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PRIMARY RESEARCH PAPER

Biodiversity distribution patterns of echinoderms from the Gulf of Mexico and adjacent waters: species richness, beta diversity and endemism

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Abstract Echinoderms are a predominantly benthic group with selective substrate preferences, and the Gulf of Mexico exhibits a great diversity of substrates across a well-established physiographic regionalization. Therefore, a spatially structured distribution of this group in the region is expected. However, this hypothesis has not yet been tested at the community level across the entire Gulf. Our objective was to analyze biodiversity distribution patterns of echinoderms in the Gulf of Mexico and adjacent waters. Occurrence records were compiled from the GBIF and OBIS databases and peer-reviewed literature to evaluate the sampling effort, expected richness, beta diversity, and endemism. Sampling effort was higher on the continental shelf of the Yucatán and Florida Peninsulas. Higher expected richness was observed on the continental slope of the region and in the center of the Gulf, while higher endemism was observed in shelf zones and the oceanic Caribbean. Beta diversity allowed the recognition of distinct assemblages that coincide with previously proposed biogeographic areas. This study contributes to establishing a biogeographic baseline of the group in the region. Future perspectives to improve the echinoderm biogeographic knowledge in the Gulf include homogenization of sampling effort, accurate taxonomic identifications, and testing the assemblages identified.

Keywords Echinodermata · Biogeography · Macroecology · Biological assemblages · Western Atlantic

Introduction

The biogeographical patterns of echinoderms have been well-studied at a global scale in recent years (e.g., Ameziane & Roux, 1997; Stöhr et al., 2012; Pérez-Ruzafa et al., 2013; Zamora & Rahman, 2017; Bribiesca-Contreras et al., 2019; O'Hara et al., 2019; Victorero et al., 2023), although most studies have focused on specific clades, such as echinoids or asteroids, either considering benthic or fossil organisms, providing a partial view of the distributional patterns of the group. Echinoderms play a crucial role in the structure and function of marine ecosystems since most of them are filter feeders that contribute to the organic and inorganic carbon cycle, while others

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maintain algal densities controlled (Lebrato et al., 2010; Alvarado & Solís-Marín, 2013). Therefore, studying their distributional patterns is fundamental to understanding their ecology and biogeography. Studies like those of Bribiesca-Contreras et al. (2019), Granja-Fernández et al. (2023), and Maya-Alvarado et al. (2023) have proved this aspect, highlighting the utility of beta diversity for assessing the distributional patterns of echinoderms at global and regional scales. Despite this, the biogeographical knowledge of echinoderms in some regions of the world, such as the Gulf of Mexico, is scarce (Martínez-Melo et al., 2015; Caballero-Ochoa et al., 2017), preventing for recognizing biodiversity and endemism patterns, which are fundamental to the bioregionalization of the region and the conservation of the group.

The Gulf of Mexico is a semi-closed basin of the Atlantic Ocean that provides several ecosystem services derived from its geomorphology and biodiversity (Neigel, 2009; Fautin et al., 2010). The continental shelf of the Gulf represents a continuous that varies in both extent and composition. It reaches its greatest extent in the Yucatán and Florida Peninsulas, exhibiting karstic and shallow features (~50–200 m depth). The rest of the continental shelf is comparatively narrow, conformed by muds and sands of terrigenous origin (Davis, 2017). The region's hydrology is influenced by the Caribbean Current System, which enters the Gulf via the Yucatán Channel, subsequently becoming the Loop Current and finally exiting through the Florida Straits (Davis, 2017; Ward & Tunnell, 2017). The location of the Gulf results in the convergence of warm-temperate (north) and tropical (south and Caribbean) biotas, contributing to high biodiversity and endemism (Engle & Summers, 2000; Neigel, 2009; Ahuatzin-Hernández et al., 2023), which has motivated numerous studies on the diversity distribution of different taxa (e.g., Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023). Due to these characteristics, in addition to the structured physiography of the region (Davis, 2017) and the preference of some echinoderms for specific substrates and habitats, such as rocky, sandy, reef, or seagrass beds (Celaya-Hernández et al., 2008; Pérez-Ruzafa et al., 2013; Doll et al., 2022), a spatially structured distribution of echinoderm diversity is expected. Unfortunately, there is an evident lack of studies assessing the diversity and distributional patterns of echinoderms at a community level considering the entire Gulf of Mexico, so this hypothesis has not been addressed, leaving a gap in the biogeographical knowledge of this group in the region.

