


Research

Evaluation of diversity patterns of echinoderms with cryptic habits used Autonomous Reef Monitoring Structures (ARMS) in two reefs of Gulf of Mexico and Mexican Caribbean Sea

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Abstract

Echinoderms are a conspicuous group on coral reefs. Juvenile and small-sized species often hide in living or inert substrates to protect themselves from predation. This cryptic behavior makes it difficult to count, identify, and capture them during fieldwork, resulting in a poor understanding of their ecology and an underestimation of their abundance. Autonomous Reef Monitoring Structures (ARMS) provide a protected environment that mimics natural habitats and is capable of recruiting echinoderm cryptofauna. They also serve as a standard structural measurement unit, allowing comparisons between samples and detection of spatiotemporal patterns of compositional change. To explore these patterns, we deployed and recovered 50 ARMS on two reefs in the Yucatan Peninsula from 2018 to 2020. A total of 976 individuals belonging to 36 species and five morphotypes were collected. The dominant class was Ophiuroidea, which accounted for 92.4% of the abundance. Bajo de Diez Reef (B10) hosted approximately 92% of the total abundance. Both reefs shared only around 37% of their species. Although species abundance and composition changed over time, no species with pioneering or late-settlement tendencies were identified. October 2019 saw the lowest recruitment abundances on both reefs. This decrease may be linked to the effects of the positive phase of ENSO, in synergy with the massive flux of *Sargassum* spp. during summer and autumn of 2019. Since cryptic echinoderm abundance and composition seem to be influenced more by resource availability and environmental conditions than by community succession, future studies should compare environmental factors and variations in benthic groups that serve as resources for echinoderms to test our conclusions.

Keywords Dominance · Non-successional patterns · *Ophiactis* · Yucatan reefs · Cryptic epifauna

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1 Introduction

Echinoderms are a conspicuous component of shallow tropical coral reefs [1]. These systems are estimated to be home to around one-third of the planet's marine diversity, with nearly 500 million people depending on the exploitation of their resources [2]. The biodiversity of these systems is sustained by the structural complexity of their coral assemblages and their associated benthic groups, such as algae, sponges, and microbiota, which together provide shelter, breeding grounds, and food for a rich and diverse biological community [2, 3]. Echinoderm biotic activity influences ecological processes and modifies the species composition of these associated benthic groups. Additionally, they contribute to shaping the structure of abiotic components, including calcareous and rocky matrices, as well as soft bottoms [1, 3].

In addition to predatory and grazing species in the benthos, echinoderms also include detritivores and suspension feeders, such as sea cucumbers and various species of brittle stars [1]. These species play a crucial role in water column and soft sediment cleaning processes. Through their feeding activity, they contribute to nutrient recycling and the transport of matter to higher trophic levels [4]. Echinoderms are a key part of the diet for several reef-associated species, including fish, mollusks, and crustaceans, many of which are commercially important [3].

In the last fifty years, the ecological study of echinoderms has gained significant importance. This increased focus on reef echinoderms is closely linked to the negative impacts of population anomalies, such as outbreaks and mortality events, on reef biodiversity [5]. Notable examples include population outbreaks of the corallivorous starfish *Acanthaster* spp. on the Great Barrier Reef, Australia, and in Espiritu Santo Island, Mexico [6, 7], as well as the alarming decline in population of the grazing sea urchin *Diadema antillarum* in the Caribbean, caused by pathogen-induced disease [8]. These events highlight the critical need to understand the ecological roles of echinoderms in order to fully comprehend the functioning of coral reefs.

Ecological assessments of echinoderms require continuous monitoring of reef communities, which in turn necessitates the design of standardized techniques to measure abundance and species richness. In the coral reefs of the Gulf of Mexico and the Mexican Caribbean, various methods have been implemented to evaluate the diversity of the echinoderm assemblages. The most commonly employed techniques include manual collection using diving equipment [9, 10], substrate sampling (corals, algae, sand, etc.) along with their associated fauna [11], and the use of visual transect censuses [12]. Although these techniques have provided valuable ecological insights into echinoderms communities, each has its own limitations, complicating a comprehensive understanding of the phylum.

The lack of standardization in sampling methods, particularly in manual collections, can introduce biases in abundance estimates due to inconsistent sampling areas or volumes [13]. Additionally, the extraction of natural substrates for analysis may result in damage to their structures and diversity [14]. Visual censuses, while less invasive, often underestimate the contribution of small-sized species (< 50 mm) and those with cryptic habits [15]. This underestimation of small and cryptic species introduces a significant bias in understanding and evaluating their ecological roles in coral reef ecosystems. In the case of echinoderms, many species, especially in their juvenile stages, are small in size and exhibit cryptic behavior, making them particularly difficult to detect with conventional monitoring techniques [16, 17].

One promising solution for conducting periodic and standardized evaluations of echinoderm cryptofauna is the use of Autonomous Reef Monitoring Structures (ARMS) [18]. These structures were developed by the Coral Reef Ecosystem Division (CRED) of the United States National Oceanic and Atmospheric Administration (NOAA) to standardize and quantify benthic habitat sampling. These structures reduce the costs associated with monitoring and ecological research and enable comparisons across various substrates in geographically separated regions using a single, consistent material [19]. Although the initial investment in materials and installation may be required, the easily accessible and durable materials allow for reuse in future campaigns once the biological samples are removed, offsetting the cost. ARMS provide a protected environment that mimics coral matrices or rock crevices and is capable of recruiting juvenile and small echinoderm cryptofauna. This method reveals assemblages of species often underestimated by other techniques. Pearman et al. [18] compared visual benthic reef surveys with photo analysis of ARMS plates, showing that ARMS can reveal cryptic species that visual censuses often overlook.

Since ARMS is not widely used to assess cryptic echinoderm communities, its advantages and disadvantages still need more exploration. For example, Palomino-Álvarez et al. [20] found fewer recruited individuals compared to other invertebrate phyla, using ARMS, suggesting it may not be the best method to characterize the whole echinoderm assemblage in reef communities. However, the possibility of obtaining standardized abundance measures for the least-studied portion of the assemblage remains a strong reason to use this method.

This study aimed to investigate the spatio-temporal changes in echinoderm diversity over three-year recruitment period (2018–2020), in two sites, one in the Gulf of Mexico and the other in the Mexican Caribbean, each subject to different environmental conditions (Fig. 1), using Autonomous Reef Monitoring Structures (ARMS) as experimental units.

2 Material and methods

2.1 Study area

2.1.1 Bajo de Diez Reef

Located on the Campeche Bank, northeast of the Gulf of Mexico, approximately 23 km offshore from Puerto Sisal (21°20′53.82″ N, 90°08′45.48″ W) (Fig. 1), Bajo de Diez (B10) is a reef bank characterized by depths ranging from 3 to 10 m. Its substrate comprises a matrix formed by calcareous rock and sand, supporting a diverse assemblage of benthic organisms, including calcareous algae, fleshy algae, hard corals (primarily genera *Siderastrea* and *Oculina*) and hydrocoral *Millepora*, soft corals, sessile polychaetes, bryozoans, hydroids, and sponges. The average sea surface temperature (SST) is around 26 °C and the area experiences three well-defined seasons: the "Nortes" cold fronts (winter), a dry season (spring), and a rainy season (summer-autumn). Due to its proximity to the coast, the reef is subject to significant fishing pressure and is influenced by wave action, which leads to sediment resuspension. Additionally, the region is impacted seasonally by tropical hurricanes and winter storms [21–23]. Under these conditions, Sisal scleractinian corals form numerous colonies (9 colonies per m²), but their development is poor (average diameter of 5 cm), limiting the availability of refuge for the fauna associated with these systems [21].

