recorded. Rocky microhabitats had a cumulative specific richness of 11 species, and coral microhabitats had a cumulative richness of 9 species (Table 1). Specific richness depends on sampling effort (Magurran 2003); therefore, long-term spatiotemporal studies will significantly improve the quality of the biological inventory of both microhabitats.

On the other hand, in this study, the average density of CRF in rocky microhabitats was 24.68 ± 4.06 $\text{ind}\cdot\text{m}^{-2}$, which was very similar to the 20.9 ± 1.7 $\text{ind}\cdot\text{m}^{-2}$ reported by González-Cabello and Bellwood (2009) in Loreto Bay, Gulf of California. Contrary to our results, these authors observed relatively low densities in coral colonies, where *Protemblemaria bicirris* (20.66%) and *A. crockeri* (14.37%) were the dominant species. On the other hand, in this study, we observed that coral microhabitats (9.05 ± 1.75 $\text{ind}\cdot\text{m}^{-2}$)

had higher densities of *A. crockeri* than rocky microhabitats (0.65 ± 0.46 ind·m^{-2}), whereas González-Cabello and Bellwood (2009) observed an opposite pattern for this species, which was more abundant in rock (5.00 ± 1.24 ind·m^{-2}) than in coral heads (*Pocillopora*) (1.50 ± 0.85 ind·m^{-2}). This suggests that local factors, along with habitat availability and structure, influence both the distribution and habitat preferences of species (Arias-González et al. 2006). Therefore, our hypothesis was partially confirmed. Despite the higher density values recorded in coral microhabitats, these did not correspond to an increase in richness. We expected that habitat complexity would be a determining factor under the premise that corals would have greater structural complexity. However, the analyses showed no significant differences in 3D rugosity, which suggests that corals were not structurally more complex than rocky microhabitats.

It is important to note that only *P. panamensis* has been detected as an important species in the construction of

Table 1. Average density and similarity percentage analysis (SIMPER) of all cryptobenthic reef fish (CRF) species collected in coral microhabitats (*Porites panamensis*) and rocky microhabitats. *Endemic species of the Cortez biogeographic province (Palacios-Salgado et al. 2012).

	Average density (ind·m^{-2})			
Species	Coral ($\bar{x}$ ± EE)	Rocky ($\bar{x}$ ± EE)	Average contribution (%)	*P* value
Elacatinus puncticulatus	19.05 ± 7.26	4.11 ± 1.25	17.66	0.020
*Acanthemblemaria crockeri**	9.05 ± 1.75	0.65 ± 0.46	12.21	0.001
Lythrypnus dalli	9.05 ± 4.15	1.73 ± 0.79	10.70	0.008
*Barbulifer pantherinus**	7.62 ± 3.48	1.73 ± 0.56	7.37	0.094
*Crocodilichthys gracilis**	4.76 ± 1.99	6.28 ± 1.99	7.27	0.995
Lythrypnus pulchellus	4.29 ± 2.65	4.11 ± 2.73	6.80	0.967
Apogon retrosella		2.16 ± 0.50	3.11	0.713
*Chriolepis semisquamata**		1.73 ± 0.85	2.35	0.991
Coryphopterus urospilus		1.30 ± 0.67	2.21	0.981
Tigrigobius digueti	0.95 ± 0.95		0.76	0.023
*Chriolepis zebra**		0.43 ± 0.29	0.63	0.981
*Malacoctenus hubbsi**		0.43 ± 0.43	0.54	0.987
Starksia spinipenis	0.48 ± 0.48		0.47	0.021
*Xenomedea rhodopyga**	0.48 ± 0.48		0.47	0.021

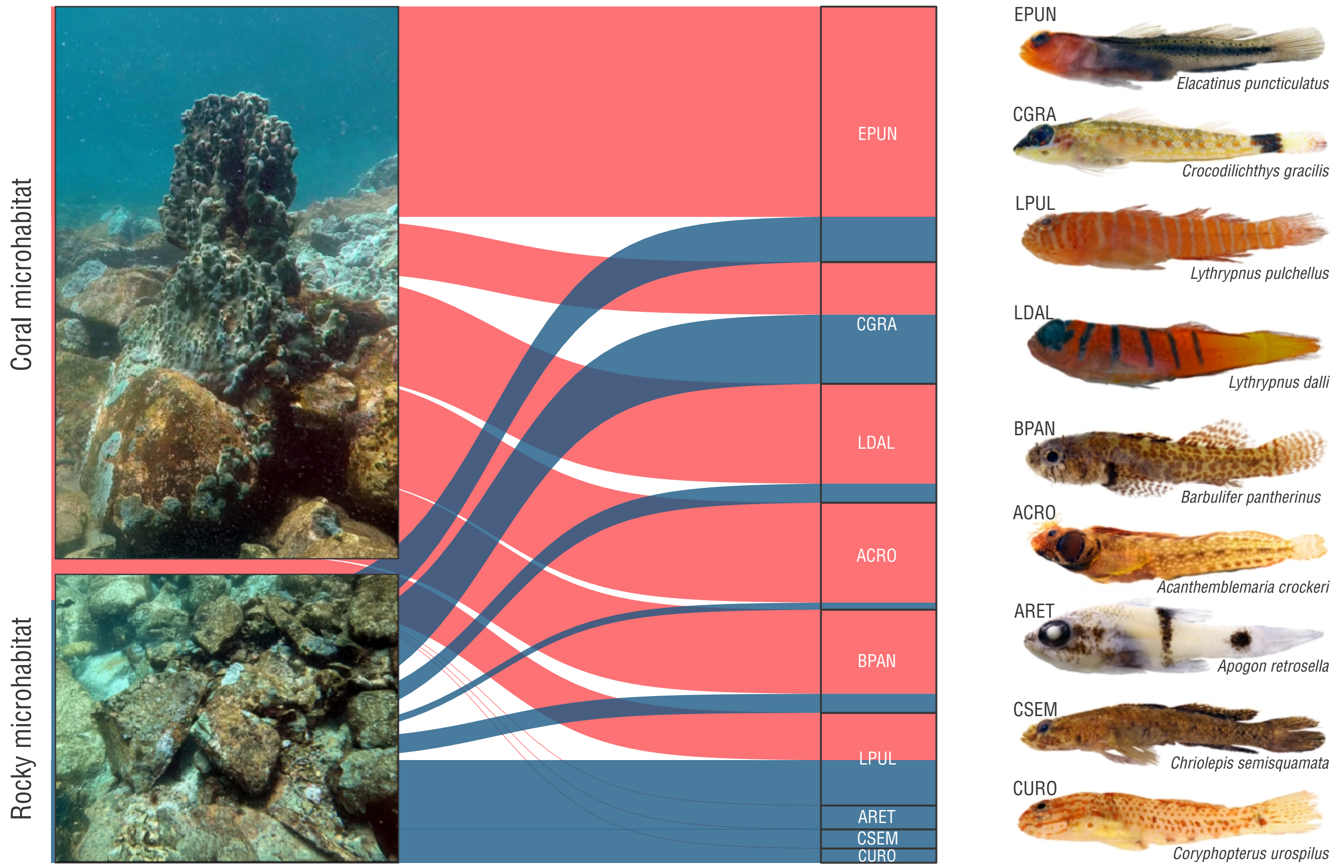

Figure 4. Alluvial diagram of the preference of the most abundant cryptobenthic reef fish species and their affinities towards coral and rocky microhabitats. EPUN = *Elacatinus puncticulatus*, CURO = *Coryphopterus urospilus*, CGRA = *Crocodilichthys gracilis*, LPUL = *Lythrypnus pulchellus*, LDAL = *Lythrypnus dalli*, BPAN = *Barbulifer pantherinus*, ACRO = *Acanthemblemaria crockeri*, ARET = *Apogon retrosella*, CSEM = *Chriolepis semisquamata*. The thickness of the lines is proportional to the average density of each species in each microhabitat.

shallow coral reefs in Bahía de los Ángeles, whereas further south (i.e., Loreto), it has been reported that other species of hard corals that form coral reefs are more important in terms of coral cover (i.e., *Pocillopora*). Therefore, the results of González-Cabello and Bellwood (2009) and those of this study could indicate that there are CRF assemblages for each coral species. Troyer et al. (2018) determined that there is a CRF structure for each type of substrate in shallow reefs of the Red Sea, where the abundance, diversity, and richness of species was greater in rubble microhabitats than in coral reefs or sandy substrates; however, at the species assemblage level, they identified particular species for each type of microhabitat. In fact, Brandl et al. (2018) and Brandl et al. (2020) have described unique assemblages for each type of substrate or microhabitat and have determined that, in addition to a marked differentiation in assemblages of species, there is a marked intra- or interspecific partitioning of the trophic niche.

In the northern Gulf of California, *P. panamensis* likely plays a crucial functional role as a microhabitat for CRF, similar to what has been observed for cryptobenthic species in other regions of the world (Brandl et al. 2018, Troyer et al. 2018). The importance of CRF in reef trophodynamics was not evaluated in this work; however, CRF are known to contribute substantially to the recycling of matter and energy in the Gulf of California. Galland et al. (2017) demonstrated that, in the Gulf of California, CRF represent more than 40% on average of the species richness per site, more than 95% of the total fish abundance, and up to 56% of the metabolic requirements on a reef. These authors divided the Gulf of California into north and south (Bahía de los Ángeles is in the north of this division), and reported that there is a greater contribution of CRF in biomass, abundance, and metabolism in the north. Therefore, the authors suggest that CRF are a crucial group of fish in the recycling of matter and energy, although this contribution seems to have greater relevance in the islands of the northern Gulf of California than in the south. Furthermore, Ackerman and Bellwood (2000) obtained similar results on Orfeo Island, Australia; these authors determined that fish less than 10 cm in length can use more than 57% of the metabolism of the ecosystem. Brandl et al. (2018) also demonstrated that CRF have much higher metabolic rates, mortality rates, and fecundity than conspicuous fish, and concluded that, as a biological group, CRF have very high turnovers in the ecosystem, categorizing CRF as the "pivotal" part of the reefs.

CONCLUSIONS

The Gulf of California is among the most diverse and productive ecosystems in the world, where 104 species are CRF (40% are endemic to the Gulf of California; Galland 2013). Because CRF have no commercial value for human consumption, they have generally been excluded from ichthyological evaluations in the Mexican Pacific. However, they play crucial roles within ecosystems by having close associations with the benthos, providing vital energetic links between the benthos and nekton and playing an important role in the trophodynamics of coral reefs by providing energy towards larger consumers (Galland et al. 2017). In the present study, the structure and composition of CRF assemblages differed between rocky and coral microhabitats, with higher CRF density in coral microhabitats. Furthermore, 5 species contributed 76.62% of the total abundance. This work represents one of the first efforts to understand the structuring of CRF in the shallow reefs of the Mexican Pacific. Future efforts should focus on understanding the role of CRF in reef trophodynamics in the region and sites further south, especially as the coral recovery and restoration programs proposed in recent decades in the central-southern Mexican Pacific have not evaluated CRF, despite the crucial role they likely play in these processes. Furthermore, the low environmental tolerance, rapid population turnover times, and scarce exploitation of CRF (Brandl et al. 2018) make them a model group to generate ecological hypotheses in ichthyological studies in the Mexican Pacific.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

Supplementary Material

The supplementary material for his work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3495/420421150.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: All; Data curation: LMJD; Formal analysis: LMJD; OMV, LBL Funding acquisition: OMV; Investigation: All; Methodology: LMJD, RDCO; Project administration: OMV; Resources: OMV; Software: LMJD; Supervision: OMV, LECA, LBL; Validation: OMV, LECA, LBL; Visualization: LMJD; Writing–original draft: LMJD, RDCO, LECA, OMV; Writing, review, and editing: OMV, LMJD, RDCO, LECA.

Data availability

The data for this study are available from the corresponding author upon reasonable request.

Ethical approvals and permissions for animal studies

We obtained the corresponding fishing permits for this study: PPF/DGOPA-035/21 and PPF/DGOPA-085/22. Likewise, on each field trip, the staff of the *Comisión Nacional de Áreas Naturales Protegidas* (CONANP) of the *Bahía de los Ángeles, Canales de Ballenas y Salsipuedes* Biosphere Reserve was informed to obtain approval and the no-objection documentation.

Use of AI tools

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

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Night surveys reveal abundant populations of sea urchins with high erosive potential in Cayo Arenas, Campeche Bank

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ABSTRACT. Sea urchins perform key ecological functions in coral reefs, such as herbivory and erosion of calcareous structures, which intensify at night. The Cayo Arenas reef, Campeche Bank, Mexico, is located far from the coast, which has helped to protect it from direct anthropogenic threats. However, there is no information available on the status of sea urchin populations and the bioerosion processes they perform in the reef. For this reason, we conducted diurnal and nocturnal surveys to characterize urchin density as a function of the diel cycle and to calculate their bioerosive potential. The surveys were conducted at 3 sites with different depths (10–19 m) and varying reef heterogeneity related to 2 components: coral cover and sand cover. All surveys were conducted in July 2023. In general, an abundant population of urchins was observed, which was mainly composed of *Diadema antillarum*. At night, the abundance (14.5 ± 3.8 ind) and bioerosion rate (1.55 ± 0.53 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$) were higher than during the day (2.6 ± 0.8 ind and 0.2 ± 0.06 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$). In addition, depth and reef geomorphology seemed to influence the pattern of urchin density. At sites with high reef heterogeneity, sea urchin density was higher at night, which could be associated with a greater availability of refuge from predators. Our results show an underestimation of urchin population densities in daytime surveys and, therefore, their impact on the ecosystem as bioerosion agents because sea urchins are mostly nocturnal but are commonly surveyed during the day.

Key words: echinoderms, geoecological functions, keystone species, carbonate budget, *Diadema antillarum*, Campeche Bank.

INTRODUCTION

Coral reefs are characterized by complex three-dimensional structures of calcium carbonate ($CaCO_3$) developed mainly through the interaction of 2 geo-ecological processes: (1) $CaCO_3$ gross production, driven primarily by scleractinian corals, and (2) bioerosion, derived from the activity of numerous organisms that remove carbonate directly from the reef matrix (Chave et al. 1972, Perry 2011), as well as processes of cementation, lithification, and physical exportation of materials (Cornwall et al. 2021). As mentioned in Sheppard et al. (2018), production and erosion processes are present in a reef in ecological balance. However, a positive balance (i.e., production rate greater than erosion rate) is necessary for the reef to grow. Despite the importance of erosion processes in reef ecosystems, many studies have focused mainly on the production processes of coral $CaCO_3$ (Perry and Lange 2019); in the case of bioerosion, the number of species-specific studies is much smaller and limited to a few sites and environmental gradients (Brown et al. 2020, Perry et al. 2023).

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Understanding the role of bioeroders is particularly relevant in the current context, where increasing human pressures (e.g., rising temperatures, coastal development, and overfishing) are affecting not only calcifiers but also bioerosion processes, which can vary at different spatial and temporal scales (Perry et al. 2014, Schönberg et al. 2017, Molina-Hernández et al. 2022). Currently, the scenarios observed reflect those reported by Molina-Hernández et al. (2020), in which the low levels of bioerosion are determining the direction (i.e., accretion or net erosion) and speed with which carbonate balances shift towards neutral scenarios (~1–0 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$) in various highly degraded Caribbean reefs.

Sea urchins are important bioeroders in coral reefs (Bak 1994, Glynn and Manzello 2015). Historically, the main eroding urchin in the tropical Atlantic Ocean has been *Diadema antillarum* (Bak 1994, Hutchings 2011). However, given the mass mortality of this species as a result of a disease outbreak in the 1980s, its populations drastically decreased throughout the region (Lessios et al. 1984). At present, most Caribbean reefs are characterized by low urchin abundance (Hughes et al. 2010). *Diadema antillarum* has shown localized recovery in certain sites (Jorgensen et al. 2008, Keller 2011, Johnston et al. 2021), but recent disease outbreaks have caused new mortality events (Levitan et al. 2023), which could be reversing recovery trends in its populations (Tuohy et al. 2020). In the Gulf of Mexico, current urchin populations are larger than in the Caribbean; however, they are dominated by urchins of the genus *Echinometra* (González-Azcárraga 2009, Morales-Quijano et al. 2017, Johnston et al. 2021). Mass mortality events have not only reduced *D. antillarum* populations, but also their contribution to coral reef bioerosion, going from values of up to 5.3 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ (Scoffin et al. 1980) to only 0.1 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ (Perry et al. 2014). Currently, parrotfishes are considered the dominant bioerosion agents in the Caribbean (Perry et al. 2014, Molina-Hernández and Álvarez-Filip 2024).

Rates of urchin bioerosion have decreased by up to 90% due to low population densities in the Caribbean (Perry et al. 2014). However, the population of urchins could be underestimated as most surveys are performed during the day, when urchins retreat into their shelters (Mills et al. 2000, Tuya et al. 2004, Young and Bellwood 2011). Most urchin species are nocturnal and have a peak in their movement patterns (movement on the substrate) during the night when they feed. Their activity decreases as dawn breaks, and urchins are cryptic during the day (Smith et al. 2024). Likewise, under experimental conditions, 90% of sea urchins show negative phototaxis and seek refuge when exposed to ultraviolet light (Adams 2001). However, it remains to be confirmed whether this behavior in natural conditions is related to other variables such as depth and solar radiation (Adams 2001). In addition, reef structural heterogeneity can influence the population density of sea urchins; as depth increases, colonies tend to have flatter morphologies (due to decreased light), and the amount of sand increases, so there is less space available for shelter (Griffin et al. 2003). This is important because erosive species (*D. antillarum*, *Echinometra* spp., and *Eucidaris tribuloides*) prefer rocky and coral substrates (Celaya-Hernández et al. 2008, González-Azcárraga 2009), with bigger population densities at depths of 3–5 m for *D. antillarum* (Sellers et al. 2010), 1–6 m for *Echinometra viridis* (Griffin et al. 2003), and 1–3 m for *E. tribuloides* (McPherson 2018).

In the Campeche Bank, and in most of the Gulf of Mexico, sea urchin research has focused mainly on the taxonomy (Durán-González et al. 2005, Solís-Marín et al. 2013) and the distribution and species composition of all echinoderm groups (Vázquez-Bader et al. 2008). Few studies have focused on the taxonomic diversity, the description of urchin habitat, and variations in *D. antillarum* population density between day and night, although the latter has been addressed in a very lax manner (Celaya-Hernández et al. 2008, González-Azcárraga 2009). Almost all the information available for the southeastern Gulf of Mexico is restricted to the Veracruz Reef System (VRS) (Durán-González et al. 2005, Celaya-Hernández et al. 2008, González-Azcárraga 2009).

For this region, some authors report *Echinometra lucunter* as one of the most abundant species at shallow depths, both in the crest area and in the reef lagoon, where it is associated with rocky-coral substrate (Lara et al. 1992, Celaya-Hernández et al. 2008). González-Azcárraga (2009) found that population density and species diversity are greater in the Gulf of Mexico than in the Mexican Caribbean, and observed higher values for the 2 variables at shallow depths (1–10 m) than at greater depths (10–15 m) in both regions. However, in recent years, *D. antillarum* has shown low population densities (~0.5 $ind \cdot m^{-2}$) in both regions (Celaya-Hernández et al. 2008, González-Azcárraga 2009).

The above indicates that the study on the ecological functionality of sea urchins with erosive potential (i.e., *D. antillarum*, *E. viridis*, *E. lucunter*, and *E. tribuloides*) still presents gaps, both ecological and geographical, in the Gulf of Mexico and, especially, in the Campeche Bank. Therefore, in this study, we evaluated and compared the abundance of sea urchins and their bioerosion potential between diurnal and nocturnal visual surveys conducted at 3 sites with different characteristics of reef heterogeneity. Due to the nocturnal habits of sea urchins, we expected greater variation in urchin abundance between day and night in locations with greater reef heterogeneity and, consequently, higher bioerosion rates.

MATERIALS AND METHODS

Study area

Cayo Arenas (Fig. 1) belongs to a set of reefs on the Campeche Bank in the Gulf of Mexico (Logan et al. 1969, Sanvicente-Añorve et al. 2014). The Campeche Bank does not have reef barriers, which leaves the platform devoid of physical protection from wave and wind energy, and open to the influence of the Loop Current in the western part of the Gulf of Mexico (Logan et al. 1969). Cayo Arenas is considered a platform reef with complex reef structures, called "walls", with depths up to 30 m (Tunnell and Chávez 2013). In addition, it is a remote reef with limited access located ~200 km from the coastal area. Various authors have classified these reef structures based on their location: the northeastern structure, which is the largest formation with 2 emergent zones, and the southeastern structure, the smallest of the structures with one small emergent zone, which receives the greatest energy from the wind and waves along with the Northeast wall. The eastern structure has a lagoon on the windward side and a cay with vegetation on sand blocks and coral skeletons; due to its location, the structure is protected from wave and wind energy (Logan et al. 1969, Chávez et al. 2007, Tunnell and Chávez 2013).

The study area covered 3 sites (Bajo Tortugas, Cayo Arenas 1 [CA1], and Cayo Arenas 14 [CA14]), located in the protected zone of the reef, with different depths and benthic components, such as coral, sand, and hard substrate (i.e., calcareous matrix that is not covered by coral tissue). Bajo Tortugas is a submerged reef that was sampled between 12 and 13 m depth. This site had a well-developed coral community, with a coral cover of 23%, absence of sand cover, and a hard substrate cover of 77%, which made it the site with the greatest heterogeneity and, therefore, available habitat. In Bajo Tortugas, the reef structure was mainly formed by corals with massive and large morphologies such as *Orbicella* spp. and *Colpophyllia natans*. In contrast, CA1 was located leeward in the eastern zone and had discontinuous coral patches separated by large sand areas. In addition, this site presented 20% coral cover, 11.6% sand cover, and 68.4% hard substrate cover. Therefore, CA1 showed medium reef heterogeneity. Cayo Arenas 14 was located in the leeward reef lagoon and was sampled down to 19 m. The site had a mixed composition of corals and algae, with 12% coral cover, 8.5% sand cover, and 79.5% hard-substrate cover. Compared to CA1, CA14 had more continuous coral patches, but low reef heterogeneity.

Field work

Diurnal and nocturnal visual surveys were conducted following the ReefBudget methodology (Perry and Lange 2019). For day and night surveys, we deployed 10 × 1 m band transects. However, for night surveys, transects were modified to 20 × 0.5 m to focus on a smaller area and make data collection with the diving lights more efficient during sampling. The transects were 10 m² for all cases. In each transect, the number of urchins per species and the size of the testa were recorded following size classes of 20 mm (i.e., 0–20, 21–40, 41–60, 61–80, and 81–100 mm). The records were made considering only eroding species, including *D. antillarum*, *E. viridis*, *E. lucunter*, and *E. tribuloides*. All surveys were conducted with scuba diving equipment in July 2023. Daytime surveys were conducted between 08:00 h and 14:00 h, whereas night durveys were conducted one hour after sunset at all sites (i.e., around 20:00 h). Figure 1 shows the exact monitoring schedules for each site. Current intensity and reef depth complicated monitoring efforts; therefore, the number of transects varied between sites and between diurnal and nocturnal surveys. In CA1, 5 transects were done during the day at 8 m depth and 7 transects at night at 9.8–10 m depth. In Bajo Tortugas, 6 transects were done during the day at 7.5–11.2 m depth and 5 transects at night at 8.5–11 m depth. Finally, in CA14, 6 transects were done for both times of the day, at 18.5 m depth during the day and 17 m depth at night. For all sites, monitoring was only conducted once a day and once at night. The sampling depths were random because transects were deployed on coral substrate.

Estimation of abundance and rate of urchin bioerosion

Urchin abundance per site (number of individuals) was estimated from the surveys. Urchin bioerosion rate was estimated according to species identity, the number and size of urchins (based on testa diameter), and constants from previously published species-specific regression equations compiled in Perry and Lange (2019). These equations describe the relationship between the size of urchin and the bioerosion values (g urchin$\cdot$d^{-1}) based on the analysis of stomach content, reported for different urchin sizes (see Perry and Lange 2019). The annual rate was calculated from the daily rate multiplied by 365 (days of the year), and was standardized to 1 m²; values are reported in kg $CaCO_3\cdot m^{-2}\cdot y^{-1}$ (Perry and Lange 2019). This approach assumes constant bioerosion rates throughout the year.

Benthic description of sites

Coral, sand, and hard substrate cover data were obtained through orthomosaic analysis. The information collected helped to determine the reef heterogeneity of the sites based on the amount of coral cover, hard substrates, and sand. Underwater images were obtained with scuba diving using 2 cameras equipped with waterproof housing. For each site, orthomosaics were constructed using underwater photogrammetry following the methodology proposed by Hernández-Landa et al. (2020). This consisted of delimiting plots of ~400 m² with transects and polyvinyl marks (6 m × 0.6 m). Each plot was divided in 2 by the central mark and each half was photographed by 2 divers swimming at a speed of ~5 m$\cdot$min^{-1}. Photographs were taken 2 m above the average depth of the reef bottom. Depth was recorded at the beginning and end of each transect with a standard dive computer. For each site, ~4,000 images were obtained with a high level of overlap (>70%). The images were processed in AgiSoft Metashape v. 2.0.3 (Agisoft 2024) with Structure from Motion algorithms. To build orthomosaics and digital elevation models, 3 steps were followed: (1) initial processing (internal and external orientation of the camera and creation

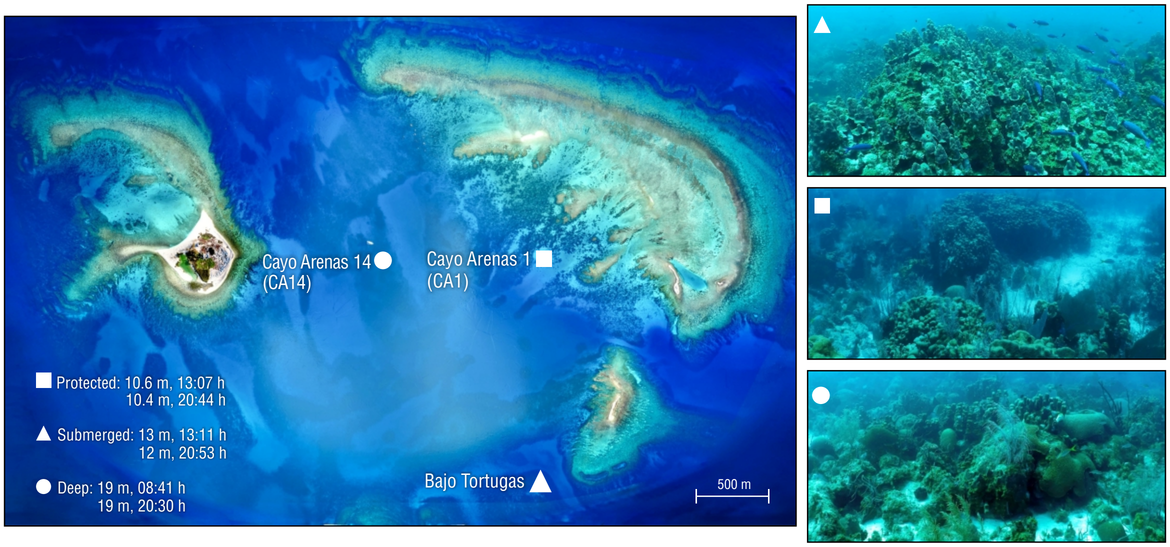

Figure 1. Location of the 3 sampling sites in Cayo Arenas, Campeche Bank. The photos show the representative characteristics of the coral community and the depth and sampling schedule for each Site. The photo of Cayo Arenas is an orthomosaic composed of photos taken by drone; the flights and construction of the orthomosaic were done by Lorenzo Alvarez-Filip. Lorenzo Alvarez-Filip and Esmeralda Pérez-Cervantes took the photos of the reef.

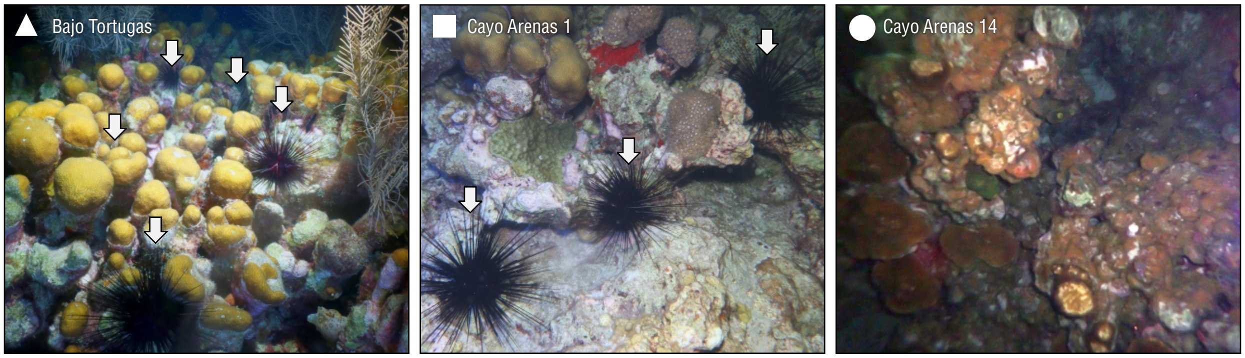

Figure 2. Graphic representation of the number of *Diadema antillarum* urchins during nocturnal surveys at the 3 sampling sites. A gradient is observed in the abundance of urchins that decreases from left to right: Bajo Tortugas (5 urchins), Cayo Arenas 1 (3 urchins), and Cayo Arenas 14 (no urchins). Lorenzo Alvarez-Filip and Esmeralda Pérez-Cervantes took the photos of the urchins.

of sparse clouds); (2) generation of point clouds and meshes; and (3) digital surface modeling (DSM) and orthomosaic construction. Because the images did not have geolocation, the polyvinyl marks were used as a contrast measure to transform the model into absolute measurements (Hernández-Landa et al. 2020).

The orthomosaics were analyzed in ArcMap v. 10.6 (ESRI 2017). Sections of each plot were joined along the center mark using spatial snap extension. One orthomosaic was constructed per site, and the scleractinian coral colonies were identified to the species level (Human and Deloach 2002, Lang and Marks 2018). For each colony, coral cover of living tissue was manually digitized following its contour, considering colonies ≥ 5 cm^2. Data matrices were created to estimate the cover (cm^2) at each site. For each site, vector layers of coral cover and sand cover were generated in an area of 380 m^2. The cover of other hard substrates (i.e., calcareous matrix that is not covered by coral tissue) was estimated by subtracting the digitized area from the total area analyzed.

Data analysis

To explore potential differences between sites and sampling times (day and night monitoring), we used 2 generalized linear models (GLM). We opted for GLM instead of linear models due to their ability to fit distributions of response variables that do not follow a normal distribution. The first model analyzed urchin abundance (total number of individuals observed [1]), whereas the second evaluated bioerosion rates (kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ [2]). To evaluate differences between individuals between day and night we used abundance instead of density (ind·m^{-2}) because the model requires discrete data (Crawley 2005). However, we present the results using density units to facilitate comparison with previous studies. We fit the models using the 'glm()' function. The dependent variables were urchin abundance (Y1) and bioerosion rate (Y2), whereas predictor variables included the site (Bajo Tortugas, CA1, and CA14), the survey time (diurnal or nocturnal), and the interaction between both variables. Data were not transformed for analysis; however, different distributions were used to address the non-normal distribution for the response variables: (1) a Poisson distribution with log link (log) for abundance and (2) a Gaussian distribution with identity link function for the rate of urchin bioerosion. Model validation was carried out using residual plots generated with the 'simulateResiduals()' function of the 'DHARMa' package. Subsequently, for each model, we performed a 2-way analysis of variance (ANOVA) (Type II Wald chi-square tests using the 'Anova()' function from the 'car' package. We performed post hoc tests using adjusted marginal means analyses with the Bonferroni correction with the 'emmeans()' function from the package of the same name. All analyses were performed in R v. 2023.12.0 (R Core Team 2023).

The models used were mathematically represented as follows:

$$\log(Y_1) = \beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + \beta_3 \cdot (X_1 \cdot X_2) \quad , \qquad (1)$$

$$X_2 = \beta_0 + \beta_1 \cdot X_1 + \beta_2 \cdot X_2 + \beta_3 \cdot (X_1 \cdot X_2) + \epsilon , \qquad (2)$$

where Y_1 and Y_2 represent the dependent variables (urchin abundance and bioerosion rate, respectively); β_0 is the intercept; β_1 and β_2 are the coefficients associated with the survey time (X_1) and the site (X_2), respectively; β_3 corresponds to the interaction coefficient between survey time and site ($X_1 \cdot X_2$); and ϵ is the residual error term, which follows a normal distribution.

RESULTS

Urchin abundance

Cayo Arenas had greater urchin abundance during the night (14.5 ± 3.8 ind) than during the day (2.6 ± 0.8 ind). This pattern was observed at the sites Bajo Tortugas and CA1 (Fig. 3). For the 3 sites, the most abundant species was *D. antillarum*, both in the diurnal (1.4 ± 0.4 ind) and nocturnal (10.2 ± 3.3 ind) surveys, followed by *E. viridis* (0.18 ± 0.1 ind and 3.9 ± 1.2 ind, respectively), and *E. lucunter* (1 ± 0.4 ind and 0.16 ± 0.2 ind, respectively); *E. tribuloides* was only observed during the night (0.2 ± 0.2 ind). Site evaluation showed that Bajo Tortugas had lower urchin abundance in diurnal surveys (2.7 ± 0.95 ind) than in nocturnal surveys (28.4 ± 09.5 ind); the same occurred for CA1 (diurnal: 5.6 ± 1.9 ind; nocturnal: 16.8 ± 3.2 ind). In CA14, there was only one record of the species *D. antillarum* at night (Table 1).

The 2-way ANOVA showed differences in urchin abundance between sites ($\chi^2_{(2)} = 33$, $P < 0.05$), between diurnal and nocturnal surveys ($\chi^2_{(1)} = 93.9$, $P < 0.05$), and between the interaction of these variables ($\chi^2_{(2)} = 14$, $P < 0.05$). The post hoc test showed differences between diurnal and nocturnal abundance in Bajo Tortugas ($P < 0.05$) and in CA1 ($P < 0.05$) (Fig. 3).

Bioerosion potential

The bioerosion potential for Cayo Arenas was significantly higher in nocturnal surveys (1.55 ± 0.53 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$) than in diurnal surveys (0.2 ± 0.06 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$). In Cayo Arenas, the species with the greatest contribution to the bioerosion potential, both during the day and at night, was *D. antillarum* (0.19 ± 0.06 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ and 1.5 ± 0.53 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$, respectively), followed by *E. viridis* (0.002 ± 0.001 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ and 0.05 ± 0.014 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$, respectively), *E. lucunter* (0.013 ± 0.006 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ and 0.003 ± 0.003 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$, respectively), and *E. tribuloides* (0.003 ± 0.002 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ in nocturnal surveys). In Bajo Tortugas, the diurnal bioerosion rate was 0.29 ± 0.1 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ and the nocturnal bioerosion rate was 3.9 ± 1.49 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$. In CA1, diurnal and nocturnal bioerosion rates were 0.33 ± 0.13 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ and 1.18 ± 0.12 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$, respectively; in CA14, the nocturnal bioerosion rate was 0.02 ± 0.02 kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$ (Table 1).

The statistical analyses used to compare bioerosion rates between sites and between diurnal and nocturnal surveys showed differences in the bioerosion rate between sites ($\chi^2_{(2)} = 14.8$, $P < 0.05$) and between the 2 types of survey ($\chi^2_{(1)} = 11.4$, $P < 0.05$). Furthermore, urchin bioerosion rates in Cayo Arenas showed a significant interaction between both variables ($\chi^2_{(2)} = 12.7$, $P < 0.05$). The post hoc test showed differences between sites and between the 2 types of survey (Fig. 4); however, only Bajo Tortugas showed differences between nocturnal and diurnal bioerosion rates ($P < 0.05$) (Fig. 4).

DISCUSSION

In this study, we found significant changes in population densities and bioerosion potential between diurnal and nocturnal surveys in Cayo Arenas. In addition, the most abundant species with the greatest changes in diurnal and nocturnal abundance was *D. antillarum*. Due to its high nocturnal abundance, *D. antillarum* boosted the total bioerosion potential, which is, the summed effect of the 4 species of eroding urchins found in the study sites. Furthermore, we observed that the site with the greatest changes between day and night for both variables was the site that had the reef with the greatest reef heterogeneity, that is, with continuous coral patches and without sand patches (Bajo Tortugas). At the site with the greatest depth and largest sand patches, only one urchin (CA14) was recorded. In general, the results indicated that bioerosion rates are proportional to the abundance of urchins (Figs. 3, 4), therefore, in sites where they are still abundant, such as in Cayo Arenas, urchins have an important role in the carbonate dynamics in the reef.

Our findings evidence that there are still reef sites dominated by *D. antillarum*, despite historical and current reports of the mortality of this species (Lessios 2016, Levitan et al. 2023). Currently, the density of urchins in the Caribbean continues to be zero for some sites (Kuffner et al. 2019) and very low for others, such as for the back reefs in the Florida Keys, where the average density of *D. antillarum* urchins ranges between 0.017 to 0.026 ind·m^{-2} (Chiappone et al. 2013), or the front reefs of the northern Mexican Caribbean (Molina-Hernández et al. 2020). Studies that have reported the abundance of urchins in the Gulf of Mexico have recorded values similar to those of Cayo Arenas. For example, in VRS, average urchin densities have been estimated between 0.646 (González-Azcárraga 2009) and 1.4 ind·m^{-2} (Horta-Puga et al. 2017), whereas, for the reef banks of Flower Gardens and Stetson Bank in the northern Gulf of Mexico, reports show average densities between 0.28 to 1 ind·m^{-2} (Nuttal et al. 2020, Johnston et al. 2021). In these studies, the data were obtained during diurnal surveys, which suggests that there is a possibility that urchin densities in VRS and Flower Gardens are higher; therefore, it is recommended to confirm these findings in these and other systems in the Gulf of Mexico through nocturnal surveys, particularly in reefs with high structural heterogeneity.

Regarding the species reported for Cayo Arenas, the one with the highest density was *D. antillarum* (diurnal and nocturnal surveys), which highlights the importance of the populations of this species in a regional context, since *D. antillarum* has experienced severe population losses throughout its range (Chiappone et al. 2002, González-Azcárraga 2009, Levitan et al. 2023). The 2 species of the genus *Echinometra* recorded in this study had much lower densities compared to what was reported in the reef systems of Veracruz, Mexico (González-Azcárraga 2009, Morales-Quijano et al. 2017).

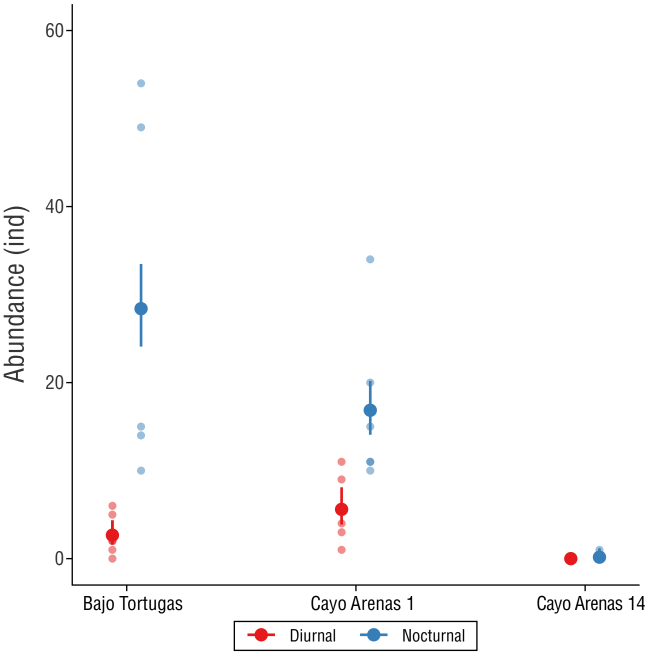

Figure 3. Urchin abundance (number of individuals) in the Cayo Arenas reef, Campeche Bank. The points indicate the predicted means for each site and survey type (diurnal and nocturnal), and the error bars represent the 95% confidence intervals (CI). Both calculations come from the adjusted marginal means based on the generalized linear model. Non-overlapping 95% CI are significantly different.

Table 1. Abundance and estimates of diurnal and nocturnal bioerosion rates of the species of eroding urchins in Cayo Arenas.

		Abundance (ind)		Bioerosion rate (kg CaCO$_3$·m^{-2}·y^{-1})	
Site	Species	Diurnal	Nocturnal	Diurnal	Nocturnal
Bajo Tortugas	*Diadema antillarum*	2.2 ± 0.7 *n* = 13	24.6 ± 9.0 *n* = 123	0.28 ± 0.1	3.85 ± 1.5
	Echinometra viridis	0.17 ± 0.2 *n* = 1	03.6 ± 1.0 *n* = 18	0.003 ± 0.003	0.05 ± 0.01
	Echinometra lucunter	0.33 ± 0.2 *n* = 2	-	0.005 ± 0.003	-
	Eucidaris tribuloides	-	0.2 ± 0.2 *n* = 1	-	0.008 ± 0.008
	Site mean	2.7 ± 0.95 *n* = 16	28.4 ± 9.5 *n* = 142	0.29 ± 0.1	3.9 ± 1.49

(*continued on next page*)

Table 1 (*continued*)

		Abundance (ind)		Bioerosion rate (kg $CaCO_3 \cdot m^{-2} \cdot y^{-1}$)	
Site	Species	Diurnal	Nocturnal	Diurnal	Nocturnal
Cayo Arenas 1	*Diadema antillarum*	2.2 ± 1.0 *n* = 11	8.4 ± 1.0 *n* = 59	0.29 ± 0.12	1.1 ± 0.13
	Echinometra viridis	0.4 ± 0.2 *n* = 2	7.6 ± 2.4 *n* = 53	0.003 ± 0.003	0.09 ± 0.03
	Echinometra lucunter	3.0 ± 1.0 *n* = 15	0.43 ± 0.4 *n* = 3	0.04 ± 0.013	0.007 ± 0.007
	Eucidaris tribuloides	-	0.43 ± 0.4 *n* = 3	-	0.003 ± 0.003
	Site mean	5.6 ± 1.9 *n* = 28	16.8 ± 3.2 *n* = 118	0.33 ± 0.13	1.18 ± 0.12
Cayo Arenas 14	*Diadema antillarum*	-	0.17 ± 0.17 *n* = 1	-	0.02 ± 0.02
	Site mean	*n* = 0	0.17 ± 0.17 *n* = 1	-	0.02 ± 0.02
Species	*Diadema antillarum*	1.4 ± 0.4 *n* = 24	10.2 ± 3.3 *n* = 183	0.2 ± 0.06	1.5 ± 0.5
	Species mean	5.9 ± 1.8 *n* = 207	-	0.86 ± 0.3	-
	Echinometra viridis	0.18 ± 0.1 *n* = 3	3.9 ± 1.2 *n* = 71	0.002 ± 0.001	0.05 ± 0.01
	Species mean	2.1 ± 0.7 *n* = 74	-	0.03 ± 0.008	-
	Echinometra lucunter	1.0 ± 0.4 *n* = 17	0.16 ± 0.2 *n* = 3	0.013 ± 0.006	0.003 ± 0.003
	Species mean	0.6 ± 0.2 *n* = 20	-	0.008 ± 0.003	-
	Eucidaris tribuloides	-	0.2 ± 0.2 *n* = 4	0 ± 0	0.003 ± 0.002
	Species mean	0.11 ± 0.1 *n* = 4	-	0.002 ± 0.001	-
Cayo Arenas	Mean	2.6 ± 0.8 *n* = 44	14.5 ± 3.8 *n* = 261	0.2 ± 0.06	1.55 ± 0.53

Data are shown as the mean ± standard error and number of individuals (*n*). Diurnal surveys were conducted between 08:00-13:00 h and nocturnal surveys at around 20:00 h (see Fig. 2). No individuals found for the species monitored transect (-).

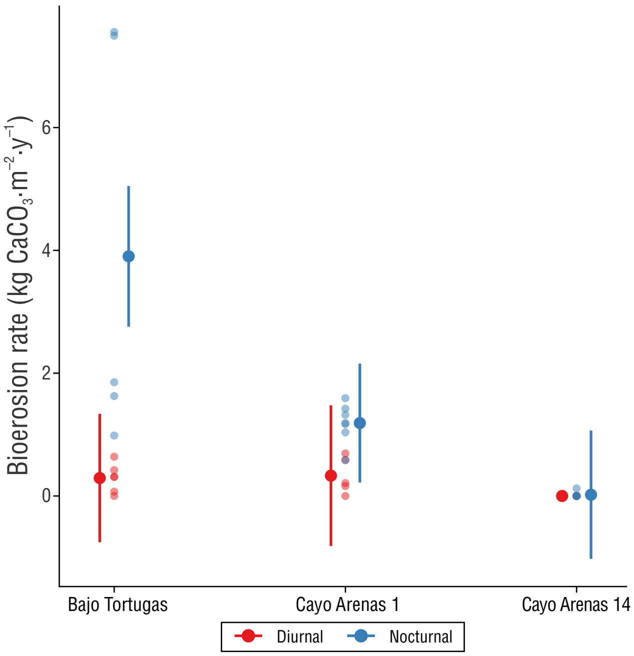

Figure 4. Contribution of sea urchins to the bioerosion potential in the Cayo Arenas reef, Campeche Bank. The points indicate the predicted means for each site and the type of survey (diurnal and nocturnal), and the error bars represent the 95% confidence intervals (CI). Both calculations come from the adjusted marginal means based on the generalized linear model. Non-overlapping 95% CI are significantly different

For example, in the Lobos-Tuxpan Reef System, Veracruz, average densities for *E. viridis* and *E. lucunter* were 6.8 ind·m^{-2} and 3.6 ind·m^{-2}, respectively (Morales-Quijano et al. 2017), whereas in the VRS, the values recorded for these species were 2.5 and 0.34 ind·m^{-2}, respectively (González-Azcárraga 2009). These values are higher than those reported for *D. antillarum* in the same studies (0.59 ± 0.18 ind·m^{-2}, Fig. 3) and those recorded for all urchin species in this study in diurnal and nocturnal surveys. This suggests that, in reefs with low abundance of *D. antillarum*, *E. viridis* and *E. lucunter* have become the main reef eroders due to their greater abundance (Dunn et al. 2017, Morales-Quijano et al. 2017), which could be reflected in a reduced bioerosion potential, as is currently occurring in Caribbean reefs (Perry et al. 2014). Unfortunately, there are few records of urchin populations, such as *D. antillarum*, prior to the mass mortality event of the 1980s. The only source of evidence we found is for the Flower Gardens reefs, where *D. antillarum* densities were reported to range between 0.5 to 1.40 ind·m^{-2} before the mass mortality event (Johnston et al. 2021), which is slightly higher than what was found in the present study.

Our results show a clear pattern between surveys carried out during the day and those conducted at night. All urchin species had greater densities during the night, when they are most active. This could be related to urchins coming out at night to search for food because this protects them against predators (Shulman 2020, Smith et al. 2024). This is particularly important in reefs with high structural heterogeneity given that greater heterogeneity (González-Azcáraga 2009, Tuohy et al. 2020) provides more refuge spaces for urchins, which reduces their energy expenditure to avoid predators (Bodmer et al. 2021) and even modulates their functionality in the reef (Lee and Hessen 2006). This suggest that shelter quality can minimize predator attacks (Carpenter 1984). The more evident changes in *D. antillarum* between day and night could be due to the greater distances traveled by this species during the night (3.7 m, Tuya et al. 2004) compared to those traveled by *E. viridis* and *E. lucunter* (10 and 5 cm, respectively; Shulman 2020). This was most evident in Bajo Tortugas, the site with high reef heterogeneity, which not only had the highest urchin densities but the greatest difference between day and night urchin densities, probably because the calcareous structures provide them with greater refuge from natural predators during the day. Conversely, CA14 was predominantly covered by large patches of sand and had the lowest population density. Site CA1 represented an intermediate case; this site was covered by small coral patches interspersed with sand patches and had medium urchin density, without significant changes between day and night. This shows that the abundance of urchins in Cayo Arenas is still subject to reef heterogeneity.

Bioerosion is key in coral reefs because it modulates other processes such as reef accretion and sediment production (Perry and Alvarez-Filip 2019). Our observations show that there are healthy populations of urchins, particularly of *D. antillarum*, in Cayo Arenas, which have the potential to play an important role in carbonate dynamics. The bioerosion rates reported in this study are the first for Campeche Bank reefs. However, we were able to compare our rates with those of VRS, where studies report a diurnal urchin bioerosion rate, mainly related to *E. viridis*, of 0.43 kg $CaCO_3·m^{-2}·y^{-1}$ (Cabrera-Rivera 2022). This value triples when compared to the nocturnal erosion of Cayo Arenas. An important finding of our study is that the potential for nocturnal urchin bioerosion in our study area (1.55 ± 0.53 kg $CaCO_3·m^{-2}·y^{-1}$) can exceed the $CaCO_3$ production by corals, even in reefs with high gross production such as Bonaire reefs (>5 kg $CaCO_3·m^{-2}·y^{-1}$, Perry et al. 2018). For example, Bajo Tortugas would have to have exceptionally high gross production (~9 kg $CaCO_3·m^{-2}·y^{-1}$) to remain in a state of net accumulation. The results reported here suggest that the surveys conducted during the day could be underestimating the density and bioerosion values; however, more studies are needed in other reefs to corroborate this.

Although not analyzed in this study, it is possible that differences in abundances observed between diurnal and nocturnal samplings are also reflected in the estimation of other key functions performed by urchins, such as herbivory, since this function also depends on species, size, and abundance (Ogden and Lobel 1978, Lange and Perry 2019, Williams 2022). Future research will be necessary to characterize possible variations, not only in urchin erosion rates, but also herbivory along different environmental gradients. Considering the relevant functional spectrum of urchins in reef systems, this information will contribute, in a comprehensive manner, to the implementation of conservation and management strategies (Molina-Hernández and Álvarez-Filip 2024), especially at sites with reported increase in urchin abundance (Myhre and Acevedo-Gutiérrez 2007, Vermeij et al. 2010, Keller 2011, Johnston et al. 2021).

Although it has been observed that reefs in good condition can withstand high erosion rates (Hoey and Bellwood 2008), any impact that affects calcification processes will have serious implications for the delicate balance between erosion and $CaCO_3$ production, potentially causing an abrupt transition to net erosive states (Cornwall et al. 2021). This is particularly relevant in reef systems such as Cayo Arenas, where despite no documented mass bleaching events or coral diseases, any event that results in significant coral mortalities will increase the impact of urchin bioerosion, which could lead to immediate imbalances in net production rates with negative consequences at the reef scale. An example of this was observed in the reefs of the tropical eastern Pacific, where an increase of up to 42% in the rate of urchin bioerosion was estimated after a mass coral mortality event, causing widespread degradation of reefs in the region (Alvarado et al. 2016).