Recognizing geographical areas based on the distribution of biotas is of practical interest not only for future decision-making about the management and conservation of natural resources but also for understanding the evolutionary history of a region and the biota that inhabits it (Costello et al., 2017). In this sense, the Gulf of Mexico is geographically divided into the Temperate Northern Atlantic and Tropical Atlantic realms (including the Carolinian and Caribbean Provinces) (Spalding et al., 2007) and the Northern Gulf of Mexico, Southern Gulf of Mexico, and South Florida/Bahamian Atlantic ecoregions (Wilkinson et al., 2009), both schemes suggesting two principal components (north and south). However, these regionalizations are either based on oceanographic and physiographic variables (not necessarily reflecting the distributional patterns and endemism of the biotas) (Wilkinson et al., 2009) or restricted to coastal and shelf areas (Spalding et al., 2007), providing a partial biogeographic view of the region. In this zone, diverse studies have delimited geographic areas considering different taxa, mainly estimating alpha and beta diversity (e.g., Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023). Regarding echinoderms, efforts have been temporarily constant, although spatially and taxonomically punctual (e.g., Beddingfield & McClintock, 2000; Celaya-Hernández et al., 2008; Hernández-Herrejón et al., 2008; Martínez-Melo et al., 2015; Caballero-Ochoa et al., 2017). For instance, previous biodiversity studies only considered some regions of the Gulf (either north or south), excluding neighboring waters, such as the Caribbean, which is crucial to understanding the biodiversity of the region (Pawson et al., 2009; Solís-Marín et al., 2013, 2014a). Consequently, this study aimed to assess the distribution of echinoderm diversity at the community level in the Gulf of Mexico and adjacent waters through the analysis of their richness, endemism, and the recognition of biological assemblages.

Materials and methods

Data acquisition and cleaning process

Locality records of nominal species, subspecies, and genera of echinoderms were obtained from the

Global Biodiversity Information Facility (GBIF, 2023, 2025), the Ocean Biodiversity Information System (OBIS, 2023), and peer-reviewed literature (mainly from the Mexican territory, where sampling effort is lower) (Table 1). Data were retrieved using the search criteria of preserved specimen and material citation. Duplicate records and those falling on land were flagged and removed using the *cc_dupl* and *cc_sea* functions of the 'CoordinateCleaner' R package v. 3.0.1 (Zizka et al., 2019). The World Register of Marine Species (www.marinespecies.org) was then used to reconcile taxa names (including subgenus), correcting synonyms, invalid taxa, and typos. In order to validate the occurrence of each taxon in the study area and increase the certainty of the dataset, each taxon was cross-checked with the most recent inventories of the region (i.e., Abreu-Pérez et al., 2005; del Valle García et al., 2005; Hernández-Herrejón et al., 2008; Laguarda-Figueras et al., 2009; Pawson et al., 2009; Alvarado, 2011; Rodríguez-Barreras & Messing, 2013; Solís-Marín et al., 2013; Martínez-Melo et al., 2016; Gabino-García et al., 2021) and the documented distribution range provided by WoRMS (2024), removing the taxa not reported in these works (Online Resource 1). The data was then coded into two community matrices with species in the columns and quadrants of $1° \times 1°$ in the rows. The size of the quadrants was defined based on the distribution of records (we tested different scales and found that smaller sizes, such as $0.5° \times 0.5°$ resulted in a great number of distributional discontinuities among the quadrants, while larger scales such as $2° \times 2°$ prevented us from recognizing local patterns) and upon previous studies (Engle & Summers, 2000; Ahuatzin-Hernández et al., 2023). The first matrix indicated '1' for the presence of each taxon in each quadrant and '0' for its absence (occurrence matrix) (Online Resource 2). The second matrix was employed to assess the sampling effort by counting the number of records for each taxon in each quadrant (records matrix) (Online Resource 3).