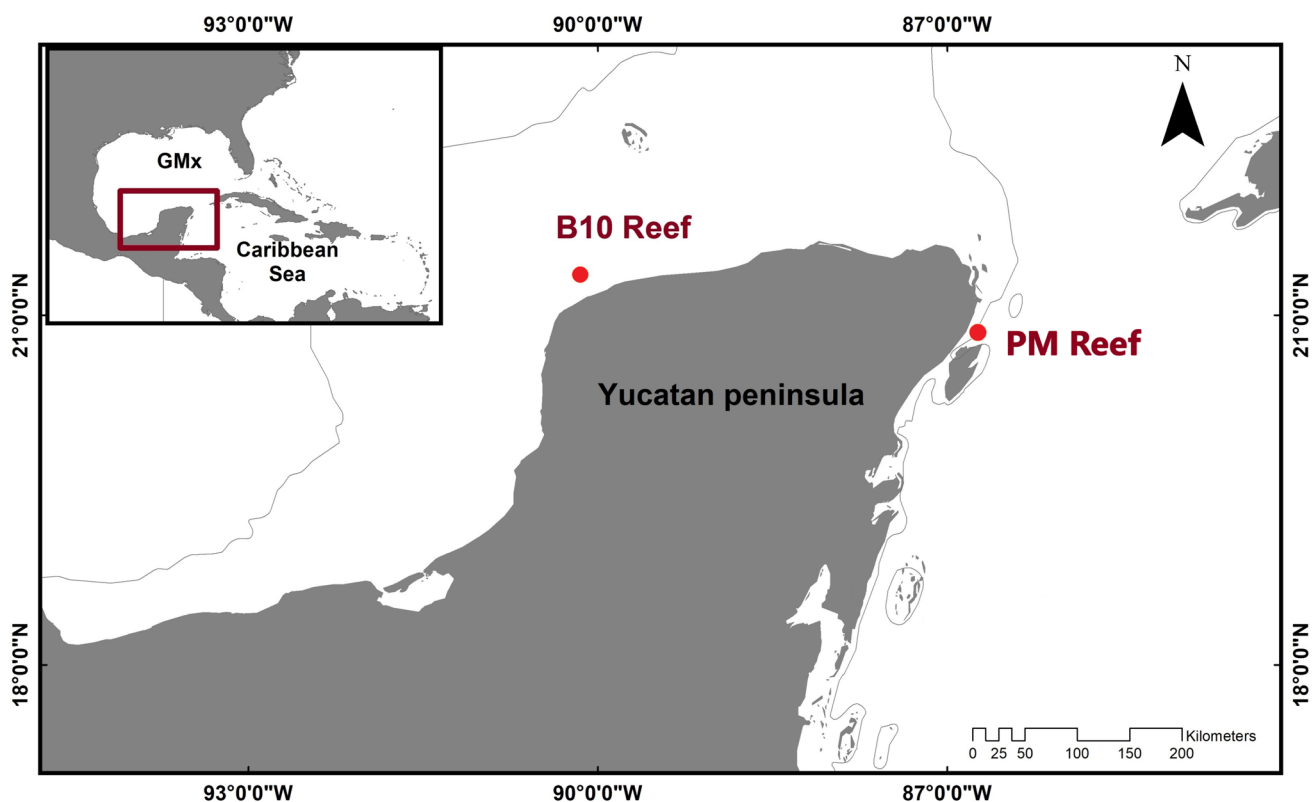


Fig. 1 Location of Autonomous Reef Monitoring Structures (ARMS) deployed in two sites. *GMx* Gulf of Mexico, *B10* Bajo de Diez Reef, Yucatan, Mexico, *PM* Puerto Morelos Reef, Quintana Roo, Mexico

2.1.2 Puerto Morelos Reef

Located in the Mexican Caribbean, approximately 25 km south of Cancun, La Bonanza Reef (20°57'53.54" N, 86°48'52.194" W) (Fig. 1) is part of the extensive reef lagoon of Puerto Morelos (PM), which stretches along the northeastern coast of Quintana Roo. These shallow reefs, ranging from 2 to 5 m depth can become exposed during spring low tides and are interconnected with other systems, such as sea grass beds and mangroves, which provide coastal protection. The region experiences two distinct seasons: a winter season (November to April) with the influence of cold fronts known as "Nortes"; and a summer season characterized by tropical conditions, low waves, and occasional hurricanes and storms. The substrate consists of calcareous sands covered by seagrass, along with calcareous pavements colonized by large patches of coral from genera *Acropora*, *Orbicella* and *Pseudodiploria* as well as other coral species that contribute to the reef's structure, together comprising 23% of the benthic cover. Other sessile organisms present include soft corals, fleshy algae and algal turfs. While the reef's conservation status is considered regular, due to the low rates of coral recruitment and biomass of key commercial fish species, it remains vulnerable to various natural and anthropogenic stressors, such as thermal anomalies, *Sargassum* spp. blooms, coral and echinoderm diseases, and overfishing [24, 25].

2.2 ARMS deployment and collection

The spatio-temporal variation in cryptic echinoderms assemblages was assessed by deploying 50 ARMS in the subtidal zone on carbonate substrates, which were not occupied by living coral colonies, at depths of approximately 4–7 m on two reefs: B10 (26 ARMS) and PM (24 ARMS). The ARMS were spaced 3–5 m apart within each reef. The detailed methodology used for constructing, assembling and deploying the ARMS is described in Palomino-Álvarez et al. [24, 40]. Authorization for deployment was granted by the Secretary of the Navy. To install the structures, an Exception Permit was obtained from the Secretary of the Navy (SEMAR-EX.006/06/18). The original design involved deploying 12 structures for one year, gradually recovering three structures every 3 months (3 M, 6 M, 9 M, 12 M), and repeating the process in the second year with the same structures. However, environmental and logistical challenges caused by COVID-19 and other events led to delays in recovery, with some structures being retrieved up to 6 months late. The total number of recovered structures, the duration of the experimental recruitment period, and the recovery dates are detailed in Fig. 2.

In the ARMS recovery process, a mesh was used to cover them, thus preventing the loss of mobile fauna during the ascent. The ARMS were submerged in filtered and aerated seawater, placed in individual plastic boxes, and transported to the Marine Biodiversity Laboratory, UMDI-Sisal, UNAM for subsequent processing [24, 40].

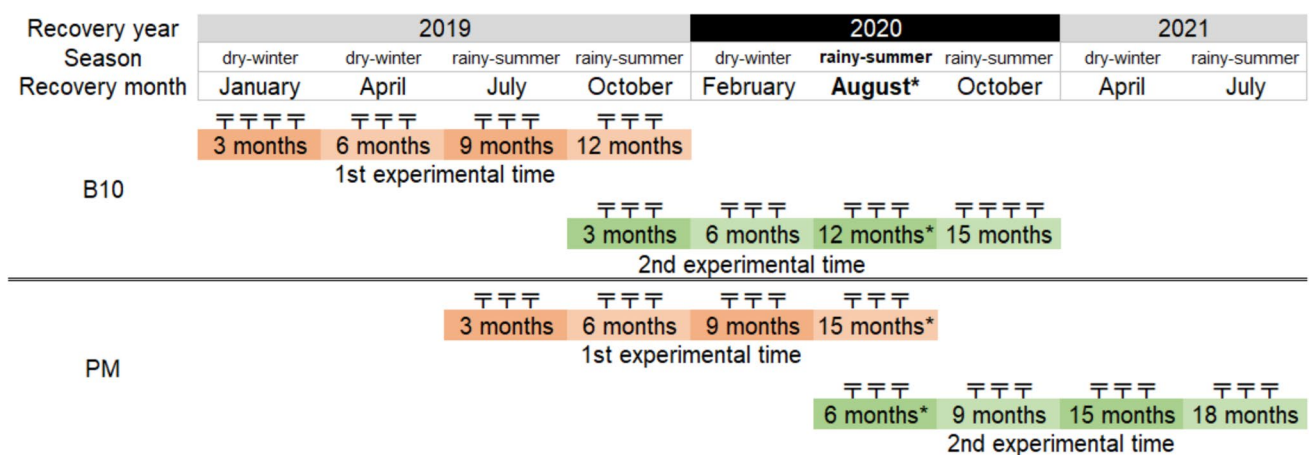


Fig. 2 Recovery scheme of Autonomous Reef Monitoring Structures (ARMS). *PM* Puerto Morelos Reef (Mexican Caribbean), *B10* Bajo de Diez Reef (Gulf of Mexico), T ARMS unit, months=Duration in months of the recruitment period. Orange color indicates the first experimental time. Green color indicates the second experimental time. Gray and black colors indicate annual separation. The asterisk (*) indicates samples for which the recovery time was extended due to the COVID-19 pandemic

2.3 Echinoderm fauna preservation

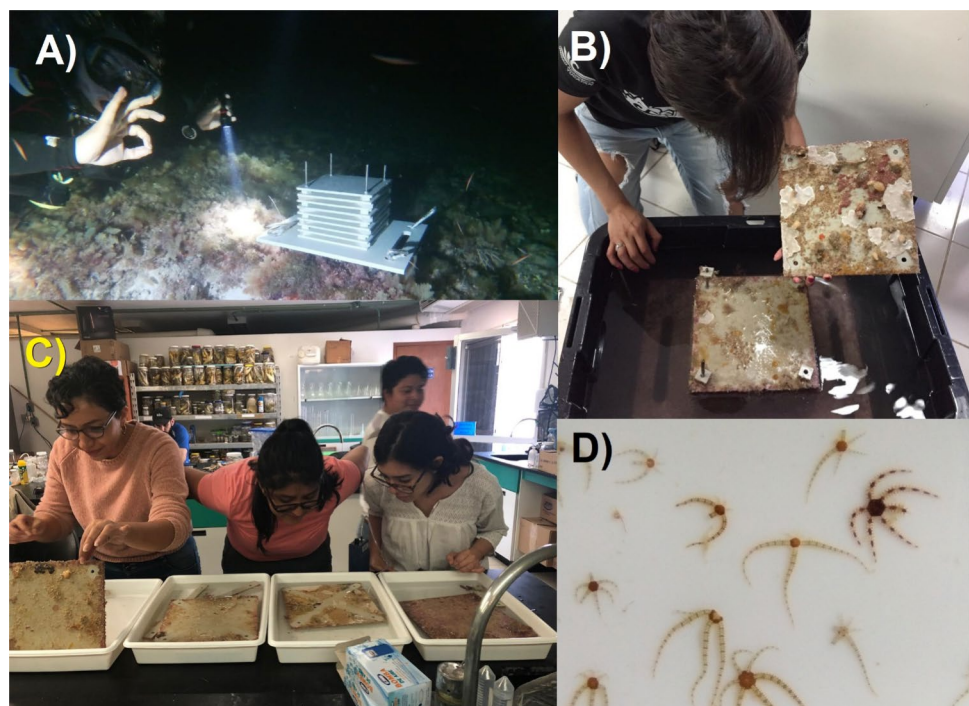
Each ARMS unit was disassembled plate by plate and placed in individual plastic trays containing seawater. Mobile individuals were manually collected using fine brushes and dissecting forceps. Specimens were placed in a plastic container with a 4% magnesium chloride solution in seawater to induce anesthesia. Ophiuroids were brushed into a "comet" position to maintain the visibility of key morphological characters for taxonomic identification. This method ensured the proper preservation of diagnostic features and facilitated subsequent specimen handling and manipulation. Individuals were then fixed in 70% ethanol, labeled, and stored in bottles (Fig. 3). Collected specimens were deposited in the Regional Collection of Echinoderms of Yucatán Peninsula (COREPY for the Spanish acronym), integrated into *Biodiversidad Marina de Yucatán* (BDMY) project at Sisal-UNAM. Macrostructures of both live and preserved specimens were examined using a Velab Stereo VE-S5C stereomicroscope, while sea cucumber ossicles were observed under Velab Prime VE-T300 optical microscope. Individuals were identified to the species level following the criteria outlined in [15, 25–27]. Voucher information can be consulted in digital dataset COREPY-BDMY [26]. Additional details on collection and preservation techniques can be found at [27].