In general terms, our study showed that the size of the urchin populations is larger than previously recognized and that they have a high erosive potential in the reef system of Cayo Arenas, Campeche Bank. It is still necessary to explore in more detail the ecological factors that could influence this circumstance, such as reef zones, the heterogeneity of the reef substrate, depth gradients, macroalgae cover, and the presence of natural predators. Nevertheless, it is likely that the remoteness from the coast has provided Cayo Arenas with a certain level of protection from direct anthropogenic threats, which contributes to the conservation of coral reefs and indirectly benefits the habitat of *D. antillarum*, maintaining it as the most abundant eroding urchin compared to other reefs in the Gulf of Mexico and the Caribbean. Furthermore, given that fishing pressure is relatively low due to the distance from the coast (Ocaña et al. 2019), it is possible that ecological interactions of predation could even control urchin population booms and, therefore, erosion pressure on these reefs. However, there is still little information about this reef and the rest of Campeche Bank and it is extremely important to continue and encourage long-term research in this system. With this, important information can be generated to allow us to understand ecological processes, responses to anthropogenic threats, possible recovery mechanisms of urchin populations, and important reef functions of urchin in other reefs of the Atlantic Ocean, where their populations continue to be decimated.

CONCLUSIONS

Cayo Arenas is a reef with high densities of eroding urchins, which was more evident during the night when the urchins emerge from their shelters and are easier to observe. This pattern was observed in the site with the greatest reef heterogeneity, and especially with the species *D. antillarum*, which had the highest population density. In this reef system, urchins are still subject to natural conditions such as substrate heterogeneity, depth, and environmental changes (i.e., between day and night). Likewise, these organisms continue to perform geo-ecological functions, since they show a high bioerosion potential dominated by *D. antillarum*. Continued monitoring is important in this area to understand the dynamics of urchin populations and their possible interaction with natural predators and geo-ecological variables in the face of the effects of climate change on these remote reefs.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

Supplementary Material

This work includes no supplementary material.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: LA-F, EC-R; Data curation: EC-R, EP-C, AM-H; Formal analysis: LA-F, EC-R; Funding acquisition: LA-F, RR-N; Investigation: LA-F, EC-R, AM-H, FM-M; Methodology: LA-F, EP-C, AM-H, FM-M, SG-G, AEM-V; Project administration: LA-F, RR-N; Resources: LA-F, RR-N; Validation: LA-F, RR-N; Writing–original draft: LA-F, EC-R, AM-H, FM-M, RR-N, SG-G, EP-C; Writing, review, and editing: LA-F, EC-R, AM-H, FM-M, RR-N, SG-G, EP-C.

Data availability

The data for this study are available from the corresponding author by reasonable request.

Use of AI tools

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

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SPECIAL ISSUE
Research Article

Physiological acclimation of *Porites panamensis* (Scleractinia: Poritidae) under high-latitude marginal conditions

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ABSTRACT. Hermatypic corals living at high latitudes face suboptimal environmental conditions associated with seasonal changes. In the central Gulf of California, the coral *Porites panamensis* is acclimated to eutrophication, low light availability, and a wide range of seasonal fluctuations in sea surface temperature (SST). The physiological adjustments of its resistance thresholds are associated with phenotypic plasticity. This study evaluated the interannual acclimation responses of *P. panamensis* to the warm and cold seasons of 2022 and 2023 using the physiological markers of endosymbiont density, chlorophyll *a* (Chl *a*) concentration, and the total lipid content in coral tissue. In addition, the abiotic variables of SST, Chl *a*, particulate organic carbon (POC), and the diffuse attenuation coefficient (K_d490) were compared between seasons. The results indicated a significant difference in endosymbiont density between seasons (cold season: $\sim 4 \times 10^6$ cell·cm^{-2}; warm season: $\sim 2 \times 10^6$ cell·cm^{-2}), and an increase in the Chl *a* concentration during the warm season of 2023. We also observed a significant increase in total lipid content in the warm season of 2023. However, seasonal changes did not negatively affect lipid content, likely due to the high concentrations of Chl *a* and POC throughout the year (2022: 4.47 ± 1.75 mg·m^{-3}; 2023: 403.3 ± 132.2 mg·m^{-3}), suggesting the existence of a potential year-round food source for *P. panamensis*. Our results indicate that *P. panamensis* acclimates to seasonal changes in temperature and turbidity. We suggest that regulating mixotrophy could be a key nutritional strategy for *P. panamensis* to withstand fluctuating environmental conditions. The ability to alternate between different nutritional pathways according to seasonal environmental conditions may allow *P. panamensis* to distribute throughout the Eastern Tropical Pacific, even inhabiting suboptimal regions for reef development.

Key words: marginal corals, phenotypic plasticity, coral heterotrophy, acclimation, seasonal changes.

INTRODUCTION

The study of hermatypic corals has focused on tropical coral reef ecosystems, where the optimal environmental conditions are oligotrophic, non-turbid, and thermally stable (Hoegh-Guldberg 2011, Soares 2020). Nevertheless, coral communities inhabiting suboptimal environmental conditions (i.e., high turbidity and sedimentation rates, eutrophication, wide temperature fluctuations, and low pH) have been documented worldwide, suggesting that these communities have a greater capacity to tolerate suboptimal conditions (Camp et al. 2018, Burt et al. 2020, Soares 2020).

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Marginal coral communities are ecologically distinct from tropical coral reefs; they show lower biodiversity, a lack of reef accretion, and coral coverage that is represented by species with wide tolerance thresholds (Perry and Larcombe 2003, Browne and Bauman 2023, Schoepf et al. 2023). Based on these and other characteristics, it has been hypothesized that these coral communities have the potential to face stressful local and regional conditions and, therefore, to cope with the effects of climate change (Perry and Larcombe 2003, Schoepf et al. 2023).

Climate change is predicted to be multifactorial, negatively affecting coral reef ecosystems in various ways (Veron et al. 2009), potentially increasing bleaching events (i.e., the loss of photosynthetic endosymbionts) and, eventually, degrading reef ecosystems. This could provoke a loss in the ecological and economic services that coral reefs provide (Veron et al. 2009, Oliver et al. 2018, Sully et al. 2019). Currently, some marginal coral communities inhabit environments resembling those predicted under climate change, allowing for an a priori evaluation of how tropical corals may respond to future environmental changes, as they may face suboptimal conditions (Perry and Larcombe 2003, Camp et al. 2018, Schoepf et al. 2023).

The Gulf of California (GC) represents the northeastern limit of the distribution of hermatypic corals in the Eastern Tropical Pacific (Glynn and Ault 2000). Bahía de los Ángeles (BLA) is located in the central region of the GC, near the Midriff Islands Region, and is considered a high-latitude environment for coral communities (29° N). Thirteen coral species have been reported in BLA, of which 2 are hermatypic (*Porites panamensis* and *Porites sverdrupi*), and 11 are ahermatypic (Reyes-Bonilla et al. 2007). The coral community of BLA is not capable of building a reef due to the extremely low temperatures in cold seasons, high turbidity, and high productivity (Reyes-Bonilla et al. 2007). A previous study in BLA reported that *P. panamensis* colonized rocky areas with a mean coverage of 2.5% (Halfar et al. 2005).

The wide latitudinal distribution of *P. panamensis* extends from the equator (–0.26° S) to the northern GC (31° N) (Glynn et al. 1994, Reyes-Bonilla et al. 2007), with this coral species being present even in suboptimal environments, such as CO_2 seep vents, estuaries, and high latitudes (Norzagaray-López et al. 2015, Zapata and Lozano-Cortés 2015, Oporto-Guerrero et al. 2018). *Porites panamensis* shows less susceptibility to thermal anomalies than other coral species distributed in the Eastern Tropical Pacific. For example, the 1997–1998 El Niño event triggered massive coral bleaching, leading to 90% mortality in *Pocillopora* spp. but only 50% mortality in *P. panamensis* (Carriquiry et al. 2001, Reyes-Bonilla 2001). Furthermore, Reyes-Bonilla et al. (2002) reported widespread bleaching during the 1998–1999 La Niña event, with higher mortality of *Pocillopora* spp. than other coral taxa, including *Porites* spp.

Physiological markers, such as endosymbiont density, pigment concentration, and total lipid content, are commonly used to assess coral health. Quantifying the energetic resources and reservoirs of corals allows us to understand acclimation at local and temporal scales, as well as the stress responses of different coral taxa (Kemp et al. 2014, Nielsen et al. 2018, Martínez-Castillo et al. 2020, Chapron et al. 2022). *Porites panamensis* has developed different physiological strategies that allow it to successfully acclimatize to the local and regional environmental conditions of the Eastern Tropical Pacific (Martínez-Castillo et al. 2020, Santiago-Valentín et al. 2023). However, the physiological response of *P. panamensis* to the suboptimal conditions of BLA remains unknown, although lower calcification (Cabral-Tena et al. 2013, Norzagaray-López et al. 2015) and high recruitment rates have been reported in this area, which contrasts with what has been reported for their tropical conspecifics (Tejada-Begazo et al. 2022), demonstrating the ability of *P. panamensis* to cope with suboptimal conditions.

The main objective of this study was to describe the physiological changes involved in the acclimation of *P. panamensis* to suboptimal environmental conditions in BLA. We hypothesized that *P. panamensis* would present seasonal acclimation with high lipid content, high endosymbiont density, and low chlorophyll *a* concentrations during the cold season compared to the warm season. This study contributes to the ongoing efforts to understand the physiological plasticity of marginal coral communities and the physiological mechanisms responsible for the wide tolerance of *P. panamensis*.

MATERIALS AND METHODS

Study area

Our study area was located southeast of La Llave Island, within BLA, in the central-western region of the GC (Fig. 1). This area is characterized by large seasonal fluctuations in sea surface temperature (SST), ranging from ~14 °C to ~34 °C, and nutrient enrichment due to vertical mixing in Canal de Ballenas caused by tidal changes and the complex bathymetry (Álvarez-Borrego 2007, Torres-Delgado et al. 2013). Moreover, northwesterly winds in winter and southeasterly winds in summer generate upwelling conditions along the eastern coast of the bay (Martínez-Fuentes et al. 2022) that result in high productivity and eutrophic and turbid water conditions (Halfar et al. 2005, Ledesma-Vázquez et al. 2009, Torres-Delgado et al. 2013, Martínez-Fuentes et al. 2022). The oceanographic conditions of Canal de Ballenas strongly affect the physicochemical conditions of BLA, as the channels connecting the bay facilitate the transport of eutrophic and acidified waters (Amador-Buenrostro et al. 1991, Martínez-Fuentes et al. 2022). Bahía de los Ángeles has 2 well-defined seasons: the cold season (December to May), characterized by low SST and higher nitrate concentrations, and the warm season (June to November), characterized by high SST and lower nitrate concentrations (Martínez-Fuentes et al. 2022).

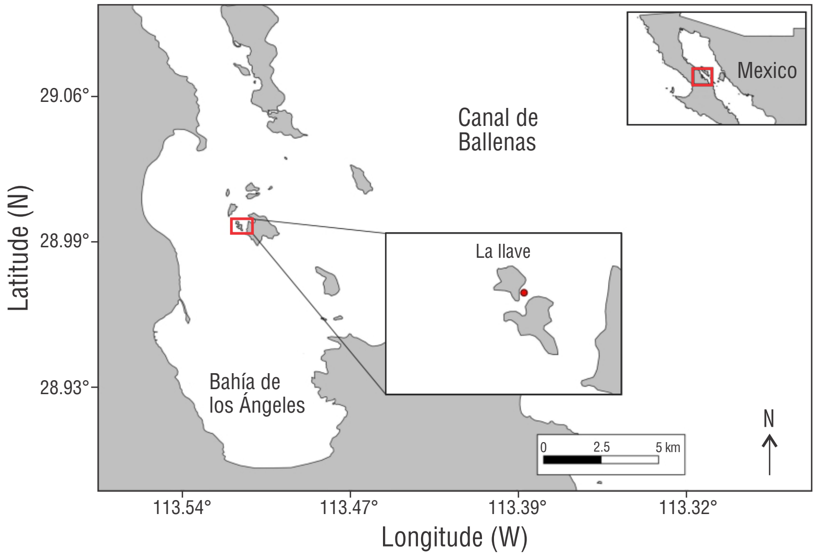

Figure 1. Study area of La Llave Island, Bahía de los Ángeles, central-western Gulf of California. The sampling site is shown with a red dot.

Field sampling

In total, 2 sampling campaigns were conducted during the cold season (March 2022 and March 2023), and 2 sampling campaigns were conducted in the warm season (October 2022 and August 2023). Healthy colonies were randomly selected in the study area, and coral nubbins (2-cm long [March 2022: n = 15; October 2022: n = 30; March 2023: n = 30; August 2023: n = 30]) were collected (5–10 m depth) during each campaign. Sampling was conducted in triplicate. All samples were individually fixed with a 10% solution of formaldehyde in filtered seawater, transported to the laboratory, and stored at room temperature (~20 °C) until further processing.

Environmental characterization

To characterize the environmental conditions of the waters surrounding our study area during the sampling campaigns, we used SST; the diffuse attenuation coefficient (K_d490), as an indicator of turbidity; the chlorophyll *a* (Chl *a*) concentration, as a proxy of the nutrient concentration and primary production; and particulate organic carbon (POC), as a proxy of productivity. The data points represent measurements averaged over 8 days (4 km^2 resolution). In addition, we obtained historical SST data (2002–2024) to evaluate the effect of El Niño in BLA. All data were downloaded from the AquaMODIS Giovanni online data system (GIOVANNI 2024). This data was used to correlate the physiological responses of corals with environmental conditions.

Physiological markers

Endosymbiont density and chlorophyll a concentration

Samples were washed with filtered seawater (FSW) and decalcified with 10% acetic acid for ~16 h. The exact area of decalcified tissue was calculated with ImageJ software (Abrámoff et al. 2004). Tissue was homogenized in 1 mL of FSW through 2 sonication cycles (15 s each), with an intermediate dwell time of 15 s, and an amplitude of 70% (Q500, QSONICA, Newtown, USA). Samples were diluted (1:10) with FSW, stained with Lugol, and counted with a hemocytometer (8 counts per sample) using a Motic BA310E microscope (Motic, Hong Kong, China). Counts were normalized to 1 cm^2 and are reported as $cell \cdot cm^{-2}$.

Endosymbiont pigments were extracted from 200 µL of tissue previously homogenized with FSW. Prior to pigment extraction, samples were centrifugated at 1,500 × *g* for 5 min to eliminate the supernatant. Salt residues were washed with 1 mL of MiliQ and centrifuged under the same conditions. Once the tissue had settled, the supernatant was decanted, and the tissue was immediately resuspended in 1 mL of 100% methanol with a sterile plastic pestle and left to incubate for 24 h at –20 °C in the dark. Chlorophyll *a* was quantified by spectrophotometry and estimated with the equation of Parsons et al. (1984) with a turbidity blank correction:

$$\mathit{Chlorophyll\ a} = 11.85(E_{664}) - 1.54(E_{647}) - (E_{630}) \ , \tag{1}$$

where E is the value of wavelength absorbance corrected with the turbidity blank. The total Chl *a* concentration was normalized per cell. The estimations are expressed as picograms (pg) of Chl $a \cdot cell^{-1}$.

Total lipid content

Lipids were extracted following the method of Folch et al. (1956) modified by Rodríguez-Troncoso et al. (2010). Briefly, 0.15 g of coral tissue was washed with distilled water and dried at 60 °C for 24 h. Lipids were extracted with a 2:1 chloroform:methanol solution. Precipitation was carried out with KCl (8%), followed by washing with a 1:1 methanol:water solution, vortex mixing, and decanting of the supernatant. The chloroform was evaporated in an oven at 60 °C for 12 h. Finally, the lipids were weighed and expressed as grams of lipids per gram of dry tissue (g of lipid·g^{-1} DW). All physiological markers are expressed as the mean ± standard deviation (SD).

Statistical analysis

Neither physiological markers nor environmental data exhibited normality or variance homogeneity. Therefore, non-parametric Kruskall–Wallis (α = 0.05), Dunn pairwise tests (α = 0.05), and Bonferroni *P*-value adjustments were used to assess statistical differences in physiological markers and environmental variables between seasons. Due to the high variability in K_d490, Chl *a*, and POC, as well as the lack of a clear seasonal pattern (Fig. S1), only the relationships between SST and physiological markers were analyzed using Spearman correlation tests. All analyses were performed using R Statistical Software v. 4.1.3 (R Core Team 2022). Dunn's pairwise comparisons were conducted with the 'FSA' (v. 0.9.5) package. All plots were constructed in GraphPad Prism v. 5.00 (GraphPad Software, La Jolla, USA).

RESULTS

Environmental characterization

Sea surface temperature varied ~15 °C between the warm and cold seasons (Fig. 2a). The warmest temperatures were observed from July to September (29.42 ± 1.24 °C), and the coldest temperatures were observed from December to March (16.1 ± 1.04 °C). The results of the Kruskal–Wallis test indicated that significant differences in SST were present between seasons (H = 64.65, P = 0.003) (Fig. S1a). Dunn's pairwise comparisons revealed significant differences between cold and warm seasons (P < 0.001) (Table S1). The K_d490 values varied substantially throughout the year, with peaks in February, April, and August of 2022 and in February, March, April, and November of 2023 (Fig. 2b). Nevertheless, there were no significant differences among seasons (H = 6.3436, P = 0.09) (Fig. S1b). Chlorophyll *a* exhibited high variation over time (Fig. 2c), with peaks in February and April of 2022 and a larger peak in November of 2023. Mean values of Chl *a* ranged from 3.7 to 6.6 mg·m^{-3}, but no significant differences were found (H = 5.4722, P = 0.14) (Fig. S1c). Particulate organic carbon also showed high fluctuations over the year (Fig. 2d), with higher concentrations in February, April, and August of 2022 and in January, February, November, and December of 2023. However, the POC concentrations remained above 200 mg·m^{-3} during all months. The results of the Kruskall–Wallis test revealed significant differences between 2 seasons, and those of Dunn′s test revealed a signficant difference between the warm season of 2023 and cold season of 2023 (H = 11.29, P = 0.01) (Fig. S1d), as well as a significant difference between the warm season of 2022 and the cold season of 2023 (Z = –2.74, P = 0.03) (Table S1).

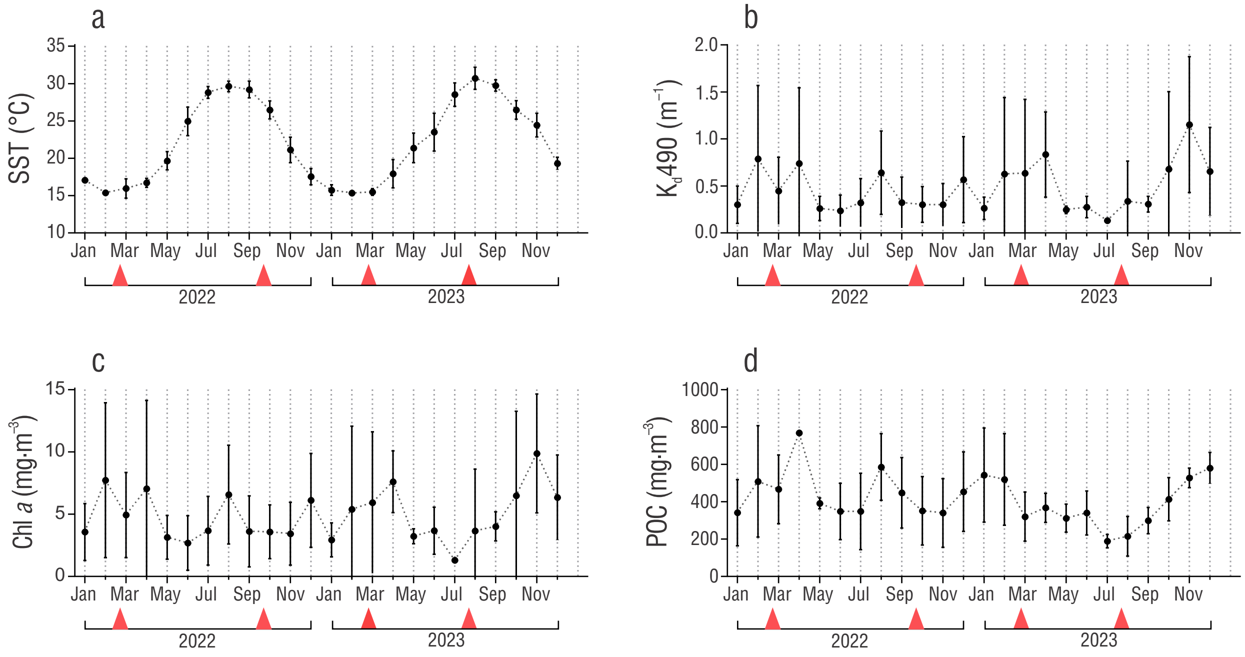

Figure 2. Environmental characterization of sampling years. Sea surface temperature (SST) (**a**), diffuse attenuation coefficient (K_d490) (**b**), chlorophyll *a* (Chl *a*) concentration (**c**), particulate organic carbon (POC) (**d**). Red triangles indicate sampling months. Data points are the monthly average ± SD.

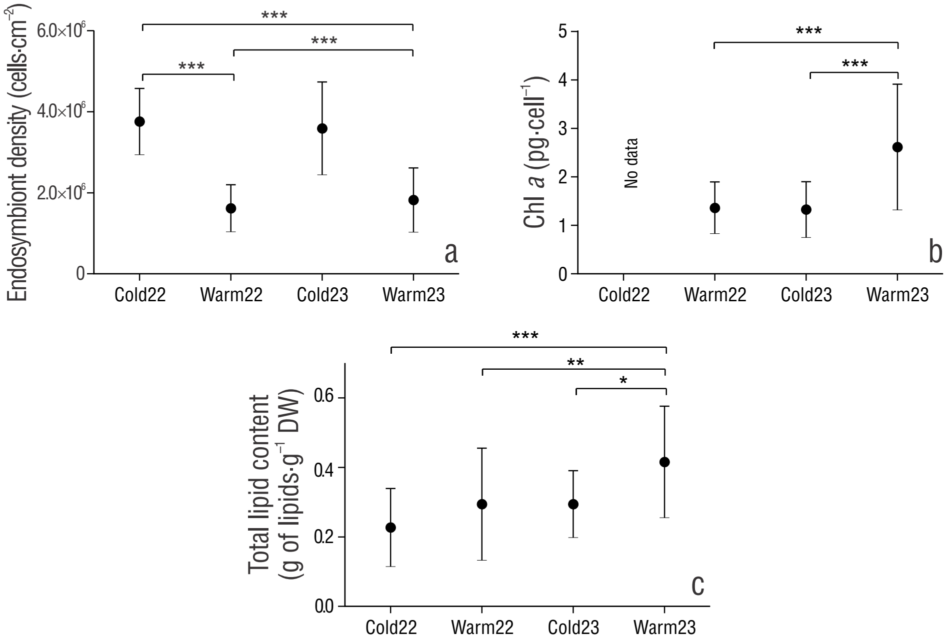

Figure 3. Physiological markers in *Porites panamensis* used in the present study. Endosymbiont density (**a**), endosymbiont chlorophyll *a* (Chl *a*) concentration (**b**), and total lipid content (**c**). Values are means ± SD. Asterisks denote the level of significance of pairwise Dunn tests: *** ($P < 0.001$), ** ($P < 0.01$), and * ($P < 0.05$).

Endosymbiont density and chlorophyll *a*

Endosymbiont density was ~2-fold higher in the cold seasons ($3.6 \times 10^6 \pm 1.04 \times 10^6$ cell·cm^{-2}) compared to the warm seasons ($1.7 \times 10^6 \pm 0.7 \times 10^6$ cell·cm^{-2}) in both years (Fig. 3a). The Kruskal–Wallis test showed significant differences ($H = 55.3$, $P < 0.001$) in endosymbiont density between seasons, and the pairwise comparison revealed significant differences ($P < 0.001$) (Table S2) between the warm and cold seasons. The endosymbiont Chl *a* concentration (Fig. 3b) was found to range from 1.3 pg·cell^{-1} (warm season) to 2.6 pg·cell^{-1} (cold season). We observed significant differences in Chl *a* between seasons ($H = 24.60$, $P < 0.001$); a significant increase was identified in the warm season of 2023 compared to that of the warm season of 2022 ($Z = -3.99$, $P < 0.001$) (Table S2) and the cold season of 2023 ($Z = 4.61$, $P < 0.001$).

Total lipid content

The mean total lipid content in *P. panamensis* ranged from 0.22 ± 0.11 g of lipid·g^{-1} DW to 0.41 ± 0.16 g of lipid·g^{-1} DW in the warm and cold seasons, respectively. The Kruskal-Wallis test showed significant differences among seasons ($H = 17.66$, $P < 0.001$), and the pairwise comparison indicated a significant increase (Table S2) in total lipid content in the warm season of 2023 (Fig. 3c) compared to that of the warm season of 2022 ($Z = -2.92$, $P = 0.01$), the cold season of 2022 ($Z = 3.83$, $P < 0.001$), and the cold season of 2023 ($Z = 2.69$, $P = 0.02$). We did not observe changes in total lipid content between cold seasons.

Spearman correlations

Sea surface temperature and endosymbiont density were significantly and negatively correlated ($r = -0.60$, $P < 0.001$). On the other hand, endosymbiont Chl *a* and total lipid content were significantly and positively correlated with SST ($r = 0.37$, $P < 0.001$; $r = 0.51$, $P < 0.001$, respectively).

DISCUSSION

Endosymbiont regulation by the host in response to temperature changes as an acclimation mechanism has been widely studied in branching corals, such as *Pocillopora damicornis*, *Acropora humilis*, and *Acropora formosa* (Stimson 1997, Fagoonee et al. 1999, Jandang et al. 2022), and the tropical *P. panamensis* conspecific (Martínez-Castillo et al. 2020, Santiago-Valentín et al. 2023). Sea surface temperature plays a crucial role in regulating coral physiology (Saxby et al. 2003, Al-Sofyani 2013). Periods of warm temperature increase respiration and photosynthetic rates (Coles and Jokiel 1977, Borell et al. 2008, Al-Sofyani 2013), while cold temperatures decrease metabolism, photosynthetic efficiency, and the translocation of photosynthates to the host (Saxby et al. 2003, Rodríguez-Troncoso et al. 2014). In both cases, if the temperature exceeds the thermo-tolerance limit of the coral, then oxidative stress is induced, resulting in the loss of endosymbionts and, consequently, in bleaching (Brown 1997, Saxby et al. 2003, Lesser 2011). In this sense, despite collecting samples under 3 different temperature regimes, we did not observe bleaching, confirming the wide thermotolerance threshold of *P. panamensis*.

We sampled in August of 2023, during an El Niño Southern Oscillation (ENSO) event, which caused the fourth global bleaching event (Reimer et al. 2024). In the southern Mexican Pacific, this ENSO event increased SST by ~2 °C above historical records for at least 4 months, causing widespread bleaching and mortality rates of 50–93% in coral cover, affecting the 3 most important reef-building corals: *Porites* sp., *Pocillopora* sp., and *Pavona* sp. (López-Pérez et al. 2024). In our study, we observed a positive thermal anomaly of ~1.48 °C in August 2023 (Fig. 4); however, these conditions did not trigger bleaching in *P. panamensis*. Previous studies have shown that upwelling due to tidal mixing processes could diminish the effect of El Niño events in the Midriff Islands Region (Santamaría-del-Angel et al. 1994, Álvarez-Borrego 2007), which could explain the observed SST patterns in BLA during 2023. Our results could be interpreted in 2 ways. First, the thermal anomaly during August could be an El Niño effect, which highlighted the thermotolerance of *P. panamensis*. Second, the effect of the thermal anomaly was masked by upwelling processes, suggesting that BLA is a potential thermal refuge for corals amid rising SST.

Seasonal variation in endosymbiont density in natural coral populations has been widely studied, with higher endosymbiont density observed in winter than in summer (Stimson 1997, Fagoonee et al. 1999, Martínez-Castillo et al. 2020, Jandang et al. 2022). The reduction in endosymbiont density during the warmer season has been associated with a host antioxidant response, a strategy to cope with rising temperatures (Liñán-Cabello et al. 2010, Madeira et al. 2015), when dinoflagellate proliferation and photosynthesis accelerate (Coles and Jokiel 1977, Patthanasiri et al. 2022). This effect was observed with a 50% reduction in endosymbiont cells with warm temperatures (Fig. 5a), as a regulatory response of the host to endosymbiont activity. Cold temperatures reduce photosynthesis and photosynthate translocation due to a reduction in photosystem II development (Saxby et al. 2003), with a subsequent reduction in the Chl *a* concentration (Roth et al. 2012, Rodríguez-Troncoso et al. 2014). We did not observe reductions in the Chl *a* concentration during periods of either the coldest or highest temperatures, indicating that dinoflagellates, as hosts, also demonstrate high thermotolerance (Fig. 5b). Nevertheless, the high density of endosymbionts during the cold season suggests that the host allowed dinoflagellate proliferation to compensate for the low translocation of photosynthates needed to supply its energetic reservoirs. This is consistent with what has been reported for *Pocillopora verrucosa* when exposed to cold stress in the eastern Pacific (Rodríguez-Troncoso et al. 2014). In field studies, this pattern has also been observed in *Acropora humilis* and *Pocillopora damicornis* in Thailand (Jandang et al. 2022) and in the tropical *P. panamensis* conspecific (Martínez-Castillo et al. 2020), where Chl *a* in dinoflagellates decreased with cold temperatures despite an increase in the number of endosymbiont cells in the host.

Several studies have documented a positive correlation between endosymbiont density and nutrients, especially with inorganic nitrogen (Marubini et al. 1996, Nalley et al. 2023, Zhang et al. 2023). Martínez-Fuentes et al. (2022), following a 2-year monitoring campaign in BLA near La Llave Island, reported an increase in the nitrate concentration during the cold season (13 ± 5 µM) compared to that of the warm season (2 ± 1.5 µM). Considering the positive correlation between endosymbiont density and nutrients in several corals, another explanation of the observed temporal variation in endosymbiont density could be related to the natural fluctuations in nutrient concentrations in BLA. However, we did not measure the nutrient concentration in the water column during the sampling campaigns to evaluate this. Nonetheless, satellite chlorophyll data (Fig. 2c) showed high variability and eutrophic conditions in both years. A continuous supply of nutrients could enhance the proliferation of endosymbiont density within the host.

At the local scale, we observed 5 times more endosymbionts (cell·cm^{-2}) compared to that reported for the tropical *P. panamensis* conspecific (Martínez-Castillo et al. 2020, Santiago-Valentín et al. 2023), but with lower Chl *a* concentration (Table 1). Moreover, the K_d490 values indicated that BLA waters were 5 times more turbid than the waters of the tropical *P. panamensis* conspecific (Rodríguez-Troncoso et al. 2023) due to a high concentration of particulate organic matter, which rapidly attenuated light (Devlin et al. 2008). Corals respond in different ways to dim-light conditions; for example, the host can induce the proliferation of endosymbiont cells, which could increase the amount of photosynthetic pigments (Hoegh-Guldberg and Smith 1989, Fagoonee et al. 1999, Titlyanov et al. 2001, Titlyanov et al. 2002).

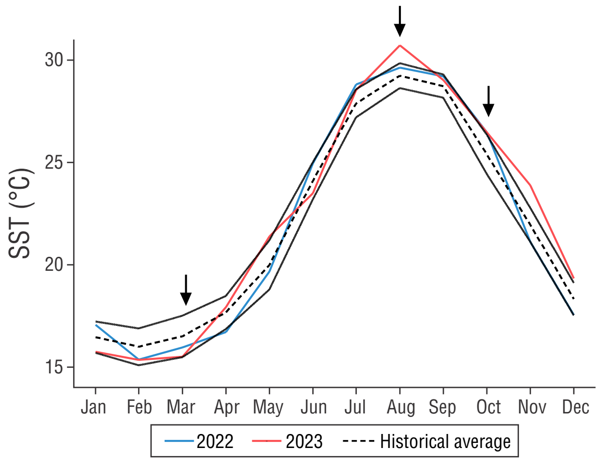

Figure 4. Historical average ± SD of satellite sea surface temperature (SST) data (2002–2024) for Bahía de los Ángeles, Gulf of California. Red and orange color lines refer to the sampling years of this study. Black arrows denote the sampling months.

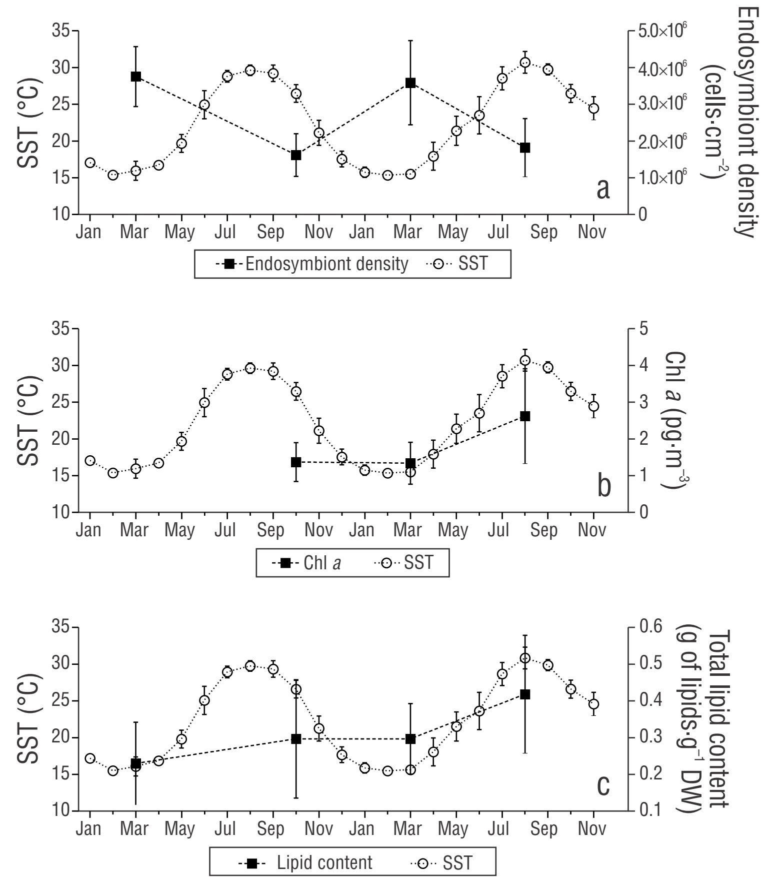

Figure 5. Effect of sea surface temperature (SST) on physiological markers Endosymbiont density (**a**), endosymbiont chlorophyll *a* (Chl *a*) concentration (**b**), and and total lipid content (**c**). Values are means ± SD.

Table 1. Comparison of environmental conditions in 3 sites in the Mexican Pacific containing *Porites panamensis* and the physiological markers evaluated in this study. SST: sea surface temperature; K_d490: diffuse attenuation coefficient; chlorophyll *a* (Chl *a*); POC: particulate organic carbon; DW: dry tissue.

	Variable	Bahía de los Ángeles (29° N)	Islas Marietas (20° N)	Oaxaca (15° N)
Environmental conditions	SST	22.2 ± 5.6[*]	28.7 ± 2.2	28.3 ± 2.1[¶]
	K_d490	0.4 ± 0.2[*]	0.08 ± 8.8 × 10^{-3}[§]	0.13 ± 1.0[¶]
	Chl *a*	4.5 ± 5.2[*]	-	-
	Nitrate	4 ± 4.1[†]	0.36 ± 0.6[‡]	-
	POC	403.3 ± 132.2[*]	-	-
Physiological marker	Endosymbiont density (cell·cm^{-2})	2.6 ± 1.3[*]	0.4 ± 0.04[‡]	0.2 ± 0.1[¶]
	Chl *a*	1.7 ± 1.0 (pg·cell^{-1})[*]	33.4 ± 5.6 (ng·cell^{-1})[‡]	26.5 ± 12.5 (pg·cell^{-1})[¶]
	Total lipid content (g of lipid·g^{-1} DW)	0.32 ± 0.15[*]	0.2 ± 0.03[‡]	0.22 ± 0.1[¶]

[*]Present study, [†]Martínez-Fuentes et al. (2022), [‡]Martínez-Castillo et al. (2022), [§]Rodríguez-Troncoso et al. (2023), [¶]Santiago-Valentín et al. (2022).

Dinoflagellate endosymbionts can absorb solar energy at different wavelengths of the light spectrum. While Chl *a* absorbs light at ~680 nm, other pigments, such as peridinin, absorb a broader spectrum of light (~450–550 nm) (Roth 2014). Therefore, the persistent turbidity in the study area and low penetration of light with short wavelengths could explain the slight variation observed in Chl *a*, highlighting the role of accessory pigments in dinoflagellate photoacclimation. Furthermore, our results revealed that endosymbiont regulation by the host plays an important role as a photoacclimation mechanism in *P. panamensis* under turbid conditions.

The primary energy source for corals in oligotrophic areas is sunlight; photosynthesis is conducted by endosymbionts, which translocate up to 90% of photosynthates to the host (Muscatine and Hand 1958, Trench 1971, Falkowski et al. 1984, Oku et al. 2003). Seasonal changes affect the energetic budget in natural populations of *Goniastrea aspera*, *Acropora millepora*, and the tropical *P. panamensis* conspecific (Table 1), showing high and low lipid content in colder and warmer months, respectively (Yamashiro et al. 2005, Conlan et al. 2020, Martínez-Castillo et al. 2020, Santiago-Valentín et al. 2023), due to the endosymbiont contributing more than 50% of total lipid content within the holobiont, as has been shown for *Acropora hyacinthus* (Zhang et al. 2023). This contribution of lipids from the endosymbiont to its coral host might be a general pattern in corals, given that a positive correlation between endosymbiotic cell density and lipid content has been reported in at least 8 coral species (Yamashiro et al. 2005). However, we did not observe lipid loss during the warm season despite the ~50% loss in endosymbiotic cells, suggesting that another energy source, such as heterotrophy, which is mainly employed by temperate corals (Ferrier-Pagés et al. 2011), contributed to lipid biosynthesis.

On the other hand, reproductive activity can also reduce lipid content in corals by 10–40% due to the maturation of lipid-enriched eggs (Oku et al. 2003, Viladrich et al. 2016, Viladrich et al. 2017, Conlan et al. 2020). *Porites panamensis* is a gonochoric breeder that is reproductively active throughout the year, with reproductive peaks during periods of warm temperatures (Glynn et al. 1994, Carpizo-Ituarte et al. 2011, Santiago-Valentín et al. 2023); however, local conditions can modify its reproductive patterns (Santiago-Valentín et al. 2018). Although there is no data on gamete maturation or the presence of *P. panamensis* larvae in BLA, high recruitment has been recorded during months of high temperatures, mainly between August and November (Tejada-Begazo et al. 2022), suggesting increased reproductive activity. Despite collecting samples in the warm seasons of both years, when lipids are presumably invested in gamete production, we did not observe a reduction in total lipid content (Fig. 5c).

Previous stable isotope analyses have revealed that corals (*Porites* spp., *Platygyra* spp., and *Pocillopora* spp.) increase heterotrophy in turbid environments (Fox et al. 2018, Travaglione et al. 2023), being able to feed on plankton, ranging in size from picoplankton to mesoplankton (particle sizes of 0.2–1,000 µm), with their consumption contributing ~15–35% to the daily metabolic requirements of healthy colonies (Houlbrèque and Ferrier-Pagès 2009). In addition, Anthony (2006) observed that coral colonies inhabiting turbid waters tend to increase their total lipid content 4-fold compared to their counterparts in clear waters. In this sense, we observed high fluctuations in Chl *a* and POC over time (Fig. 2c, d), which constitute a potential food source for *P. panamensis* that could contribute to lipid biosynthesis. If *P. panamensis* increases heterotrophy, then this increase could compensate for possible lipidic losses due to the reduction in endosymbiont density or the investment of lipids into reproductive activity during the warm season.

Corals can be autotrophic, heterotrophic, or mixotrophic, and their trophic strategy is related to their thermal tolerance. Mixotrophy, the acquisition of nutrients from photosynthesis and heterotrophy, is well-documented in corals and has been suggested to be the most successful nutritional strategy (Houlbrèque and Ferrier-Pagès 2009, Viladrich et al. 2017, Sturaro et al. 2021). Conti-Jerpe et al. (2020) observed that the nutritional strategy is highly related to coral tolerance; autotrophic corals (e.g., *Acropora samoensis*, *A. pruinuosa*, and *Goniopora lobata*) were less tolerant to thermal stress, while mixotrophic and heterotrophic corals (e.g., *Porites* spp., *Pavona* spp., *Turbinaria* spp., and *Platygyra* spp.) were notably more thermotolerant (Conti-Jerpe et al. 2020). Although we did not measure the nutritional pathways of *P. panamensis* in BLA, our observations of its thermal tolerance allow us to hypothesize that this species is a mixotrophic organism, which could explain its success under suboptimal environmental conditions due to its ability to acclimatize.

CONCLUSIONS

This study demonstrates the high phenotypic plasticity of *P. panamensis* through local adaptation to low-light and eutrophic conditions with wide fluctuations in SST. Our results highlight the role of the host through a possible induction of endosymbiont cell proliferation, a photoacclimation mechanism that improves energy uptake. Our results also suggest that *P. panamensis* exhibits a seasonal response to low-light conditions in BLA, resulting in a 5-fold increase in overall endosymbiont density. On the other hand, the prevalent conditions of high turbidity and productivity could promote a mixotrophic strategy in *P. panamensis*, which may compensate for lipidic losses in warmer months due to decreased endosymbiont density and increased reproductive activity. Furthermore, upwelling areas in the region could provide refuge from warm SST anomalies, although further studies are needed to evaluate this possibility. Moreover, future studies must also characterize other dinoflagellate pigments that could be beneficial in turbid environments. Isotopic and molecular analysis, such as RNA-seq, should be explored to confirm the mixotrophy in *P. panamensis* and unravel the fundamental cellular mechanisms involved in the acclimation and resistance of this species. The present study furthers our understanding of *P. panamensis* physiology under suboptimal conditions, and our results suggest that mixotrophy is a fundamental strategy responsible for the broad tolerance of *P. panamensis*, highlighting the importance of studying the effects of nutritional strategies in other coral species in the face of local, regional, and global climate impacts.

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3507/420421159.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Conceptualization: AETE (equal), RACT (equal), CEGS (equal); Data curation: AETE (lead), RACT (equal), APRT (supporting), LECA (supporting); Formal analysis: AETE (equal), RACT (equal), APRT (equal), LECA (supporting), OEJ (supporting); Funding acquisition: RACT (equal), CEGS (equal); Investigation: AETE (lead), RACT (equal), APRT (equal); Methodology: AETE (lead); Project administration: RACT (equal), CEGS (equal); Resources: RACT (equal), CEGS (equal); Software: AETE (lead); Supervision: CEGS (equal), LMDR (equal), APRT (equal), RACT (equal), OEJ (equal), LECA (equal); Validation: APRT (equal), RACT (equal); Visualization: AETE (equal), APRT (equal), OEJ (equal); Writing–original draft: AETE (lead); Writing–review & editing: AETE (equal), LMDR (equal), OEJ (equal), RACT (equal), CEGS (equal).

Data availability

Data for this study may be obtained from the corresponding author upon reasonable request.

Ethical approvals and permits for studies involving animals

Coral nubbins were collected with permit (*Permiso Pesca de Fomento*) PPF/DGOPA-085/22 from *Comisión Nacional de Acuacultura y Pesca* (CONAPESCA).

Use of AI tools

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

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Reef health status of the southwestern Gulf of Mexico and Mexican Caribbean coral reefs

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ABSTRACT. Coral reefs are highly diverse ecosystems that provide various environmental services; however, they remain highly threatened. Assessing the health and trends of coral reefs is vital to establishing management strategies that contribute towards their conservation and recovery. One way of contributing to this objective is through monitoring indicators of reef health. In this context, the present study focused on evaluating the health of 4 reef systems located in 2 extensive regions of Mexico: the southwestern Gulf of Mexico (SGM) and the Mexican Caribbean (MC), using the Reef Health Index (RHI). Fieldwork was conducted on 11 reefs in October 2022 in the SGM and in May 2023 in the MC. Data were collected using 5 to 6, 50 × 2 m transects per site, followed by video transects of 50 × 0.50 m to record benthic organisms along the transect. An average RHI score of 3.50 (considered "good") was obtained for SGM reefs, while for MC reefs, the average RHI score was 2.50 (considered "poor"). These results suggest that, according to the RHI criteria, SGM reefs present a better state of health than their MC counterparts. This difference was mainly influenced by the lower coral cover and higher macroalgae cover associated with the coral-algal phase shift, likely resulting from the rapid coastal development observed along the MC coasts. Lastly, for the SGM, this evaluation represents the first reef health assessment for the Lobos-Tuxpan Reef System Flora and Fauna Protection Area using a rating system coupled to ecologic indicators such as the RHI.

Key words: Mexican Caribbean, southwestern Gulf of Mexico, reef health, phase shift, reef monitoring.

INTRODUCTION

Over half of the reefs across the world are estimated to have been lost over the past 30 years, and they are currently in a state of crisis (Downs et al. 2005, Souter et al. 2021). The main factors contributing to coral reef degradation include urban and industrial development in coastal areas, agricultural activity, sedimentation, overfishing, marine pollution, and climate change, which leads to ocean warming and acidification (Bindoff et al. 2019, Obura et al. 2019, Souter et al. 2021, Feng et al. 2023). Furthermore, climate change has increased the incidence of coral diseases (Gil-Agudelo et al. 2009; Alvarez-Filip et al. 2019, 2022), and, unlike past climate events, such as those of the Paleocene, the current accelerated pace of global warming (Zeebe et al. 2016) is affecting the adaptive and resilience capacity of corals.

The year 2023 was marked as the warmest year on record, possibly in the last 100,000 years of the Earth, triggering the most severe coral bleaching and mortality event reported in the Northern Hemisphere and the Caribbean region (Goreau and Hayes 2024, Schmidt 2024). Nevertheless, 2024 had the highest ocean temperatures recorded in the Great Barrier Reef in Australia, posing a threat to coral communities in this region (Henley et al. 2024, Tollefson 2024). As a result, the biodiversity of reefs and associated communities has changed. Thus, baseline assessments and ongoing monitoring are needed to determine the health of these ecosystems, which will facilitate the design of effective

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management and conservation strategies (Downs et al. 2005, Obura et al. 2019).

In Mexico, reef health assessments have been carried out over the years, both for the reefs of the southwestern Gulf of Mexico (SGM; Horta-Puga 2003, López-Padierna 2017, Arguelles et al. 2019, Pérez-España et al. 2021) and for the reefs of the Mexican Caribbean (MC; Ruiz-Zárate 2003; HRI 2008; Caballero-Aragón et al. 2020a; McField et al. 2022, 2024), using different methodologies. The Reef Health Index (RHI) has been widely used in MC reefs. This index was implemented by the Healthy Reefs Initiative (HRI) and is one of the first regional efforts to develop reef health criteria and indicators.

Since 2008, the HRI has produced biennial reports on reef health in the region (HRI 2008; Kramer et al. 2015; McField et al. 2022, 2024), which have provided insight into the status and trends of reefs over time and the progress of restoration and conservation efforts in the MC and, on a larger scale, the Mesoamerican Reef System (MAR). However, the need to apply the RHI at more sites in the MC has been highlighted (Díaz-Pérez et al. 2016); furthermore, its expansion to reefs in the SGM has been proposed, as reef health assessments based on scoring systems are still limited in this region, with those carried out by Simoes et al. (2020) and Pérez-España et al. (2021) being particularly noteworthy.

In Mexico, the most important reefs, in terms of size and diversity, are those found in the Gulf of Mexico and the Caribbean (Horta-Puga et al. 2019). These reefs provide ecological, environmental, and economic services (SENER 2016); in addition, they serve as the connection with the rest of the coral ecosystems of the Wider Caribbean (Tunnell et al. 2007). Veracruz reefs have been considered one of the most threatened in the Wider Caribbean (Horta-Puga 2003, Pérez-España et al. 2015) because they have been exploited for centuries (López-Padierna 2017). Despite not being abundant, their uniqueness, isolation, and good state of conservation make these reefs highly relevant for research and preservation (Gil-Agudelo et al. 2020).

On the other hand, the MC hosts the most extensive reef formation in Mexico, mainly composed of fringing reefs that extend more than 350 km along the coast of the state of Quintana Roo (Ruiz-Zárate et al. 2003, Ardisson et al. 2011, Blanchon 2011). These reefs have experienced continuous devastation since the early 1980s due to anthropogenic activity in the region (Pérez-Cervantes et al. 2017).

Therefore, this study aimed to assess the health status of 11 reef sites in the SGM and MC to elucidate their current condition and evaluate the effectiveness and applicability of the RHI in these 2 regions. It also enabled the analysis of the main factors that could influence their health status, such as the natural history and demographics of both regions. Finally, the results for each of the indicators used and the RHI score will serve as a reference point prior to the severe bleaching event of 2023.

Materials and methods

Study area

The sampling sites for this research covered 2 regions of the Mexican Atlantic: SGM and MC. The reefs of SGM are located off the coast of the state of Veracruz (Tunnell et al. 2007). One of the reef systems in this region is the Flora and Fauna Protection Area *Sistema Arrecifal Lobos-Tuxpan* (APSALT, for its acronym in Spanish), located north of Veracruz. It encompasses 6 emergent and platform-type coral formations divided into 2 subsystems or polygons: north and south (González-Gándara et al. 2013, Ortiz-Lozano et al. 2013, Cancino-Guzmán 2018).

The *Sistema Arrecifal Veracruzano* National Park (PNSAV, for its acronym in Spanish) is the largest reef complex in the SGM (Chávez et al. 2007), located south of Veracruz (SEMARNAT 2017). This system encompasses approximately 50 coral reefs, of which half are emergent (fringing or platform; Ortiz-Lozano et al. 2013, Robertson et al. 2019) and the rest are submerged (Ortiz-Lozano et al. 2019), distributed in 2 groups: north and south (Horta-Puga et al. 2015, Pérez-España et al. 2015).

The MC region is part of the MAR and extends 400 km along the coast of the state of Quintana Roo (Rioja-Nieto and Álvarez-Filip 2019), from Isla Contoy and Cabo Catoche in the north, to Xcalak and Banco Chinchorro in the south (Carricart-Ganivet and Horta-Puga 1993, Chávez-Hidalgo 2009). Among others, this region encompasses the systems *Arrecifes de Cozumel* National Park (PNAC, for its acronym in Spanish) in the northern zone and the *Arrecifes de Xcalak* National Park (PNAX, for its acronym in Spanish) in the southern zone.