Species richness and endemism

The echinoderm richness was calculated by implementing a rarefaction method, which allowed us to estimate the expected number of species (ES) for each quadrant, considering an uneven sampling effort across the units corresponding to the study

Table 1 List of peer-reviewed literature consulted to supplement the occurrence records dataset

Reference	Jurisdictional territory
Agassiz (1877)	Mexico/USA
Arriaga-Ochoa et al. (2012)	Mexico
Barbosa-Ledesma et al. (2000)	Mexico
Borrero-Pérez et al (2024)	Mexico/USA
Bravo-Tzompantzi et al. (1999)	Mexico
Bribiesca-Contreras et al. (2013)	Mexico
Caso (1979a)	Mexico
Caso (1979b)	Mexico
Caso (1990)	Mexico
Caso (1996a)	Mexico
Caso (1996b)	Mexico
Caso (1996c)	Mexico
Caso et al. (1994)	Mexico
Celaya-Hernández et al. (2008)	Mexico
de la Cruz-Francisco et al. (2017)	Mexico
De los Palos-Peña et al. (2021)	Mexico
del Valle-García et al. (2008)	Cuba
Downey (1971)	Mexico/USA
Downey (1972)	Mexico
Downey (1973)	Mexico/USA/Cuba
Downey (1980)	Mexico
Durán-González et al. (2021)	Mexico
Durán-González et al. (2024)	Mexico
Esteban-Vázquez et al. (2021)	Mexico
González-Gándara et al. (2015)	Mexico
Hendler & Turner (1987)	USA/Cuba
Hendler et al. (1995)	USA
Hernández-Díaz et al. (2013)	Mexico
Hernández-Herrejón et al. (2008)	Mexico
Kuk-Dzul et al. (2019)	Mexico
Laguarda-Figueras et al. (2001)	Mexico
Laguarda-Figueras et al. (2004)	Mexico
Laguarda-Figueras et al. (2009)	Mexico
Laguarda-Figueras et al. (2013)	Mexico
Lawrence et al. (2018)	Mexico/USA
Mah (2015)	USA
Márquez-Borrás et al. (2016)	Mexico
Martín-Cao-Romero et al. (2017)	Mexico
Martin-Cao-Romero et al. (2021)	Mexico
Martínez-Melo et al. (2014)	Mexico
McClintock et al. (2013)	USA
Messing (1978)	USA
Meyer et al. (1978)	USA
Miller & Pawson (1979)	USA/Cuba
Pawson (2018)	Mexico

Table 1 (continued)

Reference	Jurisdictional territory
Pawson et al. (2015)	USA
Quijano et al. (2017)	Mexico
Quiroga Pastor et al. (2019)	Mexico
Rathbun (1885)	Mexico/USA
Rodríguez-Barreras et al. (2007)	Cuba
Rodríguez-Muñoz et al. (2023)	Mexico
Solis-Marín & Laguarda-Figueras (2010)	Mexico
Solís-Marín et al. (1997)	Mexico
Solís-Marín et al. (2007a)	Mexico
Solís-Marín et al. (2007b)	Mexico
Solís-Marín et al. (2014b)	Mexico
Solís-Marín et al. (2015)	Mexico
Thomas (1962)	USA
Zulliger & Lessios (2010)	USA

area. This analysis was conducted with the records matrix, considering 15 randomly chosen subsamples from the original dataset and calculating the mean number of species every 15 records (ES15). A subsample size of 15 was chosen over the global subsample size of 50 due to the low number of records at some sites. This calculation was conducted with the *rarefy* function of the 'vegan' R package v. 2.6.10 (Oksanen et al., 2022), considering the criteria of Hurlbert (1971). Standard errors (SE) were estimated on Heck et al. (1975) (Online Resource 4). Endemism was assessed with the corrected weighted endemism index (CWE). First, we calculated weighted endemism using the *weighted_endemism* function of the 'phyloregion' R package v. 1.0.8 (Daru et al., 2020) on the occurrence matrix, and then each value was divided by the local species richness. Additionally, a mean CWE value was calculated, taking into account all the quadrants conforming to the study area to identify those quadrants with values higher than the overall mean. Finally, in order to evaluate the bias due to an unequal sampling effort on the biodiversity estimators, the Spearman rank correlation coefficient was calculated independently between the sampling effort vector and raw richness, expected richness, and CWE.