2.4 Statistical analyses

To evaluate differences in echinoderm assemblages, we used a three-level nested hierarchical design of permutational analysis of variance (PERMANOVA) with fixed effects, using the factors S_i = Site (B10, PM), E_t = Experimental time (1, 2), and D_u = Duration (3, 6, 9, 12, 15, 18) with the equation: $Y = \mu + S_i + S_i(E_t) + S_i(E_t(D_u)) + \epsilon_i$. The contribution of each species to spatio-temporal variation was evaluated using percentage similarity analysis (SIMPER).

To visualize changes in assemblage composition between sites and experimental times, a Principal Component Ordination (PCO) was generated, applying centroid distance metrics. In addition, a shaded plot was generated using average abundance values for the nested factors site (S_i) in the experimental time (E_t) and Duration (D_u). All statistical analyses were based on a Bray–Curtis dissimilarity matrix, constructed with an abundance matrix for level of ARMS ($N = 50$), after previously applying a fourth root transformation to avoid the bias associated with the dominance of abundant species, and we also applied a "dummy" variable to correct the effect of empty values. Statistical analyses and graphs were created using the software $\text{\textcircled{R}}$ PRIMER-PERMANOVA v.7 [28], $\text{\textcircled{R}}$ Inkscape v.0.92.1–1 [29], RStudio v. 2024.04.2, with the packages ggplot2, cowplot, readxl, stats, FactoMineR, plotly, ggfortify, vegan, scales, and ggrepel [30].

Fig. 3 Process of ARMS deployment and recovery, followed by the separation, classification, and identification of the associated echinoderm fauna. **A** ARMS deployed on hard reef substrate. **B** ARMS recovery in individual plastic box containers for transport to the laboratory. **C** Manual separation of echinoderm fauna from the recruitment plates. **D** Example of echinoderm fauna being anesthetized for preservation



3 Results

Over the three-year period, ARMS units recruited a total of 976 echinoderms, representing four classes, eight orders, 16 families, 23 genera, 36 species, and five morphotypes (Fig. 4, Table 1). The morphotypes could not be identified to the species level due to their very small size and early developmental stages.

The class with the highest species richness and abundance at both reefs was Ophiuroidea, with 17 species and 848 individuals in B10, and 14 species and 54 individuals in PM, representing 92.4% of the total abundance of the samples (Table 1, Fig. 4).

Bajo de Diez had the greatest species richness, with 24 species and four morphotypes across four classes. In comparison, Puerto Morelos recruited 24 species and two morphotypes, but these were divided into three classes. The number of taxa was similar in both reefs; only ~37% of species were shared between the two sites (Fig. 4).

The sites show differences in species composition (Fig. 4) and their abundances (Fig. 5). Bajo de Diez maintained the highest abundance throughout the study, with recruitment densities ranging from 0.7 to 58 individuals per ARMS, with an average of 32.7 individuals per ARMS, while Puerto Morelos showed much lower values (0 to 7.7 individuals per ARMS, \bar{x} = 3.28 individuals per ARMS) (Fig. 5).

3.1 Spatio-temporal patterns

The PERMANOVA test revealed significant differences in echinoderm assemblage composition at all three levels of variation: reefs (Si), experimental times on each reef (Et (Si)), and durations for each experimental time (Du (Et (Si))) (Table 2). A post-hoc test (Appendix Table 1) showed that the experimental times exhibited significant changes only in PM. This same test showed that B10 presented differences during the first recovery period (3 months).

This first and second recruitment periods (3 and 6 months) have the greatest richness and number of echinoderm species across all experimental times (Figs. 5, 6). During the second experimental time, the paired test detected significant differences between the 3-month recruitment period and the 15-month period (Appendix Table 1); these periods had the lowest and largest values of richness and abundance of the second experimental time in B10, respectively. The richness and abundance between the months of recruitment in PM did not show significant differences, however, it is important to note that in October 2019 (6 months from the first time), no echinoderms were recruited (Appendix Table 1, Figs. 5, 6).

The SIMPER test between sites highlighted that the ophiurans *Ophiactis savignyi*, *Amphipholis squamata*, *Amphiura stimpsonii* and *Ophiactis lymani*, and the sea urchin *Arbacia punctulata* explained 49.63% of the dissimilarity. The heat map (Fig. 6) shows a higher density and presence of these species in the ARMS of B10. Meanwhile, in PM *O. savignii*

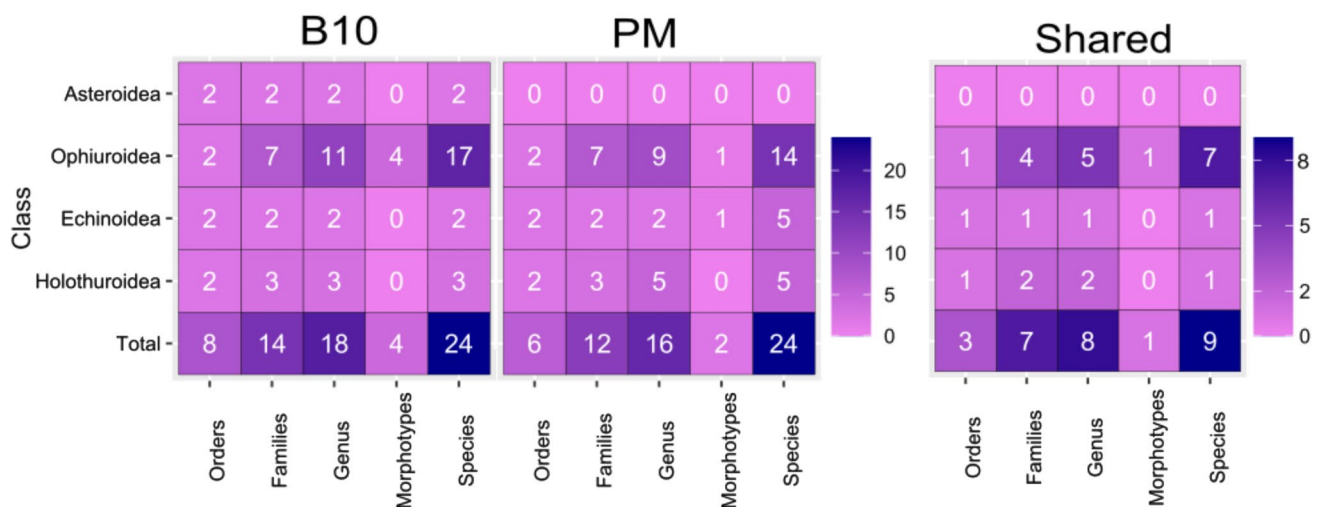


Fig. 4 The heat map shows the number of species, morphotypes, genera, families, and orders for each class at each reef, as well as the taxa shared between both. *B10* Bajo de Diez Reef, *PM* Puerto Morelos Reef

Table 1 Taxonomic list of echinoderm species recruited in ARMS

Phylum echinodermata	B10	PM
Class Asteroidea		
Order Spinulosida		
Family Echinasteridae		
Genus <i>Echinaster</i>		
<i>Echinaster (Othilia) echinophorus</i> Verrill, 1899	1	
Order Valvatida		
Family Oreasteridae		
Genus <i>Oreaster</i>		
<i>Oreaster reticulatus</i> Ljungman, 1866	1	
Class Ophiuroidea		
Order Amphilepidida		
Family Amphiuridae		
Genus <i>Amphiodia</i>		
<i>Amphiodia</i> sp. A. Agassiz, 1863	6	
Genus <i>Amphipholis</i>		
<i>Amphipholis januarii</i> (Lamarck, 1816)	7	
<i>Amphipholis squamata</i> (Stimpson, 1854)	14	13
Genus <i>Amphiura</i>		
<i>Amphiura fibulata</i> H.L. Clark, 1933		2
<i>Amphiura stimpsonii</i> Ljungman, 1872	41	12
Genus <i>Microphiopholis</i>		
<i>Microphiopholis gracillima</i> Lütken, 1856	1	
Genus <i>Ophiocnida</i>		
<i>Ophiocnida scabriuscula</i> (Müller & Troschel, 1842)	2	
Family Ophiactidae		
Genus <i>Ophiactis</i>		
<i>Ophiactis</i> sp. Lütken, 1856	11	1
<i>Ophiactis algicola</i> (Lütken, 1859)	10	
<i>Ophiactis lymani</i> (Lamarck, 1816)	54	
<i>Ophiactis muelleri</i> (Müller & Troschel, 1842)	1	
<i>Ophiactis savignyi</i> (H.L. Clark, 1900)	667	1
Family Ophiolepididae		
Genus <i>Ophiolepis</i>		
<i>Ophiolepis</i> sp. (Say, 1825)	1	
Family Ophionereididae		
Genus <i>Ophionereis</i>		
<i>Ophionereis olivacea</i> Müller & Troschel, 1842	1	1
<i>Ophionereis reticulata</i> Lütken, 1856	1	2
<i>Ophionereis squamulosa</i> Müller & Troschel, 1840	21	6
Family Ophiothrichidae		
Genus <i>Ophiothrix</i>		
<i>Ophiothrix</i> sp. Müller & Troschel, 1840	1	
<i>Ophiothrix (Ophiothrix) angulata</i> H.L. Clark, 1900	5	
<i>Ophiothrix (Ophiothrix) oerstedii</i> (Say, 1825)	2	7
Order Ophiacanthida		
Family Ophiocomidae		
Genus <i>Ophiocoma</i>		
<i>Ophiocoma echinata</i> Koehler, 1914		3
Genus <i>Ophiocomella</i>		
<i>Ophiocomella ophiactoides</i> Lütken, 1856	2	
Genus <i>Ophiomastix</i>		