For the APSALT, we selected the Tuxpan and Enmedio reefs (Fig. 1), which are both located within the Tuxpan subsystem in the southern portion and are emergent and platform-type reefs, respectively (González-Gándara et al. 2013, Ortiz-Lozano et al. 2013). In the PNSAV, we selected the Blanca, De Enmedio, and Santiaguillo reefs (Fig. 1), all located in the southern group (Horta-Puga and Tello-Musi 2009); like those in the APSALT, they were all emergent and platform-type reefs (Ortiz-Lozano et al. 2013).

The reefs selected for the PNAC were Caracolillo, Paraíso Norte, and Colombia Somero, located both in the northern and southern extremes of the National Park (Fig. 1). These reefs are classified as fringing (Fenner 1988, Jordán-Dahlgren and Rodríguez-Martínez 2003) and insular (Rioja-Nieto and Álvarez-Filip 2019). For the PNAX, the Río Huach, La Poza, and Canal de Zaragoza reefs were chosen as study sites (Fig. 1) to encompass the extremes of the National Park. Río Huach, in the northern zone, is considered a nursery area for fish and marine invertebrates of ecological and commercial importance, whereas the Canal de Zaragoza, in the south, is identified as a vessel entry zone (Villegas-Sánchez et al. 2023). These are all considered fringing reefs (Weidie

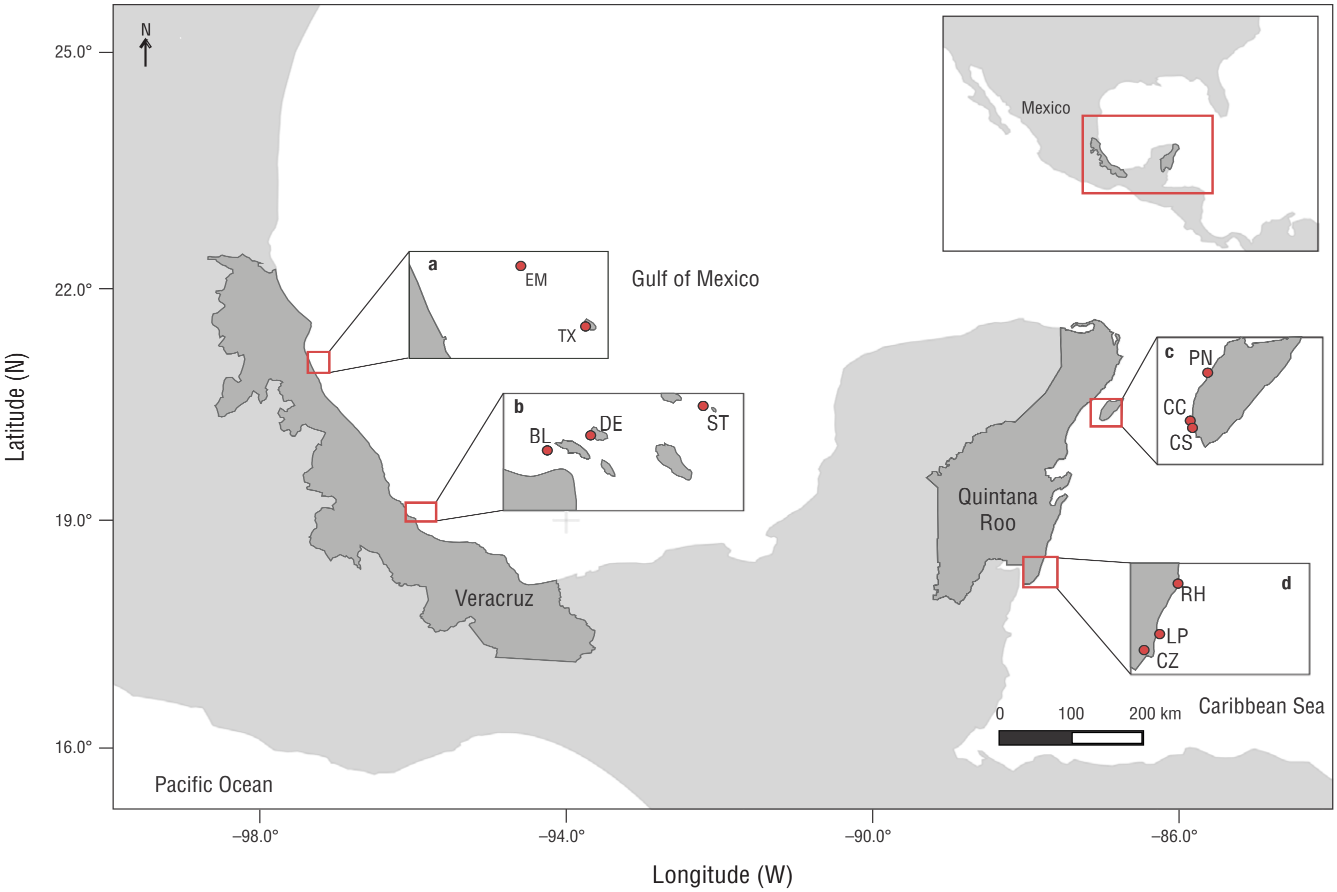

Figure 1. Map illustrating the study area and sampling sites: southwestern Gulf of Mexico (SGM) and Mexican Caribbean (MC). Lobos-Tuxpan Reef System Flora and Fauna Protection Area (APSALT, for its acronym in Spanish) (**a**); *Sistema Arrecifal Veracruzano* National Park (PNSAV, for its acronym in Spanish) (**b**); *Arrecifes de Cozumel* National Park (PNAC, for its acronym in Spanish) (**c**); *Arrecifes de Xcalak* National Park (PNAX, for its acronym in Spanish) (**d**); Tuxpan (Tx); Enmedio (EM); Blanca (BL); De Enmedio (DE); Santiaguillo (ST); Paraíso Norte (PN); Caracolillo (CC); Colombia Somero (CS); Huach River (RH); La Poza (LP); Zaragoza Channel (CZ).

1985, Jordán-Dahlgren and Rodríguez-Martínez 2003, Arias-González et al. 2008).

We chose to sample the leeward zone on all reefs in the SGM and CM (Jordán-Dahlgren and Rodríguez-Martínez 2003, Hongo and Kayanne 2009) to ensure similar exposure conditions. This zone has been recorded as having the greatest coral development in the APSALT and PNSAV (Lara et al. 1992, Escobar-Vásquez and Chávez 2012, Horta-Puga et al. 2015, González-González et al. 2016) and in the PNAC and PNAX (Fenner 1988). Samplings were carried out at depths between 7 and 12 m to minimize variations in environmental conditions such as light and temperature, which influence coral cover.

The composition of these reefs on a broad geographic scale, such as the Mexican Atlantic, is considered similar and has 3 main structural zones: fore reef, reef crest, and back reef (Jórdan-Dahlgren and Rodríguez-Martínez 2003). This zonation is primarily determined by wave impact, light, and depth (Escobar-Vásquez and Chávez 2012, Rioja-Nieto and Álvarez-Filip 2019).

Fieldwork

Sampling was done in October 2022 in the SGM and in May 2023 in the MC. At each sampling site, 5 or 6 replicates were done to assess each indicator of interest (fishes and benthic organisms). Fish sampling was carried out using visual surveys using scuba equipment and 50 × 2 m transects (Díaz-Pérez et al. 2016). The species, size, and abundance of all observed fish were recorded on each transect. To characterize the benthic structure, 50 × 0.50 m video transects were recorded with the aid of an underwater camera over the same fish transects (Díaz-Pérez et al. 2016). A GoPro Hero8 camera (GoPro, San Mateo, USA) was used in standard mode and 4K 4:3 resolution.

Estimation of health indicators

Coral and algal covers were calculated from field-recorded videos, from which 40 photographs per transect were selected for analysis using 13 fixed points (Villegas-Sánchez et al. 2015, Barrera-Falcón et al. 2021). Photographs for each video were automatically captured using VLC Media Player v. 3.0.18 Vetinari (VLC Media Player, Inc., Paris, France), setting time intervals according to the length of each video. Photo analysis was carried out using the AEFEBE v. 1.1 software (Lara-Arenas and Villegas-Sánchez 2016) on a Linux operating system. Under each fixed point, predetermined by the software, the substrate type was identified, including coral and fleshy macroalgae cover, following a modification of the method described by Aronson et al. (1994). The guides of Humann and Deloach (2013) and Vargas-Hernández et al. (2017) were used to identify hard coral species.

The biomasses of herbivorous fishes from the families Scaridae and Acanthuridae and commercial fishes from the families Lutjanidae and Serranidae were calculated using the length–weight relationship equation (Equation 1):

$$W = aL^{b} \quad , \qquad (1)$$

where W is the total weight of the fish, L is the total length, a is the coefficient scale, and b is the parameter determining fish body shape (Kuriakose 2014). The parameters a and b were obtained from FishBase (Froese and Pauly 2023).

Reef health index (RHI)

Finally, we estimated the RHI, which considers 4 indicators: live hard coral cover, fleshy macroalgae cover, herbivorous fish biomass, and commercial fish biomass (HRI 2012; McField et al. 2022, 2024). Reef-building hard corals were considered for the live coral cover. This is an important indicator since these corals are responsible for the structural complexity of reefs, fish abundance, and overall diversity in reef ecosystems (Graham and Nash 2013).

Large, soft algae, such as species from the genera *Dictyota*, *Lobophora*, *Halimeda*, and *Sargassum*, were included for the macroalgae cover (Delgado-Pech 2016). These fleshy macroalgae are associated with coral reef degradation because they compete with corals for space, negatively impacting larval settlement and adult coral survival (Adam et al. 2015, Ceccarelli et al. 2020, Quezada-Pérez et al. 2023).

The RHI considers the families Scaridae and Acanthuridae for the herbivorous fish biomass because these reduce the amount of fleshy macroalgae. For commercial fish biomass, it considers the families Lutjanidae and Serranidae due to their commercial importance and their trophic role as carnivores (McField and Kramer 2007). Indicator ratings and scores were based on the criteria and thresholds established by McField et al. (2024) (Table 1) for the MAR. This standardized assessment allowed us to evaluate the health status of the SGM and MC and understand the performance of these criteria in the SGM.

The average value of the indicators was converted to an ordinal scale with values ranging from 1 to 5, resulting in 5 health values: critical (1), poor (2), fair (3), good (4), and very good (5). The final values of each indicator were averaged to obtain the RHI rating (McField et al. 2022, 2024); the standard error was then calculated to determine its variation by region, system, and reef site.

Statistical analysis

To identify interactions or factors with a significant effect on the community structure of hard corals, a type II permutational multivariate analysis of variance (PERMANOVA) was performed with 1,000 permutations (Anderson and Walsh 2013), considering 3 factors: fleshy macroalgae cover, herbivorous fish biomass, and commercial fish biomass. Prior to the analysis, the coral cover matrix was square-root transformed, and the Bray–Curtis similarity index was calculated. This analysis was performed using the PRIMER statistical package with PERMANOVA V7 (Clarke and Gorley 2015).

RESULTS

Southwestern Gulf of Mexico: coral and fleshy macroalgae cover

In total, 26 stony coral species were recorded in the SGM, of which *Siderastrea siderea*, *Siderastrea radians*, *Montastraea cavernosa*, *Pseudodiploria strigosa*, *Colpophyllia natans*, *Porites colonensis*, *Orbicella annularis*, *Orbicella faveolata*, *Porites astreoides*, and *Acropora cervicornis* had the highest cover values. The APSALT had greater coral cover (55.66%) than the PNSAV (22.14%; Fig. 3). The reefs Tuxpan (68.46%) and De Enmedio (23.92%) had the highest cover in each system, respectively (Table 2, Fig. 3).

Fleshy macroalgae cover was higher in the APSALT (1.68%) than in the PNSAV (1.13%; Fig. 2). The highest cover was observed in the Enmedio reef (2.73%) in the APSALT, and Blanca reef (1.86%) in the PNSAV. The lowest cover was observed in the Tuxpan Reef (0.61%) and Santiaguillo Reef (0.42%) for the APSALT and PNSAV, respectively (Table 2, Fig. 3). It should be noted that macroalgae cover did not exceed 3% in all SGM reefs.

Southwestern Gulf of Mexico: herbivorous and commercial fish biomass

In total, 11 herbivorous fish species were recorded in the SGM. The species *Scarus guacamaia*, *Acanthurus chirurgus*, *Scarus iseri*, *Scarus vetula*, and *Sparisoma viride* had the highest biomasses, which constituted 91% of the total biomass. The families Acanthuridae and Scaridae had the highest biomass in the APSALT (3,258.95 g·100 m^{-2}; Table 2, Fig. 2).

Table 1. Criteria and thresholds established for each of the 4 indicators of the reef health index. Values taken from McField et al. (2024). Coral and fleshy macroalgae cover in percentage and biomass of herbivorous and commercial fish in grams per 100 m².

Score	Coral cover (%)	Fleshy macroalgae cover (%)	Herbivorous fish biomass (g·100 m^{-2})	Commercial fish biomass (g·100 m^{-2})
Very good (5)	40	1	3,290	1,620
Good (4)	20	5	2,740	1,210
Fair (3)	10	12	1,860	800
Poor (2)	5	25	990	390
Critical (1)	<5	>25	<990	<390

In this system, the Enmedio Reef (4,916.64 g·100 m^{-2}) had the highest values of this indicator, whereas for the PNSAV (1,337.62 g·100 m^{-2}), the Santiaguillo Reef had the highest values (2,512.18 g·100 m^{-2}; Table 2, Fig. 3). It should be noted that the biomass of scarids exceeded that of acanthurids in both reefs.

In the SGM, 19 commercially important fish species were recorded. The species *Ocyurus chrysurus*, *Lutjanus griseus*, *Epinephelus adscensionis*, *Cephalopholis cruentata*, *Mycteroperca bonaci*, *Lutjanus cyanopterus*, *Lutjanus analis*, *Lutjanus synagris*, and *Mycteroperca phenaxhighest* had the highest biomasses, which constituted 90% of the total biomass. The families Lutjanidae and Serranidae had the highest biomasses in the APSALT (808.59 g·100 m^{-2}; Table 2, Fig. 2), where the Enmedio Reef (944.54 g·100 m^{-2}) had the highest values for this indicator. For this reef, the biomass of lujanids was higher than that of serranids. In the case of the PNSAV (500.66 g·100 m^{-2}), the Blanca Reef had the highest values (666.44 g·100 m^{-2}; Table 2, Fig. 3), with higher biomass of serranids than of lujanids

Mexican Caribbean: coral and fleshy macroalgae cover

In the MC, 24 species of hard corals were recorded, of which *S. siderea*, *O. faveolata*, *P. astreoides*, *Agaricia tenuifolia*, *Agaricia agaricites*, *Porites porites*, *Porites furcata*, and *Porites divaricata* had the highest cover values. The PNAC showed greater coral cover values (14.96%) compared to the PNAX (6.02%; Fig. 2); the Caracolillo (24.27%) and Río Huach (8.85%) reefs had the highest cover values within these systems, respectively (Table 2, Fig. 3).

Fleshy macroalgae cover was similar in PNAC (37.13%) and PNAX (37.20%; Fig. 2). The highest cover values were recorded in the Colombia Somero Reef (55.35%) and in Canal de Zaragoza (46.03%) for the PNAC and PNAX, respectively (Table 2, Fig. 3). The lowest cover values were observed in the Paraíso Norte (24.33%) and Río Huach (29.76%) reefs for the PNAC and PNAX, respectively (Table 2, Fig. 3).

Mexican Caribbean: biomass of herbivorous and commercial fish

In the MC, 10 herbivorous fish species were recorded. *Sparisoma viride*, *Sparisoma aurofrenatum*, *Acanthurus coeruleus*, *Sparisoma chrysopterum*, *S. iseri*, and *S. vetula* contributed the highest biomasses, which represented 90% of the total biomass. The families Acanthuridae and Scaridae had the highest biomass values in the PNAC (1,073.85 g·100 m^{-2}; Table 2, Fig. 2). At PNAC, Paraíso Norte Reef had the highest biomass value (1,123.00 g·100 m^{-2}); at PNAX (851.41 g·100 m^{-2}), La Poza Reef had the highest values (1,134.54 g·100 m^{-2}; Table 2, Fig. 3). In both reefs, the biomass of scarids exceeded that of acanthurids.

In the MC, 13 commercially important fish species were recorded. *Lutjanus griseus*, *Lutjanus apodus*, *O. chrysurus*, *Lutjanus mahogoni*, *L. synagris*, and *Lutjanus jocu* contributed the highest biomasses, which represented 90% of the total biomass. The families Lutjanidae and Serranidae had the highest biomass values in the PNAC (2,709.45 g·100 m^{-2}; Table 2, Fig. 2). The Colombia Somero Reef in the PNAC had the highest biomass (4,507.27 g·100 m^{-2}); in the PNAX (1,108.91 g·100 m^{-2}), La Poza Reef had the highest values (2,340.58 g·100 m^{-2}; Table 2, Fig. 3). The biomass of lujanids exceeded that of serranids in both reefs.

Reef health index (RHI)

Overall, the SGM obtained a health rating of good (3.50). The APSALT had a RHI rating of 4.25, which classified its condition as good, as observed for the Tuxpan Reef (3.50).

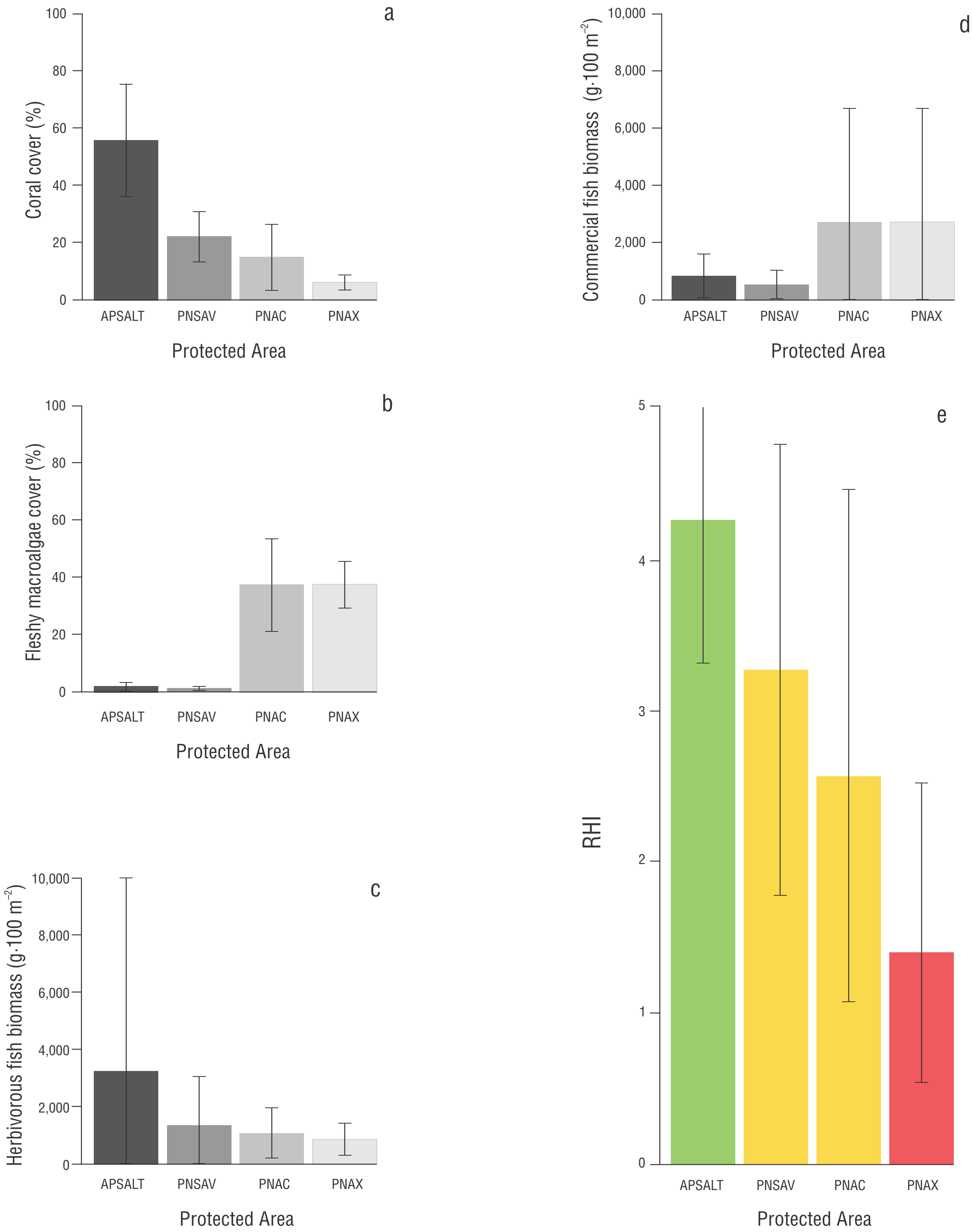

Figure 2. Values obtained for each indicator and reef health index (RHI) score for each system. Average cover of hard corals (**a**); average cover of fleshy macroalgae (**b**); average biomass of herbivorous fish (**c**); average biomass of commercial fish (**d**); RHI score (**e**). Lobos-Tuxpan Reef System Flora and Fauna Protection Area (APSALT, for its acronym in Spanish); *Sistema Arrecifal Veracruzano* National Park (PNSAV, for its acronym in Spanish); *Arrecifes de Cozumel* National Park (PNAC, for its acronym in Spanish); *Arrecifes de Xcalak* National Park (PNAX, for its acronym in Spanish).The green, yellow, and red colors indicate the RHI qualitative rating: green (good), yellow (fair), and red (critical). The gray tones represent the reef systems. The error bars correspond to the standard deviation values.

Table 2. Reef Health Index (RHI) results for each region, system, and reef. The 5 ratings are indicated by the following colors: blue (very good), green (good), yellow (fair), orange (poor), and red (critical). Southwest Gulf of Mexico (SGM); Lobos-Tuxpan Reef System Flora and Fauna Protection Area (APSALT, for its acronym in Spanish); *Sistema Arrecifal Veracruzano* National Park (PNSAV, for its acronym in Spanish) ; Mexican Caribbean (MC); *Arrecifes de Cozumel* National Park (PNAC, for its acronym in Spanish); *Arrecifes de Xcalak* National Park (PNAX, for its acronym in Spanish).

Region/System/ Reef	RHI	Corals (%)	Fleshy macroalgae (%)	Herbivorous fish ($g \cdot 100\ m^{-2}$)	Commercial fish ($g \cdot 100\ m^{-2}$)
SGM	3.50🟢	38.90🟢	1.41🔵	2,298.28🟡	654.62🟠
APSALT	4.25🟢	55.66🔵	1.68🔵	3,258.95🟢	808.59🟡
Tuxpan	3.50🟢	68.46🔵	0.61🔵	1,601.25🟠	672.64🟠
Enmedio	4.50🔵	42.85🔵	2.73🔵	4,916.64🔵	944.54🟡
PNSAV	3.25🟡	22.14🟢	1.13🔵	1,337.62🟠	500.66🟠
Blanca	3.25🟡	22.02🟢	1.86🔵	383.32🔴	666.44🟡
De Enmedio	3.00🟡	23.92🟢	1.11🔵	1,117.36🟠	266.26🔴
Santiaguillo	3.50🟢	20.48🟢	0.42🔵	2,512.18🟡	569.28🟠
CM	2.50🟠	10.49🟡	37.16🔴	962.00🔴	1,908.50🔵
PNAC	2.75🟡	14.96🟡	37.13🔴	1,073.85🟠	2,709.45🔵
Caracolillo	2.50🟠	24.27🟢	31.72🔴	1,023.94🟠	1,043.08🟡
Colombia Somero	2.75🟡	16.00🟡	55.35🔴	1,074.62🟠	4,507.27🔵
Paraíso Norte	2.25🟠	4.60🔴	24.33🔴	1,123.00🟠	2,578.01🔵
PNAX	1.50🔴	6.02🔴	37.20🔴	851.41🔴	1,108.91🟡
La Poza	2.25🟠	4.43🔴	35.79🔴	1,134.54🟠	2,340.58🔵
Río Huach	1.25🔴	8.85🟠	29.76🔴	721.32🔴	196.71🔴
Canal de Zaragoza	1.25🔴	4.78🔴	46.03🔴	698.37🔴	789.45🟠

🔵very good, 🟢good, 🟡fair, 🟠poor, 🔴critical.

The Enmedio Reef was the only one with a health status classified as very good (4.50; Table 2). The PNSAV, with an RHI rating of 3.25, was classified as having fair health. In this system, only Santiaguillo Reef (3.50) showed a health status classified as good, whereas the statuses of the Blanca (3.25) and De Enmedio reefs (3.00) were classified as fair (Table 2).

In contrast, the MC system had a health status classified as poor (2.50), lower than the SGM system. The PNAC had an RHI score of 2.75, a condition classified as fair. In this system, the conditions of the Caracolillo (2.50) and Paraíso Norte (2.25) reefs were classified as poor, whereas the condition of Colombia Somero (2.75) was classified as fair. The PNAX showed a critical health condition (1.50). In addition, in this system, the Río Huach (1.25) and Canal de Zaragoza (1.25) reefs had conditions classified as critical. On the other hand, La Poza showed a condition classified as poor (2.25; Table 2).

Regarding RHI indicators, the value of coral cover for the SGM was good (38.90%). In this context, the very good cover values of the APSALT and Tuxpan reefs were notable (55.66% and 68.46%, respectively). In the MC, cover was fair (10.49%; Fig. 4); however, in this region, Caracolillo Reef was distinguished by a cover value classified as good (24.27%). It is worth noting that the cover value for PNAX (6.02%) was classified as critical, as were the values for La Poza (4.43%) and Canal de Zaragoza (4.78%) within this system. For all SGM reefs, macroalgae cover values were very good and did not exceed 3% in all cases. Conversely, for MC reefs, the macroalgae cover values were critical, with values greater than 24% in all cases. Particularly in this region, on the Colombia

Somero Reef, macroalgae cover exceeded 50% (Table 2), which indicated a reef dominated by fleshy macroalgae.

For the SGM, the biomass of herbivorous fish was fair (2,298.28 g·100 m^{-2}), and only the Blanca Reef showed a critical state (383.32 g·100 m^{-2}). For the MC, the biomass of herbivorous fish was critical (962 g·100 m^{-2}), since all reefs had poor biomass values, except for Río Huach (721.32 g·100 m^{-2}) and Canal de Zaragoza (698.37 g·100 m^{-2}), which had critical biomass values (Table 2).

For the MC, the value of commercial fish biomass was very good (1,908.50 g·100 m^{-2}), with the Colombia Somero, Paraíso Norte, and La Poza reefs standing out with very good values. Río Huach was the only reef with critical biomass values (196.71 g·100 m^{-2}). On the other hand, the SGM had a rating considered poor (654.62 g·100 m^{-2}), with the De Enmedio Reef being the only one with a critical biomass value (266.26 g·100 m^{-2}).

The type II PERMANOVA showed that only the fleshy macroalgae cover factor was significantly related to coral community structure ($P < 0.05$, $P = 0.001$; Table 3), indicating that areas with low fleshy macroalgae cover (RHI = good and very good) differ significantly from those with high macroalgae cover (RHI = poor and critical) in terms of coral community structure. Finally, the interactions between the 3 factors (fleshy macroalgae cover, herbivorous fish biomass, and commercial fish biomass) were not significant ($P > 0.05$).

Discussion

The health status of SGM reefs, assessed using the RHI, showed an average coral cover of 38.90% (Table 2). This indicator could reflect the interaction of processes that have occurred for approximately 220 million years (Tunnell et al. 2007), along with anthropogenic alterations that have affected the resilience and adaptive capacity of corals in this region. The importance and coral development of these reefs has been highlighted in previous studies (Horta-Puga 2003, Escobar-Vásquez and Chávez 2012), suggesting that, despite environmental pressures, these ecosystems have maintained a significant size and cover (Gil-Agudelo et al. 2020).

The SGM reefs are located on a terrigenous continental shelf (Morelock and Koenig 1967, Tunnell et al. 2007) and are exposed to turbid conditions (Tunnell 1988, 1992) due to their proximity to the coast (Horta-Puga et al. 2015). This turbidity results from the discharge of siliciclastic sediments transported by numerous hydrological basins during the rainy season (Carriquiry and Horta-Puga 2010, Mateos-Jasso et al. 2012, CONABIO 2013) and the resuspension of sediments generated by cold fronts (Avendaño-Álvarez et al. 2017). Despite these adverse conditions, SGM reefs have demonstrated a remarkable capacity for adaptation across geological scales (Roche et al. 2018, Dee et al. 2019).

In Singapore, for example, reefs that persist in disturbed, urbanized environments and chronic turbidity have been observed to transition to more tolerant species to withstand current and future disturbances (Januchowski-Hartley et al. 2020).

Furthermore, coral reefs in environments with natural turbidity tend to be more resilient than those with anthropogenic turbidity because the latter have only had short periods to acclimate and adapt (Roche et al. 2018). For example, in the Great Barrier Reef in Australia, reefs such as Middle Reef have been able to survive and maintain high growth rates over the past 9,000 years, despite experiencing high terrigenous sedimentation. The authors suggest that this rapid reef growth is linked to post-death coral skeleton preservation, favored by high levels of terrigenous sediment. This terrigenous sediment tends to coat the skeletons, protecting them from bioerosion and wave action for longer, keeping them intact and, therefore, converting them into stable substrates for new corals to establish. Over time, this process has contributed to reef growth despite adverse turbidity conditions (Perry et al. 2012).

However, although some reef systems, such as those in the SGM, can persist in high turbidity environments, it is important to understand their tolerance limits to sedimentation (Browne et al. 2012). This is especially relevant given that sediments in these reefs come from both natural sources and anthropogenic activities (Tuttle and Donahue 2022).

The PNSAV is located opposite the city of Veracruz, one of the oldest cities in the Americas, founded in 1519 (Melgarejo-Vivanco 1960). Since then, these reefs have been exploited to extract coral to use in construction (Heilprin 1890, Tunnell et al. 2007, Gil-Agudelo et al. 2020) and have been exposed to the impact of port activities (Horta-Puga and Tello-Musi 2009, Horta-Puga et al. 2015, Argüelles et al. 2019). These conditions have subjected the corals to a continuous state of stress for approximately 500 years.

Similarly, APSALT reefs, off the cities of Tuxpan and Tamiahua, have been subjected to pressure since the creation of the port of Tuxpan in 1580 and have been affected by port activities and fuel spills (Ortiz-Lozano et al. 2013, Lozano-Nathal and Ponce-Jiménez 2018). Thus, the natural events that characterize this area, along with the impacts endured by the APSALT and PNSAV reef systems progressively and throughout history, could be favoring the adaptive potential of these reef systems.

The upwelling of oceanic water from the Campeche cyclonic gyre is another natural factor that could be contributing to the good health of SGM reefs (Salas-Pérez et al. 2012, Guerrero et al. 2020); this upwelling limits coral bleaching by bringing in cool waters (<22 °C) and favors coral development with the contribution of nitrogen used by zooxanthellae (Carrasco 2022, Salas-Monreal et al. 2022).

In addition, natural temperature variability in the SGM, where waters cool in the winter (Escobar-Vásquez and Chávez 2012), could increase reef resilience, as reef areas with greater water temperature variability have been shown to be more resistant to thermal stress and bleaching (Safaie et al. 2018, Lachs et al. 2023). Furthermore, reefs in the Gulf of

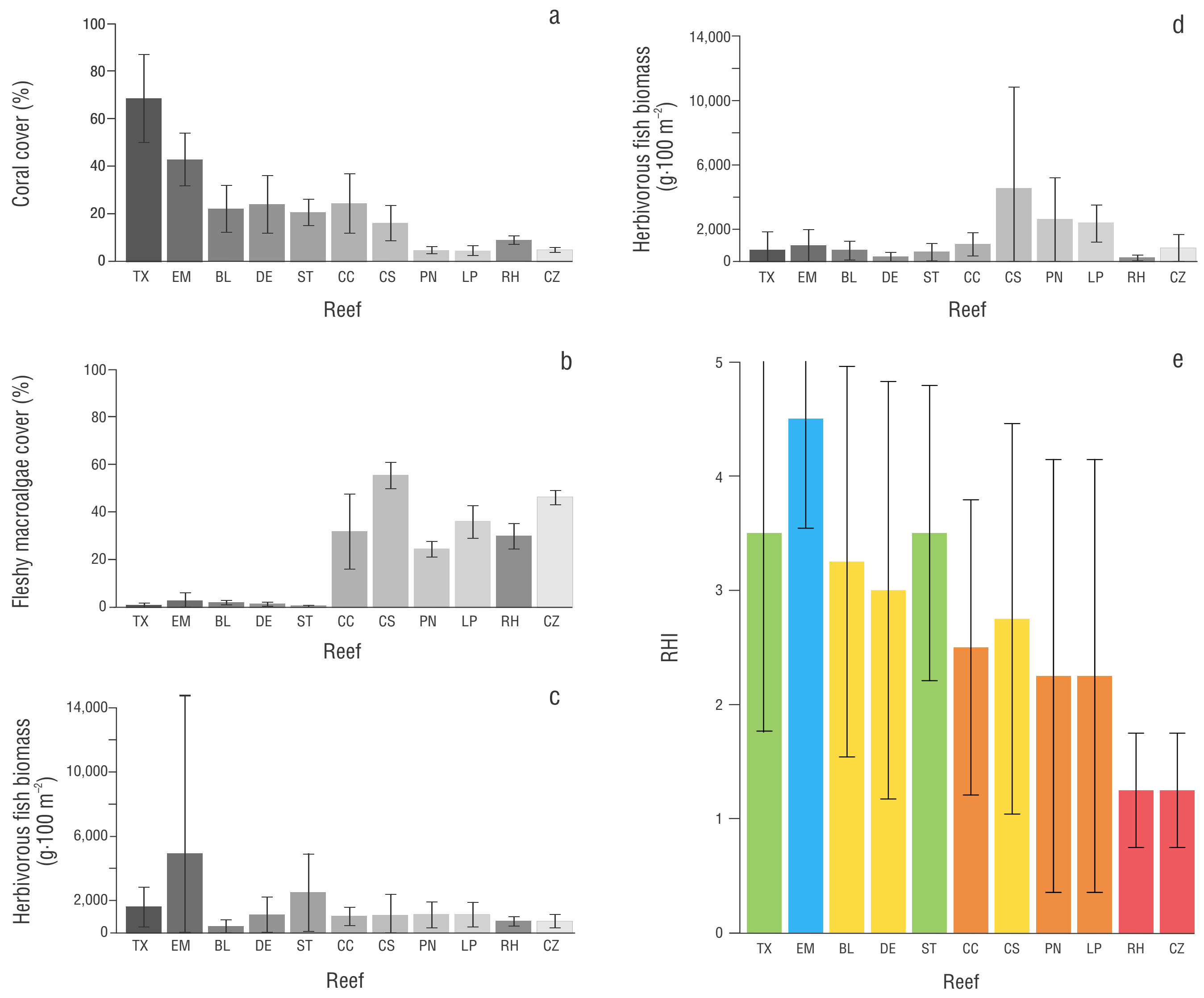

Figure 3. Values obtained for each indicator and RHI score for each reef. Average cover of hard corals (**a**); average cover of fleshy macroalgae (**b**); average biomass of herbivorous fish (**c**); average biomass of commercial fish (**d**); Reef Health Index (RHI) score (**e**). Tuxpan (Tx); Enmedio (EM); Blanca (BL); De Enmedio (DE); Santiaguillo (ST); Caracolillo (CC); Colombia Somero (CS); Paraíso Norte (PN); La Poza (LP); Río Huach (RH); Canal de Zaragoza (CZ). The green, yellow, and red colors indicate the qualitative RHI score: green (good), yellow (fair), and red (critical). The gray tones represent the reef systems. The error bars correspond to the standard deviation values.

Mexico have experienced thermal stress since 1878 (Kuffner et al. 2015), and the siliciclastic nature of the gulf may make corals more resilient than those found in carbonate environments (Dee et al. 2019). These factors combined could explain the high resistance and resilience of the reefs in the region, especially in species such as *C. natans*, *M. cavernosa*, and *P. strigosa*, which tolerate high sedimentation rates (Horta-Puga et al. 2015) and, in fact, had some of the highest cover values in the region.

In the Yucatán Peninsula, MC reefs developed in oligotrophic waters on a carbonate platform, with little influence of fluvial currents due to the karst nature of the region (Weidie 1985, Merino et al. 1990, Merino 1997, Tunnell et al. 2007). The high permeability of the soil enables water to infiltrate into aquifers, where soils act as natural filters for contaminants (Carballo-Para 2016, Estrada-Medina et al. 2019).

Historically, the region has not shown high sedimentation rates (Horta-Puga et al. 2019). However, in recent decades, there has been an increase in nutrients and sediments associated with human activities (Arias-González et al. 2017, Rogers and Ramos-Scharrón 2022), and, recently, the waters have come to be considered non-oligotrophic (Velázquez-Ochoa and Enríquez 2023). Thus, it is likely that, due to the lack of natural sedimentation throughout its history, the hard coral species of the MC have not had sufficient time to adapt to the effects of anthropogenic sedimentation (Roche et al. 2018).

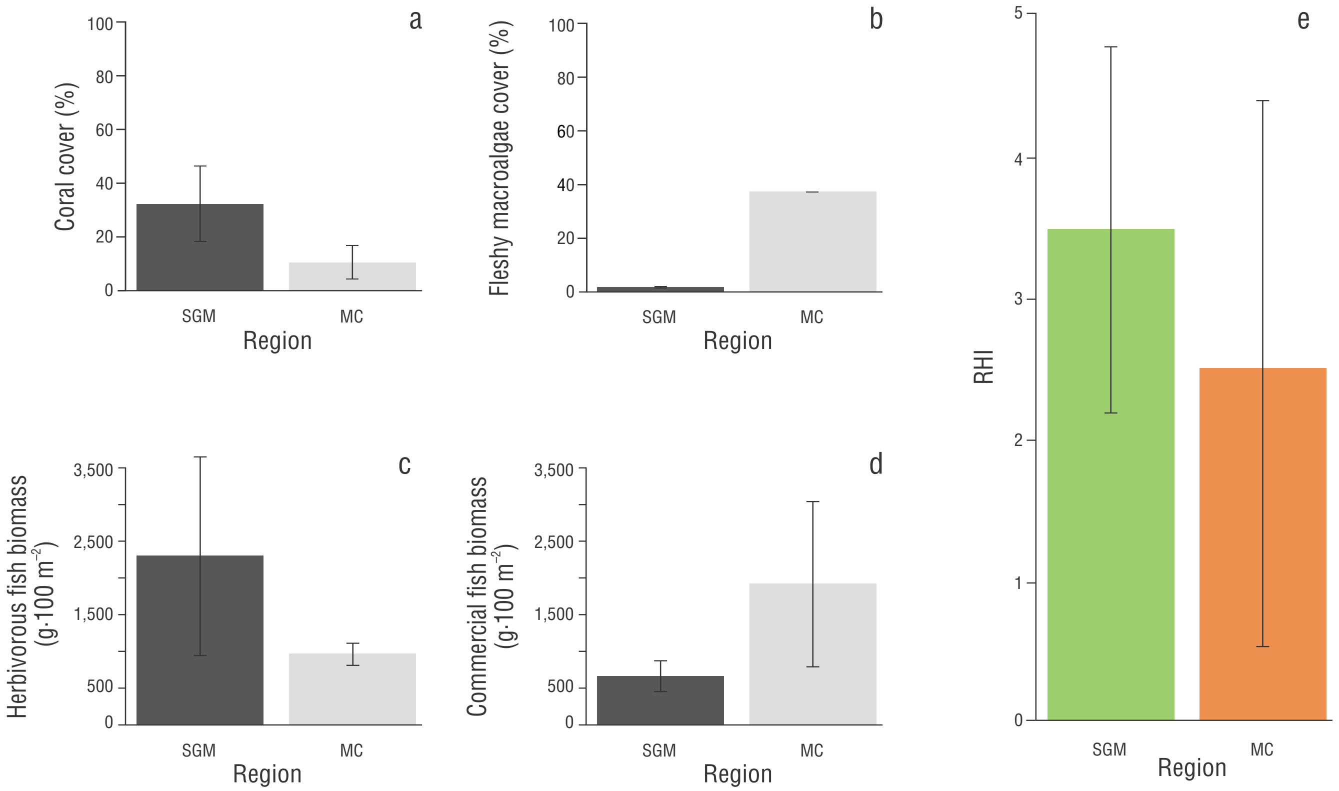

Figure 4. Values obtained for each indicator and RHI score for each region. Average cover of hard corals (**a**); average cover of fleshy macroalgae (**b**); average biomass of herbivorous fish (**c**); average biomass of commercial fish (**d**); Reef Health Index (RHI) score (**e**). Southwestern Gulf of Mexico (SGM); Mexican Caribbean (MC). The green and orange colors indicate the qualitative RHI score: green (good), orange (poor). The gray tones represent the regions. The error bars correspond to the standard deviation values.

The state of Quintana Roo is still young (founded in 1974; State Congress 2001); however, coastal development rates in the MC over the past 14 years have been very high (Arias-González et al. 2017), increasing from 88,000 inhabitants in 1975 to 1.5 million in 2015 (Suchley and Alvarez-Filip 2018). This could be associated with a more intense and abrupt impact on the reefs of the MC compared to those of the SGM; this impact could have negatively affected the adaptive capacity of coral species (Roche et al. 2018) and the resilience of these ecosystems (Sandin et al. 2008, Graham et al. 2013, Anthony et al. 2015).

In MC reefs, an accelerated phase shift has been documented, driven by eutrophication and sedimentation as a result of inadequate wastewater treatment (Martínez-Rendis et al. 2015, Suchley et al. 2016, Arias-González et al. 2017, Rioja-Nieto and Álvarez-Filip 2019, Randazzo-Eisemann et al. 2021). These impacts are closely linked to coastal development (Arias-González et al. 2017, Suchley and Álvarez-Filip 2018, Rioja-Nieto and Álvarez-Filip 2019).

The data generated confirmed that the community structure of hard corals is determined by the presence of fleshy macroalgae (Table 3). Although macroalgae are primary producers and a fundamental part of food chains (Pereira 2021), high covers can negatively affect reefs by competing with corals for space, inhibiting larval settlement and hindering their recovery (Díaz-Pulido et al. 2010). This highlights the importance of considering this indicator in reef health assessments in the region.

This could be associated with the shift in reef-building species in the MC, from dominant genera, such as *Orbicella*, *Montastraea*, and *Acropora*, to opportunistic and more tolerant genera, such as *Porites* and *Agaricia* (Fig. 5), which also contribute very little to calcium carbonate accumulation and reef structural complexity. Furthermore, this trend has consistently been observed across other Caribbean reefs (Barranco et al. 2016, Caballero-Aragón et al. 2020b, Dahlgren et al. 2020, Lima et al. 2022, McField et al. 2022, CCMI 2023, Eagleson et al. 2023).

These results are concerning because it is important not only to conserve high coral cover but also to maintain cover of reef-building corals (e.g., *Acropora* spp., *Orbicella* spp.; Alvarez-Filip et al. 2013, González-Barrios 2019, Guendulain-García et al. 2024). The loss of structural complexity affects the three-dimensional structure

Tabla 3. Reef community structure. Result summary of the 3-factor Type II PERMANOVA.

Factor	Pseudo-*F*	*P*(perm)
Fleshy macroalgae cover	7.1975	**0.001**
Herbivorous fish biomass	1.0246	0.455
Commercial fish biomass	1.3092	0.185

*Results that showed a significant relationship ($P < 0.05$) are indicated in bold.

of reefs and impacts their function as coastal protectors, as they lose the capacity to reduce wave energy (Carlot et al. 2023). This increases the risk of coastal erosion and affects nearby ecosystems, such as mangroves and seagrass beds (Zepeda-Centeno et al. 2018).

Low cover values of fleshy macroalgae (1.41%) indicated that the status for this indicator in the SGM was very good (Table 2), which positively influenced the RHI score for the region (3.50). This value contrasts with that of the MC, where the status for this indicator was critical (Table 2). In the PNSAV, the benthic community is dominated by turf algae, whereas fleshy macroalgae have a lower presence (Horta-Puga et al. 2020). This suggests that low cover values of fleshy macroalgae in SGM reefs do not necessarily imply high herbivore biomasses, but rather a possible association with the dominance of turf algae, as has been observed in this region (Dee et al. 2019).

According to Horta-Puga et al. (2020), it is not possible to establish that the reefs of the PNSAV are in a stable state as in the MC, but rather in an unstable or intermediate state. This is because a stable state is characterized by changes in key elements of the system that result in a dramatic and lasting impact on species composition and ecosystem functioning (Simenstad et al. 1978), whereas an unstable or intermediate state is characterized by high spatial and temporal variability of the key elements, and not necessarily a dominance of any of them (Bellwood and Fulton 2008, Goatley et al. 2016). In coral reefs, there are 2 stable states, one dominated by corals and the other dominated by fleshy macroalgae (Mumby and Steneck 2008, Mumby 2009).

A shift from a steady state of a coral reef to a stable state dominated by fleshy macroalgae has already been reported in the MC (Randazzo-Eisemann et al. 2021). Likewise, such events have been reported in other ecosystems, such as the shift from a steady state of macroalgae forests to rocky, sterile, and low-biodiversity marine environments, as a consequence of high urchin abundances (Ling et al. 2015, McPherson et al. 2021, Eger et al. 2024). Nevertheless, unstable or intermediate states have also been recorded in coral reefs, where other benthic organisms, in addition to fleshy macroalgae, become dominant (e.g., sponges, gorgonians, turf algae; Norström et al. 2009, Graham et al. 2014) in response to constant anthropogenic disturbances (Norström et al. 2009). These intermediate states tend to become stable when large-scale coral mortality occurs, creating positive feedback loops, which amplify and reinforce the process, preventing the reef from recovering to its original state (Norström et al. 2009, Van de Leemput et al. 2016).

Therefore, PNSAV reefs could likely be heading towards an unstable or intermediate state dominated by turf algae (Horta-Puga et al. 2020). This could also be the case for APSALT reefs, as an increase in turf algae cover has also been reported in the area (Escobar-Vasques and Chávez 2012, Cancino-Guzmán 2018, González-Gándara and Salas-Pérez 2019), which would consequently have implications for the coral cover of the reefs.

Although not reflected in our reported results, turf algae had higher cover values than fleshy macroalgae during the SGM frame analysis (SGM: 17.81%; APSALT: 14.38%; PNSAV: 20.11%; Enmedio: 14.90%; Tuxpan: 13.85%; Blanca: 27.70%; De Enmedio: 19.50%; Santiaguillo: 13.17%). This could be encouraging for the reefs of this region, since coral recruits have been shown to establish and grow, albeit slowly, in dense mats of turf algae (Birrell et al. 2005, 2008). Conversely, this process of coral recruit settlement does not occur when fleshy macroalgae dominate the seafloor.

Thus, if recruitment continues, corals could surpass turf algae (Birrell et al. 2005, 2008; Swierts and Vermeij 2016). However, it is important to note that turf algae can also be displaced by fleshy macroalgae (Fung et al. 2011), where herbivory by fish and sea urchins would play an important role in the competition between these 2 algal groups (Arias-González et al. 2017).

These results suggest that special attention should be paid to the cover of both algal groups in the SGM and that they should be monitored because the current state could take 2 paths: (1) an ideal state, with reefs dominated by corals, or (2) a less desirable scenario, with a dominance of turf algae,

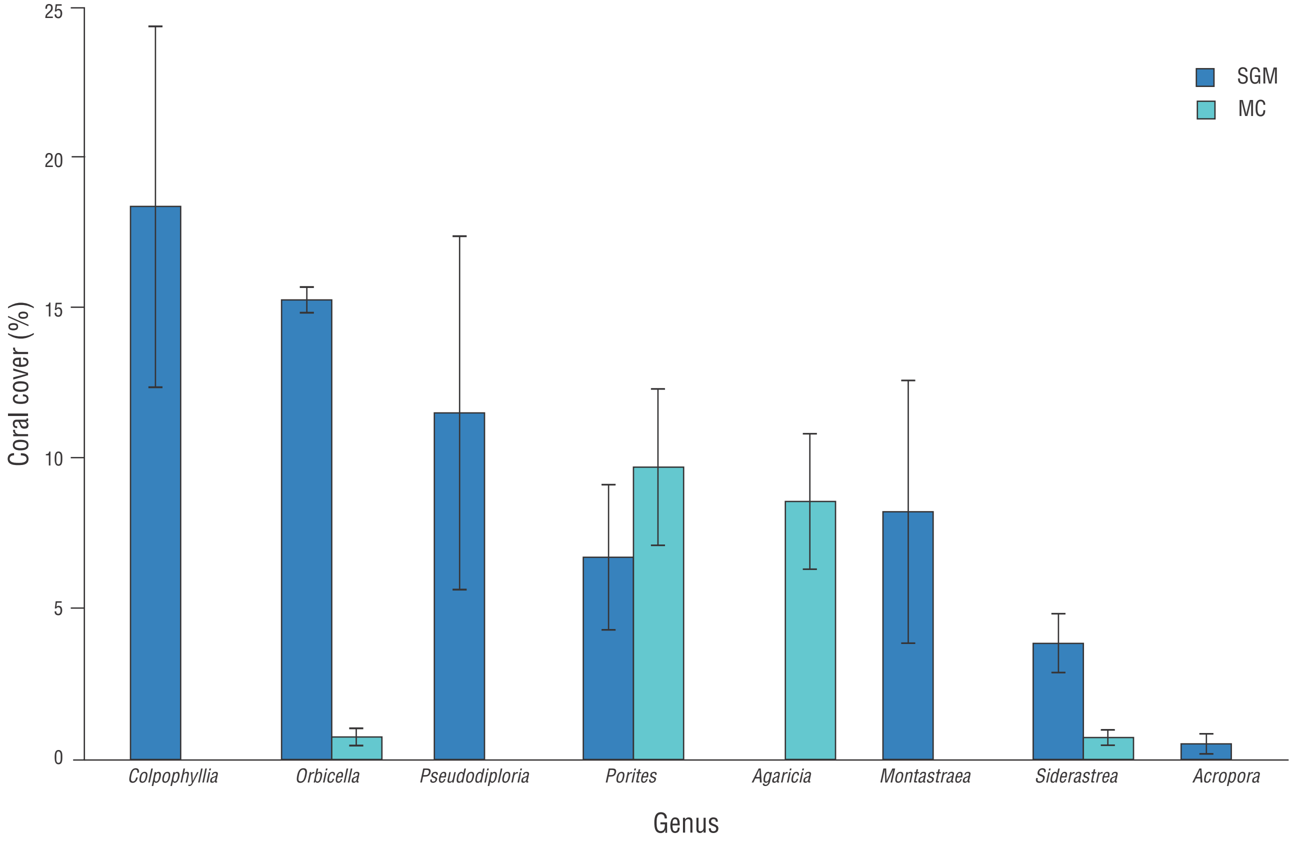

Figure 5. Average cover for the 8 genera of hard coral with the highest cover in the southwestern Gulf of Mexico (SGM) and the Mexican Caribbean (MC). Error bars correspond to standard deviations.

which would imply a phase shift, similar to that experienced in the MC with fleshy macroalgae. This is especially relevant considering that some authors, such as Harris et al. (2015), have pointed out that an increase in the abundance of turf algae is expected in the future, given that they can survive in conditions unfavorable to corals.