Echinoderm assemblages

The echinoderm assemblages were identified by estimating the beta diversity of the occurrence matrix. For this task, hierarchical clustering with contiguity constraint was employed using the *constr.hclust* function of the 'adespatial' R package v. 0.3.24 (Dray et al., 2022). The dissimilarity matrix was estimated using the form $D[ik]=\text{sqrt}((b+c)/(a+b+c))$ of the Jaccard index, where i and k designate two rows of matrix Y. In this context, $D[ik]$ is the dissimilarity between rows i and k, a is the number of shared species between i and k, b is the number of exclusive species of i, and c is the number of exclusive species of k (Legendre & De Cáceres, 2013). The Ward (1963) grouping criterion was employed to identify clusters at three cut-off levels ($k=4$, 6, 8), which is handy for analyzing the assemblage dynamism through different dissimilarity degrees (Vilhena & Antonelli, 2015). Likewise, a principal coordinate analysis (PCoA) was performed with the *pcoa* function of the 'ape' R package v. 5.8.1 (Paradis & Schliep, 2019), utilizing the previously estimated dissimilarity matrix, associating each quadrant of the study area with the cluster to which it was previously assigned. The objective was to analyze the affinity among the assemblages through a spatial gradient. As the dissimilarity matrix possesses Euclidian properties (see Legendre & De Cáceres, 2013), no correction method was employed, as no negative eigenvalues were generated. All the data needed to reproduce the maps (quadrant centroids, biodiversity estimators, including standard errors and biological assemblages) are provided in the Online Resource 4. Analyses were performed in R 4.4.2. (R Core Team, 2024).

Results

Species richness and endemism

After data cleaning, 43,421 echinoderm records were obtained for the study area, corresponding to 624 taxa, including species, subspecies and genera. The geographic distribution of the echinoderm records in each quadrant suggests a higher sampling effort on the continental shelf of the Florida Peninsula, the northern and western part of the Yucatán Peninsula, and the Mexican Caribbean (Fig. 1a). Raw richness showed a similar distribution pattern to that of sampling effort (Fig. 1b). On the other hand, higher values of expected species richness (ES15) were observed throughout the continental slope, escarpment, and oceanic zones (Fig. 1c). The higher values of the CWE index were observed in the northeast and southeast of the study area, mainly in the border of the Florida platform, surrounding western Cuba, in the northeastern and southeastern of the Yucatán Peninsula, and in the Caribbean Sea (Fig. 1d). The Spearman's rank correlation coefficient between the sampling effort and biodiversity estimators proved the raw richness as strongly biased (Spearman $\delta = 0.92$; $P < 0.0001$). Nevertheless, expected richness (Spearman $\delta = 0.61$; $P < 0.0001$) and CWE (Spearman $\delta = 0.32$; $P < 0.0001$) proved to be not influenced by unequal sampling effort.

Echinoderm assemblages

The three cut-off levels evidenced a high turnover in the northern shelf areas of the Gulf of Mexico. When $k = 4$, the 'Northern' assemblage distributes in all the shelf zones of the northern Gulf, encompassing all of the Florida Peninsula and the Coasts of Louisiana, Alabama, Mississippi, and Texas. The 'Sigsbeean' assemblage is distributed in a transitional zone between the continental shelf, the Sigsbee escarpment, and deep oceanic waters in the central region, having a distinctive echinoderm composition that