Table 1 (continued)

Phylum echinodermata	B10	PM
<i>Ophiomastix wendtii</i> (Say, 1825)		1
Family Ophiidermatidae		
Genus <i>Ophioderma</i>		
<i>Ophioderma brevispinum</i> (Linnaeus, 1758)		1
<i>Ophioderma cinereum</i> (Lesueur, 1824)	6	1
<i>Ophioderma rubicundum</i> (Théel, 1886)	5	
Family Ophiomyxidae		
Genus <i>Ophiurochaeta</i>		
<i>Ophiurochaeta littoralis</i> (Koehler, 1913)		3
Class Echinoidea		
Order Arbacioida		
Family Arbaciidae		
Genus <i>Arbacia</i>		
<i>Arbacia punctulata</i> (Delle Chiaje, 1828)	31	
Order Camarodonta		
Family Echinometridae		
Genus <i>Echinometra</i>		
<i>Echinometra lucunter</i> Koehler, 1914		1
<i>Echinometra viridis</i> Lütken, 1859		6
Family Toxopneustidae		
Genus <i>Lytechinus</i>		
<i>Lytechinus</i> sp. (Lamarck, 1816)		1
<i>Lytechinus variegatus</i> (Pourtalès, 1851)		1
<i>Lytechinus variegatus carolinus</i> (Lamarck, 1816)	1	1
<i>Lytechinus variegatus variegatus</i> (Pourtalès, 1851)		1
Class Holothuroidea		
Order Apodida		
Family Chiridotidae		
Genus <i>Chiridota</i>		
<i>Chiridota rotifera</i> Selenka, 1867	1	4
Family Synaptidae		
Genus <i>Synaptula</i>		
<i>Synaptula hydriformis</i> (Forsskål, 1775)	2	7
Order Dendrochirotida		
Family Cucumariidae		
Genus <i>Thyonella</i>		
<i>Thyonella pervicax</i> (Linnaeus, 1758)	1	
Genus <i>Holothuria</i>		
<i>Holothuria (Halodeima) floridana</i> A. Agassiz, 1863		1
<i>Holothuria (Halodeima) grisea</i> A. Agassiz, 1863		1
<i>Holothuria (Thymiosycia) impatiens</i> (Lamarck, 1816)		1
TOTAL	897	79

B10 Bajo de Diez Reef (Gulf of Mexico), PM Puerto Morelos Reef (Mexican Caribbean)

and *A. stimpsonii* presented low and moderate abundance respectively, and *O. lymani* and *A. punctulata* were absent. *A. squamata* was present in two reefs with similar densities, however, in B10 it throughout the entire experimental period, but in PM it was absent in early months of both experimental times (Table 3, Fig. 6).

In B10, the species *O. savignyi*, *A. punctulata*, *Ophiactis algicola*, and *A. stimpsonii* explained 58.26% of the dissimilarity between times, with *O. savignyi*, *A. punctulata*, and *A. stimpsonii* being more abundant at the first experimental time, while *Ophiactis algicola* was only present during the second experimental time (Table 3, Fig. 6).

Fig. 5 Richness and density for each experimental time and duration (in months of recruitment). *B10* Bajo de Diez Reef (Gulf of Mexico), *PM* Puerto Morelos Reef (Caribbean Sea). The numbers 1 and 2 indicate the experimental time. The label “ND” indicates the months without sampling. Border lines: orange = dry seasons, blue = rainy seasons

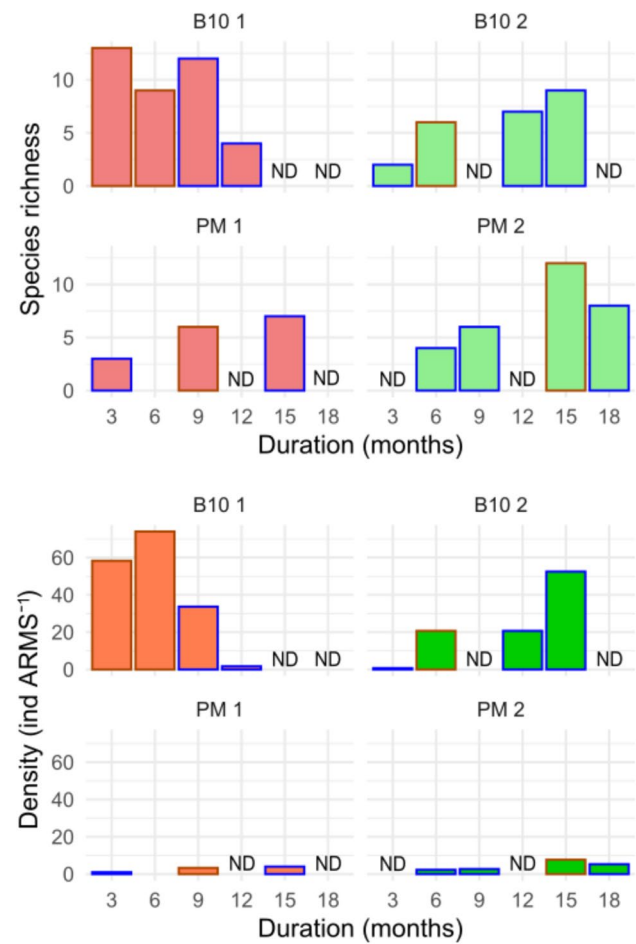


Table 2 PERMANOVA results for variation between sites (Si), experimental times (Et) and recruitment duration in months (Du)

Source	df	SS	MS	Pseudo-F	P-value	Unique perms
Si	1	19211	19211	14.14	0.0001	9946
Et (Si)	2	6244	3122	2.2979	0.0187	9931
Du (Et (Si))	12	37870	3155.8	2.3227	0.0001	9874
Res	34	46194	1358.6			
Total	49	1.10E+05				

For PM, the SIMPER test identified the sea cucumbers *Chiridota rotifera* and *Synaptula hydriformis*, and the ophiuroids *Ophionereis squamulosa*, *Amphipholis squamata*, and *Amphiura stimpsonii* as the species contributing most to the dissimilarity between experimental times (52.62%). The heat map shows that these species had higher abundance and frequency of appearance during the second experimental time, compared to the first (Fig. 6).

A PCO analysis was used to explore changes between reefs and experimental times (Fig. 7). The analysis reveals a consistent pattern of change in echinoderm assemblages at both reefs over time, although this pattern did not show any clear trends related to seasonal variation or recruitment duration. Reef B10 exhibited the greatest variations in species composition during both experimental periods. It is notable how the richness and abundance of cryptic echinoderms progressively decreases during the first experimental time in B10, but recovers for the second experimental time (Fig. 7). Thus, the final experimental period of the second time point (15 months) presents an assemblage similar to the first periods (3 and 6 months) of the first experimental time (Figs. 6, 7). On the other hand, PM exhibited greater similarity between periods with very low abundances, highlighting the third period (15 months) of the second experimental time as the one with the highest recruitment (Figs. 6, 7).

4 Discussion

Previous studies have demonstrated that Autonomous Reef Monitoring Structures (ARMS) create microenvironments capable of recruiting representative assemblages of cryptic biota from the surrounding reef [18]. Consequently, the micro-communities recruited into ARMS serve as valuable tools for exploring the recruitment and colonization processes that sustain the diversity and biomass production of cryptic taxa on reefs. However, as noted by Palomino-Álvarez et al. [20], recruitment efficiency varies across phyla, meaning that groups like echinoderms may represent only a fraction of the reef community. Nevertheless, this fraction provides valuable insights by including species often overlooked by manual capture methods or visual censuses, which are limited by the diver's ability to detect organisms with the naked eye in a short time frame.

To illustrate this point, we can compare the taxonomic lists available for B10 and PM with the species assemblage obtained from the ARMS in this study. For B10, only two previous studies include taxonomic lists for echinoderms. In the first, Hernández-Díaz [31] used manual and substrate collections, reporting 17 species, 10 of which are also found in our study. More recently, Palomino-Álvarez et al. [20] recovered four ARMS after one year of sampling, recording 17 species, 14 of which are reported in our work. The 14 species not previously reported in B10, recorded by our study after three years of sampling, demonstrate that ARMS are a valuable tool for complementing local inventories.

In contrast, the PM echinoderm assemblage is better characterized, with general [32] and specific inventories for Echinoidea [33] and Ophiuroidea [34]. These lists include almost all species reported in our study, except for the brittle star *Ophiurochaeta littoralis*. However, none of these previous studies report abundance data that allow for an exploration of community dynamics on the reef. The closest approximation is the community analysis by Güemez-Pérez [35], who examined the dynamics of six echinoderm species recorded through visual censuses on band transects within the PM reef. Of these, only two species are shared with our results. Therefore, ARMS can also be a tool to assess changes in abundance at both the population and community levels for species that, due to their small size or cryptic behavior, evade detection by visual census techniques. Having abundance data allows us to evaluate community structure patterns that species richness alone cannot reveal.

Among coral communities, echinoderms stand out as a highly abundant and ubiquitous phylum [1, 3], exhibiting opportunistic habits in their use of both food and shelter resources [36, 37]. This dietary and habitat plasticity is evident in the fact that, while there are species assemblages commonly associated with reef systems, few exhibit an exclusive distribution within these systems. It is also common to find them in adjacent environments such as sandbanks, algal beds, seagrasses, and mangroves [17, 38, 39]. The flexible colonization of various habitats complicates the identification of specific resources or environmental factors that promote or inhibit their presence on reefs. However, an initial step toward understanding the structure of these assemblages is to identify dominant species, which are those that maintain the highest abundance and consistent occurrence over time [40].