The better health status of the APSALT (good) compared to the PNSAV (fair) (Table 2) coincides with the idea that the reefs in northern Veracruz (APSALT) are in better condition than those in the south (PNSAV; Chávez et al. 2007). Nonetheless, attention should be directed toward fish communities, especially in PNSAV and the Tuxpan reef of APSALT, whose ratings ranged from critical to fair (Table 2).

This could reflect the pressure of artisanal fishing on the coast of Veracruz (Ortiz-Lozano et al. 2019). Another factor to consider is that only reefs from the southern group were sampled in both systems, which could have influenced the results, as the conservation status of reefs of the southern group of the PNSAV has been reported to be better than that of the northern group (Chávez et al. 2007).

Regarding the scores obtained, the work by Simoes et al. (2020) classifies the health status of the SGM, APSALT, and PNSAV as fair, using different indicators and criteria than those used for the RHI. Nevertheless, we can compare these results with those obtained in the present study (Table 2), where the scores were good for the SGM and APSALT, and fair for the PNSAV.

On the other hand, Pérez-España et al. (2021) used the RHI to assess the health status of 15 reefs in the PNSAV. Although the individual scores for each indicator differed from those obtained in this study, probably due to an adjustment made by these authors to the RHI criteria based on recent studies in the PNSAV (last 10 years), the average score obtained (fair) coincides with that of this study. In the present study, we did not use the adjusted criteria of Pérez-España et al. (2021) because we selected the RHI criteria established by the HRI for a standardized assessment. It is important to note that there are no previous studies for the APSALT based on the RHI, which limits the comparison with the results presented here.

The PNAC showed the best health status within the MC (fair), which coincides with that reported by McField et al. (2022), where the PNAC was identified as one of the best conserved sites in the MC and MAR, with 35% of its reefs under full protection, higher than anywhere else in the region.

Previous studies in the PNAC that use the RHI also indicate that the biomasses of herbivorous and commercial fish are in good health (Pérez-Cervantes et al. 2017); these values are the highest in the MAR (McField et al. 2022).

The improved health status of the PNAC could be the result of the conservation strategy implemented by the *Comisión Nacional de Áreas Naturales Protegidas* (CONANP) in 2019, which included the temporary suspension of tourist activities in certain areas of the National Park to promote recovery from the impact of the white syndrome (CONANP 2019). Furthermore, the circulation of currents in the area could mitigate the effects of sedimentation and continental debris (Contreras-Silva et al. 2020).

The corals of the PNAC are considered among the most resilient in the MC, with high coral cover (Barranco et al. 2016, Contreras-Silva et al. 2020), where the leeward reefs show greater development because they are protected from winds and storms (Fenner 1988). In addition, the critical state for the PNAX is consistent with that observed by the HRI (2012) and, more recently, by Díaz-Pérez et al. (2016), who reported highly deteriorated and critical conditions for the PNAX.

This is likely due to local anthropogenic pressure, derived from tourism and agriculture, and inadequate reef management in the southern part of the MC (Contreras-Silva et al. 2020). Therefore, our results reflect the intensity and pressure exerted by the rapid coastal development of the last 14 years in the MC, where PNAC reefs still present the best conditions.

The SGM and PNAC reefs are the most resilient in the MC (Contreras-Silva et al. 2020) and could act as resilience hotspots, that is, areas where corals have demonstrated a greater capacity to resist and recover from environmental and anthropogenic disturbances, such as climate change and human activity (Nyström et al. 2008; McClanahan et al. 2012; McLeod et al. 2019, 2021). These areas are characterized by their ecological stability and their potential to serve as natural sanctuary areas, making them key sites for reef conservation in the region (McClanahan et al. 2014, McLeod et al. 2019, Bang et al. 2021, Moritsch and Foley 2023). However, the speed of climate change is likely to exceed the speed at which corals can adapt (Frieler et al. 2013).

Therefore, further studies are needed for SGM reefs to help expand on and understand the ecological and environmental processes that make the persistence of these reefs possible in an environment of high sedimentation and turbidity, as suggested by Salas-Pérez and Granados-Barba (2008) for the PNSAV. In addition, their tolerance thresholds need to be determined because the future trend is towards greater deposition of anthropogenic sediments and thermal stress, which will also be catastrophic for the less resilient reefs of the MC.

Finally, the biomass results should be interpreted with caution because samplings were conducted during different periods in the 2 regions, and fish abundance may fluctuate seasonally. In addition, it is important to consider that commercial fish species tend to be highly mobile, traveling long distances, so sampling for this indicator should be conducted more frequently to obtain results representative of the current status of this indicator (McField and Kramer 2007).

The RHI has proven to be key to understanding reef conditions at the regional level, such as the MAR. However, to gain more detailed knowledge of other regions, it is essential to consider other local indicators, such as water quality, as suggested by Horta-Puga and Tello Musi (2009) and Simoes et al. (2020) for the Gulf of Mexico, because environmental conditions, such as water quality, have been observed to influence the cover of algal groups (Horta-Puga et al. 2020).

It is essential to implement an ongoing reef health assessment program for reefs in the SGM and MC. Periodic assessments facilitate comparing trends over time to provide a true measure of reef health. These assessments, along with resilience-based management strategies (McLeod et al. 2019, Obura et al. 2019, Vardi 2021, Moritsch and Foley 2023), will be key to reef management and conservation in the Mexican Atlantic.

Conclusions

The results obtained using the RHI led to the following key conclusions: (a) reefs in the SGM had greater coral cover than those in the MC; (b) a phase shift is already evident in the MC, whereas in the SGM, the low cover of fleshy macroalgae would indicate that it is still in an intermediate stage; (c) the high cover of fleshy macroalgae in the MC negatively affected its health status; (d) the lower biomasses of herbivorous fish reported in the MC could corroborate their relationship with the high macroalgae cover observed; (e) the higher biomasses of commercial fish recorded in the MC, particularly in the PNAC, suggest the effectiveness and importance of conservation strategies; and finally, (f) reefs in the SGM had better health conditions than those in the MC, which could be related to the natural and anthropogenic history of both regions.

English translation by Claudia Michel-Villalobos.

Declarations

Supplementary Material

This work includes the following supplementary material: (1) a database of coral cover, (2) a database of turf algae cover, and (3) photographs of the sampled reefs. The supplementary material for this work can be downloaded from the following links: (1) https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3501/420421182, (2) https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3501/420421183, and (3) https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3501/420421185.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: DC, CAVS; Data curation: DC, CAVS; Formal analysis: DC, CAVS; Funding acquisition: DC, CAVS; Investigation: DC, CAVS; Methodology: DC, CAVS, HPE; Project administration: CAVS; Resources: DC, CAVS; Software: DC, CAVS; Supervision: CAVS, HPE, LAF; Validation: CAVS, HPE, LAF; Visualization: DC, CAVS, HPE, LAF; Writing—original draft: DC, CAVS; Writing— review, and editing: CAVS, HPE, LAF.

Data availability

The data are available as supplementary material.

Ethical approvals and permits for animal studies

This study was conducted with ethical approval from CONANP and all necessary permits (F00.9.DPNAC/174/2023 and F00.9.DPNAX/210/2023). The study complied with all applicable regulations for the justified use of animals in research and their welfare.

Use of AI Tools

The authors did not use any artificial intelligence tools for this work.

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SPECIAL ISSUE
Research Article

Taxonomic and functional richness of fish in temperate and tropical reefs of the Mexican Pacific

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ABSTRACT. Taxonomic and functional diversity patterns of fish in temperate reefs in the Mexican Pacific have not been analyzed in integrative biodiversity studies. Thus, this study compared the taxonomic, phylogenetic, and functional diversity of reef fish in 4 biogeographic provinces: Californian, Cortez, Panamic, and Oceanic Islands. Species checklists were compiled from the literature, museum collections, and monitoring data from 21 sites in marine protected areas (MPAs) and 45 non-protected sites. Based on this data and 6 biological traits (size, mobility, period of activity, gregariousness, position in the water column, and diet), we calculated species richness (S), average taxonomic distinctness ($\Delta+$), number of functional entities (FE), functional redundancy (RED), functional vulnerability (FV), and functional volume ($FVol$). We registered 1,045 species; the dominant categories were benthic, highly site-attached, diurnal, solitary, medium-sized, and invertivores. The Cortez province showed the highest S and FE values, whereas the Californian province presented the lowest values. Notably, $FVol$ was >70% across the 4 biogeographic provinces, suggesting that the range of ecological functions and processes was maintained across provinces despite their contrasting biodiversity levels, environmental conditions, and evolutionary histories. A "regional backbone" was identified, consisting of 74 species and 58 FE (the fundamental species and shared ecological roles across provinces). At the regional level, low RED (<3 species·FE^{-1}) and high FV (>55% of FEs represented by a single species) were observed. All provinces presented high values of $\Delta+$ (>80%), reflecting the broad range of taxonomic lineages within the region. The MPAs presented higher S and RED than non-protected sites; however, further research is needed to elucidate the positive effects of protection.

Key words: marine protected areas, marine ecosystems, ichthyofauna, biogeographic patterns, biological traits.

INTRODUCTION

Marine and coastal ecosystems worldwide are increasingly threatened by human activities (e.g., fishing, pollution, and habitat fragmentation), as well as by environmental factors associated with climate change (e.g., increasing sea temperatures and rising sea levels), which could result in a loss of species and the functions and services they provide (Halpern et al. 2015, Morzaria-Luna et al. 2018). Understanding how fish diversity varies across biogeographic provinces with distinct environmental conditions and evolutionary histories is crucial for developing effective

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conservation strategies (Stuart-Smith et al. 2013, McLean et al. 2021). These comparisons can help identify regions with unique or vulnerable assemblages that require targeted management efforts (Olivier et al. 2018). In the face of the loss of species, functions, and services, marine protected areas (MPAs) serve as a primary conservation tool to safeguard biodiversity and improve ecosystem resilience (Hernández-Andreu et al. 2024).

Although taxonomic diversity-based studies are common for describing spatial and temporal differences (Mora et al. 2008, Lin et al. 2020, Pham et al. 2023), it has been reported that these studies are not highly sensitive to the effects of disturbances on ecological processes (Mouillot et al. 2013). An alternative is to use trait-based approaches that consider the biological information of each species as an approximation of their role in the ecosystem and assess the loss of species and their functions (Francisco and De la Cueva 2017). Using species presence and their biological traits makes it possible to calculate functional indices and describe spatial patterns such as biodiversity "hotspots" or functionally vulnerable areas at the global level (Mouillot et al. 2014). Moreover, based on a functional diversity analysis, it has been reported that no-take zones inside MPAs were not sufficiently representative to safeguard ecosystem functions in tropical reefs (Hernández-Andreu et al. 2024).

Regional descriptions of the functional patterns of reef fish have been extensively reported given the ample biological information available, the wide variety of functions they perform, and the economic importance of some species (Mouillot et al. 2014, Olivier et al. 2018). Mouillot et al. (2014) analyzed the taxonomic and functional richness of 6,316 tropical reef fish species at a global level, evaluating data from 169 locations. The authors found the highest species richness (S = 3,689 species) in the Central Indo-Pacific region and the lowest richness in the Eastern Atlantic (S = 403 species) and Eastern Tropical Pacific (ETP) (S = 570 species). However, Mouillot et al. (2014) reported that even the later regions with low species richness could be able to maintain the ecological processes necessary to sustain tropical reefs, as they presented similar functional volume values and shared most of the key functions with richer faunas, such as those found in the Central Indo-Pacific. Moreover, these authors reported that even highly diverse systems, such as tropical reefs, could be threatened by species loss, as fish species tended to be disproportionately packed into a few specific functional entities, leaving many functions highly vulnerable.

McLean et al. (2021) analyzed 2,786 fish species. These authors reported a consistent variety of traits (the dominant categories were invertivore diets; demersal, diurnal, and solitary behavior; and small-medium size), including a "backbone" of 21 functional entities common to the 89 studied ecoregions, highlighting the existence of shared ecological roles in shallow reefs worldwide. Even though the authors found more species in tropical reefs than in temperate regions, they reported similar trait compositions among fish assemblages under similar environmental conditions (even when thousands of kilometers separated study sites), despite the assemblages hosting drastically different species from separate evolutionary lineages. These findings suggest that similar trait-based management strategies can be applied to regions with distinct species pools. Therefore, understanding taxonomic, phylogenetic, and functional biodiversity patterns in marine regions is needed to unravel the contributions of species (and their evolutionary lineages and functional entities) to ecosystem processes and to support the development of management strategies that enhance reef resilience.

While studies have been conducted in the Mexican Pacific, a comprehensive comparison of the taxonomic and functional richness of fish across regions is missing. In the ETP, Robertson and Cramer (2009) identified a high number of resident species in the central region of the Panamic province (Panama and Costa Rica) and at the tip of the Baja California Peninsula in the Cortez province. Similarly, Dubuc et al. (2023) reported the highest values of taxonomic and functional richness in the central region of the ETP (based on an analysis of 313 species registered by visual censuses at 122 sites from Mexico to Ecuador), which was positively influenced by sea surface temperature and conservation status and negatively influenced by shelf area and the distance from the mainland. In contrast, Ramírez-Ortiz et al. (2017) found a decreasing biogeographic pattern in the functional richness of fish and macroinvertebrates towards the tropics, with the highest values in the Cortez and Oceanic Islands provinces (compared to the Panamic province), which were associated with habitat heterogeneity and the oceanographic conditions of those regions.

In the Mexican Pacific, Olivier et al. (2018) identified similar fish diversity patterns in the Gulf of California by analyzing different data sources and reported greater taxonomic and functional diversity in the southern islands associated with the oceanographic conditions of this region. Although their findings revealed low functional redundancy and high functional vulnerability at the regional level, uneven species distributions between functional entities and spatial differences in fish diversity were reported.

Despite an increase in studies of the Mexican Pacific, analyses of the regional patterns in fish diversity in temperate and tropical reefs, as well as in MPAs and non-protected sites, remain scarce. Thus, we compiled fish species presence data from 66 reefs from different sources (the literature, museum collections, and monitoring programs) to describe the spatial patterns of taxonomic, phylogenetic, and functional richness in 4 biogeographic provinces (Californian, Cortez, Panamic, and Oceanic Islands). We also sought to identify possible ecological factors that influence reef fish fauna, considering the effects of protection by MPAs on species conservation and their ecological functions. Overall, the results of this study help to elucidate common and particular traits and the taxonomic and functional diversity patterns of fish in each biogeographic province of the Mexican Pacific.

MATERIALS AND METHODS

Study area

We compiled information on fish presence in 66 sites (21 MPA sites and 45 non-protected sites) along the Mexican Pacific (Fig. 1). The study region was divided into 4 biogeographic provinces according to the regional classification of Robertson and Cramer (2009), which is based on the geographic distribution of shore fish species (i.e., resident species whose abundance or distributions indicate they exhibit self-sustaining populations in the region; Robertson et al. 2004). The Californian province extends north from 25° N along the Pacific coast of the Baja California Peninsula (Robertson and Cramer 2009). It is influenced by the California Current, which imposes its temperate features (average sea surface temperature [SST] of 16 °C; SAGARPA 2018), and the North Equatorial Current and its tropical features (SST of 29.2–25.6 °C; SAGARPA 2018) (Bernal et al. 2001, Valdez and Díaz 1996).

The Cortez Province covers the Gulf of California and the southern Pacific coast of Baja California Peninsula, reaching north to about 25° N near Magdalena Bay (Robertson and Cramer 2009); the average SST range for the province is 19.8–27.8 °C (Anislado-Tolentino 2008, SAGARPA 2018). The Cortez province is influenced by the North Equatorial Current and North Pacific Gyre (Bernal et al. 2001). Northwest winds generate upwelling events that bring nutrient-rich waters to the euphotic zone and increase primary productivity (Escalante et al. 2013). These oceanographic conditions support a high diversity of marine fauna and a great variety of habitats such as mangroves, coastal lagoons, and rocky and coral reefs (Cruz-García 2009).

The Panamic province extends from 25° N to 4° S off the Gulf of Guayaquil in Ecuador (Robertson and Cramer 2009). The mean SST of this province is 28 °C, and it is influenced

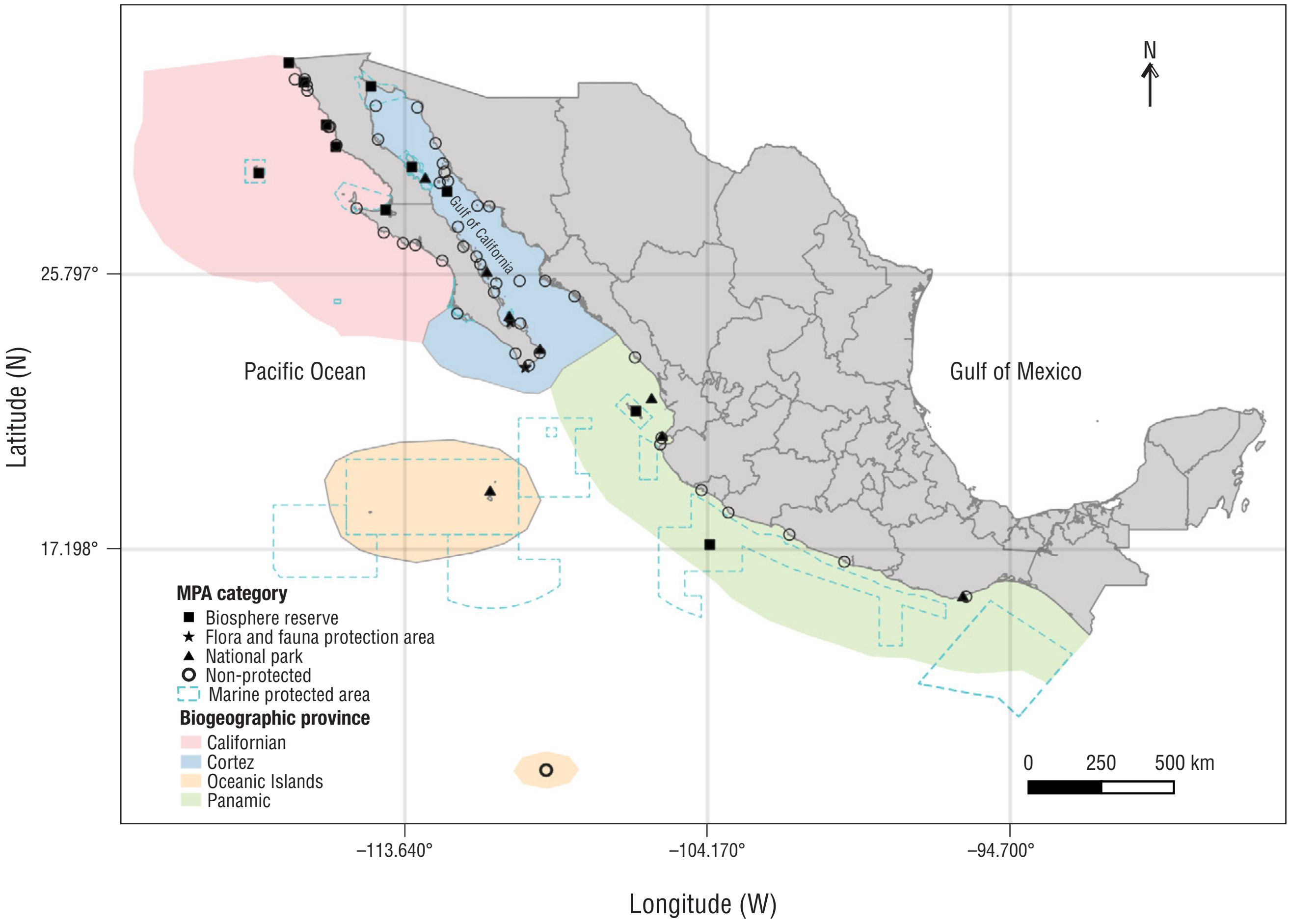

Figure 1. Map of the Mexican Pacific depicting study sites in the Californian (red), Cortez (blue), Panamic (green), and Oceanic Islands (orange) biogeographic provinces. Circles indicate non-protected sites; other markers indicate that study sites are located in marine protected areas (MPAs) (blue dashed line) with distinct protection categories: national parks (triangles), biosphere reserves (squares), and flora and fauna protected areas (stars).

by the confluence of 2 marine currents in the central Mexican Pacific, the Costa Rican Coastal Current and California Current, which merge to contribute to the formation of the North Equatorial Current (Lara-Lara 2008). This province is also influenced by northwest winds, which increase the presence of gyres and eddies, thus favoring primary productivity near the coast for most of the year (Pérez-de-Silva 2023). In addition, the upwelling zone of the Gulf of Tehuantepec, which is induced by Tehuano winds, is considered one of the most productive zones in the study region (Lara-Lara 2008).

Finally, the Robertson and Cramer (2009) classification considers oceanic islands as an independent biogeographic province relative to mainland areas, as the Oceanic Islands province hosts relatively smaller ichthyofauna, distinct functional groups, and a greater number of transpacific and endemic species. This biogeographic province is comprised of 5 islands (from north to south): Revillagigedo, Clipperton, Cocos, Malpelo, and Galapagos. In the present study, we only considered the islands of Revillagigedo and Clipperton (CONANP 2004, Ricart et al. 2016). These islands present the same average SST (28 °C), as they are mainly influenced by the North Equatorial Current and, in the case of the Revillagigedo Archipelago, by the California Current, making the area a transition zone due to the convergence of 2 water masses (CONANP 2004, Velasco-Lozano et al. 2020).

Species checklist and biological traits

We compiled a species checklist of conspicuous bony fish (Teleostei) in the Mexican Pacific from 21 sites in MPAs and 45 non-protected sites. Data sources included published literature (scientific articles [e.g., Olivier et al. 2018], reports [e.g., Del Moral-Flores et al. 2013], and MPA management programs [e.g., CONANP 2004]), museum collections (e.g., Del Moral-Flores et al. 2016), and diurnal monitoring efforts (e.g., Mascareñas-Osorio et al. 2018) (Supplementary Material 1). Using different data sources has the advantage of including rare, nocturnal, and cryptic species that usually are not considered in biodiversity analyses (Olivier et al. 2018). We excluded fish species with maximum sizes of <5 cm and minimum depths of >70 m, organisms that were not identified at the species level, and species with particular life cycles (e.g., Anguilliformes). We did not consider areas with fewer than 10 registered species; non-protected sites encompassed reefs on the continental shelf, islands, or archipelagos separated by less than 10 km and located outside of the protection polygon of an MPA, whereas the protected reefs included all sites within a protection polygon.

We characterized all species using 6 biological traits that reflected key aspects of fish ecology (Mouillot et al. 2014). Biological information was compiled from the online repository FishBase (Froese and Pauly 2024) and included categories grouped into traits that have been used in previous studies at the global (Mouillot et al. 2014) and regional (Olivier et al. 2018, Ramírez-Ortiz et al. 2022) levels: (a) maximum fish size (5–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm, 50.1–80 cm, or >80 cm), (b) mobility (highly site-attached, mobile within-reef, mobile among reefs, or very mobile with very large home ranges), (c) period of activity (diurnal or nocturnal), (d) gregariousness (solitary, pairing, small group of 3–50 individuals, or large group >50 individuals), (e) position in the water column (benthic, bentho-pelagic, or pelagic), and (f) diet (herbivores-detritivores, invertivores targeting sessile invertebrates, invertivores targeting mobile invertebrates, planktivorous, piscivores, or omnivores). Based on species presence and biological trait information, we calculated the relative frequency of each category in the biogeographic provinces. We repeated this process for an additional subset of common species for all provinces, which we considered to be the regional backbone (McLean et al. 2021). The relative frequency of each category was represented in histograms using the packages ‘tidyverse’ (Wickham and Wickham 2017), ‘ggplot2’ (Wickham 2016), and ‘gridExtra’ (Auguie 2017) in R v. 4.3.3 (R Core Team 2024).

Biogeographic patterns in the taxonomic, phylogenetic, and functional diversity of reef fish

To describe regional patterns in fish diversity in temperate and tropical reefs, we used various ecological indicators to assess distinct diversity components. For taxonomic diversity, we considered species richness (S), which is the number of species in a community at a given time; high values of this indicator reflect high diversity (Halffter et al. 2005).

For phylogenetic diversity, we used the average taxonomic distinctness index (Δ+), which measures the mean distance (according to the Linnaean classification tree) between each pair of species within a study site (Clarke and Warwick 1998). To calculate Δ+, we used 6 hierarchical levels (species, genus, family, order, subclass, and class) and Eq. (1):

$$\Delta^{+} = \frac{\left[\sum \sum_{i<j} w_{ij}\right]}{\left[\frac{S(S-1)}{2}\right]} \quad , \qquad (1)$$

where w_{ij} is the taxonomic distance between each pair of species, and S is the total number of species. Low values of this index show that the species present in a certain site share a close evolutionary origin (i.e., low phylogenetic distance between species; Clarke and Gorley 2001).

To calculate functional indices, we classified each species into a functional entity (FE) based on a combination of the categories of the 6 biological traits, which was represented by an alphanumeric code indicating the possible ecological role played by each species in the ecosystem (Villéger et al. 2017). Using this information and species presence data, we calculated 4 indices: number of FEs, functional redundancy (RED), functional vulnerability (FV), and functional volume

(*FVol*). (1) Number of *FE*s: the number of unique combinations of the categories considered for the biological traits (Mouillot et al. 2014). High values of *FE* indicate that a wide variety of functions are represented within the assemblage (Quimbayo et al. 2017). (2) *RED*: the mean number of species per *FE* (Mouillot et al. 2014). Low values of this index suggest a reduced potential for functional compensation in the event of species loss (Micheli and Halpern 2005). (3) *FV*: the percentage of *FE*s represented only by one species (Mouillot et al. 2014). This index was calculated with Eq. (2):

$$FV = \frac{FE - \sum_{i=1}^{FE} min(n_i - 1, 1)}{FE} \quad , \qquad (2)$$

where S is the total number of species, and n_i is the number of species represented in the ith *FE*. High *FV* values indicate a high risk of losing functions in the event of species loss, as most *FE*s are represented only by one species (Mouillot et al. 2014). (4) *FVol*: the volume covered by a set of species proportional to the functional space defined by the outermost vertices of the total assemblage. In the present study, *FVol* represents the distribution of *FE*s in a particular province. High *FVol* values indicate the presence of highly extreme functions within the assemblage, similar to the total registered across the entire study region (Mouillot et al. 2013, 2014).

To calculate *FVol*, we employed a principal coordinates analysis (PCoA) based on a Gower distance dissimilarity matrix, which allows for comparing different types of variables while assigning them equal weight (Gower 1971). We selected the first 5 PCoA axes, which accounted for more than 70% of the total data variance. This created a 5D space for the biogeographic provinces and regional backbone, where pairwise distances between species were congruent with their initial trait-based Gower distances (Mouillot et al. 2021). These distances represent coordinates and were used to estimate *FVol* according to the convex hull volume model of Cornwell et al. (2006), in which the outermost vertices (*FE*s with more extreme traits) define the convex hull (Villéger et al. 2008). The amount of space that the provinces and regional backbone assemblages encompassed in proportion to the total volume of the Mexican Pacific were calculated to determine *FVol* using the packages 'elbow' (Casajus 2024), 'mFD' (Magneville et al. 2022), 'geometry' (Habel et al. 2023), 'vegan' (Oksanen et al. 2022), and 'tidyverse' (Wickham and Wickham 2017) in R v. 4.3.3 (R Core Team 2024).

Finally, *S*, *FE*, and *FVol* of the fish assemblages in each province and the regional backbone were plotted to visualize spatial differences using the packages 'ggplot2' (Wickham et al. 2016) and 'gridExtra' (Auguie 2017). The ecological indicators for each site were illustrated in maps with QGIS v. 3.34.0 to describe regional patterns. Classes or intervals of *S*, Δ+, *FE*, *RED*, and *FV* values were determined using Sturges' rule.

Results

Species checklist and biological traits

We registered 1,045 conspicuous fish species in 66 temperate and tropical reefs in the Mexican Pacific (Supplementary Material 1), representing 450 genera, 148 families, and 42 orders (Supplementary Material 2). The most represented family was Serranidae (64 species and 16 genera), followed by Gobiidae (47 species and 29 genera) and Carangidae (47 species and 16 genera).

Despite the presence of distinct species between provinces, all biological trait categories were present (Fig. 2). Their relative proportions remained similar within the study region, where the most frequent biological trait categories were: benthic (Fig. 2a), highly site-attached species (Fig. 2b), diurnal (Fig. 2c), solitary (Fig. 2d), medium-sized (15–30 cm; Fig. 2e), invertivores, and piscivores (Fig. 2f). These biological trait categories were dominant in the 4 biogeographic provinces and in the regional backbone.

Biogeographic patterns in the taxonomic, phylogenetic, and functional diversity of reef fish

The Cortez province presented the highest fish diversity values (911 species, 382 *FE*s, and *FVol* = 96%), followed by the Panamic (465 species, 265 *FE*s, and *FVol* = 80%) and Oceanic Islands (393 species, 233 *FE*s, and *FVol* = 77%) provinces. The lowest values were observed in the Californian province (314 species, 196 *FE*s, and *FVol* = 73%). In comparison, the regional backbone was comprised of 74 species (30% of the total species richness registered in the study area) and 58 *FE*s, covering 38% of the total regional volume (Fig. 3). These results indicate that the range of "functions" (*FVol*) was similar between biogeographic provinces despite the differences in *S* and *FE* values. Moreover, through the regional backbone description, we identified the fundamental species and, thus, the *FE*s necessary to maintain reef processes in the Mexican Pacific.

Regarding the protection level, in sites within MPAs, 898 species and 323 *FE*s were registered, while in non-protected sites, a total of 829 species were registered and grouped into 362 *FE*s (Table 1; Fig. 4a, b); thus, *RED* was higher in MPA sites (2.78 $\text{species}\cdot FE^{-1}$) than in non-protected sites (2.29 $\text{species}\cdot FE^{-1}$). At the regional scale, for most sites, we registered low mean *RED* values (2.4 $\text{species}\cdot FE^{-1}$; Fig. 4c) and high *FV* values (55% of the *FE*s were represented only by one species; Fig. 4d) due to the high percentage of species concentrated in a relatively small subset of *FE*s. High *RED* values (~1.64–1.96) and medium *FV* values (~60–80%) were mainly observed in MPAs (e.g., Revillagigedo National Park and Islas Marias Biosphere Reserve) than in non-protected sites, which presented low *RED* values (~1–1.64) and high *FV* values (>80%). Finally, high Δ+ values (>97%; Fig. 4e) were observed in the 4 biogeographic provinces, indicating

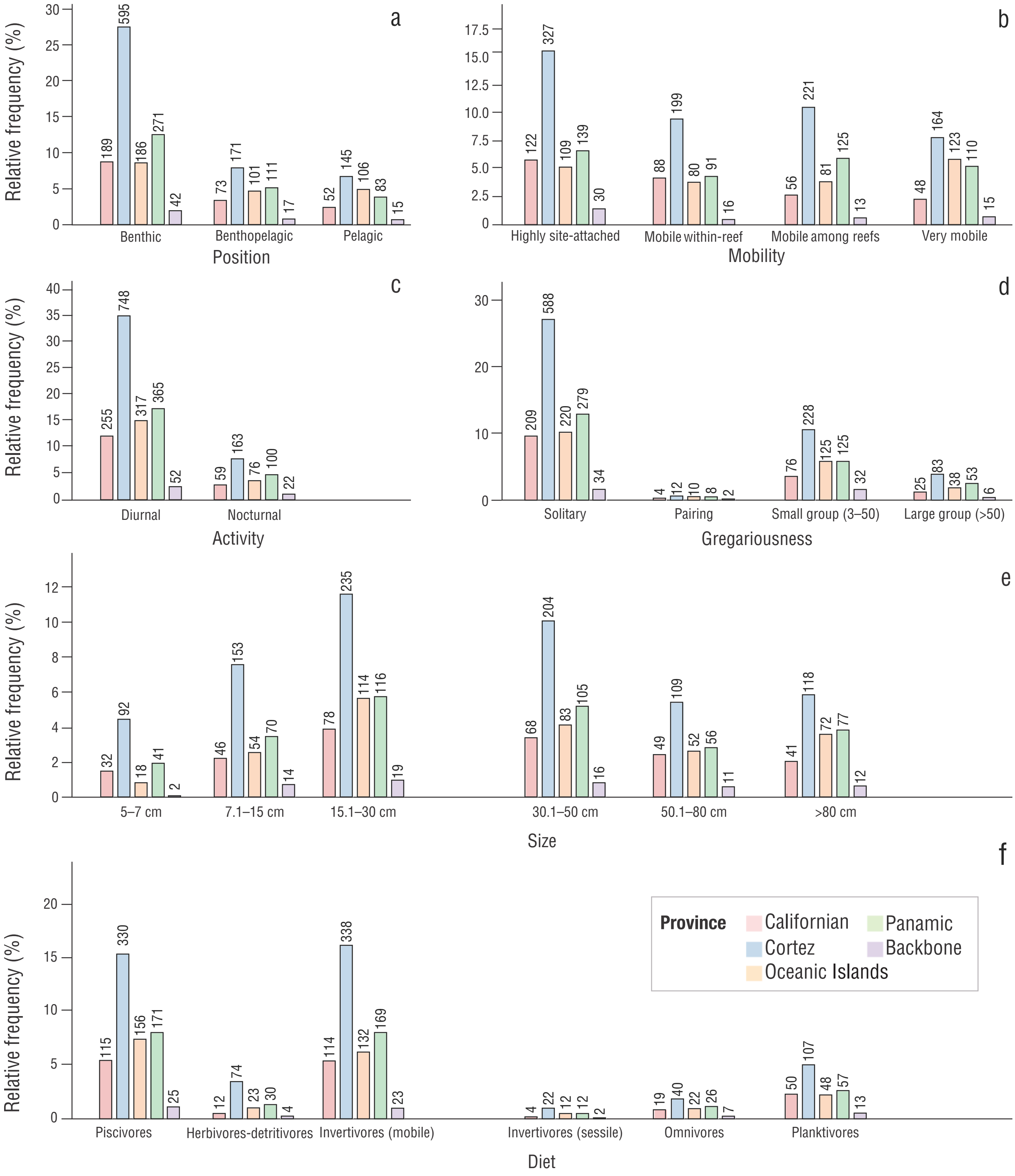

Figure 2. Relative frequency histograms showing the number of species per categories within the considered biological traits: position in the water column (**a**), mobility (**b**), period of activity (**c**), gregariousness (**d**), maximum size (**e**), and diet (**f**). Different columns represent different biogeographic provinces (Californian [red], Cortez [blue], Panamic [green], and Oceanic Islands [orange]) and the regional backbone (purple).

high phylogenetic distance (i.e., distant evolutionary origin) between the species within the study region.

DISCUSSION

Species checklist and biological traits

We reported higher values of species richness (1,045 species) in the Mexican Pacific compared to the reports of previous global studies, which have registered <580 species for the ETP (Mouillot et al. 2014, McLean et al. 2021). Despite the high fish species richness reported in this study, we found that the Mexican Pacific presented lower richness than the Central Indo-Pacific (3,689 species) and Central Pacific (2,911 species), which have been recognized as biodiversity hotspots for reef fish fauna (Mouillot et al. 2014).

Regionally, Dubuc et al. (2023) reported a total of 313 species for the Mexican Pacific, which is less than the value reported in the present study (1,045 species). This difference could be associated with our compilation of information from different sources (scientific articles, reports, MPA management programs, monitoring data, and museum collections), as well as the incorporation of data from temperate reefs of the Californian province, which allowed us to generate a more comprehensive assessment of fish diversity in the different reef habitats of the Mexican Pacific.

Our analysis revealed that the most frequent biological trait categories (benthic, highly site-attached, diurnal, solitary, medium-sized, and invertivores specialized in mobile invertebrates or piscivores) across the 4 biogeographic provinces and regional backbone are among the most common for reef fish, which aligns with global (McLean et al. 2021) and regional (islands located in the central Mexican Pacific; Morales-de-Anda et al. 2020) reports. The high frequency of these categories could be associated with the dominance of families, such as Serranidae and Gobiidae, that exhibit these functional characteristics (Morales-de-Anda et al. 2020, McLean et al. 2021). To evaluate a wider variety of categories within the considered biological traits, future regional analyses should focus on describing functional diversity across different habitats (e.g., pelagic habitats, mangroves, and estuaries). Regarding diet, invertivores specialized in mobile invertebrates were the dominant category. Still, we also found a high frequency of piscivores, which have been reported to be indicators of good conservation status, as most species are commercially important (Quimbayo et al. 2017, Morales-de-Anda et al. 2020). However, we found that MPAs hosted a similar number of piscivores (105 species) as non-protected sites (116 species). Thus, subsequent analysis should consider other ecological indicators (abundance, size, and biomass) to determine if MPA protection positively affects this trophic group at the regional level. Additionally, the high frequency of the diurnal biological trait category could be associated with the period of the day during which most data have been collected. Even though our data encompass different sources, which could help reduce information bias (compared to other studies based on one data collection method), future sampling efforts should focus on describing nocturnal assemblages to provide a more accurate description of this trait.

Biogeographic patterns in the taxonomic, phylogenetic, and functional diversity of reef fish

By comparing reef fish diversity across 4 biogeographic provinces, we found the highest values of *S*, *FE*, and *FVol* in the Cortez province, followed by the Panamic, Oceanic Islands, and Californian provinces. The high fish diversity in the Cortez province could be due to the isolation of the Gulf of California from the Pacific Ocean since the formation of Baja California Peninsula, which has favored high speciation rates (Bernal et al. 2001, Mora and Robertson 2005, Robertson and Cramer 2009). The isolation, along with habitat heterogeneity in terms of substrate (rocky reefs and coral communities) and water-column characteristics due to the influence of Tropical Surface Water, California Current Water, and Gulf of California Water, have previously been reported as key factors within the Cortez province (Lavín and Marinone 2003). These factors influence the transport and settlement of fish larvae from other areas, contributing to the high taxonomic and functional diversity due to the convergence of tropical and temperate fish faunas (Ramírez-Ortiz et al. 2017). Additionally, this province hosts the majority of the MPAs analyzed in this study (9), which have been established to conserve biodiversity and ecological functions (SEMARNAT-CONANP 2018, Dubuc et al. 2023). The management of these MPAs and the high sampling effort in these areas to evaluate their effectiveness may have positively influenced the high fish diversity values recorded in the Cortez province.

Compared to the Cortez province, the Panamic province exhibited lower values of *S*, *FE*, and *FVol*, possibly due to its more stable oceanographic conditions throughout the year, as well as its less diverse habitats, such as sandy beaches and coral reefs dominated by *Pocillopora*, which has not been found to affect fish diversity within the ETP (Glynn 2004, Ramírez-Ortiz et al. 2017, Olán-González et al. 2020). In contrast, the Oceanic Islands province, which exhibited intermediate fish diversity values, has been considered a transition zone due to the confluence of the North Equatorial and California Currents, which favor environmental variability and, thus, the presence of multiple species with different biogeographic affinities (Velasco-Lozano et al. 2020). Nonetheless, the distance of these insular territories from the coast (>1,000 km) introduces bias into the sampling efforts in this province. The fact that the Revillagigedo National Park and Islas Marias Biosphere Reserve exhibited some of the highest fish diversity values within the study region may encourage the continuation of management efforts in these areas to promote the protection of key ecological functions in these provinces (CONANP 2004).

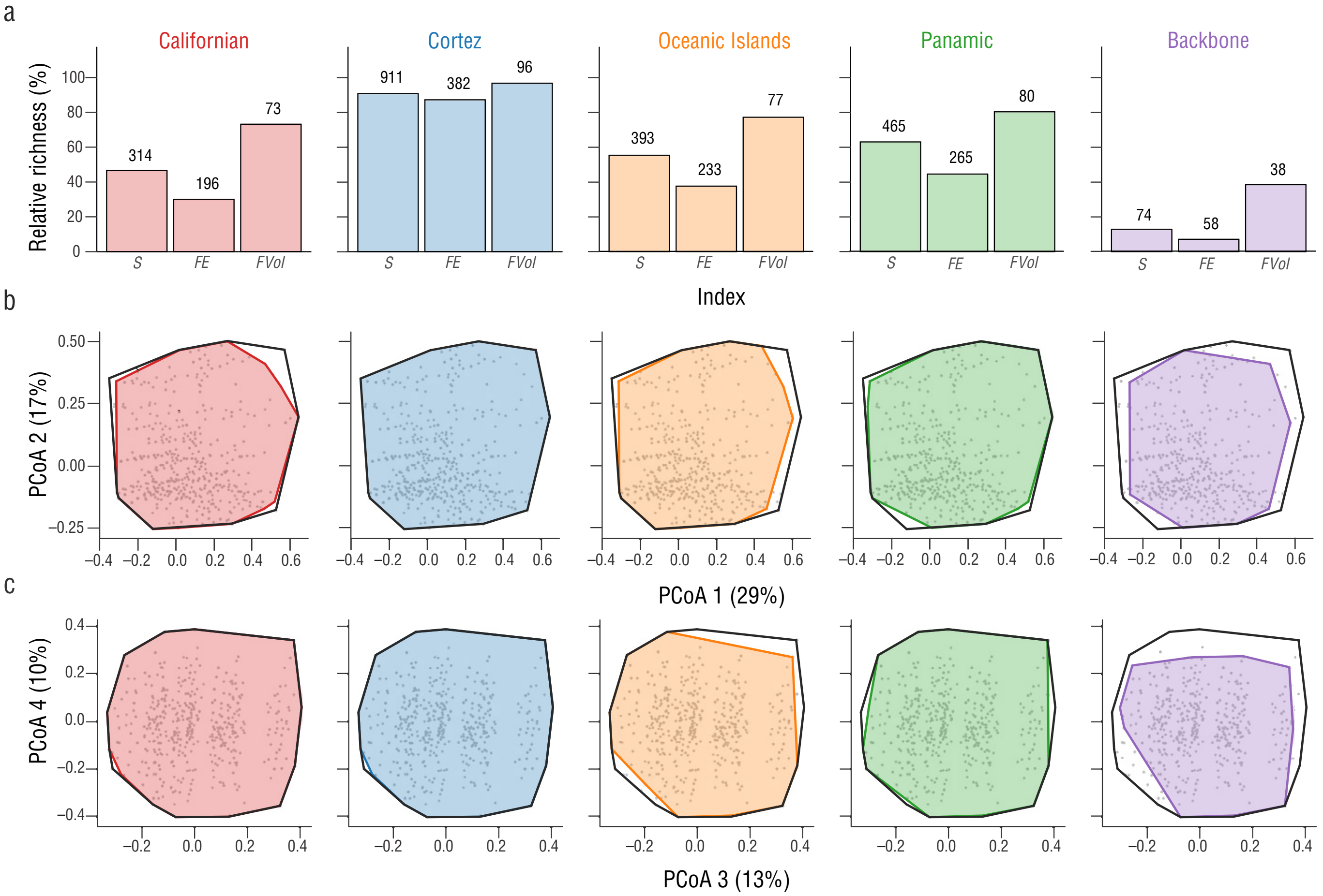

Figure 3. Taxonomic and functional indices calculated for the ichthyofauna across the 4 biogeographic provinces and the regional backbone: histograms of species richness (*S*), number of functional entities (*FE*), and percentage of the occupied functional volume (*FVol*; values are displayed at the top of each bar) (**a**). Functional space occupied by the fish assemblages in each province and the regional backbone (colored polygon) in comparison with the total FVol of the study region (black-line polygon) for axes 1 and 2 (**b**). Axes 3 and 4 of the PCoA (**c**). Gray markers indicate species distribution within the functional space.

Most of the sites in the Californian province exhibited low values of *S*, *FE*, and *FVol*, despite being considered an upwelling zone with high primary productivity (Castro-Aguirre et al. 1993, Valdez and Díaz 1996) and the presence of 6 MPAs. Previous studies have reported that reef fish taxonomic and functional diversity is strongly influenced by temperature changes, with diversity increasing towards the equator, as more species coexist in the tropics than in temperate areas (Tittensor et al. 2010, Dubuc et al. 2023). In this study, we observed this pattern of higher fish diversity in the tropical provinces, possibly due to limited species dispersal into the Californian province in contrast to the others. However, this condition might change in the near future, as extreme heat events could promote the colonization of kelp forests and rocky reefs by widely distributed and generalist species (Robertson and Cramer 2009, Dubuc et al. 2023).

Despite the differences in *S* and *FE*, the fish assemblages in each biogeographic province occupied similar volumes (>70%) within the total functional space. This is consistent with the results of McLean et al. (2021), who reported a range of functions shared between tropical and temperate regions worldwide, despite differences in species presence, environmental conditions, and evolutionary history across ecoregions. In this context, we identified 74 species and 58 *FE*s as the regional backbone, which represent the fundamental species and shared ecological roles across provinces that contribute to maintaining reef processes in the Mexican Pacific. This consistency across the study region presents an opportunity to propose trait-based approaches that could improve management outcomes in reefs under similar environmental conditions (McLean et al. 2021). Additionally, it is important to identify specific traits present in reefs with good conservation status in order to determine local priorities for trait-based management.

Regarding conservation status, we reported that although the number of non-protected study sites was higher, the MPAs exhibited greater total species richness (898 species) but

Table 1. Number of sites in non-protected zones in marine protected areas (MPAs) within the 4 biogeographic provinces according to the Robertson and Cramer (2009) classification. Additional rows show species richness (*S*) and functional entities (*FE*s) in non-protected sites and MPAs.

Biogeographic province	Non-protected sites (number of sites)	Marine protected areas (number of sites)
Californian	12	6
Cortez	24	9
Panamic	8	5
Oceanic Islands	1	1
Index		
S	829	898
Number of *FE*s	362	323

lower *FE* values (323 *FE*s) compared to the non-protected sites (829 species; 362 *FE*s). This result may indicate a positive effect of protection by MPAs, not only by increasing taxonomic diversity but also by increasing functional redundancy. However, further analysis is needed to determine whether this result can be attributed to the positive effect of reef conservation status, as influenced by the level of protection and size of the MPA (Dubuc et al. 2023), or whether MPAs, as reported in a global study (Hernández-Andreu et al. 2024), are effective for conserving species despite not always adequately protecting functions.

At regional level, we reported low average values of *RED* (2.48 species·FE^{-1}) and high *FV* values (55% of the *FE*s were represented by only one species), which were similar to the values reported for the ETP (*RED* = 2.8; *FV* = 54%; Mouillot et al. 2014). The observed pattern of low *RED* and high *FV* has been previously registered as a global phenomenon and associated with the uneven distribution of species among *FE*s (Mouillot et al. 2014). In our study, species were disproportionately concentrated into a small set of *FE*s (61% of the species were grouped into 21% of the *FE*s), leaving most *FE*s to be represented by a single species and resulting in limited potential for functional compensation in the event of species loss (Micheli and Halpern 2005). This aligns with the results of Parravicini et al. (2014), who reported that, although *RED* is important for maintaining ecosystem processes, functions dependent on few species are especially sensitive, and their loss could jeopardize the maintenance of specific processes over time. It is worth mentioning that the results of indicators based on the relationship between the number of species and *FE*s (e.g., *RED* and *FV*) should be interpreted with caution, as they can change depending on the number of categories and biological traits considered (Ladds et al. 2018). Moreover, trait-based approaches group species based on trait similarities. However, these approaches produce approximations, as each species contributes uniquely to ecosystems, and its loss could notably impact ecosystem processes in ways that are not yet predictable (Eisenhauer et al. 2023).

Finally, we recorded high values of $\Delta+$ in all study sites, indicating that the species presented a wide range of taxonomic lineages while the provinces exhibited high evolutionary diversity. These results could be attributed to the biogeographic isolation of the ETP due to the formation of the Isthmus of Panama, which favored the independent evolution of species within this region (Mora and Robertson 2005, Robertson and Cramer 2009). Nonetheless, future analyses should focus on testing the relationship between latitude, species richness, and speciation rates across marine fish in the ETP.