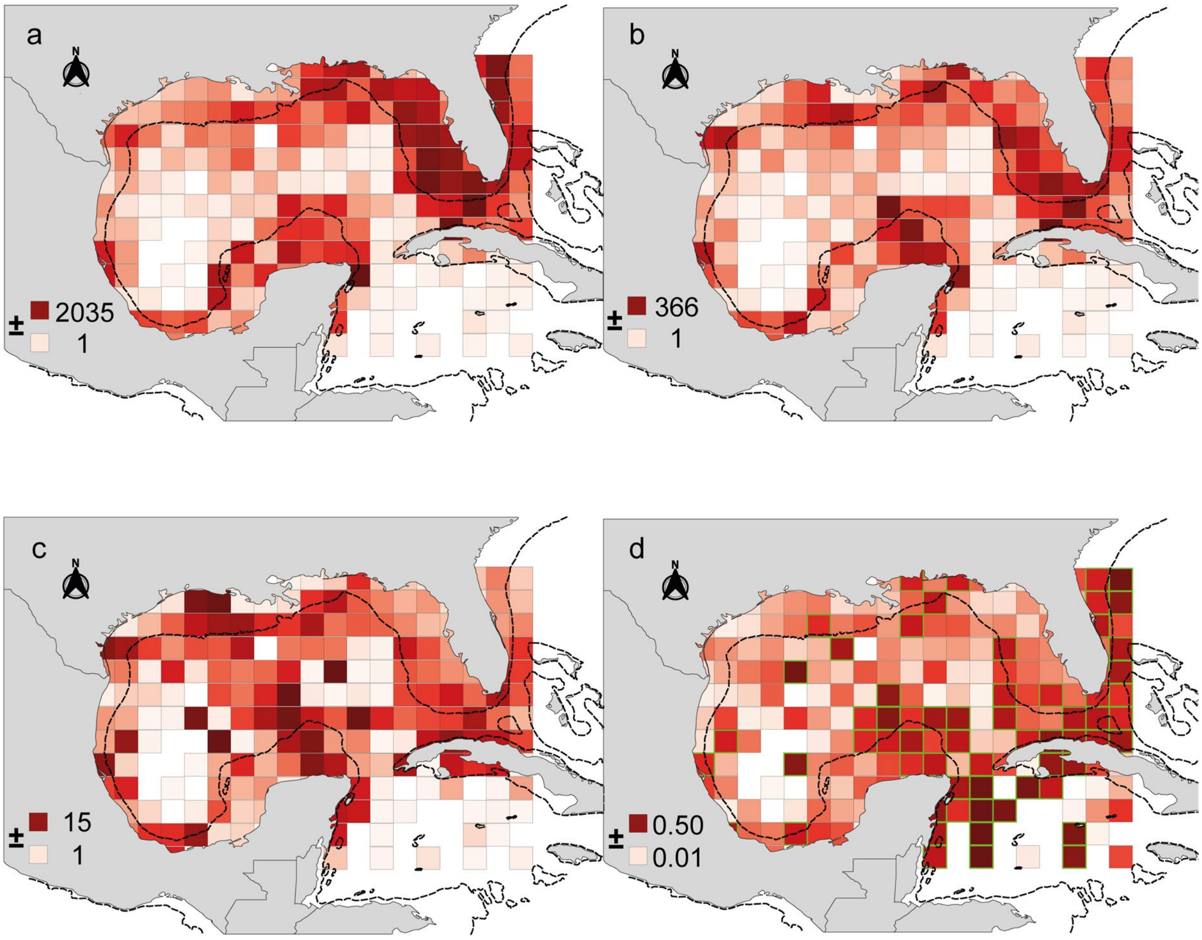

Fig. 1 **a** Sampling effort (distribution records density). **b** Raw richness per quadrant. **c** Expected echinoderm richness per quadrant (ES15). **d** Corrected weighted endemism (CWE). Quadrants with green rims have index values higher than the overall mean. The dashed line represents the 200 m isobath

shows no affinity with any assemblage. The 'Basin' assemblage is distributed mainly in oceanic waters of the basin Gulf, in front of Tamaulipas, although it also characterizes the continental shelf of the Yucatán Peninsula. The 'Transitional' assemblage characterizes the remaining study area, encompassing oceanic waters of the Caribbean Sea, Cuba, part of the central Gulf, and eastern Florida (Fig. 2a–c).

When $k=6$, the 'Transitional' assemblage splits into the 'Southern' and 'Caribbean' assemblages. The former characterizes the slope and shelf of the southwestern Gulf, the slope of Campeche, and a large area of the Yucatán Peninsula platform, showing affinity with the 'Northern' assemblage. On the other hand, the 'Caribbean' characterizes a small oceanic area of the Caribbean Sea, located in the eastern Yucatán Peninsula and southern Cuba, showing no clear affinity with other assemblages (Fig. 2a–c).

Finally, when $k=8$, the 'Northern' assemblage splits into the 'Floridan', 'Texan', and 'Northern-slope' assemblages. The 'Floridan' assemblage is distributed on the Florida Peninsula, showing affinity with the 'Southern' assemblage. The 'Texan' assemblage characterizes the northwestern shelf of the region, off the states of Texas, Louisiana, and Mississippi, showing affinity with the 'Floridan' and 'Transitional' assemblages. Finally, the 'Northern-slope' assemblage characterizes the western continental slope of the Florida Peninsula, having more affinity with the 'Southern' assemblage (Fig. 2a–c).