Although defining the set of adaptations that enable a taxon to be dominant in a system is complex, it is clear that dominant species possess competitive advantages over other taxa, allowing them to exploit available resources more efficiently [40]. In our study, species of the class Ophiuroidea were dominant, though with notable variations in abundance and composition between the two reef localities. In this context, Sloan [41] reported that between 62 and 89% of the cryptic fauna abundance associated with reef-building coral colonies in the Aldabra Atoll, Seychelles, were ophiuroids. These results coincide with previous reports from the research area, where Hernández-Díaz [42] found that 57% of the echinoderm species collected in the reefs of the northwest Yucatan Peninsula, Mexico, belonged to the class Ophiuroidea. This is largely attributed to the inclusion of cryptic habitats in the study, such as crevices, spaces under rocks, and algae clusters.

Sloan [41] proposes that the small interstitial spaces between coral heads function as refuge areas and nurseries for species with small body volumes, such as ophiuroids. Rius et al. and Higgins et al. [40, 43] further noted that species with cryptic habits and filter-feeding diets can remain in their burrows to obtain food, without needing to venture out. In our study, the interstitial spaces formed between the ARMS plates may efficiently emulate the natural interstitial spaces found in coral structures, providing suitable refuges for ophiuroids and other small echinoderms, thereby protecting them from predation.

Although specific values are not provided in our study, the ARMS deployed on both reefs exhibited a coverage by sessile filter-feeding invertebrates, including bryozoans, tunicates, sponges and polychaetes [20]. Their presence likely promotes the recruitment of detritivorous and filter-feeding species, such as ophiuroids and sea cucumbers, as many of these species opportunistically feed on particles and micro-prey that result from the activity of sessile filter-feeders

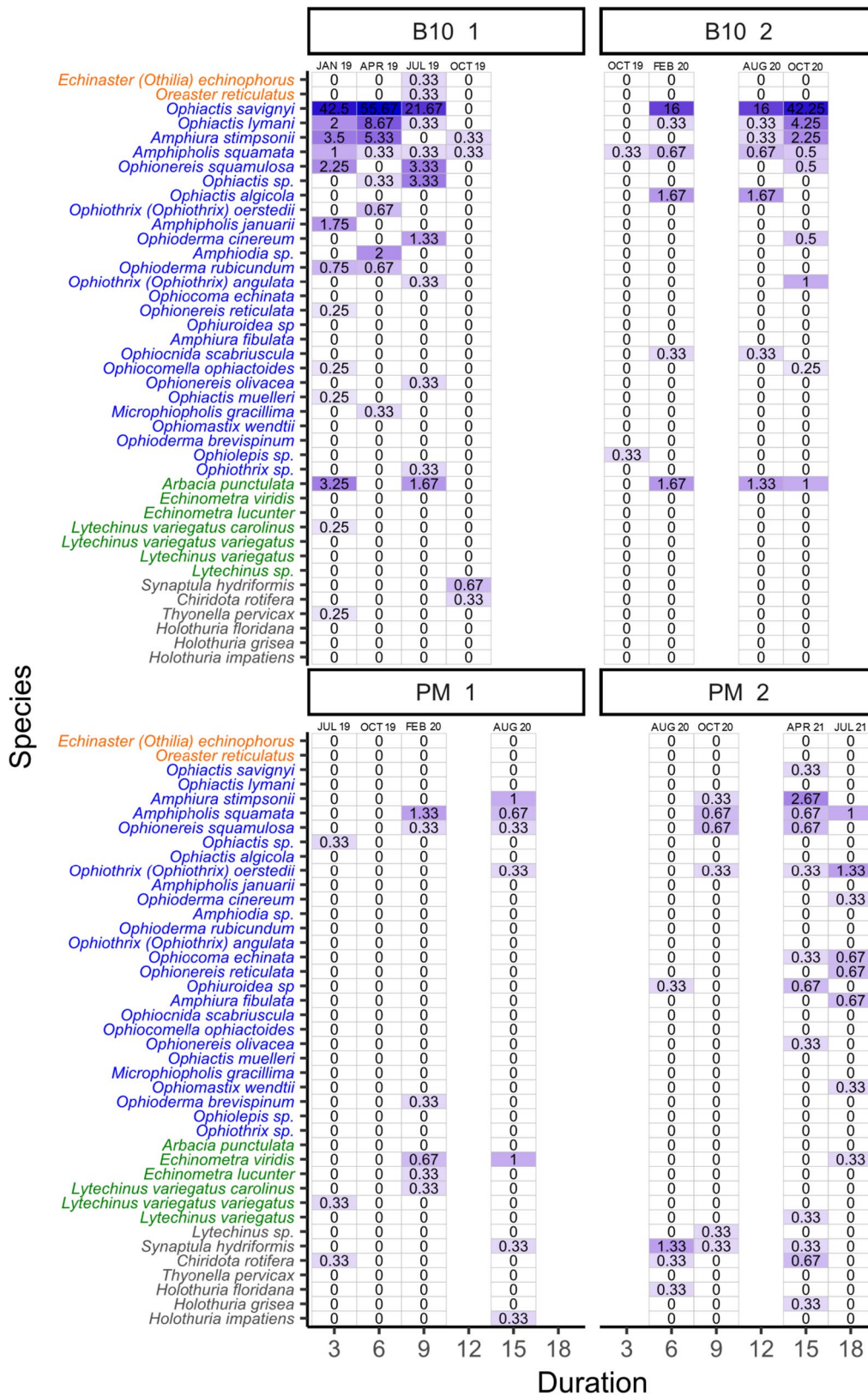


Fig. 6 Heat map of abundance expressed as density (individuals per ARMS). B10=Bajo de Diez Reef (Gulf of Mexico); PM=Puerto Morelos Reef (Caribbean Sea). Lower codes indicate the duration of the recruitment period in months (3, 6, 9, 12, 15, 18). Upper codes indicate the experimental times (1, 2), months (JAN=January; FEB=February; APR=April; JUL=July; AUG=August; OCT=October) and year (19=2019, 20=2020, 21=2021) of recovery. The colors of the species names represent the taxonomic classes: orange=Asteroidea, blue=Ophiuroidea, green=Echinoidea, black=Holothuroidea. Genera without a specific epithet (sp.) indicate morphs that could not be identified to the species level

Table 3 Results of the SIMPER analysis displaying percentage contributions to dissimilarity in echinoderms abundance between reefs and experimental times (cut-off of 50%)

Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
B10 & PM						
<i>Ophiactis savignyi</i>	1.59	0.04	18.13	1.35	19.29	19.29
<i>Amphipholis squamata</i>	0.44	0.3	8.11	0.74	8.63	27.92
<i>Amphiura stimpsonii</i>	0.51	0.21	7.26	0.75	7.72	35.65
<i>Arbacia punctulata</i>	0.64	0	7.02	1.02	7.47	43.12
<i>Ophiactis lymani</i>	0.6	0	6.12	0.86	6.51	49.63
<i>Ophionereis squamulosa</i>	0.3	0.25	5.62	0.65	5.98	55.61
B10_1 & B10_2						
<i>Ophiactis savignyi</i>	1.72	1.46	23.29	2.33	26.04	26.04
<i>Arbacia punctulata</i>	0.59	0.69	11.86	1.99	13.26	39.3
<i>Ophiactis algicola</i>	0	0.51	8.7	0.96	9.72	49.02
<i>Amphiura stimpsonii</i>	0.65	0.36	8.26	1.22	9.24	58.26
PM_1 & PM_2						
<i>Chiridota rotifera</i>	0.08	0.18	14.29	0.43	16.01	16.01
<i>Synaptula hydriformis</i>	0.08	0.28	9.78	0.67	10.96	26.97
<i>Ophionereis squamulosa</i>	0.17	0.33	8.74	0.71	9.8	36.77
<i>Amphipholis squamata</i>	0.22	0.38	7.25	0.62	8.13	44.89
<i>Amphiura stimpsonii</i>	0.11	0.31	6.89	0.67	7.72	52.62

B10 Bajo de Diez Reef, *PM* Puerto Morelos Reef, *B10_1* Bajo de Diez Reef during the 1st experimental time, *B10_2* Bajo de Diez Reef during the 2nd experimental time, *PM_1* Puerto Morelos Reef during the 1st experimental time, *PM_2* Puerto Morelos Reef during the 2nd experimental time