CONCLUSIONS

We reported higher values of species richness in the Mexican Pacific (1,045 species) compared to those of previous studies, likely because the data in the present study were obtained from diverse sources. The dominant biological trait categories of the fish species observed in the present study (benthic, highly site-attached, diurnal, solitary, medium-sized, and invertivores specialized in mobile invertebrates) align with those reported in global and regional studies. The Cortez province exhibited the highest values of species richness, number of *FE*s, and *FVol*, which could be associated with its geographic isolation, habitat heterogeneity, and water-column conditions. In contrast, the Californian province showed lower diversity, possibly due to limited species dispersal within this region. Despite differences in *S* and the number of *FE*s, the fish assemblages in each province occupied more than 70% of the total functional space, which is consistent with global studies that have reported a range of functions shared between tropical and temperate regions despite variations in environmental

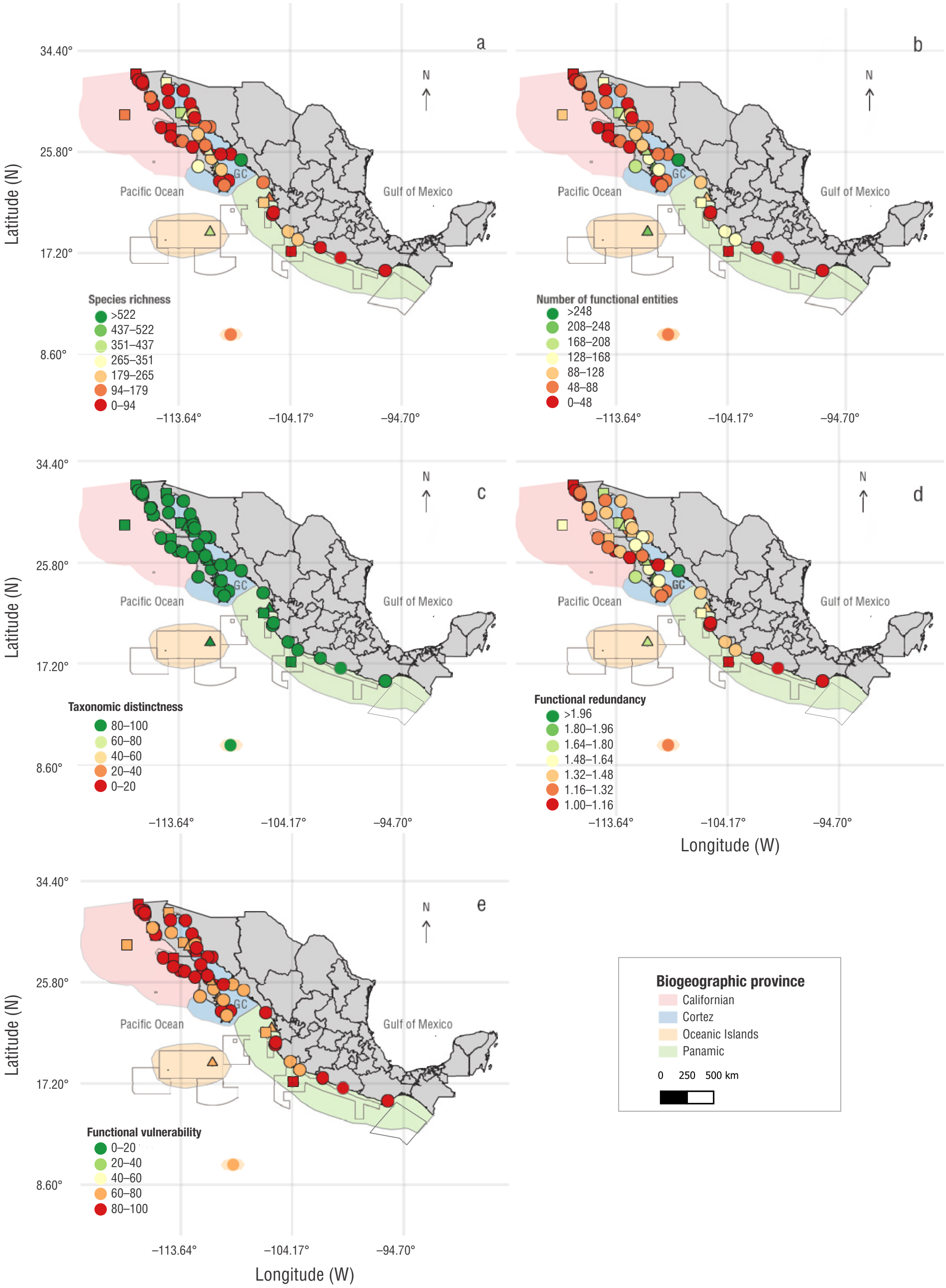

Figure 4. Geospatial representation of the ecological indicators calculated with the information of fish species presence and biological traits: species richness (*S*: total number of species per site) (**a**), number of functional entities (*FE*: number of species groups with unique combination of categories for the biological traits) (**b**), average taxonomic distinctness (Δ+: distance between each pair of species according to the Linnaean classification tree) (**c**), functional redundancy (*RED*: average number of species per functional entity) (**d**), and functional vulnerability (*FV*: percentage of functional entities [*FE*s] with only one species) for the 4 biogeographic provinces (colored polygons) within the Mexican Pacific (**e**). Markers per site indicate the interval scale for each ecological indicator: low (red), medium (yellow and orange), and high (green) values. Gray lines show the protection polygons of marine protection areas (MPAs). Circles indicate non-protected sites; other markers indicate that study sites are located in MPAs with distinct protection categories: national parks (triangles), biosphere reserves (squares), and flora and fauna protected areas (stars).

conditions and evolutionary history. This result, in addition to the identification of the regional backbone, which represents the fundamental species and common ecological roles shared across provinces, presents an opportunity to propose trait-based approaches that could improve management outcomes in reefs under similar environmental conditions. Marine protected areas exhibited higher values of *S* and *RED* than non-protected sites, but further analysis is needed to assess the positive effects of MPA protection. At the regional level, we reported low *RED* and high *FV*, which confirms the uneven distribution of species among *FE*s that has been reported globally. Finally, high Δ+ values indicated that the provinces hosted a wide range of taxonomic lineages among the fish species present, possibly due to the biogeographic isolation imposed by the formation of the Isthmus of Panama.

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://github.com/lecofym/mexpacfish/blob/main/Data/Supplementary%20Material%201.xlsx and https://github.com/lecofym/mexpacfish/blob/main/Data/Supplementary%20Material%202.xlsx.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: GRO; Data curation: RTG, EDLS, MVL; Formal analysis: RTG, EDLS, GRO; Funding acquisition: GRO, RBL, JL, LMC; Investigation: GRO, RTG, EDLS, RBL, JL, LMC; Methodology: RTG, EDLS, MVL; Project administration: GRO, RBL, JL, LMC; Resources: GRO, RBL, JL, LMC; Supervision: GRO; Validation: GRO, MVL; Visualization: RTG, EDLS, MVL; Writing – original draft: RTG, EDLS, GRO; Writing – review & editing: RTG, EDLS, GRO, MVL, LMC, RBL, JL.

Data availability

The data for this study are available from: https://github.com/lecofym/mexpacfish.

Ethical approvals and permits for studies involving animals

Field surveys at marine protected areas were conducted with all necessary permits approved by the *Comisión Nacional de Áreas Naturales Protegidas*.

Use of AI tools

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

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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

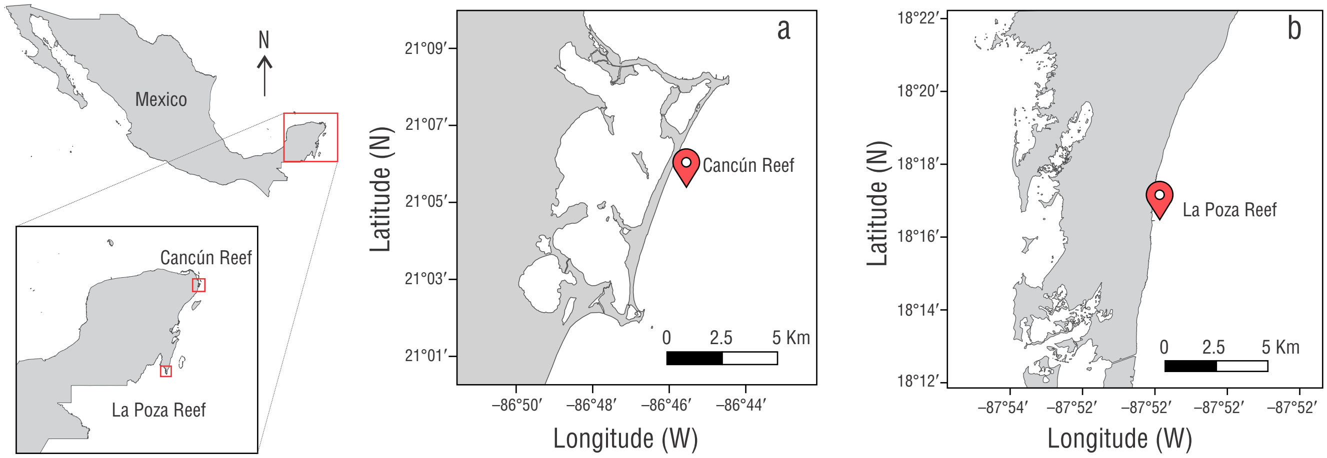

Figure 1. Study area in the Mexican Caribbean. Sampling sites: Cancún Reef in Cancún and La Poza Reef in Xcalak.

(5′-GTCTCGTGGGCTCGGAGATGTGTATAAGAGA-CAGGACTACHVGGGTATCTAATCC-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.

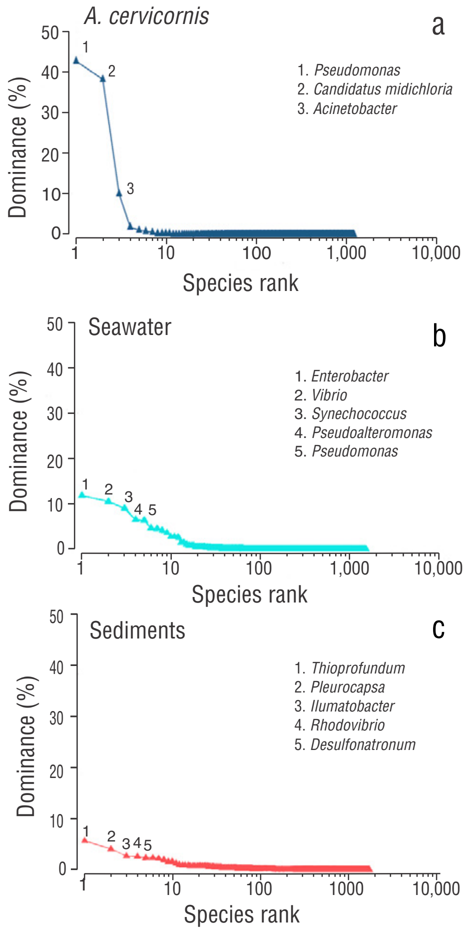

Figure 2. Rank abundance curves for the bacterial assemblages by analyzed substrate. The blue, turquoise, and coral triangles represents the bacterial genera present in *Acropora cervicornis*, seawater, and sediments, respectively.

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%).

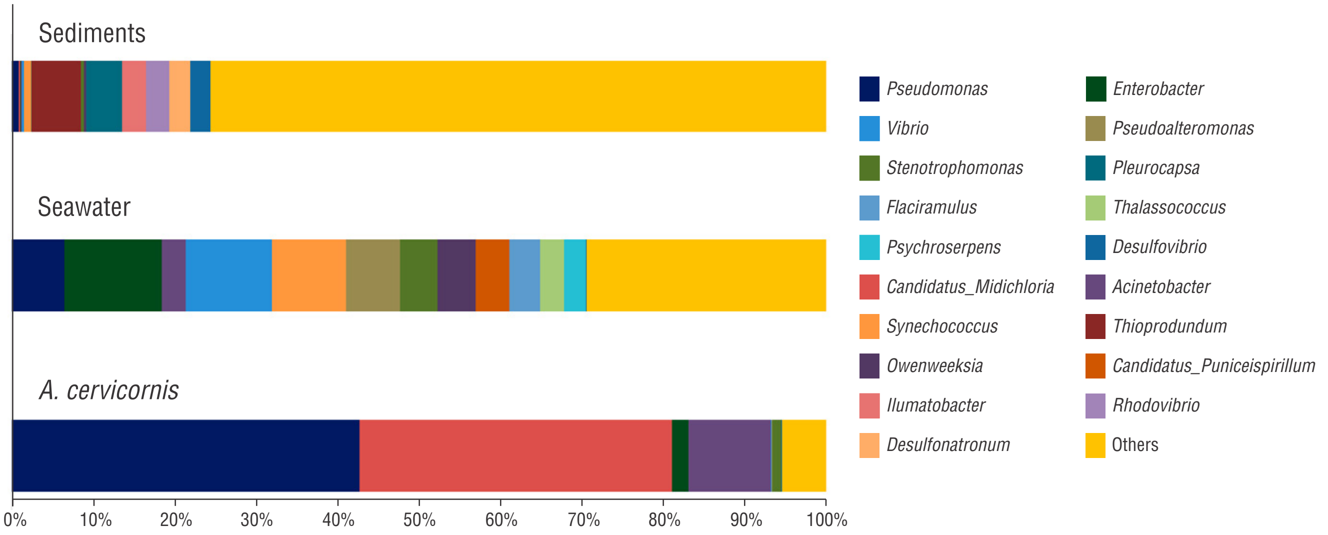

Figure 3. Dominant bacterial genera associated with *Acropora cervicornis*, seawater, and sediments in the entire study area. Each color represents a different bacterial genus in each substrate.

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 2). 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).

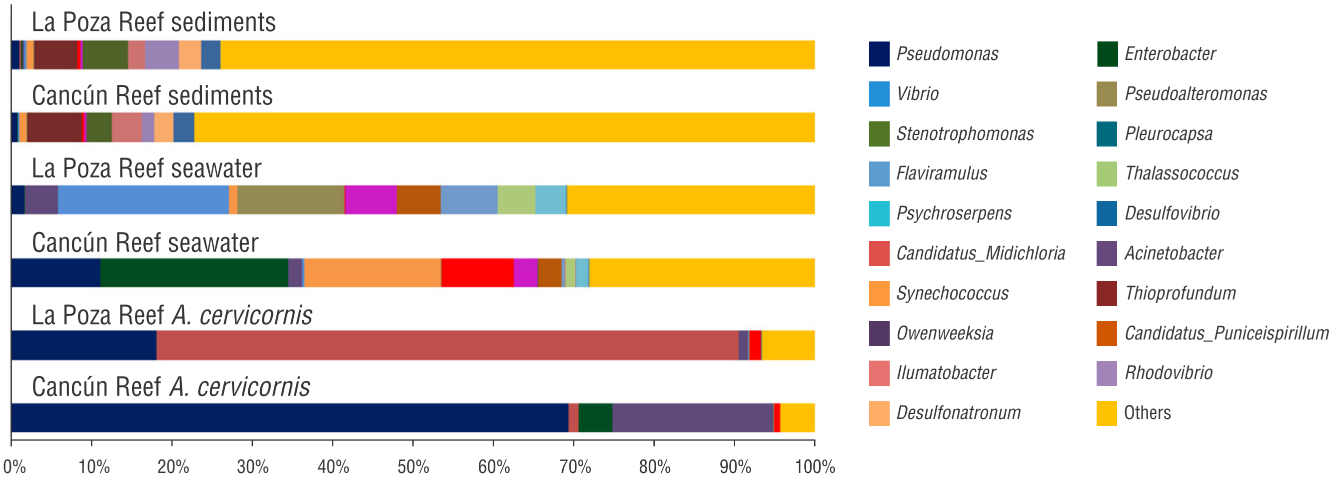

Figure 4. Dominant bacterial genera associated with *Acropora cervicornis*, seawater, and sediments per site. Each color represents a different bacterial genus in each substrate.

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

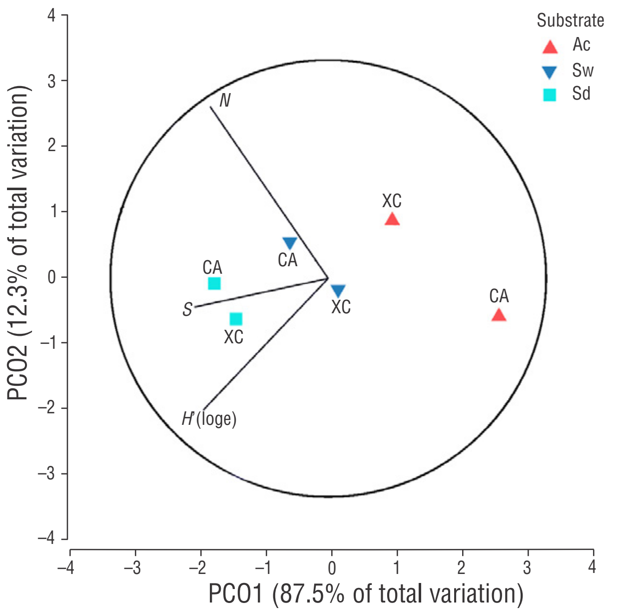

Figure 5. Principal coordinates analysis (PCO) ordination of the variation in community attributes (genera richness [*S*], abundance [*N*], and Shannon diversity [*H*′]) by substrate type and sampling site. The vectors were generated based on a multiple correlation analysis. The correlation circle represents 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

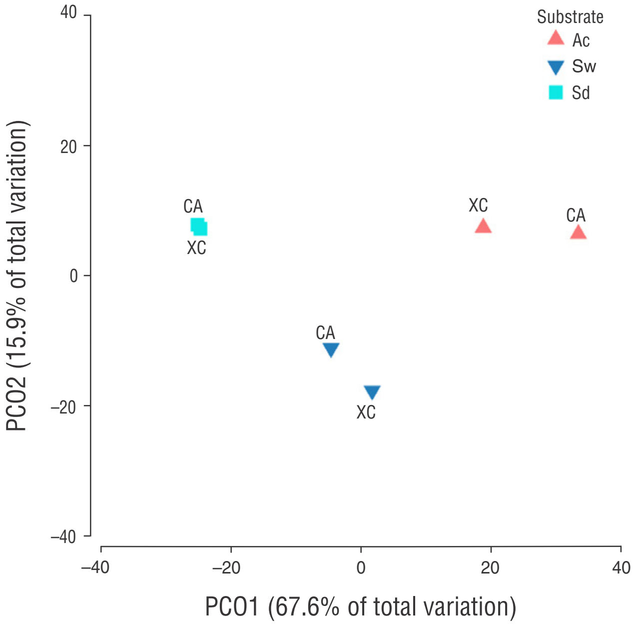

Figure 6. Principal coordinates analysis (PCO) ordination of the changes in the composition and abundance of bacterial genera by substrate type and sampling site. Codes: Cancún (CA); Xcalak (XC); *Acropora cervicornis* (Ac); seawater (Sw); sediments (Sd).

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

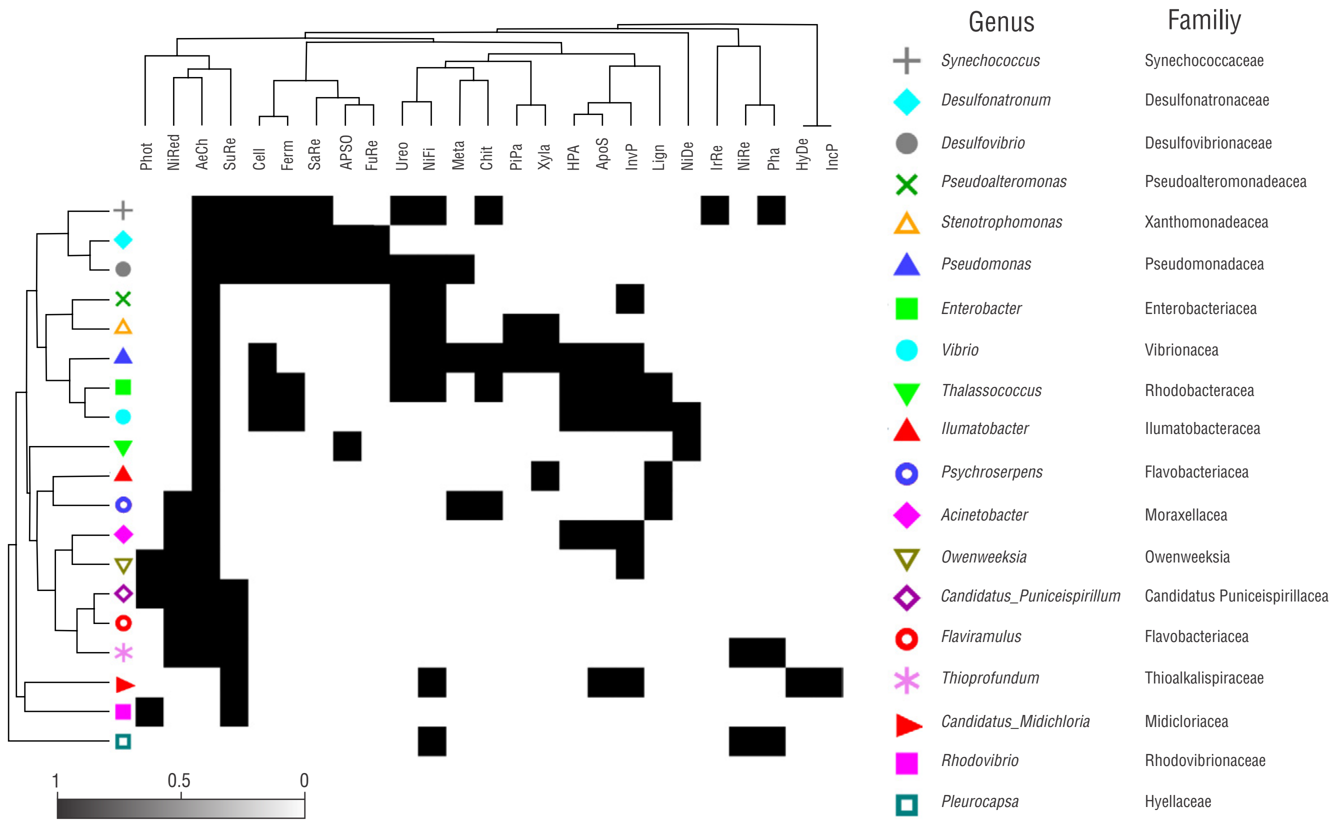

Figure 7. Shade plot of the dominant bacterial genera and respective putative metabolic functions. Codes: Photoheterotrophy (Phot); Nitrate reduction (NiRed); Aerobic chemoheterotrophy (AeCh); Sulfur respiration (SuRe); Cellulose (Cell); Fermentation (Ferm); Sulfate respiration (SaRe); Anoxygenic photoautotrophy 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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Efficiency of self-recovery in coral living tissue of donor colonies of *Orbicella faveolata* used for coral intervention in the Mexican Caribbean

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ABSTRACT. The effects of climate change and local impacts, such as disease, hurricanes, and nutrient input, have led to the rapid degradation of reef ecosystems. The implementation of active restoration methods has expanded globally to mitigate the loss of these important habitats. However, many intervention strategies are still under development, and their impact is unknown. The aim of this study was to evaluate the efficiency of self-recovery of live *Orbicella faveolata* tissue used as donor microfragments from May 2021 to May 2023 in the Puerto Morelos Reef National Park. Digital images were analyzed to measure the recovery of bare area (~1,250 mm^2), transverse diameter (mm), longitudinal diameter (mm), and number of new polyps in donor colonies. After 2 years the results showed that the area of bare tissue had an average recovery of 1,065 ± 237 mm^2 of living tissue with 97% of tissue recovered. The transverse and longitudinal diameters showed average monthly growth of 0.88 mm and 0.98 mm, respectively, with a recovery of 93–96% and an increase of approximately 18 new polyps by the end of the study period. The removal of live tissue microfragments does not negatively affect healthy donor colonies, which are capable of recovery within a relatively short time frame (24 months). This information reveals the potential of using microtransplants to accelerate live tissue recovery in colonies affected by various stressors. Despite their feasibility in coral species rehabilitation projects, it is necessary to continue investigating the long-term effects related to susceptibility to erosion and disease to establish more appropriate strategies that support the conservation of coral colonies and reef habitats, as well as the provision of ecosystem services.

Key words: coral recovery, live tissue, restoration, *Orbicella faveolata*, Mexican Caribbean.

INTRODUCTION

Coral reefs represent one of the most biodiverse and productive ecosystems on the planet, providing ecosystem services such as the provision of fishery resources, coastal protection, carbon sequestration, sediment retention for beach formation, and tourist attraction (Moberg and Folke 1999, Shepard et al. 2009). Despite their ecological and socioeconomic importance, these ecosystems have experienced accelerated degradation due to anthropogenic factors such as overfishing, eutrophication, and pollution (Hughes et al. 2003). Furthermore, over the last 2 decades, the effects of climate change, including rising temperatures, ocean acidification, and pollution, have led to the reduction of more than 60% of coral cover worldwide (Hughes et al. 2017, Boström et al. 2020). In the Caribbean, live coral cover has drastically decreased from ~50% in 1980 to ~10% in 2024 (Gardner et al. 2003, Perera-Valderrama et al. 2017, Reimer et al. 2024).

The construction and maintenance of coral reefs depend on the accumulation of calcium carbonate ($CaCO_3$) by hermatypic corals, which contribute structural complexity to the ecosystem (Spalding et al. 2001, González-Barrios et al. 2018, Tortolero-Langarica et al. 2023). Specifically, a reduction in the abundance of reef-building species such as *Acropora* spp. and *Orbicella* spp. has been documented (Álvarez-Filip et al. 2011). Although a relative recovery of coral reefs has been recorded at some Caribbean sites, this has been dominated by low-relief species with low building capacity (González-Barrios et al. 2018, Gouezo 2019). Nevertheless, the increase in frequency, intensity, and severity

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of current disturbances has notably limited natural recovery (Cheal 2017, Hughes et al. 2018).

In the face of the accelerated loss of coral cover, active restoration strategies have been implemented worldwide to mitigate reef deterioration and promote their recovery (Rinkevich 2019). Among these strategies, coral transplantation has been established as one of the most widely used and most successful in the medium and long term (Boström-Einarsson et al. 2020). In this context, microfragmentation has emerged as an alternative method for coral restoration, based on the extraction of small fragments (<3 cm²) of live tissue from a small portion of donor colonies (Page et al. 2018; Tortolero-Langarica et al. 2020, 2023). Observations indicate that the removal of a small fraction of tissue (<10% of the total) does not compromise the viability of the donor colony and promotes a relatively rapid recovery in some coral species (Padilla-Souza et al. 2023). However, regenerative capacity is primarily influenced by the health status of the donor colony, which is more efficient in healthy colonies (Rodríguez-Martínez et al. 2016). Nonetheless, some physiological processes, such as growth and reproduction, could be affected due to the redistribution of energy resources towards regeneration and repair (Carricart-Ganivet 2007).

Microfragmentation has shown promising results in coral reef restoration, but it is still in its early stages of development. Uncertainties exist regarding its effect on the health, growth, and recovery of donor colonies, which highlights the need for long-term research to evaluate its efficacy and relationship to environmental conditions. In this context, the objective of this study was to evaluate the efficiency of self-recovery of live tissue in colonies of the reef-building coral *Orbicella faveolata* used as donors and their growth response over 2 years.

MATERIALS AND METHODS

Growth parameters

The study was carried out from May 2021 to May 2023 in the Puerto Morelos Reefs National Park in the northern Mexican Caribbean (21°00′00″ to 20°48′33″N, 86°53′14.94″ to 86°46′38.94″W). Five adult colonies with the same morphology and size (~100 cm height), and a healthy appearance (no evidence of disease, erosion, bleaching, or competition) were selected at a depth of 5–8 m. For each colony, 3 to 6 small circular fragments (for a tissue transplant project) with radiuses of ~20–30 mm and depths of 20 mm were extracted using a submersible hydraulic electric drill (Nemo Power Tools, Tucson, USA) with a 30-mm diameter diamond-tipped cylindrical drill tip, producing bare areas of tissue (~1,250 mm²) with ~30-mm depths. Each month for 24 months, we monitored and evaluated the recovery of the bare tissue areas that resulted from harvesting donor tissue in terms of surface growth (area), radial growth (longitudinal and transverse diameters), and the number of new polyps formed. To achieve this, we used digital photography (Hero 10; GoPro, San Mateo, USA) in linear format and 25 MP resolution using a plastic Vernier caliper (precision: 0.5 mm) as a reference scale. Images derived from monthly samplings were processed using the freely available software ImageJ v. 1.53t (Schneider et al. 2012). To determine the recovered surface growth, the outline of the bare cavity of live coral tissue (mm²) was measured. To obtain the values for both diameters, the maximum length (mm) was measured using 2 perpendicular lines (longitudinal and transverse) taken at the same reference angle for each month. To obtain the number of new polyps, the increase (number) of calyces with living tissue from the initial bare area was recorded from an aerial perspective.

Environmental variables

The environmental variables sea surface temperature (SST, °C) and photosynthetically active radiation (PAR, µmol quanta·d^{-1}) were used in this study to describe the influence of external factors on the self-recovery of living tissue of the massive coral *O. faveolata.* Hourly data for both parameters were obtained from the Sistema Académico de Monitoreo Meteorológico y Oceanográfico (SAMMO) of the *Unidad Académica de Sistemas Arrecifales*, *Instituto de Ciencias del Mar y Limnología*, *Universidad Nacional Autónoma de México* (SAMMO 2025) for the study months (May 2021 to May 2023), which were averaged to obtain a monthly value and associate it to coral growth.

Statistical analyses

Descriptive values were calculated for each variable (mean, range, maximum, and minimum). The assumptions of normality (Kolmogorov–Smirnoff, $P < 0.05$) and homoscedasticity (Bartlett, $P < 0.05$) were also tested. Because the data did not have a normal distribution and variances were not homogeneous, we perfomed two-way analyses of variance (ANOVA) with repeated measures using generalized linear models (GLM) to evaluate differences at the colony level, in time (monthly), and in their respective interactions. Simple linear regression models (coefficient of determination, r^2) were also used to identify the relationship between growth characteristics and environmental factors (temperature and PAR). All statistical analyses were performed using Sigma Plot v. 11.0 (Systat Software, Inc., San Jose, USA), using a 95% confidence interval ($\alpha = 0.05$).

RESULTS

Surface growth

After a 24-month period, the bare areas showed an average recovery of 1,065 ± 237 mm² in live tissue area when all colonies were grouped together, with a monthly average of 29.50 ± 19.40 (range: 11.50–150.18 mm²) (Table 1) and a total recovery of 97% (Fig. 1). The results showed significant differences over time ($F_{22} = 10.212$, $P < 0.001$) (Fig. 2), but no differences were found at the colony level ($F_4 = 1.788$, $P = 0.196$) or in the interaction ($F_{88} = 0.978$, $P = 0.538$) (Table S1). A posteriori results showed differences between the months of the period June–August (lower growth) and those of the period November–February (higher growth), with the same interannual trend during both years of study (Fig. 2).

Transverse and longitudinal diameters

For transverse diameters, the average accumulated growth was 20.97 mm with an average monthly rate of 0.88 ± 0.60 mm (range: 0.35 ± 2.47) (Table 1 and 2) and a 96% recovery at the end of the study (Fig. 1). The results showed differences between colonies ($F_4 = 3.369$, $P = 0.046$) and between months ($F_{22} = 11.981$, $P < 0.001$), but not in the interaction of colonies × months ($F_{88} = 0.994$, $P = 0.502$). For longitudinal diameters, the accumulated growth was 22.77 mm with a monthly average of 0.98 ± 0.40 mm (range: 0.32 ± 3.15) and a recovery percentage of 94% (Table 2). Similarly, the results revealed no differences between colonies ($F_4 = 3.132$, $P = 0.056$), but they showed differences between months ($F_{22} = 16.274$, $P < 0.001$) and the interaction of colonies × months ($F_{88} = 1.576$, $P = 0.003$) (Table S1). In both cases, the differences were associated with the months of November and December of both years, which had the highest monthly values (Fig. 2).

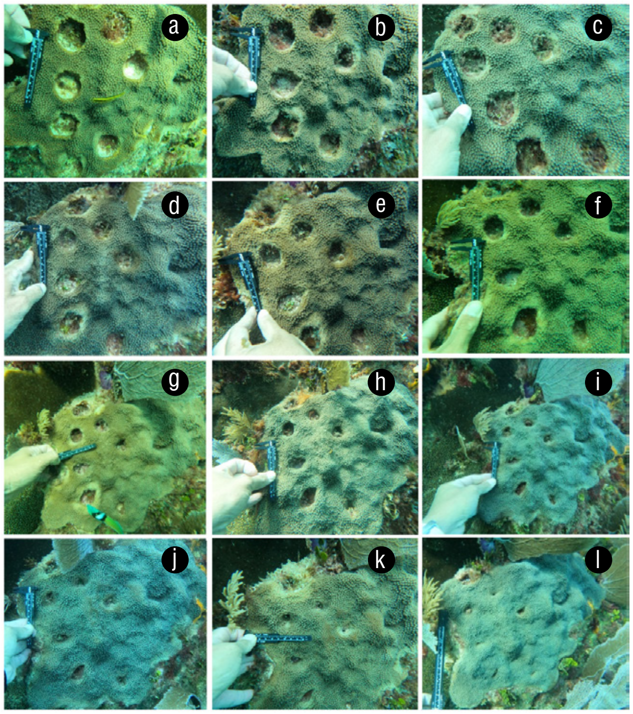

Figure 1. Coral tissue recovery experiment over a 2-year period. Bare area one month after *Orbicella faveolata* fragments were removed (June 2021) (**a**). Progress in recovery of damaged tissue in August 2021 (**b**), October 2021 (**c**), December 2021 (**d**), February 2022 (**e**), April 2022 (**f**), June 2022 (**g**), August 2022 (**h**), October 2022 (**i**), December 2022 (**j**), and February 2023 (**k**), and the recovered area at the end of the study (May 2023) (**l**).

Polyp formation

The damaged (donated) area showed a cumulative number of new polyps of 18 after 24 months of monitoring, with an increase of 0.77 ± 0.91 polyps monthly (Tables 1 and 2). The increase in the number of polyps between colonies showed significant differences, and variations were also present in time and in the interaction between colonies × months (Table S1), mainly in the warmer months (August to October) (Fig. 3) when the highest values ocurred.

Environmental variables

Monthly temperature averaged 28.62 °C (range: 25.95–30.56 °C) (Table 1). The highest temperatures were observed from July to September (~30.32 °C) and the lowest from January to February (~26.21 °C). Light averaged 52,286 µmol quanta·d^{-1}, ranging from 42,145 µmol quanta·d^{-1} (November) to 60,112 µmol quanta·d^{-1} (August) (Table 1). The highest light intensity was observed during the month of August, coinciding with the highest temperature values. Linear regression analysis only showed a negative correlation with the PAR factor and all growth parameters ($P < 0.005$) (Fig. 4).

DISCUSSION

This study demonstrates rapid recovery from microfragmentation injuries in a relatively short period (24 months) in healthy *O. faveolata* colonies. This result is similar to previous reports on tissue regeneration in coring wounds in species from the Mexican Caribbean region (Rodríguez-Martínez et al. 2016), which highlight that recovery can be high (>80%) when the donor colony is in optimal health conditions (i.e., without bleaching damage, disease, or competition for space). Nevertheless, this regenerative capacity can vary due to extrinsic factors, such as environmental microconditions, interspecific interactions, and injury severity (Meesters et al. 1996, Martínez et al. 2016).

Given the environmental regime that influenced Puerto Morelos Reefs National Park during the study period, the growth and recovery rates of live tissue in donor colonies responded primarily to intra-annual variations in light irradiance and temperature. These factors could determine the energy supplied by symbionts to the coral and, consequently, the recovery capacity (Allemand et al. 2011). The results of this study showed a relative variability (10–40%) in live tissue recovery, with improved injury repair observed when SST and PAR had average values of 28–29 °C and 48,078 µmol quanta·d^{-1}, respectively. The temporal variability pattern has also been documented in massive corals from other Pacific regions, where their recovery capacity is usually greater under optimal light (400–700 nm) and temperature (26–29 °C) conditions,

Tabla 1. Monthly averages of the growth parameters (± SD), real area (mm^2·month^{-1}), diameters (mm·month^{-1}), and number of polyps (N· month^{-1}) in fragments of *Orbicella faveolata*. Descriptions of environmental factors, such as sea surface temperature (SST) and photosynthetically active radiation (PAR), for the Puerto Morelos Reef National Park.

Month	Real area (mm^2·month^{-1})	Transverse diameter (mm·month^{-1})	Longitudinal diameter (mm·month^{-1})	Polyps (N·month^{-1})	SST (°C)	PAR (µmol quanta·d^{-1})
June 2021	48.9 ± 32.8	0.48 ± 0.46	0.62 ± 0.44	0.39 ± 0.70	29.61 ± 1.09	52,539 ± 39,084
July 2021	43.2 ± 38.6	0.35 ± 0.30	0.52 ± 0.47	0.61 ± 0.78	30.54 ± 1.02	51,542 ± 42,297
August 2021	58.7 ± 57.9	0.54 ± 0.39	0.77 ± 0.32	1.94 ± 1.47	30.56 ± 1.10	60,112 ± 40,072
September 2021	40.0 ± 41.6	0.72 ± 0.64	0.55 ± 0.67	0.22 ± 0.55	30.09 ± 0.97	54,275 ± 38,510
October 2021	44.7 ± 53.9	0.88 ± 0.88	0.87 ± 0.71	0.17 ± 0.38	29.94 ± 0.88	54,513 ± 34,755
November 2021	146.7 ± 74.3	1.77 ± 0.88	1.96 ± 1.19	0.78 ± 0.81	27.21 ± 0.87	42,145 ± 28,672
December 2021	151.8 ± 58.6	2.47 ± 1.13	2.32 ± 1.29	0.44 ± 0.51	27.02 ± 1.02	44,825 ± 28,663
January 2022	37.3 ± 62.6	0.64 ± 0.59	0.61 ± 0.74	2.61 ± 2.44	25.95 ± 1.15	42,612 ± 30,077
February 2022	22.3 ± 31.6	0.48 ± 0.53	0.32 ± 0.33	0.83 ± 0.92	26.48 ± 1.10	52,144 ± 34,325
March 2022	18.4 ± 16.0	0.35 ± 0.30	0.36 ± 0.54	0.78 ± 1.17	27.18 ± 1.11	61,573 ± 37,202
April 2022	31.9 ± 29.5	0.42 ± 0.39	0.43 ± 0.41	0.67 ± 0.84	28.01 ± 1.19	63,577 ± 40,322
May 2022	20.5 ± 12.7	0.43 ± 0.24	0.35 ± 0.27	0.33 ± 0.55	29.14 ± 0.94	61,381 ± 37,809
June 2022	29.9 ± 24.8	0.91 ± 0.73	0.88 ± 0.63	0.61 ± 0.50	29.71 ± 1.35	57,781 ± 38,243
July 2022	22.8 ± 20.4	0.37 ± 0.42	0.35 ± 0.38	0.06 ± 0.24	30.72 ± 0.91	60,327 ± 38,043
August 2022	11.5 ± 8.9	0.82 ± 0.62	0.49 ± 0.51	0.78 ± 2.10	30.98 ± 0.94	58,666 ± 38,903
September 2022	28.7 ± 25.5	0.47 ± 0.34	0.50 ± 0.47	0.67 ± 0.97	30.41 ± 1.03	52,459 ± 38,394
October 2022	42.8 ± 40.9	1.03 ± 0.71	1.03 ± 0.58	1.28 ± 1.56	28. 80 ± 1.06	53,917 ± 33,296
November 2022	78.6 ± 64.1	1.86 ± 0.75	2.72 ± 1.48	1.67 ± 1.37	28.59 ± 0.69	49,863 ± 29,993
December 2022	55.7 ± 32.5	2.29 ± 1.06	3.15 ± 0.91	1.39 ± 1.14	27.25 ± 0.86	43,210 ± 29,090
January 2023	36.0 ± 22.3	1.00 ± 0.78	1.68 ± 1.42	0.39 ± 0.50	26.5 ± 0.98	54,809 ± 51,616
February 2023	22.5 ± 9.5	0.70 ± 0.44	0.73 ± 0.36	0.33 ± 0.49	26.85 ± 0.79	75,159 ± 44,280
March 2023	20.1 ± 12.0	0.64 ± 0.37	0.54 ± 0.40	0.17 ± 0.39	27.18 ± 1.06	67,717 ± 51,804
April 2023	20.7 ± 10.5	0.72 ± 0.51	0.77 ± 0.72	0.67 ± 0.49	28.42 ± 0.84	68,402 ± 36,762

favoring physiological processes such as growth, calcification, and repair of damaged tissue (Lough and Barnes 2000, Tortolero-Langarica et al. 2020). Contrary to expectations, the warmer months (August to October) showed the lowest values for injury regeneration parameters, which was related to the highest irradiance (Fig. 3) and temperature values (Van Woesik 1998). High radiation and elevated temperatures could have influenced the reduced rate of calcification and recovery from lesions, possibly due to a decreased photosynthetic efficiency of algae (i.e., from the Symbiodinacea family) due to light stress (Allemand et al. 2011, Gutiérrez-Estrada et al. 2025). Alternatively, differences in regeneration rates may be attributable to variables such as wound size and intrinsic characteristics, including the genotypes of both the coral host and its symbiont. Studies have shown that recovery rates tend to be relatively low in large lesions (≤1,310 mm^2; Van Woesik 1998) and in colonies with disease or partial mortality (Rodríguez-Martínez et al. 2016). Therefore, it is essential to consider these intrinsic factors when using or extracting living tissue (Allemand et al. 2011, Padilla-Souza et al. 2023).

In addition, in the present study, a high percentage of live tissue recovery (>90%) and regeneration of new polyps were observed, which could favor pigmentation replacement and an improved photosynthetic efficiency (Sabine et al. 2015). Recovery from lesions has been shown to be primarily mediated by key physiological processes, such as polyp reproduction and cloning, which may exhibit seasonal patterns (Selman et

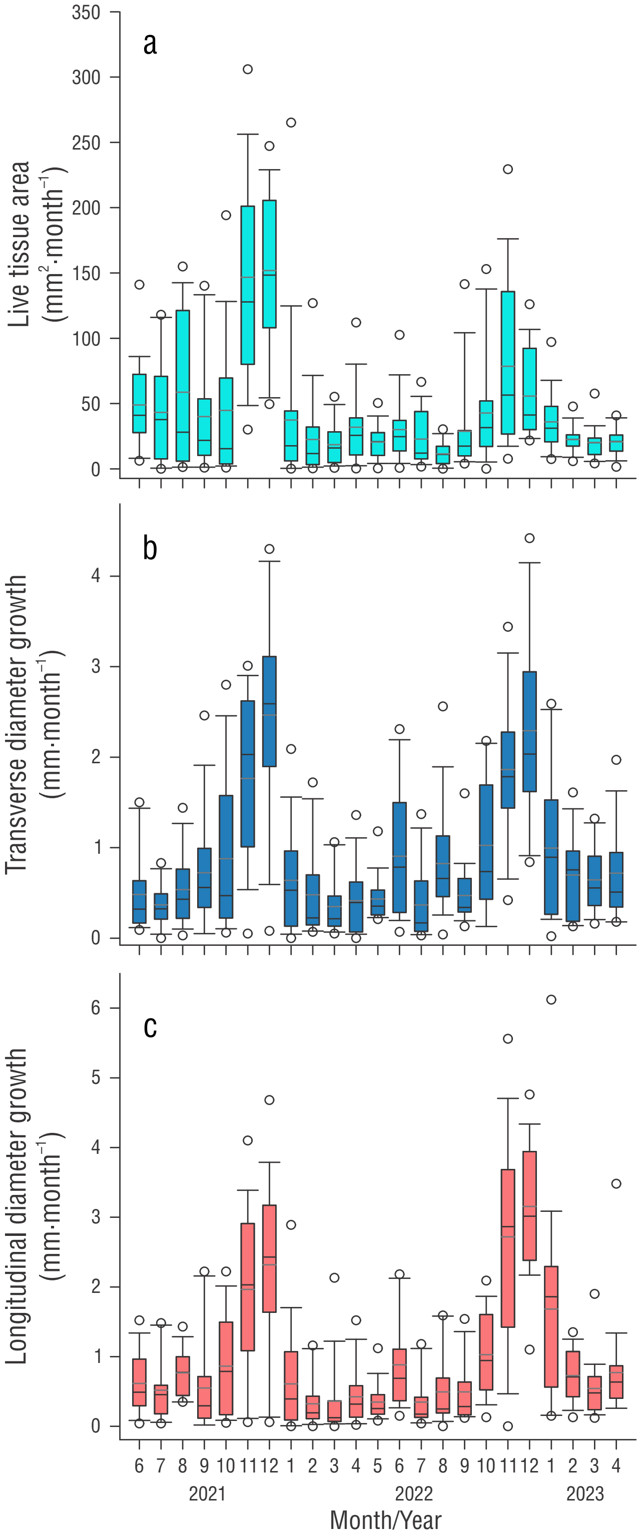

Figure 2. Box plot of monthly growth of live tissue in the coral *Orbicella faveolata* over a 2-year period. Growth rate in area (mm^2·month^{-1}) (**a**), transverse diameter (mm·month^{-1}) (**b**), and longitudinal diameter (mm·month^{-1}) (**c**).

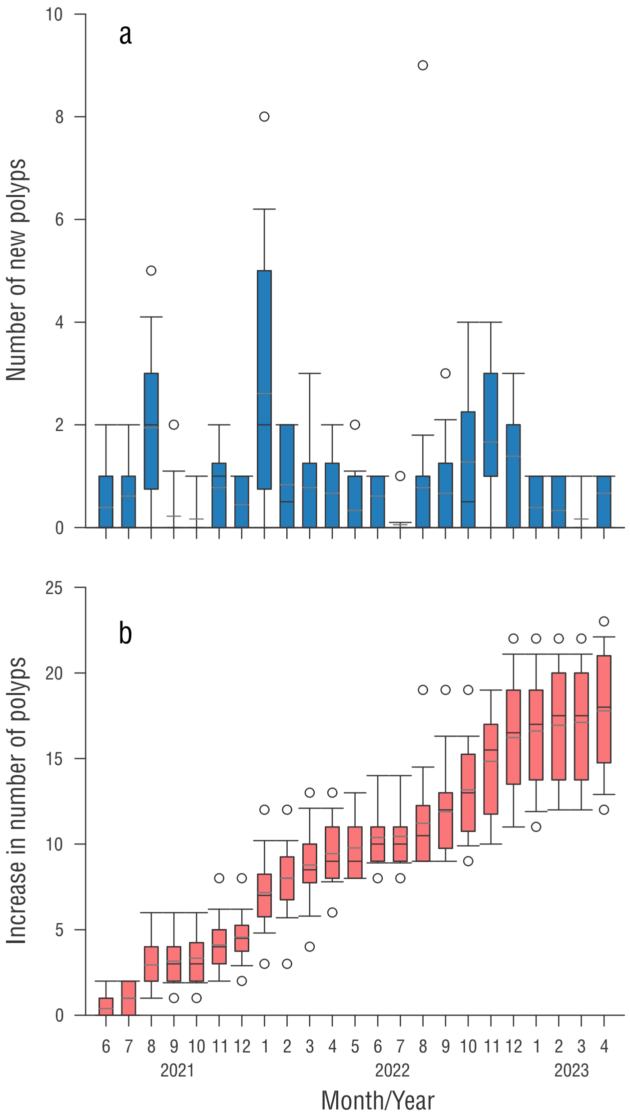

Figure 3. Box plot of new polyp formation over the study period. Number of polyps incorporated each month (**a**) and cumulative number of new polyps after a 2-year period (**b**).

al. 2012). Likewise, a lower tissue regenerative capacity has been observed before or after spawning events, because the energy requirement for gametogenesis is greater during the reproductive period (Kramarsky-Winter and Loya 2000). The observed reproductive pattern, which occurred between December and early February, suggests that coral gamete maturation coincides with the warm season. This distribution of energy between reproduction and tissue regeneration could explain the reduction in the regenerative capacity recorded in this study (Stearns 1989, Selman et al. 2012). Thus, it is essential to consider these effects when planning sampling to optimize the success of tissue regeneration, particularly in interventions involving microfragment transplantation.

CONCLUSIONS

The results suggest that the use of live tissue in massive corals can be an effective strategy for active interventions without compromising the health of donor colonies on the reef. However, several factors must be considered before this can be implemented. Among them, the health status of the colony and extrinsic factors, such as the timing of tissue extraction in relation to optimal

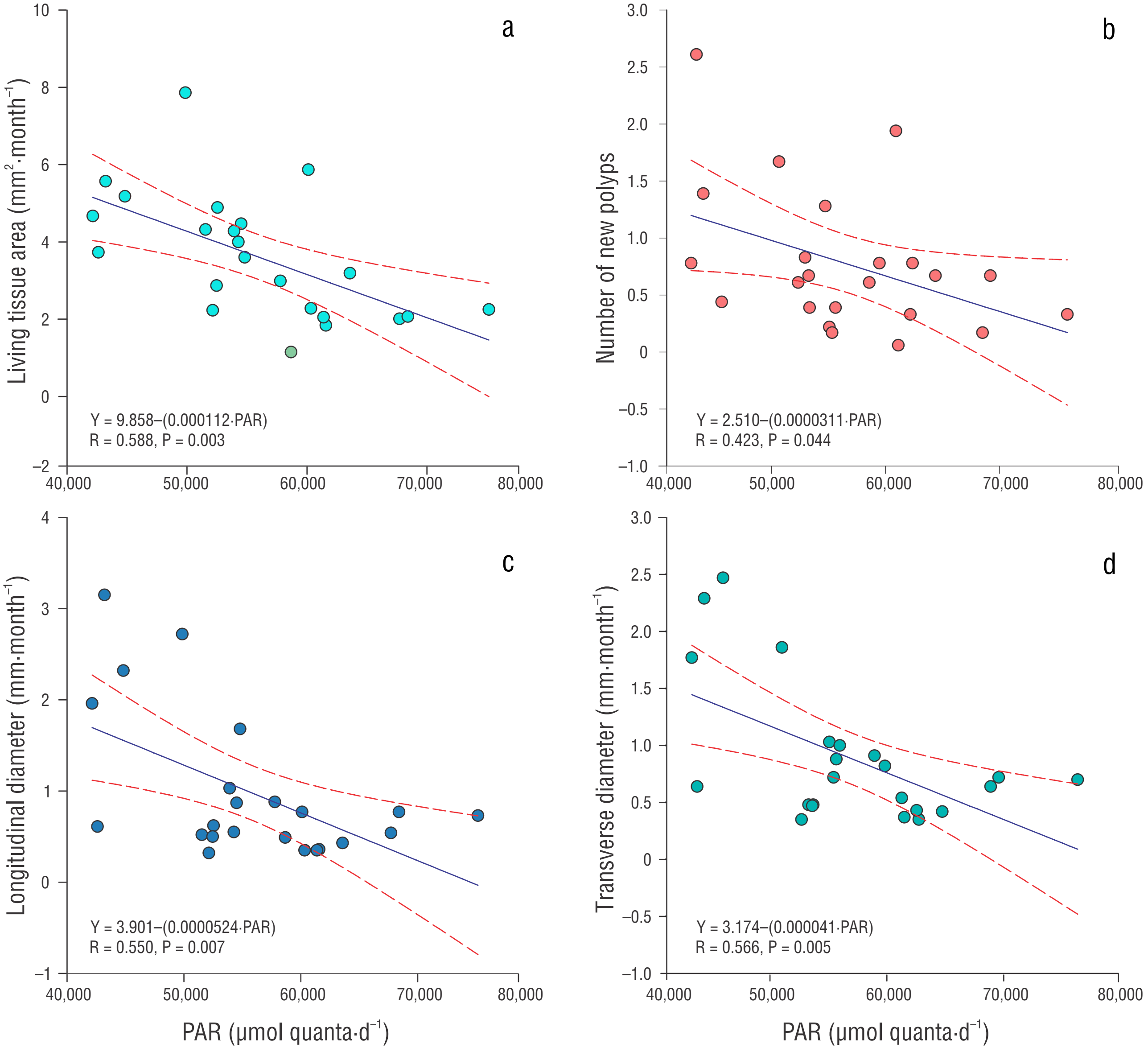

Figure 4. Scatter plot of monthly *Orbicella faveolata* parameters and photosynthetically active radiation (PAR) over 2 years (2021–2023). Area of recovered tissue vs. PAR (**a**), number of new polyps vs. PAR (**b**), transverse diameter vs. PAR (**c**), and longitudinal diameter vs. PAR (**d**). A regression line and equation for the latter relationship are shown.

Table 2. Accumulated growth (±SD) and recovery (%) for the area (mm²) and transverse and longitudinal diameters (mm) in bare tissue areas of *Orbicella faveolata*.

Month	Accumulated area (mm^2)	Accumulated area (%)	Transverse diameter (mm)	Transverse diameter (%)	Longitudinal diameter (mm)	Longitudinal diameter (%)
June 2021	48.9 ± 32.8	4.45%	0.48 ± 0.46	2.19%	0.62 ± 0.44	3.08%
July 2021	92.1 ± 60.1	8.38%	0.85 ± 0.51	3.86%	0.68 ± 0.42	3.39%
August 2021	150.8 ± 92.1	13.72%	1.39 ± 0.53	6.30%	1.28 ± 0.64	6.42%
September 2021	190.9 ± 107.4	17.36%	2.11 ± 0.78	9.59%	1.53 ± 0.57	7.64%
October 2021	235.7 ± 148.6	21.43%	2.99 ± 1.16	13.59%	2.01 ± 1.08	10.03%
November 2021	382.4 ± 197.5	34.77%	4.76 ± 1.94	21.62%	2.92 ± 1.47	14.58%
December 2021	534.2 ± 212.8	48.56%	7.22 ± 2.90	32.82%	4.75 ± 2.72	22.86%
January 2022	571.6 ± 224.7	51.96%	7.86 ± 3.05	35.73%	5.30 ± 2.29	26.52%
February 2022	594.0 ± 228.6	54.00%	8.34 ± 3.19	37.90%	5.24 ± 3.05	26.19%
March 2022	612.4 ± 225.6	55.68%	8.69 ± 3.30	39.49%	5.66 ± 2.20	28.31%
April 2022	644.3 ± 217.2	58.58%	9.10 ± 3.34	41.38%	5.99 ± 2.99	28.45%
May 2022	664.9 ± 215.5	60.45%	9.54 ± 3.48	43.35%	6.13 ± 2.31	30.65%
June 2022	694.9 ± 205.7	63.17%	10.44 ± 3.68	47.47%	6.28 ± 3.34	31.41%
July 2022	717.7 ± 200.8	65.25%	10.81 ± 3.79	49.14%	6.98 ± 3.42	34.90%
August 2022	729.2 ± 199.2	66.30%	11.63 ± 3.53	52.88%	7.44 ± 3.54	37.19%
September 2022	758.0 ± 180.6	68.91%	12.11 ± 3.54	55.03%	7.87 ± 3.56	39.36%
October 2022	800.8 ± 181.4	72.80%	13.13 ± 3.73	59.69%	8.63 ± 3.77	43.13%
November 2022	879.4 ± 206.7	79.95%	15.00 ± 4.08	68.17%	9.83 ± 4.32	49.14%
December 2022	935.1 ± 198.4	85.01%	17.29 ± 4.40	78.59%	12.98 ± 4.43	64.92%
January 2023	971.1 ± 210.0	88.29%	18.28 ± 4.30	83.11%	14.67 ± 3.93	73.33%
February 2023	993.7 ± 209.7	90.34%	18.98 ± 4.31	86.28%	15.31 ± 3.91	76.97%
March 2023	1,029.7 ± 222.8	93.61%	19.98 ± 4.32	90.81%	17.08 ± 3.92	85.38%
April 2023	1,065.7 ± 23.72	96.89%	20.97 ± 4.59	95.33%	18.76 ± 4.41	93.79%

environmental conditions (e.g., SST and PAR), are crucial for maximizing growth and the capacity for damage repair. It is recommended to avoid periods in which the influence of thermal anomalies or disease outbreaks could compromise the resilience of *O. faveolata* populations. The use of live tissue for transplantation is still in its initial development phase; thus, further exploration of its limitations is necessary for large-scale implementation. This will provide key information to improve management strategies for reefs in the Mexican Caribbean.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3511/420421209.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: JJATL and JPCG; Data curation: AMGC; Formal analysis: JJATL and AMGC; Funding acquisition: JPCG and JJATL; Methodology: GGE, JJATL; Software: AMGC and JJATL; Supervision: JJATL and JPCG; Validation: GGE, JJATL, and JPCG; Visualization: AMGC and JJATL; Writing–original draft: AMGC and JJATL; Writing–review and editing: AMGC, JJATL, GGE, and JPCG.

Data availability

Data for this study are available within the manuscript.

Ethical approvals and permits for studies involving animals

Fieldwork was conducted with the collecting permit (log number 23/LW-0103/04/21) granted by the Mexican authorities of the Puerto Morelos Reefs National Park (SEMARNAT/CONANP).

Use of AI tools

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

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SPECIAL ISSUE
Research Article

Recovery and health status of scleractinian corals facing bleaching in the Veracruz Reef System in the southwestern Gulf of Mexico

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ABSTRACT. Coral bleaching is caused mainly by heat stress, as the rise in temperature generates increasingly frequent and intense heat waves. In addition to the increase in temperature, sediment contributions in the Veracruz Reef System (VRS) could increase stress and, with it, the susceptibility of corals to bleaching. This work evaluated 2 reefs of the VRS on 2 time scales: (1) in the short term (2022 to 2023), using the bleaching response index (BRI) to assess the recovery of 104 colonies of scleractinian corals on a scale of 1 to 6 and (2) in the medium term (2008 to 2021), through the coral index (CI) to assess the health of the coral community on a scale of 1 to 5. High values reflect better condition of the corals. In addition, the number of bleached colonies was related to degree heating week (DHW) values and sedimentation rates in both periods. We found that the degrees of accumulated heat were the main cause of bleaching events, whereas sediments did not have a direct influence. In 2022, the prevalence of bleaching was 17% with values of 5 DHW, with *Montastraea cavernosa*, *Siderastrea siderea*, *Siderastrea stellata*, and *Colpophyllia natans* being the most affected species. However, most exhibited an increase in pigmentation within the first 5 months, with BRI values of 5 and 6. During the period of 2008 to 2021, the health of coral communities was classified as good, with CI values of 3.8 and 3.6. The results illustrate that scleractinian corals have been resilient to bleaching events under VRS conditions, highlighting the need to continue with in situ studies of the susceptible species in this study.

Key words: bleaching, scleractinian coral, heat stress, recovery, Veracruz Reef System.

INTRODUCTION

Coral reefs are massive, rigid, wave-resistant calcium carbonate structures built primarily by the skeletons of successive generations of scleractinian corals (Done 2011). They are ecosystems of great ecological importance. Among the ecosystem services they provide, coral reefs serve as primary coastal protection by mitigating wave force and preventing erosion during tropical storms and hurricanes (Ferrario et al. 2014). Likewise, coral reefs have a high structural complexity that provides refuge and nursery habitats for various species of commercial importance, and they are economically relevant due to the income the tourism sector generates through the sports and recreational activities that take place there (Woodhead et al. 2019).

In general, corals inhabit oligotrophic waters with low nutrient and sediment concentrations and a temperature range between 25 and 29 °C (Lough and van Oppen 2018). They are stenotolerant organisms, that is, organisms with a narrow tolerance to changes in environmental variables due to the symbiosis they maintain with endosymbiotic dinoflagellates of the Symbiodiniaceae family (Grimsditch and Salm 2005, Quigley et al. 2018). These endosymbionts, through photosynthesis, provide corals with more than 90% of the energy needed to carry out essential functions such as growth, calcification, reproduction, tissue repair after injury, mucus production, and defense against predators (LaJeunesse et al. 2018, Lough and van Oppen 2018).

Rising temperatures, sediments, and pollutants negatively impact coral health and recovery, as do human activities and

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coastal development (Grimsditch and Salm 2005). One sign of the severity of the situation is the increase in the frequency and intensity of coral bleaching events (Warner and Suggett 2016). Bleaching occurs as a stress response to changes in environmental variables (Rosenberg and Loya 2004), which cause the degradation or expulsion of zooxanthellae from polyp tissue, resulting in a loss of photosynthetic pigments (Jokiel 2004).

Rising sea surface temperatures, especially the accumulated heat to which corals are exposed, are the primary cause of stress that leads to bleaching in coral colonies (Eakin et al. 2009). Cumulative heat stress is typically measured in degrees Celsius, as the cumulative weekly temperature anomalies above the historical maximum monthly mean (MMM) of the previous 12 weeks. This indicator is known as the degree heating week (DHW), and according to its scale, bleaching occurs starting at 4 DHW. As the DHW value increases, the risk of widespread mass bleaching and high mortality increases (NOAA 2023). Nevertheless, stress and temperature are not the only triggers of bleaching. Other stressors can trigger the breakdown of symbiosis. For example, excess sediment from both rivers and wastewater discharges increases water turbidity, which triggers a reduction in photosynthetic capacity in deep zones and an increase in the energy demand for active sediment removal, which negatively affects the energy balance and survival of organisms (López-Lodoño et al. 2023). This is particularly important in reefs near river discharges because sediment stress conditions can occur recurrently.

Corals are organisms capable of recovering from bleaching injuries, whose recovery depends on several factors such as the geographic region, the type of symbiont of the colony, the percentage of affected tissue, the number of remaining symbionts, and the recovery ability and resistance of each coral species (López-Patoni 2014). For the purposes of this work, recovery from bleaching was considered as the speed with which a coral colony regains its tissue color after a bleaching event (Grimsditch and Salm 2006), and resistance to bleaching was considered as the ability of colonies to tolerate the disturbance without showing discoloration (Obura and Grimsdith 2009).

Among the species most susceptible to bleaching in the Caribbean Sea and the Gulf of Mexico are *Montastraea cavernosa*, *Colpophyllia natans*, *Porites furcata*, *Siderestrea siderea*, *Pseudodiploria strigosa*, *Orbicella franksi*, *Orbicella annularis*, *Acropora cervicornis*, *Agaricia tenuifolia*, and *Agaricia lamarcki* (González-Gándara 2008, Eakin et al. 2009, Alemu and Clement 2014, Muñiz-Castillo et al. 2024). However, coral susceptibility partly depends on their growth form; in general, genera with branched growth (acroporids) are more affected than those with massive growth, such as *Colpophyllia*, *Montastraea*, *Orbicella*, and *Siderastrea* (Loya et al. 2001).

Although the aforementioned species belong to different morphofunctional groups, they have been shown to recover from bleaching within 1–11 months, depending on the intensity of the bleaching event (Levas et al. 2018, Matsuda et al. 2020), and only *S. siderea* and *M. cavernosa* appear to be resistant to chronic sediment stress. Evidence from Caribbean islands indicates that these species are barely stressed (bleached) by sedimentation, despite being exposed to sedimentation rates of over 400 $g{\cdot}m^{-2}{\cdot}d^{-1}$ (Torres and Morelock 2002, Vargas-Ángel et al. 2007).

The Veracruz Reef System (VRS) is an exceptional case study for evaluating the effect of stress on corals, despite being considered one of the reef systems with the greatest exposure to colony stressors, both anthropogenic (e.g., pollution derived from urban growth and port, tourism, and fishing activities) and natural (e.g., atmospheric events such as *nortes* winds and hurricanes, high river discharge and sedimentation from adjacent rivers) (Salas-Pérez and Granados-Barba 2008, Ortiz-Lozano 2012). Live coral cover declined from 1960 to the late 1980s and has since remained stable at around 20% (Horta-Puga et al. 2015), although other authors have reported a decrease in cover over the same time period (e.g., Jackson et al. 2014). The VRS is located within a highly turbid environment, with average sedimentation rates during the nortes season (winter) of 500 $g{\cdot}m^{-2}{\cdot}d^{-1}$ (Pérez-España et al. 2012). The reef complex located in front of the town of Antón Lizardo is the one most exposed to constant sediment stress due to the contribution of the Jamapa and Papaloapan rivers (Salas-Monreal et al. 2022).

The constant disturbances to which VRS corals are exposed to, especially the rate of sediments from adjacent rivers, plus the increasing thermal stress we are experiencing worldwide (NOAA 2024), could increase the severity of bleaching, resulting in greater loss of coloration in the colonies and affecting their recovery process. Therefore, in the present study, we evaluated whether corals located on a reef near a river mouth were more severely affected and recovered more slowly after a bleaching event compared to those on a reef with low river influence. To this end, we assessed recovery (in terms of colony coloration) over an 8-month period following bleaching on 2 VRS reefs at different distances from river mouths. In addition, we assessed the health of the scleractinian coral community from 2008 to 2023. Both colony recovery and community health were considered individual resilience attributes, *sensu* Lam et al. (2020), of scleractinian corals.

The information obtained will serve as a baseline to understand the time it takes scleractinian corals in the VRS to recover tissue color following a bleaching event and will identify differences between species that indicate specific responses for future study. Furthermore, this study provides historical data on coral health and thermal stress and sedimentation rates for future studies in the area.

Materials and methods

Study area

The study was carried out in the VRS, located within a protected natural area in the southwestern Gulf of Mexico, on the coast of the state of Veracruz de Ignacio de la Llave (19°15′ to 19°02′N, 96°12′ to 95°47′W) (Lara et al. 1992). The reefs that comprise this system are divided into 2 groups: one to the north, located in front of the city and port of Veracruz, with the greatest anthropogenic impact; and the other to the south, in front of the town of Antón Lizardo, with more influence of sediments from the Jamapa and Papaloapan rivers (Krutak 1997).

To compare colony recovery and coral community health under different VRS stressors, sampling was carried out on 2 emergent platform reefs that, due to their location, are under different sediment exposure (Fig. 1): Blanquilla and Blanca. Blanquilla is located in the northern subgroup, 2 km off the coast in front of the port of Veracruz (19°13′24″N, 96°05′49″W), and has higher exposure to anthropogenic impacts from the population. Blanca is located in the southern subgroup, 2.6 km off the coast in front of the town of Antón Lizardo (19°05′06″ N, 95°59′57″W), and is exposed to higher sedimentation rates due to the influence of discharges from adjacent rivers (Pérez-España et al. 2015b).

Analyses of temperature and sedimentation rates

We used a time series of daily nighttime sea surface temperature (NSST) from January 2008 to July 2023 for the study area, along with DHW values calculated using satellite data at a 1-km resolution. This gave us information on the DHW to which the corals were exposed during the sampling process. Data were taken from the satellite-based early warning system for coral bleaching (SATcoral) on the Marine Coastal Information and Analysis System (SIMAR, for its acronym in Spanish) v. 02 website (SIMAR 2024).

To assess the sedimentation rate, a data series from the period 2012 to 2023 provided by the *Comisión Nacional de Áreas Naturales Protegidas* (CONANP) for the Blanquilla and Blanca reefs was analyzed. These data were collected from traps placed on the leeward side every 4 months (one per climatic season), considering the months October–February as "*nortes*," March–June as "dry," and July–October as "rainy." The sedimentation rate was calculated in units of $\text{cm}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$.

A Kruskal–Wallis test was performed considering the 3 climatic seasons and the 2 reefs to understand the variation in the sedimentation rate between seasons and between reefs. On the other hand, to determine whether bleaching was influenced by both the presence of sediments and the accumulated heat values in the study area, a Spearman correlation of the sedimentation rate and DHW was performed, with the number of bleached colonies on each sampling date of both temporal analyses (short-term: 2022 to 2023; medium-term: 2008 to 2021) (Supplementary Material 1). Both the Kruskal–Wallis test and the Spearman correlation were performed after applying normality (Shapiro–Wilk) and homogeneity of variance (F test) tests to determine the suitability of using parametric analyses. Both tests indicated that the data were homogeneous ($P > 0.05$) but did not meet normality ($P < 0.05$), thus justifying the use of nonparametric statistical techniques in data processing. The analyses were performed using InfoStat v. 2020.

Fieldwork

We used 2 timescales to evaluate the condition of scleractinian corals. The first consisted of a short-term analysis

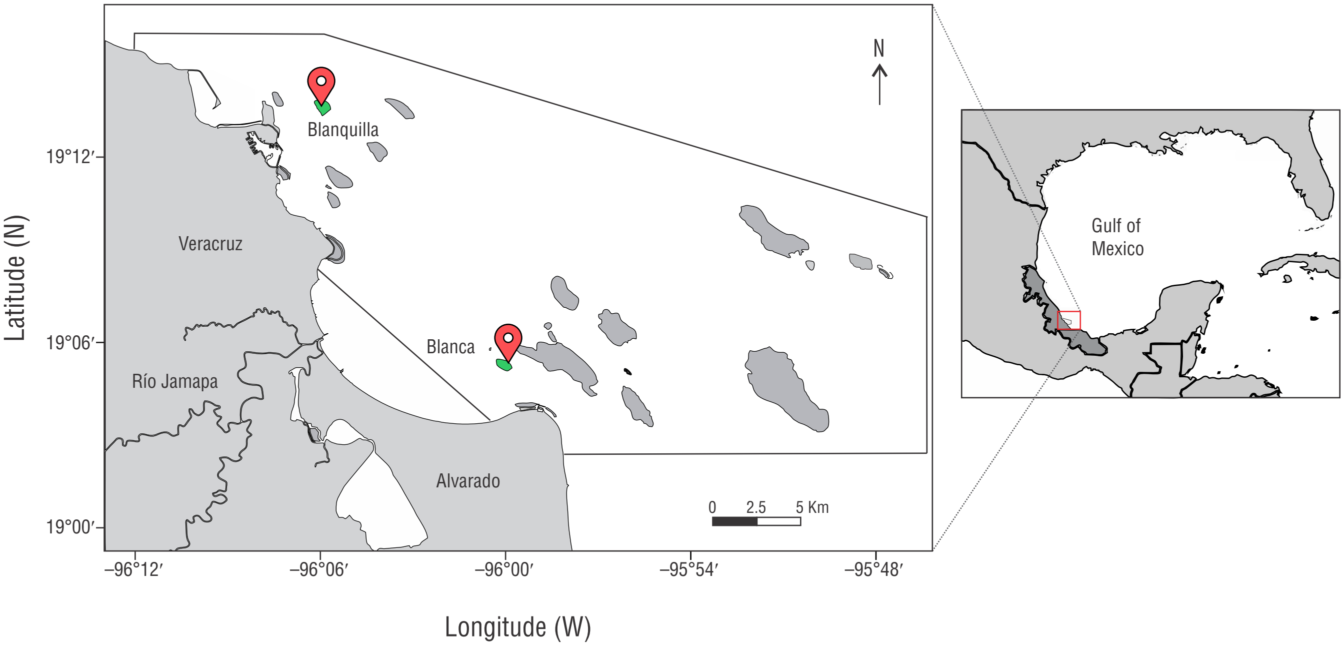

Figure 1. Map of the study area. Veracruz Reef System (VRS) with the 2 sampled reefs highlighted in green.

focusing on the process of color recovery of colonies following the 2022 bleaching event, and the second consisted of a medium-term analysis using the CI for the 2008–2021 period.

Short-term analysis: recovery of colonies

Fieldwork consisted of SCUBA sampling in the Blanquilla and Blanca reefs. During October 2022, all colonies affected by bleaching were tagged in each reef along 2 fixed strip transects (50 m × 2 m) that were placed parallel to the leeward reef slope, at depths of 8–15 m. Each marked colony was monitored using photographs taken at a distance of ~1 m with a zenith angle using a Canon G16 camera (Tokyo, Japan) with a 6.1–30.5 mm lens (ISO: 400; exposure time: 1/80 s; focal length: 18 mm; flash: not mandatory) at 15 days (to record rapid changes), at 5 months (March 2023), and at 8.5 months (July 2023; just prior to the mass bleaching event). Subsequently, the photographs were analyzed in GIMP v. 2.10, in which the percentage of bleached tissue of the colonies was determined for each sampled period. The data were captured in an Excel database for their use in the estimation species recovery (Supplementary Material 1).

In addition, at the beginning of sampling, all colonies found along the strip transect (with and without signs of bleaching) were counted to estimate the prevalence of initial bleaching by reef and species (PIB) with the equation (1):

$$Prevalence = \frac{BC}{TC} \times 100\,, \tag{1}$$

where BC is the number of bleached colonies and TC is the total number of colonies in the transect.

To determine colony recovery time, we used the bleaching response index (BRI), based on and modified from the index used by Matsuda et al. (2020). The BRI consisted of classifying the percentage of bleached tissue in the colonies into 6 categories represented by an individual indicator (ID) from 1 to 6: (1) colony with severe bleaching (>90% of affected tissue), (2) colony with serious bleaching (70–89% of affected tissue), (3) colony with moderate bleaching (50–69% of affected tissue), (4) colony with partial bleaching (30–49% of affected tissue), (5) colony with mild bleaching (1–29% of affected tissue), and (6) recovered colony (tissue not bleached). Based on this classification, the BRI was calculated per species using equation (2):

$$BRI = \frac{1}{N}\sum_{i=1}^{N} ID_i\,, \tag{2}$$

where ID is the bleaching category of the *i*-th colony (scale from 1 to 6) and *N* is the total number of coral colonies analyzed.

The BRI indicates the category with the largest number of colonies of the species; a value close to 6 indicates tissue color recovery in most colonies, and a value close to 1 represents bleaching of >90%. Because the index focuses on the recovery of bleached colonies, it was applied to species with more than 15 colonies and a prevalence greater than 10%. Due to the low number of colonies present in the other species, we established these criteria to ensure robust representation based on the number of colonies sampled. Furthermore, colonies that died completely during the study were reported under the category of mortality. This allowed us to describe the bleaching event by species over time, using the variations in prevalence.

To identify trends in associations between the BRI, time, and species, a redundancy analysis (RDA) was performed in CANOCO v. 4.5. To do this, the matrix of dependent variables (bleaching percentage, BRI, and death) was associated to a factorial matrix of independent variables (species), using the sampling time as a complementary variable. The first 2 canonical axes were considered significant; their significance was tested with the Monte Carlo test, using 999 permutations.

Medium-term analysis: coral index (CI)

A database from the period 2008 to 2021 of the "*Monitoreo del Sistema Arrecifal Veracruzano*" project provided by the coral reef laboratory of the I*nstituto de Ciencias Marinas y Pesquerías* (ICIMAP) was analyzed. This database contains data on coral cover, recruitment density, species richness, and number of bleached colonies over a 7-year period (2008, 2010, 2012, 2013, 2017, 2019, and 2021). Sampling was carried out along five 10-m long fixed transects, set parallel to the reef slope, at 10–15 m depth. Cover was estimated using video transects that were analyzed with Coral Point Count with Excel Extensions (CPCe) v. 4.1, which generates 10 random points in each image, recording the benthos and type of background where each point is placed. Thus, total abundance and coral abundance were represented by the number of points in the analyzed images. For the recruitment, we used five 25 × 25-cm quadrants for each transect (total: 0.3125 m^2 sampled per transect) and counted all bleached colonies along the transects (Pérez-España et al. 2015a).

To understand the state of the coral community of both reefs over time, we applied the coral index (CI), based on NEPA (2013) methods, to each of the 7 years of the database. This method consists of evaluating 4 essential indicators to analyze whether the coral reefs are in good condition: (1) coral cover, (2) species richness, (3) recruitment density, and (4) bleaching prevalence. The index consisted of obtaining the annual average value of the 4 indicators mentioned above for each reef. The percentage of coral cover was calculated using equation (3):

$$Coral\ cover\ (\%) = \frac{NCPT}{TNP} \times 100\,, \tag{3}$$

where NCPT is the number of coral points per transect and TNP is the total number of points. Recruitment density was calculated using equation (4):

$$Recruitment\ density\ (recruits \cdot m^{-2}) = \frac{ART}{0.3125\ m^2}\,, \tag{4}$$

where ART is the abundance of recruits per transect. The bleaching percentage was calculated using equation (5):

$$Bleaching\,(\%) = \frac{NBCT}{TCA} \times 100\,, \qquad (5)$$

where NBCT is the number of bleached colonies per transect and TCA is the total coral abundance of each reef.

Note that, because the database did not include the total abundance of colonies, we considered this to be the highest number of diseased colonies recorded in the 7 years analyzed on each reef (Blanquilla: 131 colonies; Blanca: 206 colonies).

Subsequently, the annual average of each indicator for each reef was converted into values ranging within the thresholds proposed by NEPA (2013) and Hernández-Delgado et al. (2018), which use a scale of 1 (critical condition) to 5 (very good condition). Finally, the set of scaled indicators was averaged for each year, and a final CI value was obtained. Following the intervals proposed by NEPA (2013), these values were considered very good (4.5–5), good (3.4–4.2), fair (2.6–3.4), poor (1.8–2.6), and critical (1–1.8).

RESULTS

Dynamics of temperature and sedimentation rate in coral bleaching

Using the monthly average of the NSST in the study area, a local MMM value of 29.3 ± 0.3 °C was obtained, with the warmest months being August (29–30 °C) and September (28.7–30.6 °C). In the period from 2008 to 2023, we observed that the weekly degree of warming in the VRS began each year between the months of June and July, with 2018 being the year with the highest accumulated heat (9 DHW). During 2008, 2010, 2012, 2013, 2017, 2019, and 2021, the accumulated heat reached its maximum value in September (4 ± 1 DHW) and decreased at the end of October in all 7 years (Fig. 2). During 2022, daily NSST began to increase from April onwards, exceeding the MMM in August with a value of 30.5 °C; positive anomalies from July onwards resulted in an accumulated heat stress of 5 DHW in September. At the start of sampling in 2022, corals were under 4 weeks of accumulated heat stress (4 DHW), which decreased until the end of November (<2 DHW). In 2023, the increase in temperature began a month earlier (from March onwards); by July there was already an accumulation of 2 DHW (Fig. 3).

Regarding the sedimentation rate, the studied reefs were within the VRS average (661 $cm^3 \cdot m^{-2} \cdot d^{-1}$ ± 191), with values of 657 $cm^3 \cdot m^{-2} \cdot d^{-1}$ for Blanquilla and 591 $cm^3 \cdot m^{-2} \cdot d^{-1}$ for Blanca. The Kruskal–Wallis test showed that the sedimentation rate did not vary between reefs ($P > 0.05$) (Fig. 4a), but it did vary between seasons ($P < 0.05$) (Fig. 4b); the *nortes* season had the highest sedimentation rates, with averages of 927 and 956 $cm^3 \cdot m^{-2} \cdot d^{-1}$ for Blanquilla and Blanca, respectively.

The Spearman correlation did not show a significant relationship between the number of bleached colonies in the periods 2008–2021 and 2022–2023 and the sedimentation

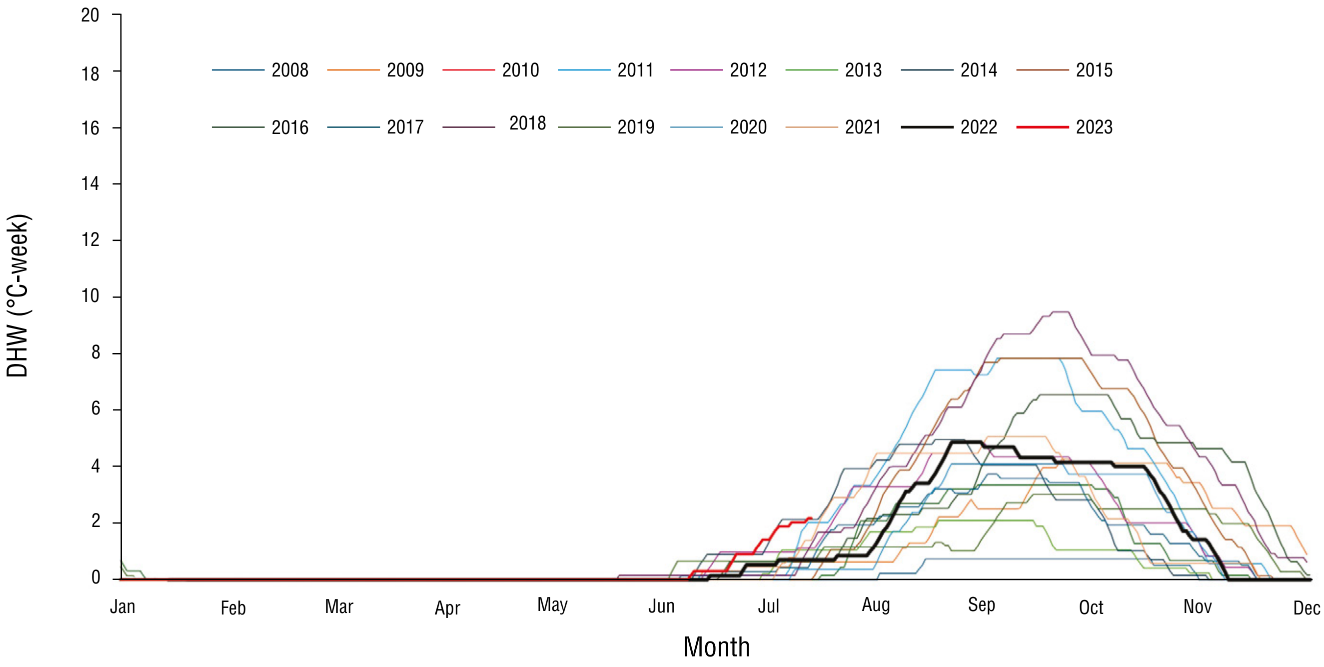

Figure 2. Degree heating week (DHW) values in the Veracruz Reef System (VRS) during the 7 years analyzed within the period from 2008 to 2023.

rate in both reefs ($P = 0.17$, $r = 0.31$), but it showed a positive correlation ($P = 0.03$, $r = 0.66$) with the DHW values.

Short-term analysis: colony recovery

Coral community composition and bleaching prevalence

For Blanca reef, across the 200 m^2 sampled, we recorded 348 coral colonies from 17 species, of which the most abundant were *S. siderea* (25.2%, 88 colonies) and *S. stellata* (23.2%, 81 colonies). At the start of sampling, 58 colonies from 9 species exhibited bleaching, whereas 8 species were unaffected (Table 1).

On the other hand, for Blanquilla reef, we identified 11 species with 278 colonies, with *Montastraea cavernosa* (42%) and *Colpophillya natans* (28.4%) being the most abundant species with 117 and 79 colonies, respectively. Bleaching occurred in 46 colonies from 5 species, whereas 6 species did not experience bleaching. For both reefs, the PIB value was 17%, with the dominant species having the highest number of affected colonies, with prevalences ranging from 14% to 32% (Table 1).

Dynamics of recovery per species

At the start of sampling, the BRI ranged between 3 and 5 on both reefs (Fig. 5a, b). *Colpophillya natans* was the most affected in Blanquilla reef, with a complete recovery of >80% of its colonies (9 colonies) at 8.5 months and the only one with a mortality rate of 9%, corresponding to one colony. Meanwhile, in Blanca reef, the species most affected by bleaching were *M. cavernosa*, with a recovery of >80% of its colonies at 5 months, and *S. stellata*, with a maximum recovery of 60% of colonies (Fig. 6).

With the exception of *C. natans* and *S. stellata*, all species in both reefs exhibited increasing pigmentation during the study period in >80% of their colonies at 5 months of recovery, with the percentage of bleaching across colonies decreasing to a mild bleaching category (*S. siderea*: 10% and 20% bleaching; *M. cavernosa*: <10% bleaching) and a recovered category (all *P. astreoides* and *A. lamarcki* colonies with no bleached tissue), with species having BRI values of 5 and 6. By 8.5 months, corresponding to July 2022, the percentage of bleaching increased in most colonies; species of the genus *Siderastrea* were the most affected (Figs. 5, 6).

The RDA showed a positive correlation ($P = 0.001$) between the presence of *P. astreoides* and *A. lamarcki* species and the BRI at 5 and 8.5 months. In contrast, the presence of *Siderastrea* species was the only variable that showed a positive relationship with bleaching. In general, the presence of the species *S. stellata*, *S. siderea*, *M. cavernosa*, or *C. natans* did not show a positive correlation with the BRI,

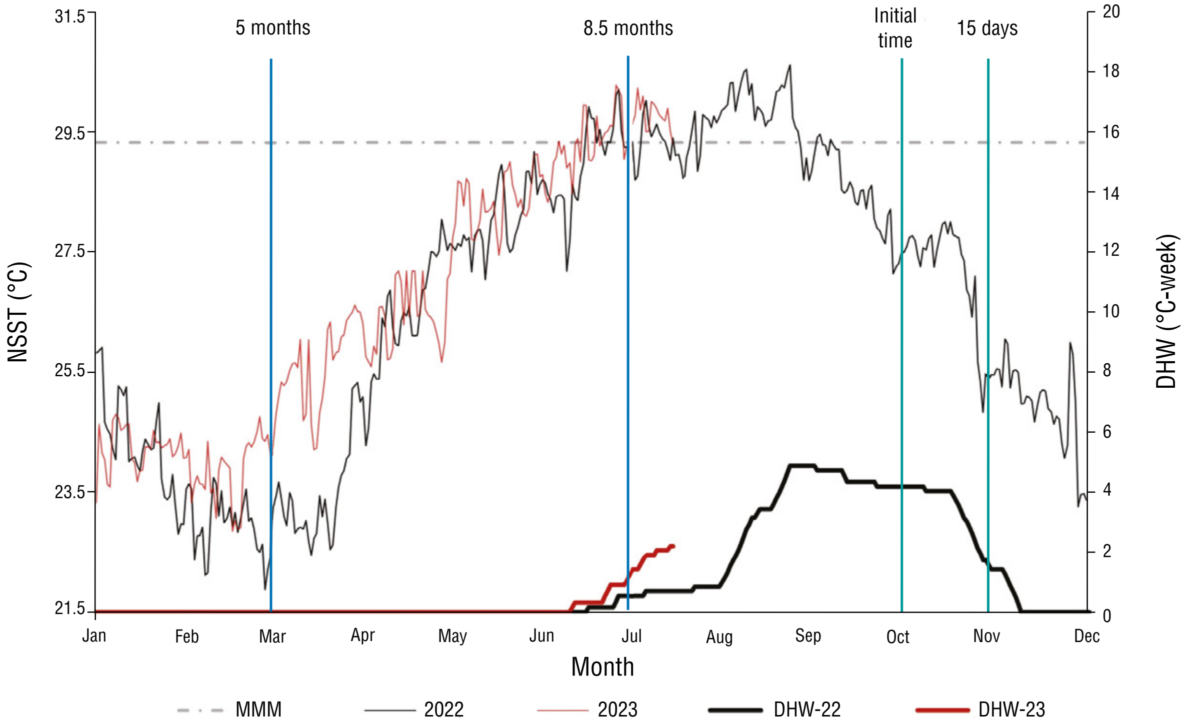

Figura 3. Daily nighttime sea surface temperature (NSST) during 2022 and 2023 in the Veracruz Reef System (VRS). Mean monthly maximum (MMM) of the study area (gray dotted line), temperature (thin lines), represented satellite-based weekly degree of warming (1-km daily) of coral bleaching (D-DHW) (thick lines), and sampling months (vertical lines).

Table 1. Prevalence and resistance of bleached colonies by species on the 2 study reefs of the Veracruz Reef System (VRS) during sampling from October 2022 to July 2023. BLE: bleached colonies; RES: resistant colonies; PIB: bleaching prevalence by species at the start of sampling.

Reef	Blanquilla			Blanca		
Species	BLE	RES	PIB	BLE	RES	PIB
Montastraea cavernosa	26	91	22	4	14	22
Colpophillya natans	11	68	14	2	19	10
Siderastrea siderea	6	13	32	20	68	23
Porites astreoides	2	13	13	3	20	13
Orbicella faveolata	0	15	0	1	24	4
Pseudodiploria strigosa	0	14	0	0	1	0
Siderastrea stellata	0	8	0	23	58	28
Stephanocoenia intersepta	0	6	0	0	18	0
Helioseris cucullata	1	1	50	2	0	100
Mycetophyllia lamarckiana	0	2	0	0	5	0
Dichocoenia stokesii	0	1	0	0	0	
Agaricia lamarcki	0	0		2	17	11
Madracis decactis	0	0		0	20	0
Agaricia fragilis	0	0		1	17	6
Agaricia agaricites	0	0		0	5	0
Siderastrea radians	0	0		0	1	0
Porites porites	0	0		0	2	0
Oculina difusa	0	0		0	1	0
Number of colonies	46	232		58	290	
Number of species	5	11		9	16	
Bleaching prevalence (%)	17			17		

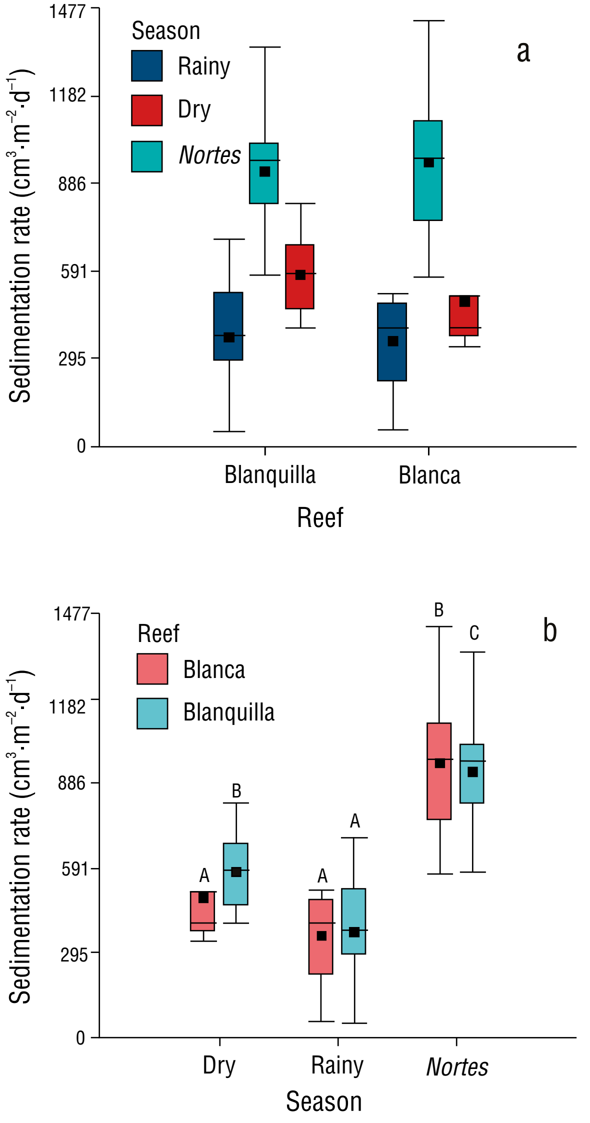

Figure 4. Sedimentation rate. Variation in sedimentation rate from 2012 to 2022 between study reefs and seasons using the Kruskal–Wallis test. Differences between the Blanquilla and Blanca reefs in the rainy season ($\chi = 0.005$, $P = 0.9$), dry season ($\chi = 3.02$, $P = 0.08$), and nortes season ($\chi = 0.00019$, $P = >0.9$) (**a**). Differences between seasons in the Blanca reef ($\chi = 15.5$, $P = 0.0004$) and in Blanquilla reef ($\chi = 19$, $P = 0.0001$) (**b**).

and of these, only the presence of *C. natans* was related to the previous death variable (Fig. 7).

Medium-term analysis: coral index (CI)

The average of each indicator over the 7 years analyzed showed that Blanquilla reef had better coral cover, whereas Blanca reef had higher recruitment density values. The bleaching percentage and species richness indicators were the same throughout the years analyzed (Table 2).

The CI varied between reefs, fluctuating between 3 and 4. The lowest CI value (3.25) for the Blanquilla and Blanca reefs, corresponding to the fair category, was observed during 2010 and 2017, respectively (Fig. 8). Low values were not directly related to the years with the highest bleaching rate. Overall, the health of the coral community in both reefs during the 7 years analyzed was categorized as good (CI = 3.6 and 3.8) (Table 2).

Discussion

Dynamics of temperature and sedimentation in coral bleaching

During the 2008–2022 period, accumulated heat (DHW) values in the VRS marked a window of thermal stress that began in June (~0.5 DHW) and ended in December (<2 DHW). September was consistently observed to be the month with the highest heat accumulation (2–9 DHW). According to the accumulated heat parameters proposed by NOAA (2024), during the 2008–2022 period, VRS corals in general were exposed to a thermal stress equivalent to a level 1 bleaching alert, which indicated a low probability of bleaching across the entire reef.

Studies conducted in the Mexican Caribbean, a region neighboring our study area in the Gulf of Mexico, have documented that corals are highly susceptible to bleaching, with a percentage of bleached colonies of 20–45% (Randazzo-Eisemann and Garza-Pérez 2021, Sellares-Blasco et al. 2022, Muñoz-Castillo et al. 2024). In this context, the bleaching prevalence recorded in this study at the beginning of the 2022 sampling in both reefs (17%) reflected a relatively low value, which was mainly determined by the accumulated weekly heat degrees to which they were exposed (5 DHW). Specifically, for the 2022 to 2023 sampling, low DHW values explained the bleaching prevalence of 17% in both reefs. Furthermore, the first samplings (October and November 2022) corresponded to the *nortes* season, when mixing in the water column helps lower temperatures (Salas-Monreal et al. 2022) and decrease thermal stress. Therefore, the bleaching prevalence observed at the start of sampling was already the highest ever reached in the area.

In the VRS, the influence of sediments from adjacent rivers varies with the climatic season (Krutak 1997). During the rainy season, the contribution of the Papaloapan River, with 1,331.4 $m^3 \cdot s^{-1}$, and the Jamapa River, with 68.2 $m^3 \cdot s^{-1}$ (CNA 2021), directly affects the reefs located in front of the town of Antón Lizardo, particularly Blanca reef, with sediment deposition on the corals; during the *nortes* season, the contribution of these rivers does not reach the reefs (Salas-Monreal et al. 2022). Despite this, in this study, a higher sedimentation rate was recorded during the *nortes* season, which could be the result of sediment traps capturing suspended particles due to mixing in the water column during this season.

On the other hand, reefs are also exposed to wastewater discharges. Blanquilla reef is exposed to input from

Table 2. Values for the coral index (CI) indicators for the study reefs converted to the threshold range according to NEPA (2013). CC: coral cover; RD: recruitment density; BLE (%): bleaching percentage; *S*: species richness; ACI: annual coral index.

Reef	Blanquilla					Blanca				
Year	CC	RD	BLE	*S*	ACI	CC	RD	BLE	*S*	ACI
2008	5●	1●	3●	5●	3.50●	3●	4●	3●	4●	3.50●
2010	5●	3●	1●	4●	3.25●	4●	5●	2●	4●	3.75●
2012	5●	4●	2●	5●	4.00●	3●	5●	2●	5●	3.75●
2013	5●	3●	2●	5●	3.75●	4●	5●	2●	5●	4.00●
2017	4●	1●	5●	4●	3.50●	2●	5●	2●	4●	3.25●
2019	4●	4●	3●	4●	3.75●	3●	5●	3●	5●	4.00●
2021	4●	4●	3●	4●	3.75●	3●	5●	3●	5●	4.00●
Indicator										
ACI	4.6	2.9	2.7	4.4		3.1	4.9	2.4	4.6	
Total CI			3.6●					3.8●		

Indicator category: ●very good, ●good, ●fair, ●poor, ●critical.

54 wastewater discharges located along the port of Veracruz, and Blanca reef is influenced by 19 wastewater discharges reported for the southern zone (Mapel-Hernández et al. 2021). This could suggest that the sedimentation rate on these reefs is influenced by both sediment input from adjacent rivers and wastewater discharges from the area, since the recorded sedimentation rate did not vary between reefs. Furthermore, although these reefs were initially selected in the hope of finding differences in sedimentation rates and species susceptibility, it ultimately became clear that in both reefs the coral colonies were under the same degree of stress from sediment accumulation.

Rising temperatures are known to be the main stress factor for coral colonies (Eakin et al. 2009), a condition that was reaffirmed in this study by the positive correlation between the number of bleached colonies and accumulated heat stress. In the VRS, corals were exposed not only to rising temperatures but also to constant sediment stress; nonetheless, in this study, sedimentation rates did not directly influence bleaching. This demonstrates a certain tolerance of the colonies to the high sedimentation rates reported for the studied reefs. Despite this, the possibility that sediments play a secondary stressor role that increases the sensitivity of the colonies should not be ruled out; during the *nortes* season, the resuspension of sediments caused by mixing in the water column, which reached an average depth of 25 m (Salas-Monreal et al. 2022), could stress corals due to the friction of particles on the tissue and cause nutritional depletion, as mentioned by Salih et al. (2000) and López-Lodoño et al. (2023).

Short-term analysis: colony recovery

During the 2022–2023 sampling, we observed that the scleractinian coral species most susceptible to bleaching in both reefs (*S. siderea*, *S. stellata*, *M. cavernosa*, and *C. natans*) were the species that most contributed to the construction of the VRS reefs (Horta-Puga and Tello-Musi 2009), which Alemu and Clement (2014) and Pérez-España et al. (2015a) reported to be among the most affected by bleaching in the Caribbean and in the VRS, respectively.

However, in this work, most species (except *C. natans* and *S. stellata*) showed a recovery in a similar time to that obtained by Matsuda et al. (2020), who reported that recoveries occurred 1 to 4 months prior to the next bleaching event, and to that obtained by Hughes and Grottoli (2013), who reported that at 4 months the colonies had concentrations of photosynthetic pigments and photoautotrophic carbon assimilation at normal levels, appearing visually healthy. Therefore, the visual decrease in bleached tissue within the first 5 months after the bleaching event in the coral colonies analyzed in this work could indicate that there was also a physiological recovery during that time.

Field studies have shown that, with elevated temperatures, reefs characterized by turbid waters are less prone to coral bleaching than reefs with clear waters (Morgan et al. 2017). The abundant particulate organic matter in turbid reefs, together with thermal bleaching, can cause some coral species to become permanently or facultatively heterotrophic (Anthony and Fabricius 2000). Hughes and Grottoli (2013) reported this same event and indicated that corals that had

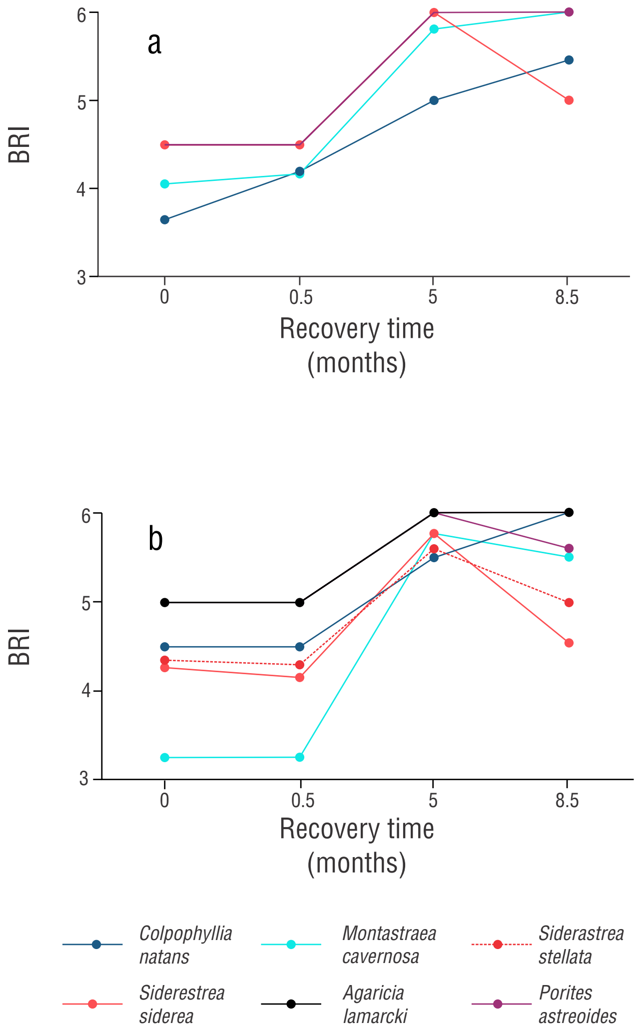

Figure 5. Bleaching response index (BRI) represented by the average score of the bleaching scale. Recovery of susceptible colonies in Blanquilla reef (**a**) and Blanca reef (**b**).

experienced bleaching had higher amounts of heterotrophic carbon assimilated during their recovery process than non-bleached corals. The VRS reef system has input from rivers that carry organic matter (Carreón-Palau 2019); therefore, the high recovery rate observed in the species analyzed in this study could be due, in part, to the access to nutrients and energy through heterotrophy during the bleaching event, which would allow the colonies to resist and recover more quickly, as mentioned by Hughes and Grottoli (2013) and Tremblay et al. (2016). However, confirmation of this event in the colonies requires specific analysis.

The analysis of the species-specific response to bleaching indicated that *C. natans* took the longest to show visually healthy tissue, in addition to being the only colony to experience mortality. This suggests a greater sensitivity of the species to thermal stress, which is consistent with the reports of González-Gándara (2008) and Pérez-España et al. (2015a), who reported that this species is among those most affected by bleaching. On the other hand, considering that there was an El Niño event in 2023, in which temperatures were above the historical record and triggered a bleaching event that affected the Pacific, Caribbean, and Gulf of Mexico (Goreau and Hayes 2024, López-Pérez et al. 2024), the sensitivity of the colonies of the genus *Siderastrea* increased during the last sampling (July 2023) due to the thermal stress to which they were exposed, since by that date there was a heat accumulation of 2 °C in the VRS (Fig. 3).

Montastraea cavernosa has been shown to be able to survive in environments with constant sediment stress, with sedimentation rates as high as 400 $g \cdot m^{-2} \cdot d^{-1}$, without showing severe bleaching or mortality (Vargas-Ángel et al. 2007). In the Blanca and Blanquilla reefs in the VRS, this species was exposed to sedimentation rates of up to 1,434 $g \cdot m^{-2} \cdot d^{-1}$ and of 600 $g \cdot m^{-2} \cdot d^{-1}$ on average. Therefore, although *M. cavernosa* was one of the most affected by bleaching, its recovery within the first 5 months demonstrated its resilience in highly sedimented environments; studies have been shown that it has the ability to stop its growth rate to direct energy resources to reject sediments (Horta-Puga and Carriquiry 2008). The same mechanism for rejecting sediments could occur in *Siderastrea* colonies, as these also showed one of the highest percentages of bleaching in their colonies and the same recovery time.