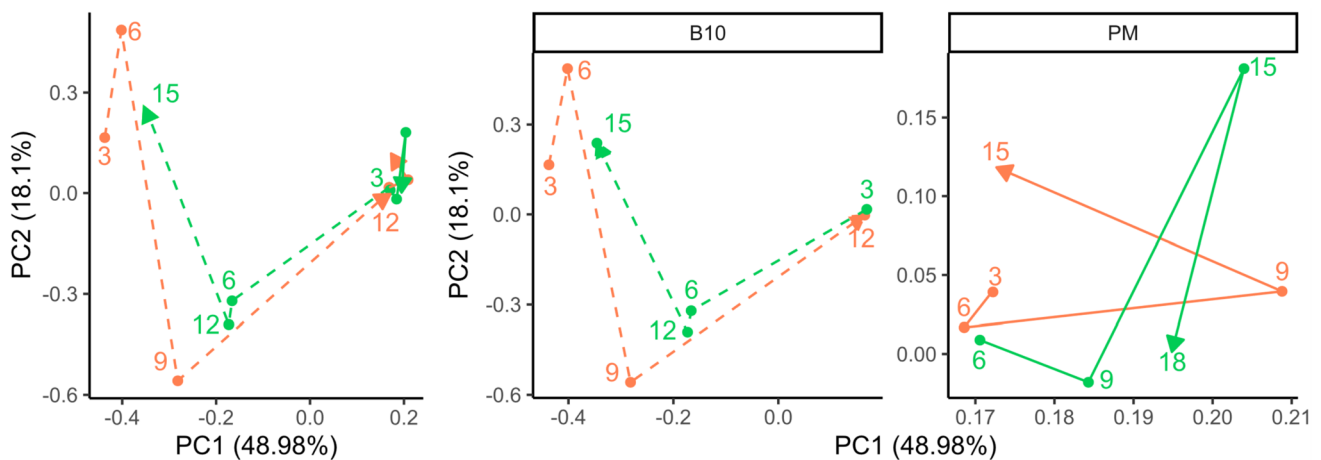


Fig. 7 Multivariate ordination (PCO) of centroids representing the structure and composition of echinoderm assemblages at reefs across experimental periods. Interconnecting lines represent temporal changes. The percentages explained by each axis are shown. *B10* Bajo de Diez Reef, *PM* Puerto Morelos Reef; orange line = 1st experimental time; green line = 2nd experimental time

[40]. This observation aligns with the findings of Hendler et al. Benavides-Serrato et al. and Hernández-Díaz [17, 39, 42], who identified the ophiuroid families dominant in our study (Amphiuridae, Ophiactidae, Ophionereididae and Ophiotrichidae) as detritivores, suspensivores and microbiota consumers. In contrast, the low presence, or even total absence, of large-volume echinoderms in the ARMS, such as certain tropical representatives of the classes Crinoidea, Echinoidea, Asteroidea and Holothuroidea may be explained by the fact that the small interstitial spaces between the plates act as a bottleneck, restricting access for large specimens with less body plasticity [44, 45].

All species recruited in the ARMS are common to the rocky-coral reefs of the Gulf of Mexico and the Caribbean [17, 32], and most have been documented across a wide range of substrates and habitats, including sandy, rocky and coral bottoms [17, 38, 39]. Therefore, their broad regional distribution patterns were insufficient to explain the variations in abundance and composition between the reefs.

Previous studies on reef echinoderms diversity in the Mexican Tropical Pacific have described how variations in biotic and abiotic factors of the reef at the meso- and micro-scale level may provide more insight into differences in assemblage composition than large-scale distribution limits or latitudinal gradients in abundance. This especially true when species with overlapping distribution ranges are sampled across different localities [46, 47].

Given that our study did not directly characterize the sessile biota recruited in the ARMS, nor the inter- and intra-annual variations in the physicochemical environmental parameters, we relied on theoretical and bibliographic analyses to identify and discuss potential ecological factors driving the differences in composition and diversity between our communities, as well as the continuous variability in recruitment patterns over time. The PERMANOVA test revealed significant differences in composition between the B10 and PM assemblages, which can be attributed to the fact that while species richness was similar in both systems, the abundance of individuals in PM represented less than 9% of the abundance reported for B10 (Table 1, Fig. 6) and B10 and PM share only ~ 37% of their species (Table 1, Fig. 4). Although both systems are shallow rocky-coral reefs [21, 25], each reef has a particular coral and benthic composition, with B10 dominated by soft corals, while PM has a higher prevalence of reef-building corals, and these differences in community composition appear to influence the availability of both trophic and refuge resources for echinoderms.

Numerous authors have discussed the importance of habitat structural complexity and shelter availability in the integration of cryptic and epi-benthic communities; as well as the influence of predation pressures, active habitat selection and fidelity to refuge sites [40, 41, 45, 48]. McClanahan and Dunn et al. [44, 45] suggest that increased predator presence on reefs alters the refuge-seeking behavior of echinoderms, shifting from random distribution patterns in predator-free environments, to an active search for protective spaces when predators are present.

Although no quantitative studies have compared the diversity and benthic cover between PM and B10 reefs, previous analyses of the B10 benthic community [21] describe a system influenced by stressors such as sedimentation and seasonal storms. Furthermore, the absence of any protected status makes the B10 more vulnerable to overfishing and disturbances associated with human activity, such as fuel pollution and accidental strandings. These conditions have likely contributed to the limited development of hard coral colonies and the proliferation of sessile and filter-feeding organisms, including fleshy algae, calcareous algae, soft corals, sponges, annelids, and other encrusting invertebrates. These heterogeneous sea beds, which may be particularly attractive to echinoderms due to the great variety of food resources [46, 47], but are potentially limited in shelter availability [48].

Additionally, the presence of a diverse predator community, including octopuses, lobsters, and predatory fishes from families Serranidae, Labridae, Haemulidae, Tetraodontidae, Diodontidae, and Balistidae, which are typical in Gulf of México and Caribbean reefs [49], could make ARMS highly attractive refuges for cryptic echinoderm fauna. Reefs with low hard coral cover, such as B10, may have a limited supply of refuge space, which could enhance the attractiveness of ARMS as settlement structures. This is especially relevant for juveniles, which feed on detritus, mucus, bacterial films, microbiota [17] and do not need to leave ARMS for sustenance. Epizoic symbionts species, such as those from the genus *Ophiactis* were notably abundant in B10. Hernández-Díaz [42] attributed the high abundance of *Ophiactis* spp. to their detritivorous and cryptic habits and their capacity for asexual reproduction, which promote colonization of living substrates.

The effect of sedimentation on marine invertebrates may be mixed. Particle abrasion can cause physical damage to both larvae and juveniles, as well as adults, especially those of small size. However, sediment resuspension can introduce nutrients, organic matter, and microbiota into the water column, which are used by detritivorous species [50]. Under these conditions, the structural complexity of ARMS in B10 may have been able to protect echinoderms from abrasion and burial, without completely blocking the supply of nutrient particles.

In contrast, the PM reefs have higher coral cover (23%) and provide more refuge opportunities, but exhibit less heterogeneity in food resources. Additionally, their lower exposure to waves, as they are located in a reef lagoon, reduces particle resuspension, which in turn lowers the amount of organic matter available in the water column for suspension-feeding species. Under these conditions, ARMS may represent a less attractive refuge for echinoderms. The search for more diverse food sources could encourage more active behaviors and lower fidelity to the ARMS [41].

Finally, echinoderms possess a unique form of locomotion controlled by the so-called water vascular system (WVS) [39]. This system, in addition to controlling movement, also regulates internal and external fluid pressure, which provides the phylum with a wide margin of bathymetric tolerance, even in specific species associated with shallow systems. Since depth measurements were not taken for each of the ARMS and the depth range between structures is less than three meters, we do not have sufficient criteria to evaluate whether depth could have influenced the abundance patterns of the assemblages. However, it would be valuable to explore this possibility in future studies, as, although these small

variations in depth may not affect echinoderms, they can influence the availability of the benthic groups with which these species are associated.

While these theories help explain the observed assemblage patterns in our studies, verifying them requires standardized measurements and comparisons of predator diversity, natural benthic cover types, and predation experiments, areas that are beyond the scope of this work. Another factor to consider is the availability of larvae, juveniles, and small adults in the waters and benthic substrates surrounding the ARMS, as well as their success in settlement, recruitment, and colonization [45]. Analyzing seasonal abundance patterns in our samples may further explain the influence of these processes.

4.1 Spatio-temporal variability

Figures 5 and 6 illustrate the fluctuating composition and abundance values for all species across both locations and experimental periods. No species exhibited a consistent recruitment pattern over time, nor as sessile communities matured on structures. In other words, we did not identify a successional pattern in the echinoderm assemblage on either reef. Even the most abundant species (such as *O. savignyi*, *A. squamata*, and *A. stimpsonii*, which contributed the most to variability between sites and experimental periods), showed inconsistent abundance patterns relative to the ARMS background time (Figs. 6, 7). Abundance did not show a seasonal pattern between the dry and rainy periods on any of the reefs. The opportunistic behavior of echinoderms and their non-selective diets likely drive constant micro-migration between ARMS and adjacent natural substrates, making it difficult to identify clear patterns of variability in species composition [44, 45].

Sloan [35] pointed out that continuous monitoring of organisms in such experiments is impractical, making it challenging to verify how long or how frequently they associate with recruitment structures. Therefore, the abundance of recruited organisms during the experimental periods serves as a “snapshot” of the community. Nevertheless, these snapshots provide valuable insights into the temporal changes in echinoderm populations. In our study, fluctuations in echinoderm diversity suggest a regional environmental anomaly, which is not necessarily reflected in the population patterns of more conspicuous species. As a result, a larger number of samples, both temporally and spatially, may be required to better characterize these community dynamics.

A notable example is the October 2019 sampling, which marked the lowest echinoderm diversity associated with the ARMS from both reefs. During the 12th month of the first experimental period, B10 experienced a loss of over 50% of its richness, recruiting only one individual each of *A. squamata*, *A. stimpsonii*, *C. rotifera*, and two specimens of *S. hydriformis*. Similarly, during the 3rd month of the second experimental period, the B10 ARMS recruited just one *A. squamata* specimen and another for the genus *Ophiolepis*. In PM, no echinoderms were recruited at all during this sampling period (Figs. 5, 7). This pattern does not appear to be seasonal, as October 2020 recorded highest richness and abundance for B10 in the second experimental period and the third highest for PM. This population anomaly is also reflected in the PCO sampling trajectories, where the proximity and similarity of the October 2019 samples are clear (Fig. 7).

For PM, this loss of richness and abundance could be linked to the massive influx of pelagic *Sargassum* spp. in the Mexican Caribbean. Over the past decade, thousands of tons of *Sargassum* spp. have been recorded annually [51, 52]. Once ashore, the algae decompose, fragment and increase bacterial and pathogen loads in the water. This results in higher turbidity, ammonium, phosphorus, and hydrogen sulfide levels, while dissolved oxygen and pH levels decrease (conditions that stress various reef taxa). Such stress has been associated with local mortality events, including those reported by [52] in urchins, ophiuroids, and sea cucumbers.

The low recruitment of echinoderms recorded in July 2019 and the complete absence of recruitment in October 2019 in PM (Figs. 4, 6), coincided with a major *Sargassum* influx event in the Mexican Caribbean. This event reached its peak in April, with 19,000 ha of algae floating and stranding along the coast of Quintana Roo [53]. However, the arrival of algae and subsequent decomposition continued through November, subjecting the region to prolonged exposure to abnormal water physicochemical parameters, which could have been detrimental to the survival of echinoderm larvae and juveniles, and may have inhibited reproduction in adults [52].

While *Sargassum* landings seem to explain the reduced echinoderm diversity in PM, there is no record of *Sargassum* affecting B10. Therefore, the cause of the recruitment decline at B10 remains unclear. An alternative explanation could be linked to the effects of the positive phase of El Niño Southern Oscillation (ENSO), which prevailed from late 2018 to mid-2019 [54]. Carrillo et al. [55], point out that during this phase, precipitation levels and storms increase along the coasts of Gulf of Mexico and Caribbean. These events result in lower salinity levels and greater sediment resuspension

in near-shore reef systems like B10 and PM. As with *Sargassum* arrivals, such conditions could negatively impact the larvae, juveniles, and adult populations of echinoderms, which are typically considered a stenohaline phylum [38, 39].

Without further environmental data, it is difficult to conclusively identify the environmental factors that influenced echinoderm assemblages during our study. However, the changes in assemblage composition observed using ARMS highlight the importance of discussing which other population and community phenomena among cryptic and epibenthic fauna remain undetected by traditional monitoring and collection methods.

In our study, the use of ARMS was combined with identification methods based on traditional taxonomy and multivariate statistical analysis, yielding valuable results but with a certain degree of uncertainty due to the lack of additional data. The incorporation of technologies such as metabarcoding, the collection of local environmental parameters through sensors, and even adjustments in the recovery times of the structures, or the combination of this collection methodology with traditional techniques like visual censuses and manual collections, could enhance the results of future research.

Since the implementation of these structures requires an initial investment in materials and the involvement of a team of specialists for the proper processing of samples, the use of ARMS may not be suitable for all types of ecological characterization of echinoderm assemblages.

Given that, coral reefs have undergone progressive degradation since the late twentieth century due to the synergistic effects of multiple environmental and anthropogenic stressors [25]. In light of the ongoing challenges posed by climate change [56], it is crucial to implement continuous, low-impact monitoring strategies like ARMS. Its proven effectiveness in recruiting and capturing small-sized species with cryptic habits makes it an especially attractive option, particularly in systems that are poorly studied, and not easily accessible for continuous monitoring.

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Author contributions All authors contributed to the study's conception and design. Material preparation and data collection were performed by P.A.A.L, H.D.Y.Q., S.N., G.C.E. and S.C.R.C. Data analyses and interpretation of results were performed by G.C.E., P.A.L.A. and S.C.R.C. The first draft of the manuscript was written by S.C.R.C. and all authors commented on previous versions of the manuscript. Funding acquisition S.N. and G.C.E. All authors read and approved the final manuscript.

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Data availability "Data are available in the dataset repository of the Marine Biodiversity of Yucatan project: <https://www.bdmy.org.mx/datasets/bdmy> and in Echinoderms from the digital repository: Gulf of Mexico and Mexican Caribbean at the «Regional Collection of Echinoderms of the Yucatan Peninsula» (<https://ipt.iobis.org/caribbeanobis/resource?r=coleccionequinodermosdeyucatan>) at UMDI-Sisal, Faculty of Sciences, UNAM, Mexico (Version 1.0) [Dataset]. Zenodo. <https://doi.org/https://doi.org/10.5281/ZENODO.3893272>."

Code availability Not applicable.

Declarations

Ethics approval and consent to participate Permission for sampling N. PPF / DGOPA-082/19 was granted by Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA) of the government of Mexico. All applicable international, national, and institutional guidelines for animal testing, animal care, and the use of animals were followed by the authors.

Consent for publication Not applicable.

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References

1. Birkeland C. The influence of echinoderms on coral-reef communities. *Echinoderm Stud.* 1989;3:1–79.
2. Sobha TR, Vibija CP, Fahima P. Coral reef: a hot spot of marine biodiversity. In: Sukumaran ST, Keerthi TR, editors. Conservation and sustainable utilization of bioresources. Singapore: Springer Nature; 2023. p. 171–94.
3. Glynn PW, Enochs IC. Invertebrates and their roles in coral reef ecosystems. In: Dubinsky Z, Stambler N, editors. Coral reefs: an ecosystem in transition. Dordrecht: Springer; 2011. p. 273–325.
4. Jangoux M, Lawrence JM. Echinoderm nutrition. 1st ed. Boca Raton: CRC Press; 2020. <https://doi.org/10.1201/9781003078920>.
5. Uthicke S, Schaffelke B, Byrne M. A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecol Monogr.* 2009;79(1):3–24. <https://doi.org/10.1890/07-2136.1>.
6. Uthicke S, Logan M, Liddy M, Francis D, Hardy N, Lamare M. Climate change as an unexpected co-factor promoting coral eating seastar (*Acanthaster planci*) outbreaks. *Sci Rep.* 2015;5(1):8402. <https://doi.org/10.1038/srep08402>.
7. Rodríguez-Villalobos J-C, Ayala-Bocos A. Depredación masiva por *Acanthaster planci* en el arrecife El Corralito, golfo de California: amenaza a corto plazo. *Rev Biol Trop.* 2021;69:S272–86. <https://doi.org/10.15517/rbt.v69iSuppl.1.46359>.
8. Vezzulli L, Colwell RR, Pruzzo C. Ocean warming and spread of pathogenic vibrios in the aquatic environment. *Microb Ecol.* 2013;65(4):817–25. <https://doi.org/10.1007/s00248-012-0163-2>.
9. Celaya-Hernández EV, Solís-Marín FA, Laguarda-Figueras A, Durán-González A, Rodríguez TR. Asociación a sustratos de los erizos regulares (Echinodermata: Echinoidea) en la laguna arrecifal de Isla Verde, Veracruz, México. *Rev Biol Trop.* 2008;56:281–95. <https://doi.org/10.15517/rbt.v56i3.27144>.
10. de la Cruz Francisco V, Morales Quijano I, González González M. Equinodermos del polígono arrecifal Tuxpan, Área de Protección de Flora y Fauna, México. *Revista de Investigaciones Marinas.* 2017;37(2):46–60.
11. Aguilera-Pérez E, de la Cruz-Francisco V. Composición taxonómica de las algas césped y su macrofauna asociada, arrecife Tuxpan, Sistema Arrecifal Lobos-Tuxpan. *Boletín Del Instituto Oceanográfico de Venezuela.* 2018;56(2):66–80.
12. Morales Quijano I, de la Cruz Francisco V, González González M, Argüelles-Jiménez J. Diversidad y abundancia de los equinodermos y su relación con la cobertura bentónica del arrecife Enmedio, Sistema Arrecifal Lobos-Tuxpan, México. *Revista Ciencias Marinas y Costeras.* 2017;9(2):51–74.
13. Cummins KW. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *Am Midland Nat.* 1962;67(2):477. <https://doi.org/10.2307/2422722>.
14. Ravinesh R, Biju Kumar A. Collection, preservation, and documentation of estuarine and marine benthic invertebrates. In: Godson PS, Vincent SGT, Krishnakumar S, editors. Ecology and biodiversity of Benthos. Amsterdam: Elsevier; 2022. p. 33–82.
15. Sayer MDJ, Poonian C. The influences of census technique on estimating indices of macrofaunal population density in the temperate rocky subtidal zone. *Uw Tech Int J Soc Uw Tech.* 2007;27(3):119–39. <https://doi.org/10.3723/175605407783360053>.
16. Clark AM. Echinoderms of coral reefs. In: Jones OA, Endean R, editors. Biology and geology of coral reefs. New York: Academic Press, Inc.; 1976. p. 95–123.
17. Hendler G, Miller JE, Pawson DL, Kier PM. Sea stars, sea urchins and allies. *Echinoderms of Florida and the Caribbean.* Washington, DC: Smithsonian Institution Press. 1995. 390 p.
18. Zimmerman TL, Martin JW. Artificial Reef Matrix Structures (ARMS): an inexpensive and effective method for collecting coral reef-associated invertebrates. *GCR.* 2004. <https://doi.org/10.18785/gcr.1601.08>.
19. David R, et al. Lessons from photo analyses of Autonomous Reef Monitoring Structures as tools to detect (bio-)geographical, spatial, and environmental effects. *Mar Pollut Bull.* 2019;141:420–9. <https://doi.org/10.1016/j.marpolbul.2019.02.066>.
20. Palomino-Alvarez LA, et al. Evaluation of the Use of Autonomous Reef Monitoring Structures (ARMS) for describing the species diversity of two coral reefs in the Yucatan Peninsula, Mexico. *Diversity.* 2021;13(11):579. <https://doi.org/10.3390/d13110579>.
21. Zarco-Perelló S, Mascaro M, Garza-Pérez R, Simões N. Topography and coral community of the Sisal Reefs, Campeche Bank, Yucatán, México. *Hidrobiológica.* 2013;23(1):28–41.
22. Winfield I, Muciño-Reyes M, Cházaro-Olvera S, Ortiz M, Lozano-Aburto M. Anfípodos bentónicos (Crustacea: Peracarida) del Sistema Arrecifal Sisal y línea de costa, noroeste de la península de Yucatán, golfo de México. *Rev Mex Biodiv.* 2020. <https://doi.org/10.22201/ib.20078706e.2020.91.3071>.
23. Jordán-Dahlgren E. Coral reefs of the Gulf of Mexico: characterization and diagnosis. In: Caso M, Pisanty I, Ezcurra E, Withers K, Nipper M, editors. Environmental analysis of the Gulf of Mexico. Corpus Christi: Harte Research Institute for Gulf of Mexico Studies; 2004. p. 340–50.
24. Coronado C, Candela J, Iglesias-Prieto R, Sheinbaum J, López M, Ocampo-Torres FJ. On the circulation in the Puerto Morelos fringing reef lagoon. *Coral Reefs.* 2007;26(1):149–63. <https://doi.org/10.1007/s00338-006-0175-9>.
25. Caballero-Aragón H, et al. Puerto Morelos coral reefs, their current state and classification by a scoring system. *Diversity.* 2020;12(7):272. <https://doi.org/10.3390/d12070272>.
26. Hernández-Díaz YQ et al. Echinoderms from the Gulf of Mexico and Mexican Caribbean at the “Colección Regional de Equinodermos de la Península de Yucatán” at UMDI-Sisal, Facultad de Ciencias, UNAM, México. Zenodo, 5 de mayo de 2020. 10.5281/ZENODO.3893272.
27. Palomino-Álvarez LA et al. Autonomous Reef Monitoring Structures (ARMS). Benthic marine fauna processing manual. Zenodo, 2021. <https://doi.org/10.5281/zenodo.5655251>.
28. K. R. Clarke y R. N. Gorley, «PRIMER v6: User Manual/Tutorial (Plymouth Routines in Multivariate Ecological Research)», Plymouth, 2006.