On the other hand, *P. astreoides* was one of the species that showed complete tissue color recovery in all its colonies 5 months after the bleaching event. According to what was reported by Levas et al. (2018), this species has the capacity to recover after a month and a half; therefore, it is possible that, in the present study, *P. astreoides* colonies reached their maximum recovery even before the 5 months sampled. Furthermore, within the analyzed species, *P. astreoides* was one of the least affected by bleaching, despite being in an environment with various stressors for corals. This result is consistent with what was reported by Green et al. (2008), who pointed out that *P. astreoides* has the potential to grow in habitats that are not optimal for most corals. Likewise, *P. astreoides* has shown high recovery rates because its symbionts are from the genus *Cladocopium* (clade C), which are characterized by high photorepair rates and a wide tolerance to variations in temperature and irradiance, compared to the symbionts of species more sensitive to bleaching (Hennige et al. 2011).

Coral mortality and recovery have been associated with bleaching severity (López-Patoni 2014, NOAA 2023). Since this study only assessed the 2022 bleaching event, with the last sampling (July 2023) occurring just before the onset of the fourth bleaching event, colony recovery corresponds to low thermal stress, as mentioned above. Therefore, the impact bleaching would have on the recovery of scleractinian coral species in the event of a severe bleaching event is unknown.

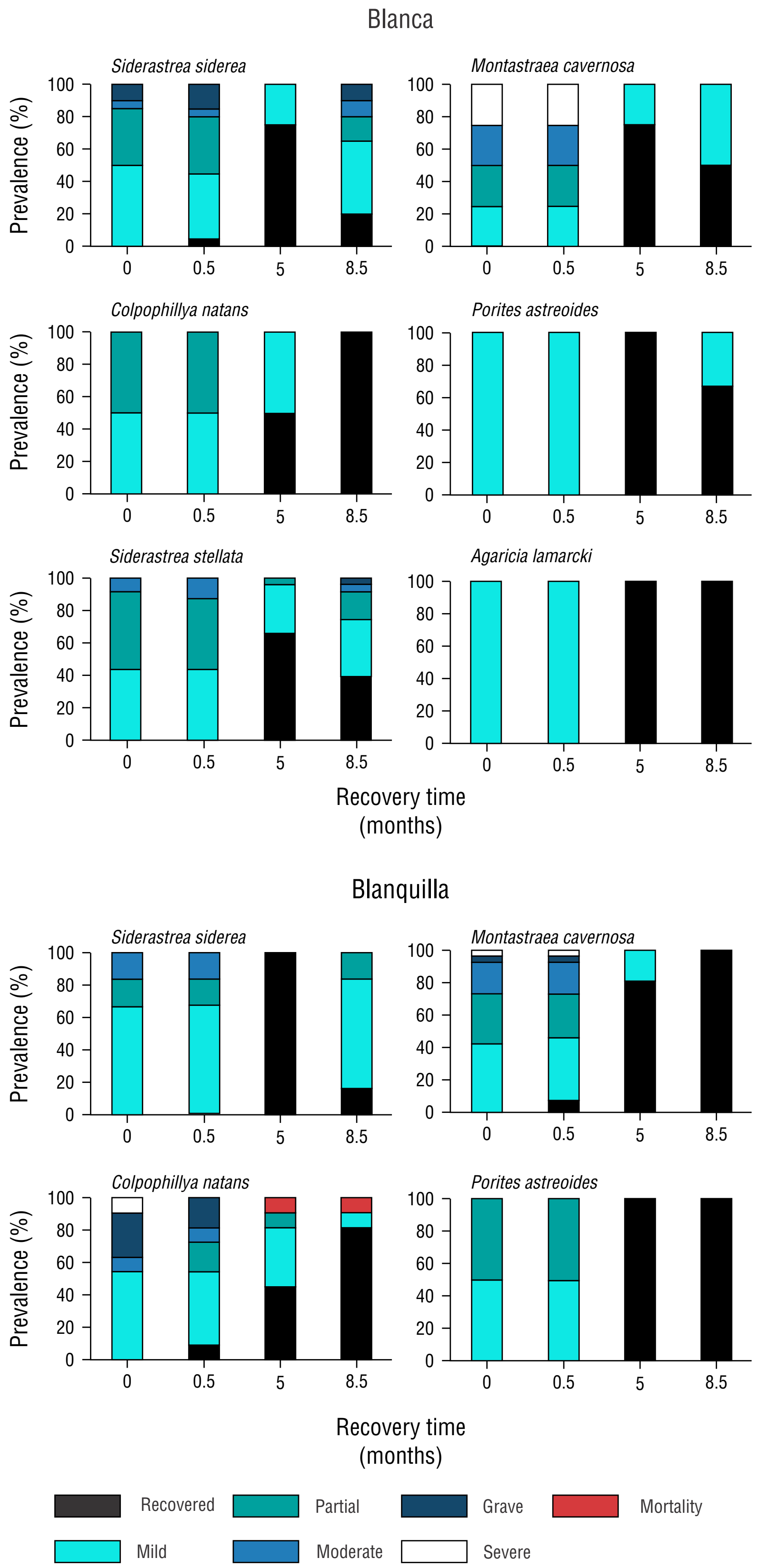

Figure 6. Prevalence per species of bleached colonies in the October 2022 sampling and at 15 days, 5 months, and 8.5 months of recovery.

Medium-term analysis: coral index (CI)

The corals of the studied reefs had high CI values during the 7 years analyzed. Although the Blanca and Blanquilla reefs are located close to the coast (2 km), the CI values were greater than 3, which contrasts with what was reported by Hernández-Delgado et al. (2018), who documented CI values lower than 2 in reefs located less than 4 km off the coast. According to what was reported by Meesters and Bak (1993), coral reefs in disturbed environments show higher rates of regeneration and pigment recovery after a period of bleaching, which is summarized as high resilience. Therefore, the good category found in both reefs could be the result of an acclimatization process in which the colonies have had phenotypic changes under the environmental and anthropogenic stress in the VRS, which has led to the readjustment of the tolerance levels of the coral colonies (Coles and Brown 2003).

Furthermore, in the deep part (>10 m), each reef shows different characteristics. Blanquilla is known to have the greatest coral cover, whereas Blanca is among those with the highest recruitment densities (Pérez-España et al. 2015a). This is consistent with our results; Blanquilla showed an average cover of 41% but a recruitment density of 5%, whereas Blanca showed a cover of 17% with a recruitment density of 16%.

The CI indicators considered in this study are essential for the coral community to be in a healthy state and recover from thermal stress (Maynard et al. 2017). In this sense, the recruitment density and coral cover indicators that characterized the study reefs have greater weight in the CI values and determine the condition of the coral community over time. However, it is important to consider that not all recruits contribute equally to the functioning of the ecosystem. Some opportunistic species can have high levels of recruitment, but limited contribution to the three-dimensional structure of the reef and, therefore, to the ecosystem services it provides (Cetz-Navarro et al. 2016). Thus, future analyses should specify recruitment composition to assess the recovery potential of the reef more accurately.

Considering colony recovery time, along with other key indicators for studying coral communities (coral cover, recruitment density, and species richness), will help us understand the response of reefs and each species over time. Horta-Puga and Tello-Musi (2009) mentioned that the VRS was dominated by species with broad tolerance limits, which we confirmed with the results of the recovery time of the dominant species. According to Lam et al. (2020), both the indicators used for the CI and the recovery of the colonies could denote that sites with a desirable set of metrics indicate greater resilience. However, due to the increasing thermal stress faced by the colonies and the anthropogenic stressors that harm their health, it is necessary to continue monitoring the colonies in situ to understand the recovery time following bleaching events, especially the 2023 event, and to identify if there are changes in the recovery of the species.

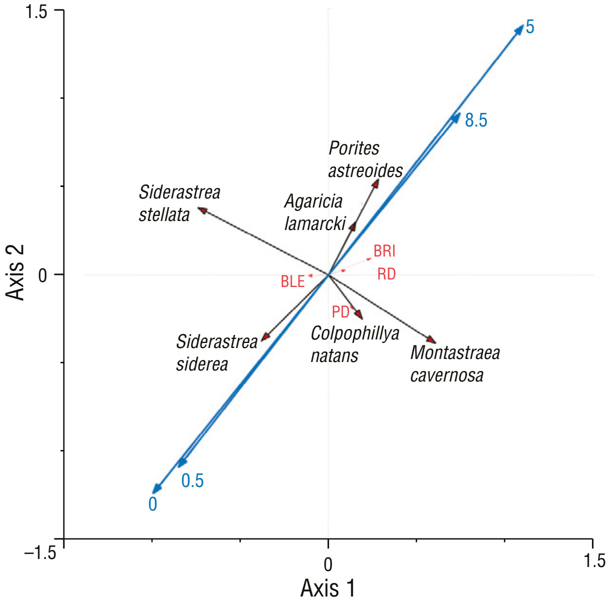

Figure 7. Partial redundancy analysis (RDA) of environmental parameters and species with months of recovery (first axis: $F = 17.862$, $P = 0.0010$; second axis: $F = 3.021$, $P = 0.0010$; 60% of the total variance explained for the first 2 canonical axes). Red arrows indicate environmental parameters. Black arrows indicate species. Blue arrows indicate recovery months. BRI: bleaching response index; BLE: bleaching percentage; PD: previous death; RD: recent death.

Furthermore, it is important to highlight that in this study, we assessed colony recovery using tissue coloration. Therefore, to better understand the bleaching process in each species, we suggest that future studies address recovery from a physiological perspective and consider other environmental variables that could influence their health status.

CONCLUSIONS

Under a cumulative heat stress of 5 DHW and a sedimentation rate of approximately 600 $\mathrm{cm^3 \cdot m^{-2} \cdot d^{-1}}$, *M. cavernosa*, *S. siderea*, *P. astreoides*, and *A. lamarcki* recovered tissue color, reaching mild bleaching in >80% of their colonies within the first 5 months after the bleaching event, regardless of the percentage of bleached tissue in the colonies, whereas *C. natans* was among the most sensitive species to heat stress and took the longest to recover (8.5 months). On the other hand, *O. faveolata*, *M. decactis*, *A. fragilis*, and *S. intercepta* were not affected by the level 1mild bleaching heat stress. The sedimentation rate to which the study reefs were exposed did not vary between reefs and did not directly influence coral colony bleaching. Rather, the main cause of bleaching was thermal stress, and recovery time depended on the decrease

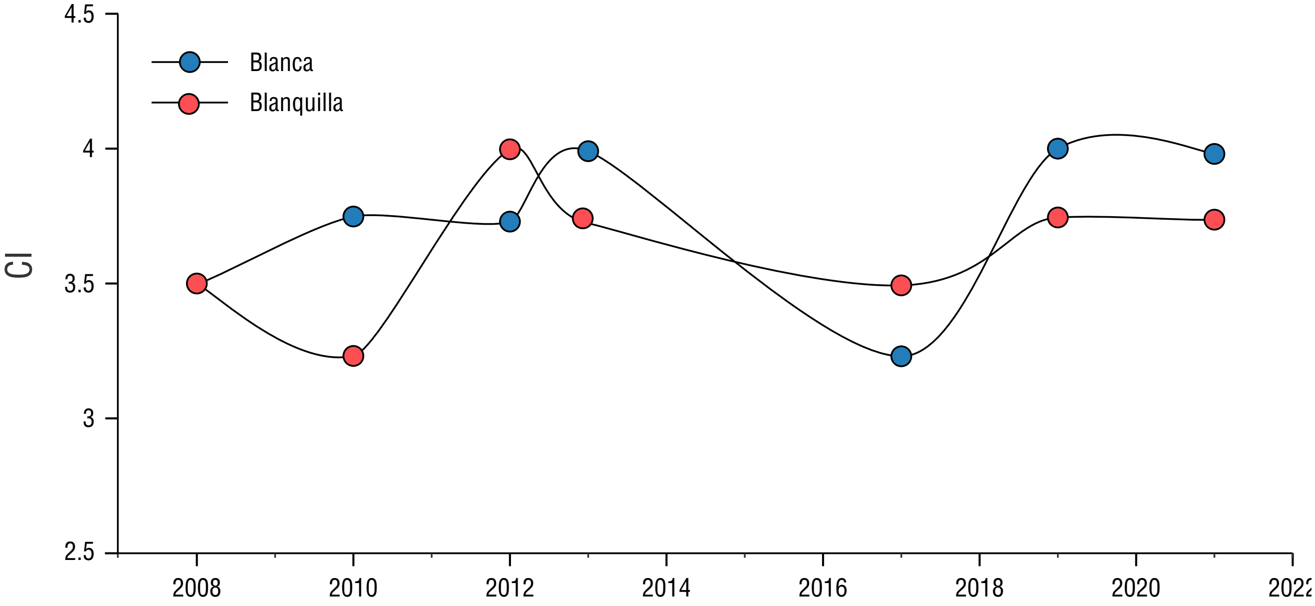

Figure 8. Coral index (CI) for each of the reefs analyzed in the period from 2008 to 2021: Blanca reef (blue circles) and Blanquilla reef (orange circles).

in accumulated heat levels. Finally, the lack of differences in the CI and BRI between reefs was influenced by the similar conditions to which the scleractinian corals of both reefs were exposed to, the recovery time of the dominant species at each reef, and the cover and recruitment density attributes that characterized them.

English translation by Claudia Michel-Villalobos.

Declarations

Supplementary Material

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3500/420421187.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: DCL and HPE (equal); Data curation: DCL; Formal analysis: DCL; Investigation: DCL (main) and HPE (support); Methodology: DCL and HPE (equal); Resources: HPE; Supervision: HPE (main), AGB, LAF; Validation: HPE, AGB, LÁF (equal); Visualization: HPE, AGB, LAF (equal); Writing—original draft: DCL (main) Writing—review, and editing: DCL (main), HPE, AGB, LAF (support).

Data availability

The data are available as supplementary material.

Use of AI tools

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

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Effect of environmental light conditions on the growth of the coral *Orbicella faveolata* in the Mexican Caribbean

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ABSTRACT. Massive corals of the genus *Orbicella* are key organisms that help maintain the physical structure of Caribbean reefs. However, they are currently threatened by environmental changes, such as increased nutrient loads and pollution, which affect the optical properties of seawater and, consequently, limit reef development. Thus, analyzing the responses in the growth of coral species to changes in light environments can help us improve mitigation and conservation strategies for coral reefs. The objective of this study was to evaluate the effect of changes in environmental light conditions on the growth rate of *Orbicella faveolata* by comparing fragments transplanted from 9 m to 3 m depth and control fragments that were transplanted under the same light conditions (3 m). The fragments of both treatments showed similar growth (16–23%), as well as comparable extension and diameter values. The annual growth rate for the control fragments and transplantation treatment fragments was 1.04 ± 0.18 $\text{cm}\cdot\text{y}^{-1}$ and 1.11 ± 0.23 $\text{cm}\cdot\text{y}^{-1}$, respectively. The results of this study reveal that the coral *O. faveolata* can physiologically acclimate to new environmental light conditions after being transplanted from a deep environment to a shallow environment in the short-term (1–9 months). This suggests great potential for the use of *O. faveolata* in restoration strategies and management programs that aim to maintain the populations and structural framework of coral reefs in the Caribbean region.

Key words: coral fragments, coral reefs, coral transplantation, massive corals, skeletal growth.

INTRODUCTION

Coral reefs are among the most complex and diverse ecosystems on the planet. They are characterized as sites for feeding, reproduction, and shelter and host approximately 25% of all marine species (Sheppard et al. 2009, Veron 2010). Coral reefs are marine benthic formations formed by the accumulation of biogenic calcium carbonate ($CaCO_3$) secreted by calcifying organisms, such as hermatypic corals, mollusks, and coralline algae (Sheppard et al. 2009). As primary producers, hermatypic corals play a key role in forming these physical structures; under optimal conditions, they can generate up to 10 kg of $CaCO_3\cdot m^3\cdot y^{-1}$ (Chave et al. 1972, Kleypas et al. 1999). In addition to increasing the three-dimensionality and complexity of habitats, hermatypic corals are fundamental to the balance of various biogeochemical cycles and ecosystem services (Perry and Alvarez-Filip 2018).

Hermatypic corals have the ability to form exoskeletons by precipitating $CaCO_3$ in the form of aragonite crystals. This process is controlled by intrinsic factors, such as genotypic variation, symbiotic community, morphology, and coral sex, as well as extrinsic factors, such as temperature, seawater chemistry, and light environment (Foster et al. 1979, Todd 2008, Allemand et al. 2011). Coral growth rates depend on carbonate calcification, which requires energy resources

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derived from photosynthesis, which are translocated by symbionts (Colombo-Pallota et al. 2010).

Both the symbiont and the host show outstanding phenotypic plasticity that allows them to develop in different light and hydrodynamic environments (Kaniewska et al. 2011). The skeletal architecture built by each polyp plays an important role in the internal light environment; optical (reflective) properties of the skeleton cause multiple light scattering, favoring photosynthesis in symbiont algae (Enríquez et al. 2017). Therefore, the role of the symbiotic community in the translocation of energy to the coral for the production of $CaCO_3$ and construction of its skeleton is highly relevant (Enríquez et al. 2005, 2017; Colombo-Pallotta et al. 2010, Scheufen et al. 2017). In this sense, the absorption and reflection properties of hermatypic coral skeletons depend on the structural arrangement that makes up their internal architecture, which modulates the dispersion of light, influencing the amount of energy available for the metabolic processes of the host (Enríquez et al. 2017). Therefore, depending on light conditions, corals can have different morphologies at the corallite level and at the colony level (Graus and Macintyre 1976, 1982; Klaus et al. 2007). In conditions of low light availability (>20 m), corals generally show plating morphologies to capture the greatest amount of light, whereas in conditions of greater light availability (1–5 m), corals have more complex morphologies (e.g., columnar or hemispherical), and colonies use self-shade to avoid excess light (Kramer et al. 2021).

Orbicella is one of the most important hermatypic coral genera in the Caribbean region and one of the most threatened by environmental changes, such as pollution or increased nutrients in seawater due to wastewater discharge (Rico-Ensenaro et al. 2023). Species of the genus *Orbicella* obtain energy from heterotrophic assimilation (15–35%) by feeding on zooplankton and from autotrophic assimilation (70–90%) through the translocation of nutrients from endosymbiotic algae (Houlbrèque and Ferrier-Pagès 2009, Yranzo et al. 2020). Symbiont photosynthetic products contribute the most to the energy balance needed for the survival and growth of *Orbicella* colonies (Teece et al. 2011). However, faced with changes in seawater quality (e.g., changes in optical or chemical properties), it is important to understand the effect that light environments have on the growth of corals and the phenotypic capacity of corals to acclimate to different environmental gradients (Merks et al. 2004).

Despite the important effect that light has on the morphology and phenotypic plasticity of corals, the information on the growth mechanisms associated with changes in light conditions is scarce (Todd 2008). In particular, how changes in light conditions affect coral growth has scarcely been explored. *Orbicella faveolata* is distributed over a wide depth gradient (1–50 m); thus, we believe it has great potential to acclimate physiologically to new light environments. Therefore, the objective of the present study was to evaluate the growth response of *O. faveolata* colonies transplanted between different light habitats (i.e., deep to shallow) and assess their acclimation capacity and potential use in restoration interventions.

MATERIALS AND METHODS

Study area

The study was performed in the *Jardines* reef of the *Arrecife de Puerto Morelos* National Park (PNAPM, for its acronym in Spanish). This protected natural area was established in 1998 and is located in front of the town of Puerto Morelos in the state of Quintana Roo (21°00′00″ to 20°48′33″ N, 86°53′14.94″ to 86°46′38.94″ W; Fig. 1). The Puerto Morelos reef is a fringing coastal reef that forms an internal lagoon, with a depth of 3–5 m, characterized by calcareous sand stabilized by seagrass meadows (CONANP 2000). The area has a well-developed back reef and reef crest, a relatively flat fore reef with some massive coral sections, and several channels that gradually descend to 20–25 m toward an extensive sand platform (Rodríguez-Martínez et al. 2010). The reef zone is composed by 41 species of scleractinian corals and 32 gorgonian corals. The most abundant hermatypic coral species in the region are *O. faveolata*, *Orbicella annularis*, *Acropora palmata*, *Acropora cervicorni*, *Millepora complanata*, *Pseudodiploria strigosa*, *Montastraea cavernosa*, *Dichocoenia stokesii*, and *Agaricia tenuifolia* (Ruíz-Rentería et al. 1998, Alvarez-Filip et al. 2019, Caballero-Aragón 2020, Molina-Ramos 2020). However, in the last 5 years, live coral cover has decreased (>60%) due to the effects of thermal anomalies, hurricanes, and diseases that cause changes in species composition and dominance (Alvarez-Filip et al. 2022).

Obtaining growth parameters

For the transplantation treatment, 16 fragments of *O. faveolata* were obtained from 4 adult donor colonies of similar size (hemispherical, 40-cm height) that appeared healthy and were in the same light gradient (9 m). For the control treatment, the same procedure was done at a 3-m depth light gradient. All fragments (3 cm^2) were extracted using a submersible hydraulic electric drill (Nemo Power Tools, Hong Kong, China). The fragments obtained at 9 m (transplantation treatment) were transplanted to the depth of the control fragments (3 m); all fragments were installed on 2 fiberglass beds. Each fragment was fixed to an acrylic plate using epoxy plasticine. After installation, the fragments were allowed to acclimate for 2 months to reduce the effect of handling stress (Fig. 2).

At the end of the acclimation period, during a period of 9 months, the following variables were measured monthly in each fragment: linear extension (cm), defined as the longitudinal distance from the base of the acrylic to the maximum height of the fragment, and the apical diameter (cm), defined as the maximum diameter from an aerial perspective. All measurements were estimated from digital images (25 MP) obtained with a GoPro Hero 9 camera (San Mateo, USA) (in linear function) using a plastic vernier (accuracy 0.05 cm) as a reference scale. The images from each monthly sampling were processed for each fragment for both treatments using the ImageJ program (Schneider et al. 2012).

This study considered the environmental variables seawater temperature (°C) and photosynthetically active radiation (PAR) to describe their influence on the growth of the massive coral *O. faveolata*. Daily values (May 2021 to February 2022) were obtained for both variables from the database of the *Sistema Académico de Monitoreo Meteorológico y Oceanográfico* (sammo.icmyl.unam.mx); these were averaged to obtain a monthly value for each variable.

Statistical analysis

Descriptive statistics were obtained for all monthly growth parameters (i.e., the average, standard deviation, ranges, and maximum and minimum values). The annual growth rate was obtained by extrapolating data from the 9 months of the study; the average value of each month was used to avoid overestimating the growth. A general monthly value was obtained, which was added to each of the 3 missing months to complete the annual period. After testing the normality and homoscedasticity of the data, various one-way analyses of variance (ANOVA) were performed, using generalized linear models (GLM), to evaluate the differences in growth parameters at the treatment and time level (monthly), including their interaction. Finally, simple linear regression models (r^2) were used to evaluate the relationship between growth characteristics and environmental factors (temperature and PAR). All statistical analyses were performed in the SigmaPlot program v. 11 (Graffiti LLC, Palo Alto, USA), using a 95% confidence interval ($\alpha = 0.05$).

RESULTS

Linear extension

At the end of the experimental period, no signs of bleaching, loss, or death of tissue were observed in any of

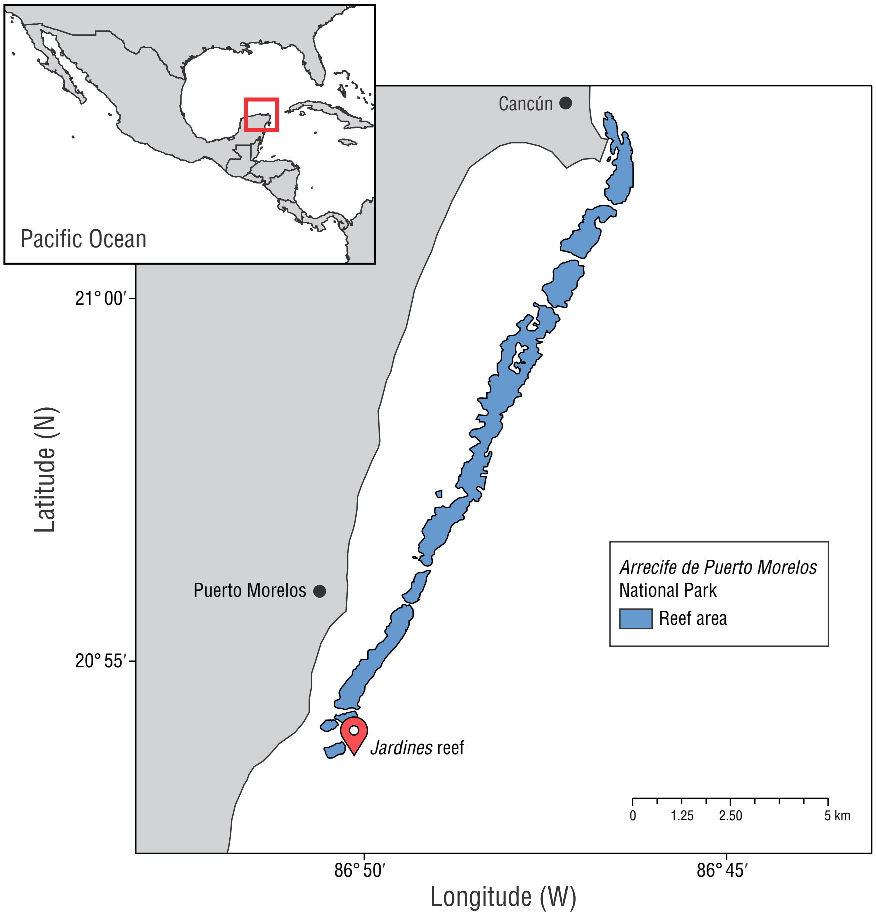

Figure 1. Map of *Arrecife de Puerto Morelos* National Park (APMNP), Mexico. The marker indicates the study site.

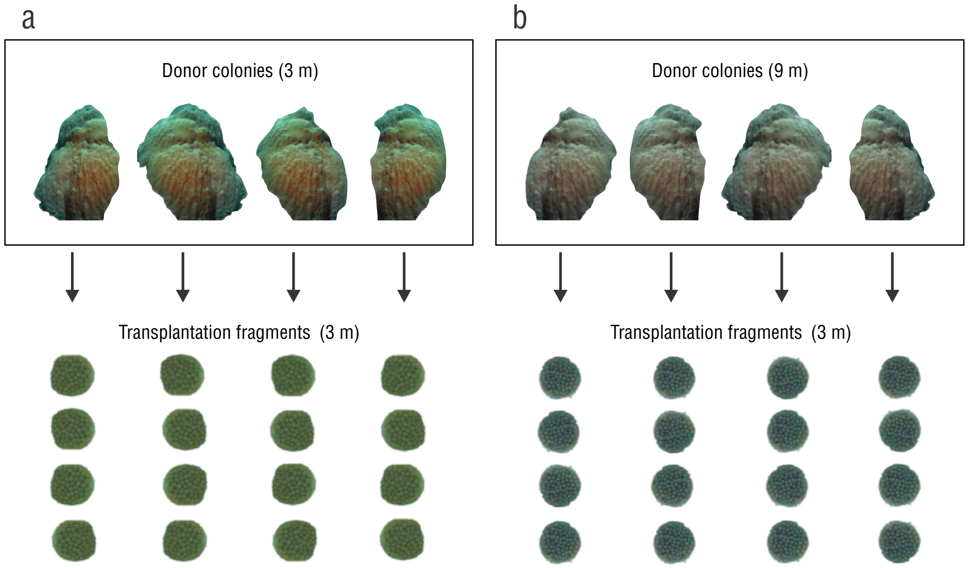

Figure 2. Experimental design. Donor coral fragments were collected at 2 depths: (**a**) 3 m (control treatment) and (**b**) 9 m (transplantation treatment). Four fragments were obtained from each donor colony, which were transplanted to a depth of 3 m.

the fragments in the 2 treatments. Growth in linear extension showed a cumulative increase of 0.74 cm for the control treatment after a 9-month period, showing a monthly growth of 0.09 ± 0.02 cm (range: 0.04–0.26) (Table 1). The transplantation treatment showed a total accumulated growth of 0.70 cm, with a monthly average of 0.08 ± 0.01 cm (range: 0.06–0.64). The annual growth of the linear extension was 1.04 ± 0.18 cm·y^{-1} and 1.11 ± 0.23 cm·y^{-1} for the control treatment and the transplanted fragments, respectively. The results obtained for the linear extension showed no significant differences between treatments ($F_{1,69}$ = 0.050, $P >$ 0.823), over time (months; $F_{6,69}$ = 2.154, $P >$ 0.061), or in interactions between both variables ($F_{6,69}$ = 0.745, $P >$ 0.616) (Fig. 3). The relative growth of the linear extension showed a similar increase (control: 16%; transplant: 15%) (Table 2).

Apical diameter

The total cumulative apical diameter growth for the control treatment after the study period was 0.96 cm, with a monthly average of 0.12 ± 0.02 cm (range: 0.06–0.17) (Table 1). The total cumulative growth of the transplantation treatment was 1.03 cm, with a monthly average of 0.13 ± 0.03 cm (range: 0.09–0.22). The annual growth of the apical diameter was 1.45 ± 0.67 cm·y^{-1} for the control treatment and 1.54 ± 0.40 cm·y^{-1} for the transplantation treatment.

The results of the apical diameter showed no significant differences between treatments ($F_{1,69}$ = 0.0641, $P >$ 0.801), over time (months; $F_{6,69}$ = 0.365, $P >$ 0.898), or in the interaction between variables ($F_{6,69}$ = 0.599, $P >$ 0.730) (Fig. 4). Apical diameter growth increased 23% for the control treatment and 24% for the transplantation treatment (Table 2).

Environmental variables

The monthly average of the sea surface temperature for PNAPM during the study period was 28.62 °C (25.95–30.56 °C) (Table 1), with the highest values during the months of August and September (~30.32 °C) and the lowest values in January and February (~26.21 °C). Irradiance remained at an average of 52,286 μmol·quanta·m^{-2}·d^{-1}, with the lowest values in November (42,145 μmol·quanta·m^{-2}·d^{-1}) and maximum values in August (60,112 μmol·quanta·m^{-2}·d^{-1}) (Table 1). August showed the highest values for temperature and light incidence; however, the results of the linear regression models showed no deterministic relationship (r^2) between the environmental variables, or with the linear extension ($P >$ 0.05), or with the apical diameter ($P >$ 0.05).

DISCUSSION

In corals, skeletal growth is controlled by various factors, such as salinity, nutrients, exposure to waves, sedimentation, aragonite saturation state, temperature, and light; the last 2 factors have the most influence (Nybakken 2001, Sheppard et al. 2009, Veron 2010, Calderón-Aguilera et al. 2017). In the case of light, it has been proposed that the average calcification rate and extension rate decrease proportionally as irradiance decreases with increasing depth (Dustan 1975, Bosscher 1993). Conversely, in shallow waters, irradiance can reach excessive energy levels and

Table 1. Growth variables (cm·month^{-1}) measured in *Orbicella faveolata* fragments for the transplantation and control treatments at 3-m depth and environmental variables measured in the *Arrecife de Puerto Morelos* National Park (PNANP, for its acronym in Spanish).

	Trasplantation		Control			
Month	Linear extension (cm)	Apical diameter (cm)	Linear extension (cm)	Apical diameter (cm)	Temperature (°C)	PAR (μmol·quanta·m^{-2}·d^{-1})
June	0.64 ± 0.67	0.15 ± 0.15	0.04 ± 0.05	0.06 ± 0.11	29.61 ± 1.09	52,539 ± 39,084
August	0.11 ± 0.09	0.18 ± 0.16	0.13 ± 0.10	0.12 ± 0.17	30.56 ± 1.10	60,112 ± 40,072
September	0.06 ± 0.07	0.09 ± 0.07	0.07 ± 0.05	0.17 ± 0.18	30.09 ± 0.97	54,275 ± 38,510
October	0.10 ± 0.07	0.17 ± 0.08	0.08 ± 0.07	0.14 ± 0.12	29.94 ± 0.88	54,513 ± 34,755
November	0.13 ± 0.14	0.09 ± 0.04	0.26 ± 0.24	0.14 ± 0.11	27.21 ± 0.87	42,145 ± 28,672
January	0.08 ± 0.10	0.10 ± 0.06	0.04 ± 0.01	0.16 ± 0.21	25.95 ± 1.15	42,612 ± 30,077
February	0.13 ± 0.09	0.22 ± 0.19	0.09 ± 0.06	0.15 ± 0.21	26.48 ± 1.10	52,144 ± 34,325

PAR: photosynthetically active radiation

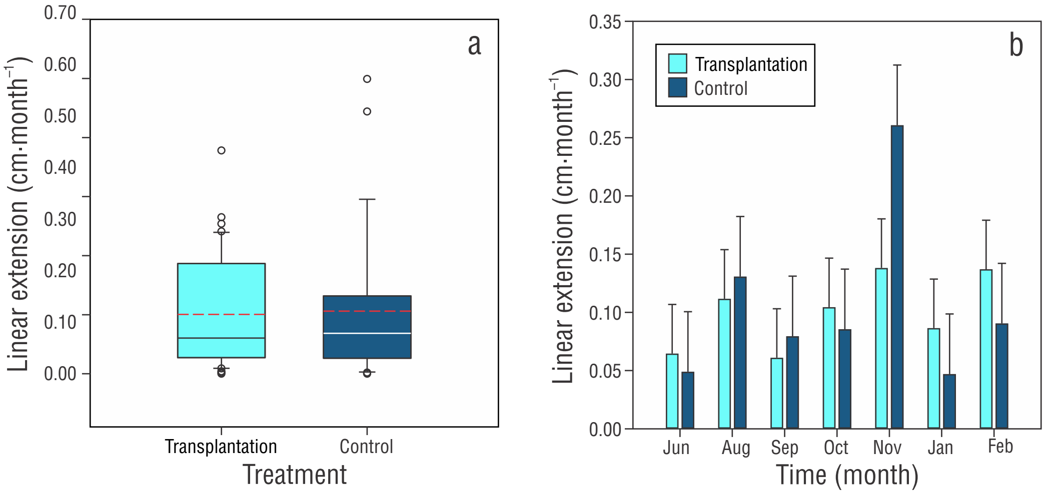

Figure 3. Boxplots of the average monthly growth of the linear extension (± SD) of *Orbicella faveolata* at 3-m depth over 9 months by (**a**) treatment (the black line represents the median, and the dashed red line denotes the mean) and (**b**) over time (months).

cause photodamage due to oxidative stress (increase in reactive oxygen species) that reduces the photosynthetic capacity of the symbiont algae (Todd et al. 2004, Rodríguez-Troncoso et al. 2014).

Previous studies focused on the relationship between coral morphology and light show that colonies modify their morphology to flatter shapes with increasing depth to increase their ability to capture light (Graus and Macintyre 1982, Willis 1987, Gutiérrez-Estrada 2017, Prada et al. 2022). Ow and Todd (2010) suggested that these morphological changes provide a long-term solution that requires less energy investment compared to the energy required for physiological adjustments.

The effect of light intensity on the characteristics and morphology of skeletal growth in hermatypic corals has been studied previously (Graus and Macintyre 1982, Hubbard and Scature 1985, Carricart-Ganivet et al. 2007, Todd 2008, Gutiérrez-Estrada 2017, Mallon et al. 2022). However, the effect of coral transplantation between depths with different environmental light conditions has been unexplored. This study shows a rapid response in the skeletal growth of the coral *O. faveolata* and its short-term physiological plasticity (1–9 months), which could be a mechanism to compensate the effects of transplantation between sites with different light gradients. Therefore, the coral *O. faveolata* shows physiological plasticity in the short-term that possibly entails morphotypic modification in the long-term (>1 year), which allows it to acclimate to new light environments.

Reports indicate that, in the Caribbean Sea, corals of the genus *Orbicella* are physiologically capable of living in shallow and deep habitats for at least 6 months after being transplanted (transplantation from shallow habitat to deep habitat and from deep habitat to shallow habitat) (Prada et al. 2022). This finding coincides with the results obtained in this study; *O. faveolata* showed physiological plasticity (in terms of growth) in response to changes in light and depth conditions. This could show that corals of the genus *Orbicella* have adapted to different light environments through an energy balance via autotrophy and heterotrophy in relation to light availability (Prada et al. 2022).

Our results demonstrated that the transplanted colonies quickly reached the growth rate of the control colonies and showed similar monthly growth during the 9-month period of the study. At 3 m depth, the annual linear extension for the control treatment and the transplantation treatment was 1.04 cm·y^{-1} and 1.11 cm·y^{-1}, respectively. These results contrast with the extension rate (0.80 cm·y^{-1}) reported for *O. faveolata* at 9 m depth in the Mexican Caribbean (Gutiérrez-Estrada 2017). A similar pattern has been reported in Florida (USA), where the linear extension of colonies in the shallow zone was higher than that of colonies in the deep zone (>6 m) during the same time period (Manzello et al. 2015). Gutiérrez-Estrada (2017) suggested that this could be due to the fact that skeletal extension depends on the number

Table 2. Increase in monthly growth percentage (%) for the linear extension and apical diameter variables in *Orbicella faveolata* fragments for the control and transplantation treatments at 3-m depth.

	Trasplantation		Control	
Month	Linear extension (cm)	Apical diameter (cm)	Linear extension (cm)	Apical diameter (cm)
June	1.37 ± 1.34	3.92 ± 3.92	1.38 ± 1.88	1.67 ± 2.84
August	2.44 ± 2.44	4.78 ± 4.70	3.50 ± 3.70	3.05 ± 4.36
September	1.16 ± 1.32	2.03 ± 1.82	1.78 ± 1.56	4.11 ± 4.33
October	2.34 ± 2.05	3.86 ± 1.90	2.08 ± 2.23	3.55 ± 3.62
November	2.54 ± 2.69	1.96 ± 0.99	4.70 ± 4.36	3.27 ± 2.72
January	2.08 ± 3.14	2.31 ± 1.60	0.88 ± 0.21	3.70 ± 5.07
February	3.07 ± 2.70	4.83 ± 4.38	1.81 ± 1.31	3.15 ± 4.23

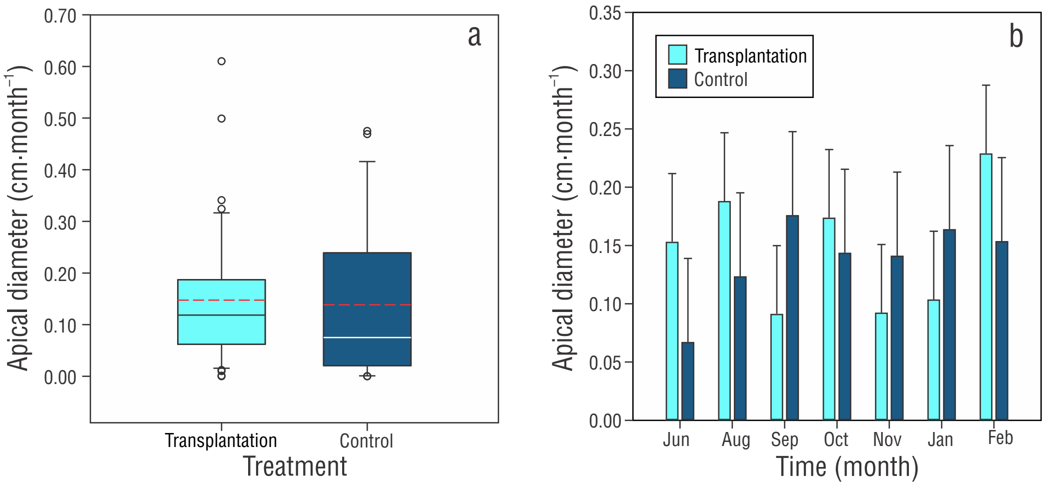

Figure 4. Boxplots of the average monthly growth of the apical diameter (± SD) of *Orbicella faveolata* at 3-m depth over 9 months by (**a**) treatment (the black line represents the median, and the dashed red line represents the mean) and (**b**) over time (months).

of exothecal dissepiments deposited per year, whereas density depends on their thickness, which are directly influenced by blue (lunar) light and conditions detected by corals at relatively shallow depths.

In light environments that facilitate optimal growth, massive colonies of *Porites* have been observed to exhibit higher growth in linear extension in contrast to colonies located in environments with high turbidity (Lough et al. 1999). Furthermore, reports indicate that colonies transplanted to shallower environments show increased lateral extension (diameter), which coincides with the results of the present study (Table 1). This could be explained by the size of the coral fragments (3–3.5 cm²), because, when a sexually mature colony fragments, the coral resources are allocated to growth and calcification processes instead of gametogenesis (Forsman et al. 2015). In this context, the transplant site and genotype of origin can influence calcification rates, resulting in an interaction effect between environmental and parental factors on the skeletal characteristics of massive corals (Smith et al. 2007). This could suggest that colony morphology varies depending on habitat, which results in high phenotypic plasticity in the skeletal characteristics of corals (Smith et al. 2007).

Previous reports with similar methodologies have found that coral species, such as *Turbinaria mesenterina*, found at depths of 1 m (shallow) and 4 m (deep) were able to adapt to the environmental conditions of both depths after transplantation; nevertheless, their growth was lower in the deep zone (Willis 1987). Other species of massive corals have shown similar patterns when transplanted to different environments. For example, Ow and Todd (2010) found higher growth in *Goniastrea pectinata* colonies transplanted to a depth of 7 m in contrast to the growth of colonies transplanted to a depth of 3 m after a short period (163 days). This could be explained by the high phenotypic plasticity and photo adaptive response to light irradiance of some genera of massive corals, such as *Porites* and *Orbicella*, which allow them to distribute over a depth light gradient (Smith et al. 2007, Todd 2008).

CONCLUSIONS

The results indicate that there were no significant differences in the linear extension or apical diameter between treatments and time periods (months). Therefore, the coral *O. faveolata* has the potential to acclimate to new environmental light conditions after being transplanted from a deep environment to a shallow environment in a short period of time. Furthermore, we suggest that transplanted colonies can achieve growth rates similar to those of control colonies relatively fast (1–9 months), which demonstrates phenotypic plasticity to changes in their light environment. Focusing on the lateral extension of the colonies, we observed a higher increase in diameter compared to the linear extension in both treatments; therefore, we can conclude that the colonies of both treatments used the available resources to repair the periphery damage caused by fragmentation.

However, the study period was relatively short to determine if the short-term response will be beneficial in the long term or if the survival and health of the colony will be compromised in the future. Therefore, we suggest conducting similar studies that consider long-term time periods (>9 months). The information from this study reveals that *O. faveolata* colonies transplanted from a deep to a shallow environment have the potential to acclimate to new light conditions in a short period of time.

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DECLARATIONS

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Conceptualization: GGE, JJATL, and JPCG; Data curation: JLJ; Formal analysis: JJATL and JLJ; Funding acquisition: JPCG; Methodology: GGE, JJATL; Software: JLJ and JJATL; Supervision: JJATL and JPCG; Validation: GGE, JJATL, and JPCG; Visualization: JLJ and JJATL; Writing—original draft: JLJ and JJATL; Writing—review and editing: JLJ, JJATL, GGE, and JPCG.

Data availability

The data for this study are available from the corresponding author upon reasonable request.

Use of AI tools

The authors did not use any artificial intelligence tools for this work.

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SPECIAL ISSUE
Research Note

Updating the understanding of lesser-known coral systems in the southern Mexican Pacific

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Abstract. Puerto Ángel (PA), Puerto Escondido (PE), and Punta Maldonado (PM) harbor coral ecosystems in the southern Mexican Pacific (SMP); however, they are among the least prospected and evaluated ecosystems. This work provides an inventory of coral species and contributes to the characterization of these systems for these areas. From 2009 to 2023, 15 sites (PA = 9; PE = 4; PM = 2) were prospected by roving survey dives and point-intercept transects, both performed by SCUBA divers and by remotely operated underwater vehicles. A total of 10 coral species (PA = 10; PE = 5; PM = 2) belonging to the genera *Pocillopora* (shallow water; <30 m depth), *Pavona*, and *Porites* (<37 m depth) were recorded. For the first time in PM, corals were recorded in deep waters (<37 m depth) and far from the coastline, which is uncommon for SMP systems. This may be due to the wider boundary of the mesophotic zone and the anomalous and extensive continental shelf formed by geological processes. Puerto Ángel had higher coral cover (30.2% ± 21.9) compared to that of PE (6.6% ± 8.7), which was dominated by rocky substrate. These percentages are lower than those reported for other regions of the SMP and are a consequence of the geomorphological characteristics of the areas, but they are mainly due to the anthropogenic disturbances they have experienced over time, such as changes in land use and the extraction of coral colonies for souvenir markets.

Key words: substrate characteristics, cover, coral, Puerto Ángel, Puerto Escondido, Punta Maldonado, Mexican Pacific, records, mesophotic zone.

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Introduction

Coral ecosystems of the southern Mexican Pacific (SMP) play a relevant role in the dispersal of organisms and in maintaining the connectivity of systems located in the central and southern portion of the eastern Pacific (Lequeux et al. 2018). Due to their extension and degree of development, the most important systems are in the areas of Ixtapa-Zihuatanejo, in the state of Guerrero, and Huatulco, in the state of Oaxaca (Glynn and Leyte-Morales 1997, López-Pérez et al. 2012). These systems have been the most studied and characterized; however, despite their great importance for regional biodiversity, other surrounding systems have been overlooked and have been scarcely explored or remain unvisited (Glynn and Leyte-Morales 1997, López-Pérez et al. 2012, Granja-Fernández et al. 2023).

In the SMP, few studies exist on the areas around Puerto Ángel and Puerto Escondido in Oaxaca, and the area around Punta Maldonado in Guerrero. However, during surveys carried out in the last century (Palmer 1928, Durham 1947, Durham and Barnard 1952, Geister 1977, Leyte-Morales 1997, Reyes-Bonilla and Leyte-Morales 1998), some coral species were recorded for a few sites in Puerto Escondido (e.g., Puerto Angelito) and Puerto Ángel (e.g., Panteones, La Guacha, and Estacahuite). Conversely, the presence of corals at Punta Maldonado has never been documented. Despite this, the relevance of these 3 areas is such that new species of fossil corals have been found and described, even in surrounding land areas (Palmer 1928, Durham 1947, Gío-Argaez et al. 2019).

Previous studies have provided information on species composition for only a few sites, but these included no data on the substrate characteristics of the coral ecosystems of these 3 areas, except the research by Reyes-Bonilla and Leyte-Morales (1998) at Puerto Ángel. Therefore, this work contributes to the knowledge of these SMP coral systems, as it provides records of coral species for a greater number of sampling sites, documents coral records for Punta Maldonado for the first time, and contributes to the characterization of sites with coral systems in Puerto Escondido and Puerto Ángel. This information is relevant to these scarcely studied areas. Furthermore, these areas are experiencing accelerated and constant anthropogenic and environmental changes associated with coastal development, and they are subject to regional interannual events, such as the El Niño-Southern Oscillation phenomenon, and large-scale processes, such as climate change.

Materials and methods

This study included 3 SMP areas with coral systems: Punta Maldonado (Guerrero), Puerto Escondido (Oaxaca), and Puerto Ángel (Oaxaca) (Fig. 1). Due to environmental conditions, the region is commonly described as a “warm pool” of the Eastern Tropical Pacific (ETP), characterized by warm, low-salinity surface waters that lay above a strong, shallow thermocline (Fiedler and Lavin 2017). The region extends across the tectonic boundary of an active convergent margin characterized by the subduction of the Cocos and the Rivera plates beneath the North American plate (Ramírez-Herrera and Urrutia-Fucugauchi 1999). As a consequence of tectonic activity, the continental shelf is very narrow; however, Punta Maldonado shows an anomalous widening of the platform known as Tartar Shoal, delimited by the Quetzala submarine canyon (Carranza-Edwards et al. 2005).

Between 2009 and 2023, coral ecosystems were surveyed and characterized intermittently using various methods: (1) 20 m intercept point transects (data obtained every 20 cm) to record the type of substrate (i.e., live coral, dead coral, rock, sand, or algae) using scuba diving equipment, (2) visual survey by roving survey dives using scuba diving equipment, and (3) roving navigation using remotely operated underwater vehicle (ROV) (BlueROV2, Blue Robotics, St. Torrence, USA; BLUEROV, Hamburg, Germany; Fifish V6, QYSEA, Shenzhen, China). In each case, the technique and number of sampling units depended on the dimensions and depth of the site and the climatic conditions at the time of the survey, so sampling periods varied between sites. The sampling techniques used at each site are listed in Table 1.

Substrate types at the sampling sites were graphically explored with a principal coordinate analysis (PCoA) based on a Bray–Curtis similarity matrix constructed with substrate type composition and coverage data; data were transformed using square root to reduce the overrepresentation (dominance) of any type of substrate. The ordination included the vectors of each type of substrate, where the length and direction of the vector indicate the relative importance of each variable in the ordination. Only those variables with a Pearson correlation > 0.7 were included in the ordination (Anderson et al. 2008). Spatial variation of substrate type was assessed using a multiscale model of a nested 2-way permutational multivariate analysis of variance (PERMANOVA) (fixed effect factor: area; random effect factor: sites nested in areas; type III model):

$$Y = \mu + area_i + site_j\,(area_i) + \varepsilon_{ij} \quad , \qquad (1)$$

where Y is the response variable, μ is the mean, and εij is the accumulated error. The PERMANOVA was done using data of the composition and coverage of substrate types; the data were transformed using the square root to reduce the relative importance of extreme data and subsequently obtain a Bray–Curtis matrix. Statistical significance of PERMANOVA was determined with 10,000 permutations of residuals under a reduced model and type III sum of squares (Anderson et al. 2008). The PCoA and PERMANOVA were performed using PRIMER 6 and PERMANOVA+ (Anderson et al. 2008).

Results

In total, 15 sites from 3 areas (Punta Maldonado [2 sites], Puerto Escondido [4 sites], and Puerto Ángel [9 sites])

(Table 1) were surveyed. Within these areas, the presence of 10 of stony coral species corresponding to the genera *Pavona*, *Pocillopora*, and *Porites* was recorded. The species *Porites panamensis* (14 sites), *Pavona gigantea* (11 sites), and *Pocillopora capitata* (10 sites) were observed in the greatest number of sites; conversely, *Pavona clavus* and *Pocillopora effusa* were recorded at a single site (Table 1).

The colonies recorded during the surveys in the Punta Maldonado area showed the presence of only 2 species of stony corals: *P. panamensis* and *P. gigantea*. In the Puerto Escondido area, 5 species were recorded; sites El Faro and Zapatito had the lowest richness (2 species), whereas Puerto Angelito had the highest richness (4 species). Of the 3 study areas, Puerto Ángel had the highest richness of stony corals (10 species). In this area, site La Tijera had the highest richness (10 species), whereas site Puerto Angelito had the lowest richness (4 species).