29. Bah T. Inkscape: guide to a vector drawing program. Prentice Hall: Hoboken, NJ, USA, 2011; Volume 559, p. 473.
30. RStudio Team, RStudio: Integrated Development for R (v. 2024.12.1)[Software]. RStudio, PBC, Boston, MA. 2024. <http://www.rstudio.com/>.
31. Hernández-Díaz YQ. Zoogeografía de equinodermos (Echinodermata) de los Bajos de Sisal y arrecife Alacranes, Yucatán, México. Ciudad de México: Tesis de Maestría, Universidad Autónoma de México; 2011.
32. Laguarda-Figueras A. Equinodermos del Caribe de México: Puerto Morelos, Quintana Roo. Ciudad de México: Universidad Nacional Autónoma de México; 2002.
33. Bravo-Tzompantzin D, Solís-Marín FA, Laguarda-Figueras A, Abreu-Pérez M, Durán-González A. Equinoideos (Echinodermata: Echinoidea) del Caribe Mexicano: Puerto Morelos, Quintana Roo, México. *Avicennia*. 1999;10/11:43–72.
34. Laguarda-Figueras A, Hernández-Herrejón LA, Solís-Marín FA, Durán-González A. Ofiuroideos del Caribe mexicano y Golfo de México. Ciudad de México: ICMYL-UNAM, Conabio; 2009.
35. Güemez-Pérez VE. Estructura comunitaria de equinodermos del Golfo de México y Mar Caribe. Chetumal: Tesis de Licenciatura, Tecnológico Nacional de México; 2015.
36. Cobb J, Lawrence JM. Diets and coexistence of the sea urchins *Lytechinus variegatus* and *Arbacia punctulata* (Echinodermata) along the central Florida gulf coast. *Mar Ecol Prog Ser*. 2005;295:171–82. <https://doi.org/10.3354/meps295171>.
37. Reyes-Luján J, Barrios J, Dwight A, Zapata-Vívenes E, Salgado W, Lodeiros C. Dieta del erizo negro *Echinometra lucunter* (Echinometra Echinoidea) en el Nororiente de Venezuela. *Rev Biol Trop*. 2015. <https://doi.org/10.15517/rbt.v63i2.23157>.
38. Borrero-Pérez G, Benavides-Serrato M, Díaz-Sánchez CM. Equinodermos del Caribe colombiano II: Echinoidea y Holothuroidea. Santa Marta: Serie de publicaciones especiales del Instituto de Investigaciones Marinas y Costeras – INVEMAR No. 30. 250 p. 2012. <http://hdl.handle.net/1834/6680>.
39. Benavides-Serrato M, Borrero-Pérez G, Díaz-Sánchez CM. Equinodermos del Caribe colombiano I: Crinoidea, Asteroidea y Ophiuroidea. Santa Marta: Serie de publicaciones especiales del Instituto de Investigaciones Marinas y Costeras – INVEMAR No. 22. 384 p. 2011. <http://hdl.handle.net/1834/6675>.
40. Rius M, Teske PR, Manriquez PH, Suarez-Jimenez R, McQuaid CD, Castilla JC. Ecological dominance along rocky shores, with a focus on intertidal ascidians. In: Hawkins SJ, Evans AJ, Dale AC, Firth LB, Hughes DJ, Smith IP, editors. *Oceanography and marine biology: an annual review*. 1st ed. Boca Raton: CRC Press; 2017. p. 55–84.
41. Sloan NA. Size and structure of echinoderm populations associated with different coexisting coral species at Aldabra Atoll, Seychelles. *Mar Biol*. 1982;66(1):67–75. <https://doi.org/10.1007/BF00397256>.
42. Hernández-Díaz YQ. Zoogeografía de equinodermos (Echinodermata) de los Bajos de Sisal y arrecife Alacranes, Yucatán, México. Tesis de Maestría, Universidad Autónoma de México, Ciudad de México. 2011. <https://repositorio.unam.mx/contenidos/64407>.
43. Higgins E, Scheibling RE, Desilets KM, Metaxas A. Benthic community succession on artificial and natural coral reefs in the northern Gulf of Aqaba, Red Sea. *PLoS ONE*. 2019;14(2):e0212842. <https://doi.org/10.1371/journal.pone.0212842>.
44. McClanahan TR. Predation and the control of the Sea Urchin *Echinometra viridis* and fleshy algae in the patch reefs of glovers reef, Belize. *Ecosystems*. 1999;2(6):511–23. <https://doi.org/10.1007/s100219900099>.
45. Dunn R, Altieri A, Miller K, Yeager M, Hovel K. Coral identity and structural complexity drive habitat associations and demographic processes for an increasingly important Caribbean herbivore. *Mar Ecol Prog Ser*. 2017;577:33–47. <https://doi.org/10.3354/meps12230>.
46. Hermosillo-Nuñez B, Rodríguez-Zaragoza F, Ortiz M, Galván-Villa C, Cupul-Magaña A, Ríos-Jara E. Effect of habitat structure on the most frequent echinoderm species inhabiting coral reef communities at Isla Isabel National Park (Mexico). *Community Ecol*. 2015;16(1):125–34. <https://doi.org/10.1556/168.2015.16.1.14>.
47. Hermosillo-Nuñez BB, Rodríguez-Zaragoza FA, Ortiz M, Calderon-Aguilera LE, Cupul-Magaña AL. Influence of the coral reef assemblages on the spatial distribution of echinoderms in a gradient of human impacts along the tropical Mexican Pacific. *Biodivers Conserv*. 2016;25(11):2137–52. <https://doi.org/10.1007/s10531-016-1182-y>.
48. Fraser KM, Lefcheck JS, Ling SD, Mellin C, Stuart-Smith RD, Edgar GJ. Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas. *Proc R Soc B*. 2020;287:20201798. <https://doi.org/10.1098/rspb.2020.1798>.
49. Zarco Perello S, Moreno Mendoza R, Simões N. Checklist of fishes from Madagascar Reef, Campeche Bank, México. *BDJ*. 2014;2:e1100. <https://doi.org/10.3897/BDJ.2.e1100>.
50. Hendrick VJ, Hutchison ZL, Last KS. Sediment burial intolerance of marine macroinvertebrates. *PLoS ONE*. 2016;11(2):e0149114. <https://doi.org/10.1371/journal.pone.0149114>.
51. Rodríguez-Martínez RE, Tussenbroek B, Jordán-Dahlgren E. Afluencia masiva de sargazo pelágico a la costa del Caribe Mexicano (2014–2015). In: García-Mendoza E, Quijano-Scheggia SI, Olivos-Ortiz A, Nuñez-Vázquez EJ, editors. *Florecimientos Algales Nocivos en México*. 1st ed. Ensenada: CICESE; 2016. p. 352–65.
52. Rodríguez-Martínez RE, et al. Faunal mortality associated with massive beaching and decomposition of pelagic *Sargassum*. *Mar Pollut Bull*. 2019;146:201–5. <https://doi.org/10.1016/j.marpolbul.2019.06.015>.
53. Chávez V, et al. Massive influx of Pelagic *Sargassum* spp. on the Coasts of the Mexican Caribbean 2014–2020: challenges and opportunities. *Water*. 2020;12(10):2908. <https://doi.org/10.3390/w12102908>.
54. Climate Prediction Center Internet Team. Cold & Warm Episodes by Season. NOAA/National Weather Service, Center for Weather and Climate Prediction. https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php.
55. Carrillo L, Horta-Puga G, Carricat-Ganivet JP. Climate and oceanography. In: Tunnell JW, Chávez EA, Kim W, editors. *Coral reefs of the southern Gulf of Mexico*. 2nd ed. Corpus Christi: Texas A&M University Press; 2007. p. 34–40.
56. Hoegh-Guldberg O, et al. Coral reefs under rapid climate change and ocean acidification. *Science*. 2007;318(5857):1737–42. <https://doi.org/10.1126/science.1152509>.