The Puerto Ángel area had the shallowest coral ecosystems (4–12 m), followed by Puerto Escondido (9.5–20 m), and, finally, Punta Maldonado (12–37 m). The depth range at Punta Maldonado limited substrate evaluation in this area; therefore, only the areas of Puerto Escondido and Puerto Ángel were evaluated. Live coral cover (mean ± SD) was relatively low at sites in the Puerto Escondido area (6.6% ± 8.7, $n = 36$) compared to those at sites located in the Puerto Ángel area (30.2% ± 21.9, $n = 48$) (Pseudo-$F_{(1,\ 82)} = 37$, $P < 0.001$). This pattern coincides with what was observed for algal cover (low values in the Puerto Escondido area and high values in the Puerto Ángel area) (Pseudo-$F_{(1,82)} = 19.9$, $P < 0.001$). Rock cover showed an inverse behavior (Puerto Escondido:

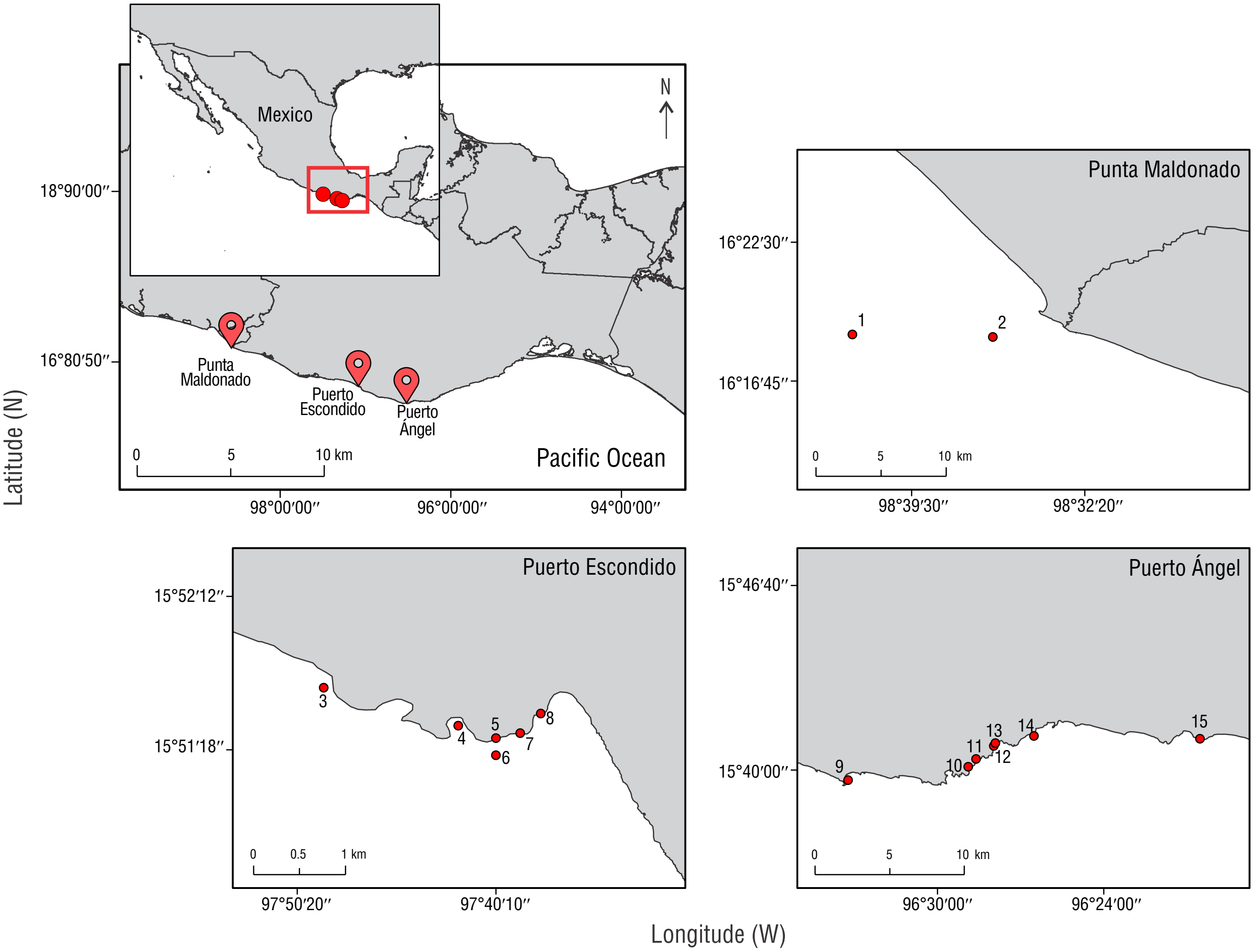

Figure 1. Map of sampling sites in the southern Mexican Pacific (SMP) region. Red markers denote the study areas of Punta Maldonado, Puerto Escondido, and Puerto Ángel. The red dots denote the sampling sites with coral systems: 1 (Las 24), 2 (Altura Baja), 3 (Bachoco), 4 (Carrizalillo), 5 (Puerto Angelito), 6 (El Faro), 7 (Zapatito), 8 (Puerto Escondido), 9 (Mazunte), 10 (Playa del Muerto), 11 (Estacahuite), 12 (La Mina), 13 (Boquilla), 14 (Tijera), and 15 (Salchi).

Table 1. Composition of stony corals by site and area in coral systems of the southern Mexican Pacific. The values in the table indicate presence.

	1^{c}	$2^{b,c}$	$3^{a,*}$	$4^{a,b}$	$5^{a,b}$	$6^{a,b}$	$7^{a,b}$	$8^{a,b,*}$	$9^{a,b}$	$10^{a,b}$	$11^{a,b}$	$12^{a,b}$	$13^{a,b}$	$14^{a,b}$	$15^{a,b}$
Pavona clavus														1	
Pavona gigantea	1			1	1	1	1			1	1	1	1	1	
Pocillopora capitata					1				1	1	1	1	1	1	1
Pocillopora damicornis				1					1	1	1	1	1	1	1
Pocillopora effusa									1					1	1
Pocillopora elegans														1	
Pocillopora grandis									1		1		1	1	1
Pocillopora meandrina									1		1			1	1
Pocillopora verrucosa					1				1	1	1	1	1	1	1
Porites panamensis	1	1		1	1	1	1		1	1	1	1	1	1	

Punta Maldonado: 1 (Las 24), 2 (Altura Baja), 3 (Bachoco), 4 (Carrizalillo), 5 (Puerto Angelito), 6 (El Faro), 7 (Zapatito), 8 (Puerto Escondido), 9 (Mazunte), 10 (Playa del Muerto), 11 (Estacahuite), 12 (La Mina), 13 (Boquilla), 14 (Tijera), and 15 (Salchi).
Sampling technique: a = transect SCUBA; b = roving survey dives SCUBA; c = roving survey ROV.
*No reef-building corals were recorded; only dead coral was recorded.

68.4% ± 18.6; Puerto Ángel: 27.9% ± 35.8; Pseudo-$F_{(1, 82)} = 37.9$, $P < 0.001$) (Fig. 2).

The first component of the PCoA ordination (Fig. 3) explained 68.4% of the variation, whereas the second component explained 24%, indicating that almost all of the variation (92.4%) among the sampling sites was explained by the analysis. The ordination showed wide variation between the sites in the Puerto Ángel area compared to sites in the Puerto Escondido area. According to the ordination, sites in the Puerto Escondido area are predominantly rocky reefs, whereas sites in the Puerto Ángel area have an important coral contribution. This is evidenced by the PERMANOVA results, which indicated significant differences between areas (Pseudo-$F_{(1,71)} = 12.8$, $P = 0.0003$) and between sites (Pseudo-$F_{(11,71)} = 3$, $P = 0.0002$).

Discussion

The results of the present study for the areas of Punta Maldonado, Puerto Escondido, and Puerto Ángel add to previous records of corals and to the characterization of the coral ecosystems of Ixtapa-Zihuatanejo, Acapulco, and Huatulco in SMP (Glynn y Leyte-Morales 1997; Leyte-Morales 1997; Reyes-Bonilla y Leyte-Morales 1998; López-Pérez et al. 2012, 2019). In particular, the survey and evaluation of Punta Maldonado and Puerto Escondido are relevant because they are the first in both areas.

On the continental part, between the entrance of the Gulf of California and Oaxaca, 25 species of zooxanthellate corals have been recorded, of which 17 correspond to the SMP (13 in Guerrero and 16 in Oaxaca) (Reyes-Bonilla et al. 2010, López-Pérez et al. 2012). The results showed that the species composition in the explored areas represents a subsample of the composition previously recorded in the states of Guerrero and Oaxaca. Despite this, the following 7 species that have been previously recorded in the 2 states were not sighted during our surveys: *Cycloseris distorta*, *Gardineroseris planulata*, *Leptoseris papyracea*, *Pavona varians*, *Pocillopora inflata*, *Porites lobata*, and *Psammocora stellata* (Glynn and Leyte-Morales 1997, Leyte-Morales et al. 2001, Reyes-Bonilla et al. 2005, López-Pérez et al. 2012). Carrying out more detailed surveys in the region will contribute to increasing the number of records of common species, such as *P. varians*, for which low cover has been observed in some sites in Ixtapa and Huatulco (López-Pérez et al. 2012, 2014). However, future surveys will struggle to increase the records for species rarely observed in the region, such as *C. distorta*, *G. planulata*, *L. papyracea*, *P. inflata*, *P. lobata*, and *P. stellata*; these have low populations and their records are largely restricted to the Gulf of California, the central and southern Mexican Pacific, and Central America (Leyte-Morales et al. 2001, Cortés and Jiménez 2003, Reyes-Bonilla et al. 2005, López-Pérez et al. 2012).

The continental coral ecosystems of the ETP are mainly characterized by the dominance of *Pocillopora* that typically occurs at shallow depths (0–8 m); however, *Pavona* and *Porites* can be found at greater depths (10–30 m) in more exposed areas and with oligotrophic characteristics, such as oceanic islands

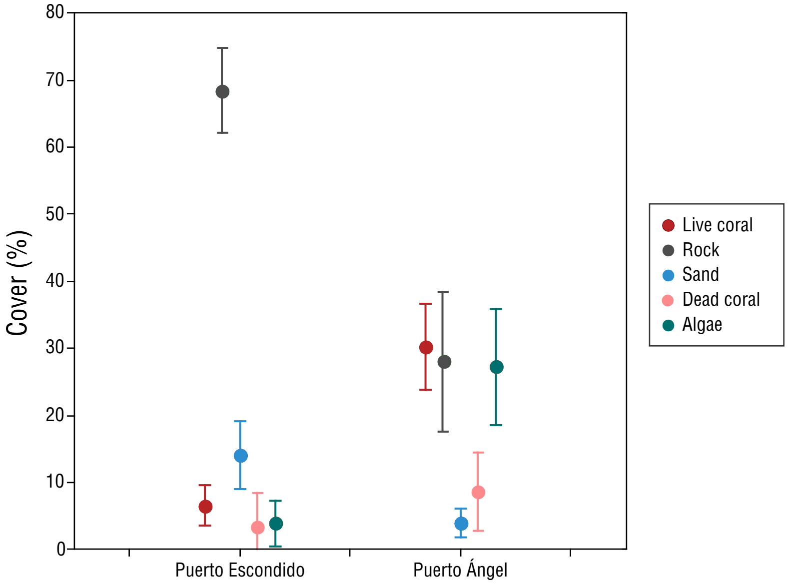

Figure 2. Substrate cover (%) in the study areas of Puerto Escondido and Puerto Ángel in the southern Mexican Pacific (SMP). Data represent the mean ± standard deviation.

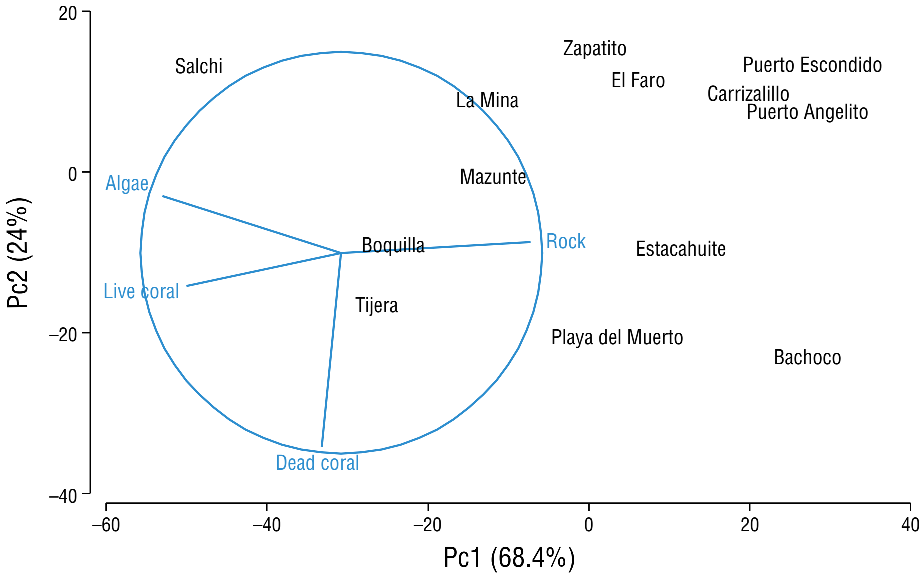

Figure 3. Ordination of the sampling sites in the study areas of Puerto Escondido (Bachoco, Carrizalillo, Puerto Angelito, El Faro, Zapatito, and Puerto Escondido) and Puerto Ángel (Mazunte, Playa del Muerto, Estacahuite, La Mina, Boquilla, Tijera, and Salchi) in the southern Mexican Pacific (SMP), depending on the type of substrate, based on the analysis of principal coordinates. On the right side are the sampling sites of the Puerto Escondido area and on the left side are the sampling sites of the Puerto Ángel area. According to the vectors, to the right side of the arrangement are the sites with significant rock cover, whereas on the left side are the sites with predominant live coral cover. In the lower portion of the ordination are the sites with a relatively high dead coral cover.

(Glynn et al. 2017). In the areas of Puerto Escondido and Puerto Ángel, sites with coral were distributed within the bathymetric ranges commonly recorded in the area and the ETP (i.e., <30 m depth) (Pérez-Castro et al. 2022). On the other hand, the shallow coastal strip of Punta Maldonado shows sandy beaches with great wave energy, where corals were detected at unusual depths (34–37 m) for the coastal areas of the Mexican Pacific (Glynn et al. 2017, Pérez-Castro et al. 2022), highlighting the presence of *P. gigantea* and *P. panamensis*, as well as the absence of the genus *Pocillopora*. In terms of depth, these species records at Punta Maldonado exceed the deepest records for the surrounding continental areas (Puerto Ángel) (Pérez-Castro et al. 2023), but add to the records of corals in oceanic sites of the Eastern Pacific (Pérez-Castro et al. 2022).

The presence of *P. gigantea* and *P. panamensis* in relatively deep sites in the Punta Maldonado area could be due to the characteristics of the seawater and the presence of specific symbionts. According to the depth and spatial location of the records, the seawater in the Punta Maldonado area could be classified as Type I Turbid Water, for which the upper limit of the mesophotic zone is 15–35 m, whereas the lower limit is 36–60 m (Table 1 in Pérez-Castro et al. 2022). Regarding the type of symbiont, the presence of corals fits the predictions made by Iglesias-Prieto et al. (2004), who indicated that the presence of specific symbionts, adapted to different light regimes, determines the vertical distribution of host corals. Particularly, the presence of *P. gigantea* could be related to the photo-physiological performance of symbionts adapted to penumbra; that is, *P. gigantea* "does not like light."

Another characteristic that draws attention is that, unlike the coral systems of the SMP located near the coastline, those of Punta Maldonado are up to 10 km offshore. This region has an anomalous widening of its continental shelf, known as Tartar Shoal, which promotes a wide extension of shallow waters, where coralline algae and rock fragments predominate (Carranza-Edwards et al. 2005). Therefore, Punta Maldonado is a viable area for the establishment of coral.

Due to the great depth and wide continental shelf of Punta Maldonado, only ROV surveys were possible. The use of this technique resulted in the discovery of a large number of sites with substrates that could host reef-building corals. Nevertheless, further surveys are needed; these could result in records of a greater number of species, including *Pocillopora* spp., in shallower sites. In addition to the marine area, terrestrial surveying is necessary, since some fossil corals from the Pliocene have been found in the Punta Maldonado Formation (Gío-Argaez et al. 2019). The results of such surveys could help understand and reconstruct the evolutionary history of corals in the region.

Due to their relatively shallow depths, it was possible to use transects to evaluate the Puerto Ángel and Puerto Escondido areas. The differing substrate cover reflects 2 stories in the surveyed area. In the Puerto Escondido area, coral cover (~7%) was consistently low across sites, whereas rock cover was relatively high (~68%). The opposite was observed in the Puerto Ángel area, where coral cover was 5 times higher and rock cover was comparatively low. Compared to the coral ecosystem cover in the areas of Ixtapa-Zihuatanejo (Guerrero) and Huatulco (Oaxaca), the recorded coral cover was substantively lower (Glynn and Leyte-Morales 1997, López-Pérez et al. 2012).

All coral ecosystems in this work are located within the warm water pool of the ETP, so the corals develop under similar environmental characteristics (Fiedler and Lavin 2017). Thus, the differences in the seafloor and the degree of development between coral systems could be related to the geomorphological and oceanographic characteristics of each area or site, such as platform extension, depth, wave intensity and direction, beach orientation with respect to wind direction, and the main currents (Kench and Brander 2006).

Areas, sites, and, consequently, coral systems have historically experienced different types and degrees of anthropogenic disturbance concurrently. For example, while Puerto Escondido and Puerto Ángel were founded in the late 1800s and early 1900s, their population growth has been uneven. Currently, Puerto Escondido is one of the most populated areas on the coast of Oaxaca (INEGI 2020). Associated with this, the deforestation and degradation of forests and jungles have been uneven, although proportional to the population increase (Leija-Loredo et al. 2016). At the same time, oral stories indicate that boats loaded to the gunwale arrived in Acapulco (Guerrero) to sell keepsakes derived from coral in souvenir markets. The demand in souvenir markets for coral keepsakes, associated with the development of the port of Acapulco, exhausted the coral systems surrounding the port. Such practices apparently ended during the late 1980s; nevertheless, the degradation was devastating.

Since then, coral systems at Puerto Escondido have not recovered and there are still patches of dead coral dotted with *Pocillopora* colonies. There are no records of the extraction of corals for souvenir markets in the Puerto Ángel area. However, the extensive change in land use in the area has the potential to contribute large amounts of terrigenous sediments and nutrients to adjacent coral ecosystems, as has been reported for Huatulco systems (Granja-Fernández and López-Pérez 2008, Leija-Loredo et al. 2016).

Conclusions

Knowledge of SMP coral ecosystems has focused on studies of areas that are large, easily accessible, and with evident coral cover. However, it is important to maximize efforts to increase information and maintain constant monitoring in regions that are relatively less extensive (Puerto Ángel), remote and difficult to access (Punta Maldonado), or degraded (Puerto Escondido). After the heat wave recorded during 2023, there is strong evidence of massive coral mortality in Huatulco, and reports indicate that mortality in the Ixtapa-Zihuatanejo area was considerable (López-Pérez et al. 2024, Reimer et al. al. 2024). Assuming that the heat wave caused equally severe damage to coral systems in all 3 study areas, the presence of mesoscale corals is currently severely compromised. Not only could millions of coral colonies have been lost, but this loss could severely undermine the current functioning of the coral ecosystems in the region and their future recovery, as these areas could function as sources of larvae and recruits for the connected communities (Lequeux et al. 2018).

English translation by Claudia Michel-Villalobos.

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Conflict of interests

The authors declare that they have no conflict of interest.

Author contributions

Conceptualization: ALP, RGF; Data curation: ALP, RGF, OVM, TGM, ERC, FARZ; Formal analysis: ALP; Acquisition of financing: ALP, LECA; Research: ALP, RGF, ERC, APM, DLL, LECA; Methodology: ALP, RGF, ERC; Project management: ALP, LECA; Resources: ALP, ERC, LECA; Writing—original draft: ALP, RGF; Writing—review and editing: ALP, RGF, OVM, TGM, ERC, APM, DLL, LECA, FARZ.

Data availability

Data for this study may be obtained from the corresponding author upon reasonable request.

Use of AI tools

The authors did not use any artificial intelligence tools for this work.

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Research Note

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Fluctuations in immune response (phenol oxidase activity) related to circadian and lunar cycles in the symbiotic anemone *Exaiptasia diaphana* (Actinaria: Aiptasiidae)

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ABSTRACT. The immune capacity of cnidarians allows them to maintain the integrity of their tissues and prevent infections when facing threats of damage. Cnidarians have an innate immune system that includes melanin and enzymes, like phenol oxidase, that is activated in the presence of pathogens and generates reactive and toxic compounds for their elimination. The anemone *Exaiptasia diaphana* is a model organism for symbiosis, nutrition, and immune studies, as it maintains a facultative symbiosis with microalgae of the Symbiodiniaceae family, like corals; *E. diaphana* can also exist in an aposymbiotic state. Therefore, *E. diaphana* is a suitable model to study the cnidarian immune system. To learn about the basic immune activity of this anemone, we asked ourselves if it exhibited variability in its immune activity throughout the day, considering 2 lunar phases (full moon and new moon). Mucus samples were taken from 6 symbiotic and 6 aposymbiotic anemones, which were previously acclimatized and maintained in 6-well plates with filtered seawater under natural light conditions. Phenol oxidase activity was estimated every 6 h for 48 h, with 2 repetitions for each moon phase. Phenol oxidase activity was highest at 14:00 h, whereas nocturnal activity was low. Enzyme activity increased under the full moon in aposymbiotic anemones ($H = 17.47$, $P = 0.0005$). We found a negative relationship between symbiont density and phenol oxidase activity ($R^2 = 0.05$, $P = 0.04$). These results allow us to suggest that this anemone can maintain a constant constitutive immunity under laboratory conditions, which responds to biological cycles such as circadian and moon cycles.

Key words: constitutive immunity, mucus, lunar phases, symbiosis, circadian cycle, symbiotic anemone, phenol oxidase, cnidarian.

INTRODUCTION

Exaiptasia diaphana is a symbiotic anemone and a model organism to study various processes in cnidarians such as symbiosis, nutrition, and immunological mechanisms (Lehnert et al. 2012, Matthews et al. 2017, Rädecker et al. 2018, Mansfield and Gilmore 2019, Dungan et al. 2020). This anemone maintains a facultative symbiosis with microalgae of the Symbiodiniaceae family (Weis et al. 2008). Cnidarians exhibit nocturnal behavior (Lewis and Price 1975, Sebens and De Riemer 1977) and establish symbiosis with microalgae, which represents a challenge for the study of basal parameters, since both are governed by different biological rhythms (Sorek et al. 2014). Biological rhythms allow organisms to anticipate and adapt to natural environmental changes (Roenneberg and Merrow 2005, Bednářová et al. 2013). Symbiotic cnidarians exhibit heterotrophic feeding habits at night (Lewis and Price 1975) and use the energy provided by their endosymbiont algae during the day; this complicates the study of their rhythmic behavior. Furthermore, they show differential behavior during the day and night; for example, non-symbiotic anemones lose their circadian rhythm when kept under constant light or darkness (Aguillon et al. 2024). In symbiotic organisms, the tentacles of anemones and the corals that allow them to feed expand at night, whereas those with a higher density of symbionts expand during the day (Sebens and De Riemer 1977).

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Lunar cycles are important for the reproduction of marine animals (Raible et al. 2017). In corals, lunar cycles regulate spawning (Harrison et al. 1984), although factors such as temperature can modify this process (Lin and Nozawa 2023). In addition, they have a correlation with the deposition of calcareous structures called dissepiments and with the growth of the calcareous skeleton of coral colonies (Winter and Sammarco).

Biological rhythms are key in controlling physiology and, therefore, the immune system (Fagiani et al. 2022). In mammals, studies have found that the circadian cycle is related to the migration of cells of the innate immune system and changes in the expression of immune molecules (Reviewed in Scheiermann et al. 2013). Furthermore, when organisms face an immunological challenge, they respond best in their active phase (Reviewed in Westwood et al. 2019). In cnidarians, the relationship between biological rhythms and the immune system has not yet been studied.

As in other invertebrates, cnidarians have an innate immune system whose function is to maintain the health of the animal (Palmer 2018). An immunological pathway commonly used by invertebrates is the proPO system, or the phenol oxidase (PO) pathway (Cerenius et al. 2008). The proPO system is activated by proteins capable of binding to peptidoglycans and lipopolysaccharides in various invertebrates, such as insects (Zhao et al. 2018), crustaceans (Liu et al. 2011), and cnidarians (Lehnert et al. 2012). Once activated, it generates cytotoxic free radicals, binding agents, and opsonin, which protect the animal without synthesizing melanin (Zhao et al. 2007, Cerenius and Söderhäll 2021). The synthesis of melanin as a final product, known as melanization, encapsulates potentially harmful microorganisms (Zhao et al. 2007, Cerenius et al. 2008). For example, Palmer et al. (2010) showed that after damage, melanin deposits appear in some corals almost instantaneously.

In some cnidarians, PO has been studied as a response to various diseases and bleaching (Mydlarz et al. 2009, Palmer et al. 2010, Rivera-Ortega and Thomé 2018). However, the study of the basal immune response and its relationship with biological rhythms has not been considered. Studying the immune response under basal conditions is important since biological processes in any living organism alternate between periods of high, low, or no activity (Cardinali 2005). Therefore, our aim was to characterize the fluctuation of PO in healthy *E. diaphana* individuals, both symbiotic and aposymbiotic, throughout the day and during the phases of full moon and new moon. In addition, to understand whether symbionts affect the immune response, PO fluctuations were compared in both symbiotic and aposymbiotic *E. diaphana*.

MATERIALS AND METHODS

Experimental design

To explore whether biological cycles influence the immune response, the experiments were done at different times throughout the day and during 2 lunar phases (full moon and new moon) using 6 symbiotic anemones and 6 aposymbiotic anemones. In each lunar phase, mucus was collected every 6 h in 2 cycles per 24 h; during the first cycle, samples were taken at 8:00 p.m., 2:00 a.m., 8:00 a.m., and 2:00 p.m. The next day, measurements of the second cycle were resumed at 2:00 p.m., 8:00 p.m., 2:00 a.m., and 8:00 a.m. Mucus extracted from the 6 symbiotic anemones and 6 aposymbiotic anemones ($n = 48$) was grouped in duplicate per lunar phase and per symbiotic state. In total, 348 anemones were used. The experiment was carried out from September to November 2023.

To determine symbiont density, 6 symbiotic anemones were used per hour of sampling. This experiment was done in a cycle for each lunar phase. In total, 48 anemones were used.

Organisms

The symbiotic anemones were collected from the aquariums of the *Unidad Académica de Sistemas Arrecifales* (*Instituto de Ciencias de Mar y Limnología, Universidad Nacional Autónoma de México*), where they grew under natural conditions. The aposymbiotic anemones came from a laboratory culture of several years. After their collection, the anemones were acclimatized for 14 d to avoid the aquarium effect. Subsequently, anemones were maintained individually in 6-well plates with filtered seawater (0.22 µm) under a light/dark regime (full moon = 67.9–985 lux; new moon = 67.4–838 lux) and at natural temperature (full moon = 28.87–29.60 °C; new moon = 28.47–29.48 °C) in a humid windowless laboratory. Anemones were fed once a week with nauplii of *Artemia* spp.

Mucus extraction

Mucus was extracted from anemones exhibiting extended tentacles and column. Before extraction, the water was completely removed from each well with a disinfected transfer pipette, wiping off the remaining water with a sterilized cotton swab. The mucus expelled by the anemone after 2 min was collected with a micropipette and stored in individual microtubes. Finally, 10 mL of filtered seawater was added to each well.

Evaluation of the immune response

To determine the basal immune response in *E. diaphana*, mucus PO activity was measured. We used 96-well plates in 90-µL reactions in triplicate, as described below. Each well contained 30 µL of mucus ($n = 6$ anemones) and 30 µL of pyrogen-free water. Subsequently, the plate was covered with aluminum and incubated for 5 min at 35 °C with shaking (60 rpm). The reaction was started by adding 30 µL of L-Dopa substrate [2.5 mM]; measurements were immediately taken in a plate reader. The absorbance reading was performed at

450 nm every minute for 10 min. The activity of PO is presented as the change in absorbance per microliter of mucus per minute.

Symbiont density

To count symbionts, the anemones were weighed and placed in microtubes with 500 µL of filtered seawater. They were homogenized manually with a plastic homogenizer until no tissue was visible. Symbionts were purified by 3 centrifugation cycles (14,000 rpm) for 1 min. They were resuspended in 500 µL of filtered seawater and fixed by adding lugol (30%). Algae were counted in a hemocytometer and calculated per milliliter. The total cell number count per anemone was normalized to grams of wet weight.

Statistical analysis

Data normality and homoscedasticity were evaluated with the Shapiro–Wilks and Levene tests, respectively. Because the data did not meet the assumptions, nonparametric statistical tests were used. To compare PO activity with the interaction between the moon and symbiotic state, the Kruskal–Wallis test and post hoc Mann–Whitney tests were used. A Pearson correlation was applied between PO activity and symbiont density. Statistical analyses were performed in RStudio v. 4.1.0 (Posit Team 2024).

RESULTS

Immune response

Circadian cycle

The activity of PO in both symbiotic and aposymbiotic anemones showed natural variability throughout the day, with 2 acrophases. The highest peak of activity was at 2:00 p.m., with symbiotic anemones at full moon showing lower PO activity compared to aposymbiotic anemones. A second smaller, but equally represented, peak was detected at 2:00 h (Fig. 1). Despite showing some biological variability, data showed no statistically significant differences (H [7] = 7.09, $P = 0.41$) throughout the day.

Lunar cycle

The analysis of PO activity, measured as the interaction between the lunar phase and the symbiotic state, showed statistically significant differences (H [15] = 17.47, $P = 0.0005$). According to the post hoc analysis, PO activity in aposymbiotic anemones was found to be significantly higher at full moon than at new moon and higher than in symbiotic anemones for both moons ($P < 0.05$). Furthermore, PO activity in symbiotic anemones at full moon was significantly higher than that observed in aposymbiotic anemones at new moon ($P = 0.032$) (Fig. 2).

Symbiont density

We found a negative relationship between PO activity and symbiont density in symbiotic anemones ($R^2 = 0.51$, $P = 0.04$) (Fig. 3). Furthermore, symbiont density varied significantly depending on the time of day (H [3] = 8.55, $P = 0.035$). According to the post hoc analysis, symbiont density was significantly higher at 14:00 h ($P = 0.006$, Fig. 4a). Taking into account the lunar phase, we found that symbiont density was similar for both the full moon (H [3] = 4.84, $P = 0.18$) and the new moon (H [3] = 4.32, $P = 0.22$) (Fig .4b).

DISCUSSION

In this study, PO activity was measured in the mucus of *E. diaphana* under basal conditions. We determined that both symbiotic and aposymbiotic anemones show PO activity throughout the day. Therefore, *E. diaphana* shows constitutive immunity, and the proPO system is part of its basal immunity. The above agrees with what was proposed by Palmer (2018), who suggests that, though immunity is commonly approached as a response activated by damage signals,

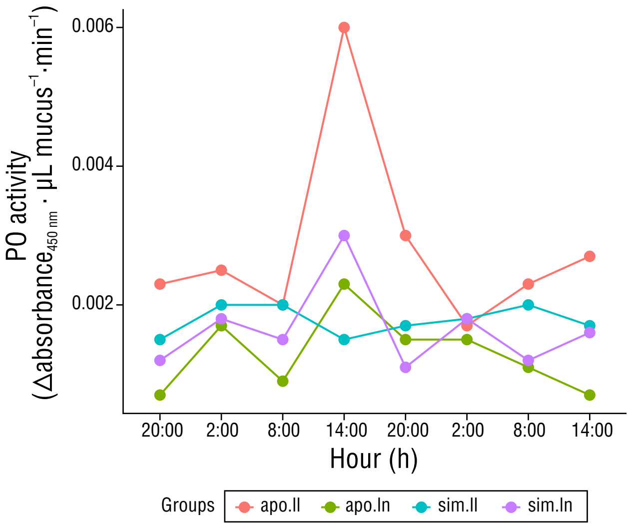

Figure 1. Variation of phenol oxidase (PO) activity during the day in *Exaiptasia diaphana.* The activity of PO was calculated in samples taken every 6 h for 48 h. Each mucus sample corresponds to a group of 6 anemones. The results of one estimation are shown; repetitions had very similar results. Abbreviations: aposymbiotic anemones at full moon (apo.ll), aposymbiotic anemones at new moon (apo.ln), symbiotic anemones at full moon (sim.ll), and symbiotic anemones at new moon (sim.ln).

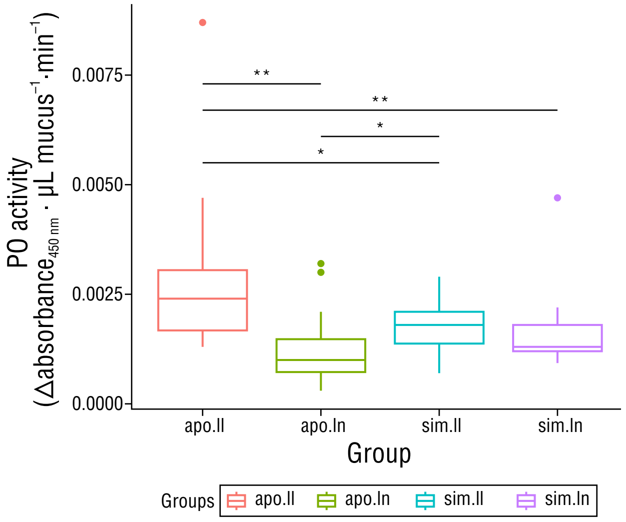

Figure 2. Comparison of phenol oxidase (PO) activity with respect to the symbiotic state and the lunar phase using the Kruskal–Wallis test. Boxplots represent the mean, first and third quartiles, confidence interval (95%), and outlier points (red dot, green dots, and purple dot). Each sample corresponds to the activity values of 6 anemones. The horizontal black lines show the comparisons between the different treatments; statistical significance of comparisons is represented by asterisks (*$P < 0.05$; **$P < 0.01$). Abbreviations: aposymbiotic anemones at full moon (apo.ll), aposymbiotic anemones at new moon (apo.ln), symbiotic anemones at full moon (sim.ll), and symbiotic anemones at new moon (sim.ln).

the immune system operates and remains active in a constitutive manner, even if it is not being challenged by a threat.

Immunity fluctuation in the circadian cycle

The PO activity in the mucus of *E. diaphana* fluctuated throughout the day, both in symbiotic and aposymbiotic anemones, with the highest PO activity at 2:00 p.m. No previous studies track PO activity throughout the day in cnidarians; our results provide a background for how the circadian cycle of *E. diaphana* affects its basal immunity.

The variability of basal immunity throughout the day could be consistent with what was observed at the transcriptomic level in symbiotic cnidarians. Gong et al. (2023) found that the corals *Acropora pruinosa* and *Pocillopora damicornis* differentially transcribe certain genes at night compared to the morning. At night, transcribed genes are mostly related to the immune system, metabolism, and signal transduction, whereas during the day, transcribed genes relate to transport and catabolism. However, Levy et al. (2011) reported that *Acropora millepora* genes associated with antioxidant activity have expression peaks at night, whereas those associated with metabolism are more expressed during the day. Furthermore, some studies report that crustaceans have a bimodal variation of PO in a diurnal cycle (She et al. 2019), whereas others have

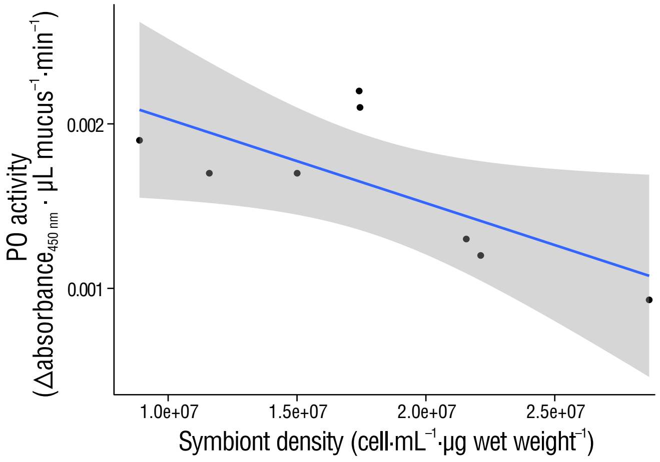

Figure 3. Relationship between phenol oxidase (PO) activity and symbiont density using a Spearman correlation test. The activity of PO decreases as symbiont density increases (cell·mL^{-1}·µg wet weight). The density of symbionts was determined in 48 anemones, grouped into 6 anemones for each sampling. The 95% confidence level is shaded.

reported greater activity during the day (Rund et al. 2016) or even constant PO activity (Pfenning-Butterworth et al. 2022). These studies illustrate the importance of considering the circadian cycle in studies of the immune system because it could help explain some variations.

Immunity fluctuations in response to the lunar cycle

The PO activity in *E. diaphana* mucus was slightly higher with the full moon than with the new moon in anemones of both symbiotic states. In corals, reproduction and growth are synchronized with lunar cycles (Boch et al. 2011). However, despite the extensive information on the influence of the moon on coral reproduction, information on the immune system is scarce and practically non-existent in *E. diaphana*. Given that the values of PO activity in the mucus of *E. diaphana* showed different behavior in the full moon than in the new moon, we can suggest that the basal constitutive immunity in this anemone also obeys the lunar cycles, regardless of its symbiotic state. This finding constitutes a novel contribution of the present study.

Symbiont density

We found a negative relationship between symbionts and the immune response that coincides with studies on the coral *Orbicella faveolata*, which reported a reduction in the expression of genes related to immunity (Fuess et al. 2020). Other studies have positively correlated immune activity with antioxidant activity and melanin synthesis (Changsut et al. 2022). Finally, it has been hypothesized that, in corals, the loss of symbionts after bleaching confers some protection, since a lower incidence of diseases has been observed

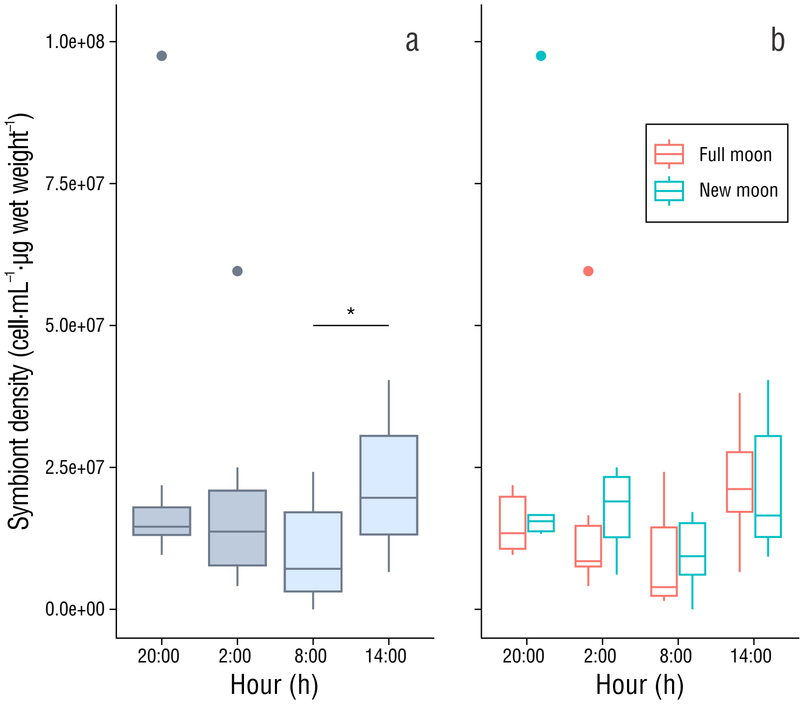

Figure 4. Comparison of symbiont density with respect to time of day and lunar phase using the Kruskal–Wallis test. (**a**) Symbiont density considering only the time of day, without taking into account the lunar phase. (**b**) Symbiont density considering lunar phase and time of day. Boxplots represent the mean, first and third quartiles, confidence interval (95%), and outliers. The asterisk (*) shows significant differences ($P = 0.035$) in the density of symbionts at 14:00 h compared to the other samples.

(Merselis et al. 2018). It is possible that symbiosis in cnidarians depends on reduced immune activity that facilitates this relationship.

CONCLUSIONS

The study of constitutive immunity and its relationship with biological cycles in *E. diaphana* is a scarcely explored field. The present study expands the understanding of PO activity as an immune response under basal conditions in aposymbiotic and symbiotic anemones, which showed basal constitutive immunity under laboratory conditions. The response varied according to biological rhythms, showing greater activity during the day and low activity at night. Furthermore, we observed that lunar cycles influenced PO activity, which was greater in the full moon phase. We also found that symbiotic status had an effect on the immune response, probably because symbiont density was negatively correlated with PO activity, with higher symbiont density observed at 14:00 h. These results not only provide evidence for constitutive immunity, but also illustrate the complexity of holobiont relationships. Future studies focusing on the relationship between immunity and biological cycles are important to achieve a more adequate interpretation of biological responses to stressors.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

Supplementary material

This work does not include supplementary material.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Conceptualization: MARJ, JRO, and PT; Data curation: MARJ; Formal analysis: MARJ; Funding acquisition: PT; Research: MARJ and JRO; Methodology: JRO and MARJ; Experimental development: MARJ; Resources: PT; Supervision: JRO and PT; Visualization: MARJ; Writing—original draft: JRO and MARJ; Writing—review and editing: MARJ, JRO, and PT.

Data availability

The raw data can be accessed at the following link: https://www.researchgate.net/publication/385169280_Raw_data_Rodriguez-Jimenez_et_al_2024.

Use of AI tools

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

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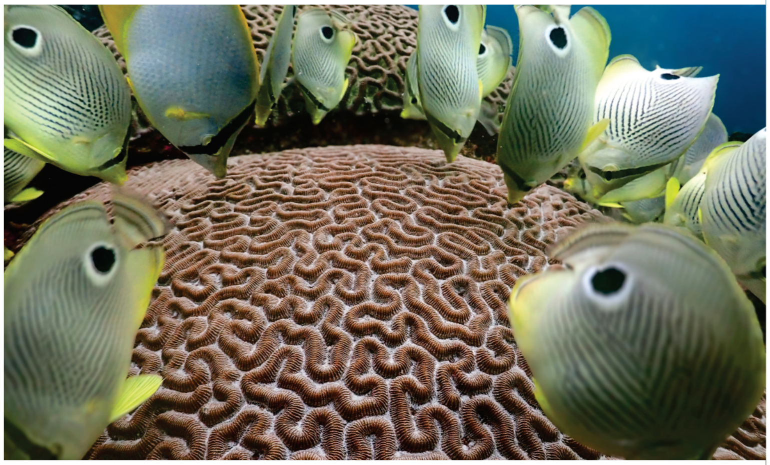

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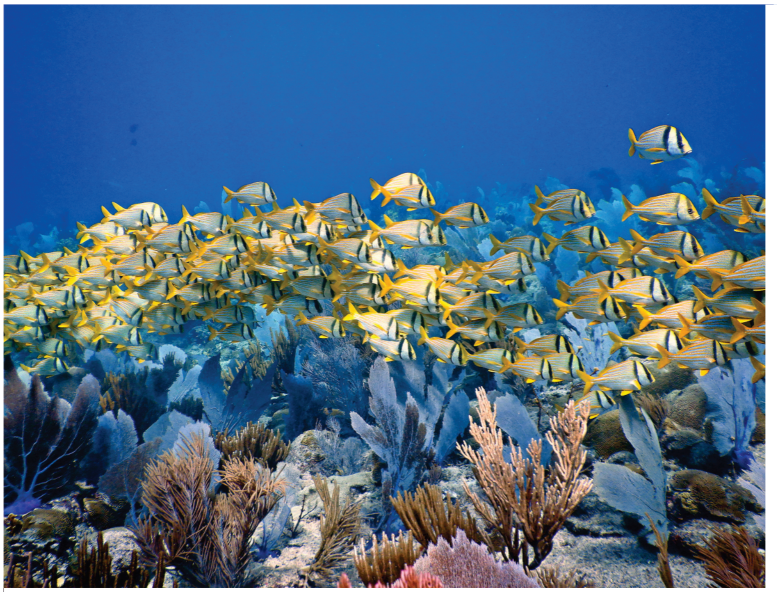

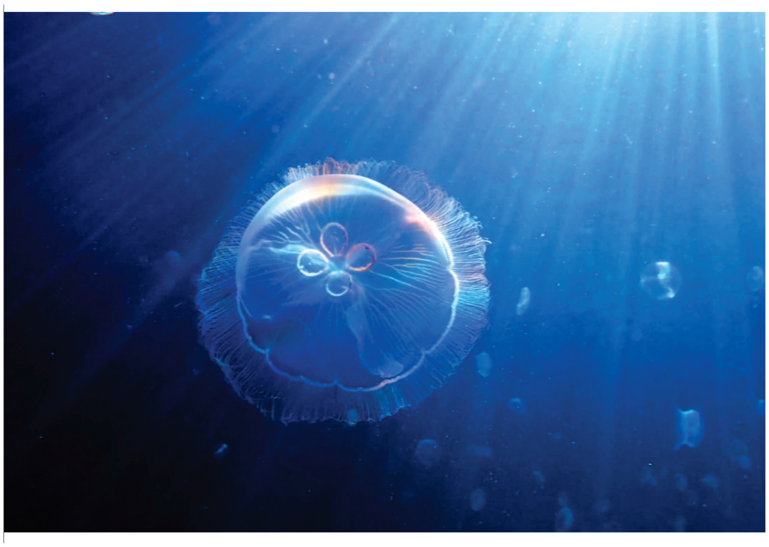

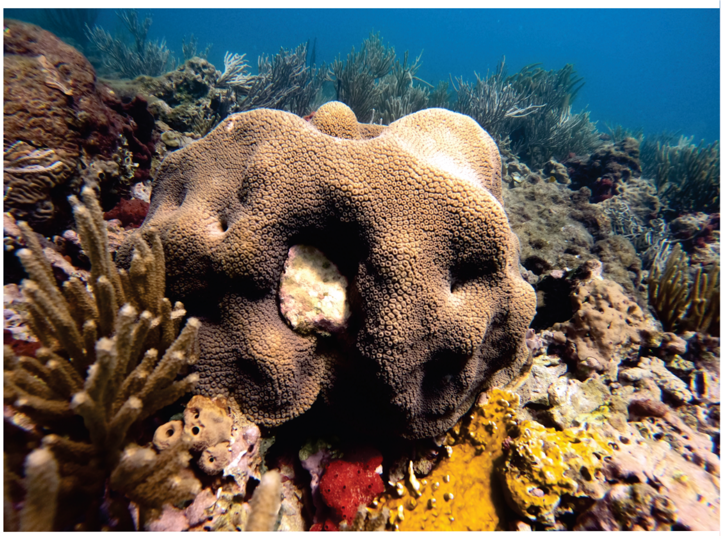

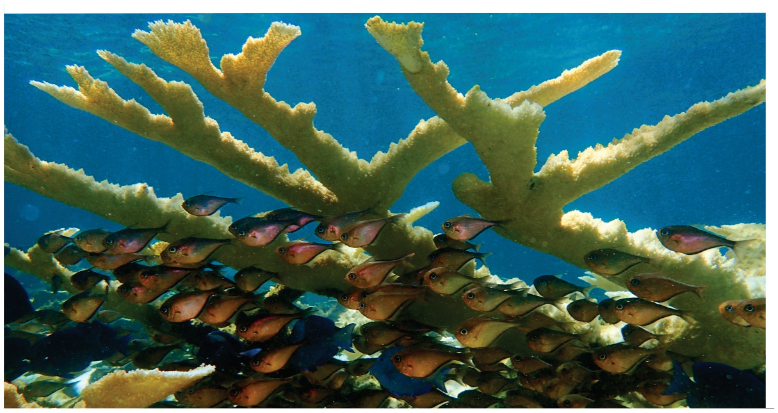

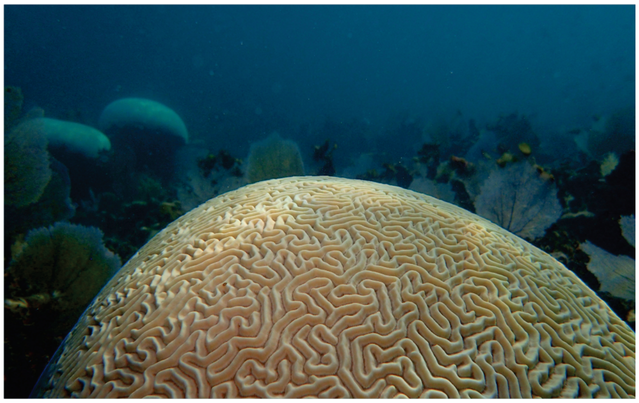

SOCIEDAD MEXICANA DE ARRECIFES CORALINOS

This collage showcases the biodiversity of marine ecosystems through images captured by participants of **XII CMAC–III CPAC**, arranged from top to bottom, left to right on each page.

Page 1 features the Fishgod Blenny *Malacoctenus ebisui* (Manuel Olán-González), the Boulder Brain Coral *Colpophyllia natans* (Adán Jordán-Garza), the Foureye Butterflyfish *Chaetodon capistratus* alongside the Symmetrical Brain Coral *Pseudodiploria strigosa* (Angela Alegria), the Caribbean Reef Squid *Sepioteuthis sepioidea* (Sergio Guendulain), and the coastal landscape of Punta Eugenia, Baja California Sur, Mexico (Abby Pañola).

Page 2 presents the California Sea Lion *Zalophus californianus* (Luis Malpica-Cruz), the Lettuce Sea Slug *Elysia crispata* with the Three Finger Leaf Algae *Halimeda incrassata* (Pedro Medina-Rosas), the longsnout seahorse *Hippocampus reidi* (Mariana Gudiño), and the Green Sea Turtle *Chelonia mydas* (Lorenzo Alvarez-Filip).

Page 3 displays the Porkfish *Anisotremus virginicus* (Manuel Olán-González), the coastal scenery of Tulum, Quintana Roo, Mexico (Tulio Villalobos), the Elliptical Star Coral *Dichocoenia stokesii* (Minerva Flores-Vargas), the Moon Jellyfish *Aurelia aurita* (Martin Serrano-Tadeo), the Mountainous Star Coral *Orbicella faveolata* (Daniela Carreño-Loaiza), the Elkhorn Coral *Acropora palmata* with Glassy Sweeper *Pempheris schomburgkii* (Esmeralda Pérez-Cervantes), and the Symmetrical Brain Coral *Pseudodiploria strigosa* (Gabriela Gutierrez-Estrada).