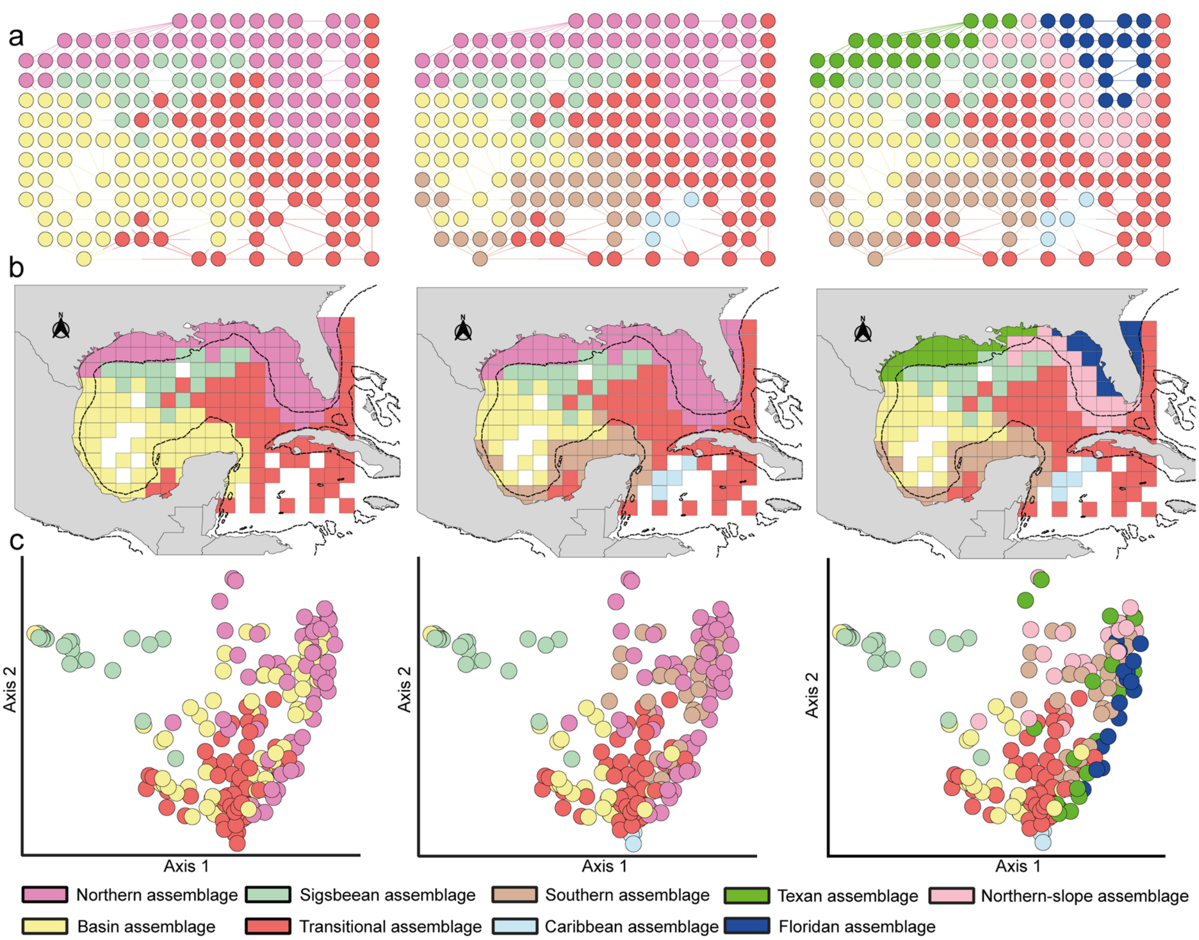

Fig. 2 Equinoderm assemblages in the Gulf of Mexico and adjacent waters considering different cut-off levels ($k=4$, 6, 8 respectively). **a** Hierarchical clustering with contiguity constraint (dotted lines represent edges with vertices in different clusters). **b** Geographic distribution of echinoderm assemblages (dashed line represents the 200 m isobath). **c** Principal Coordinates Analysis (PCoA) based on the dissimilarity matrix used to identify echinoderm assemblages

Discussion

Species richness and endemism

The uneven sampling effort across the study area can be attributed to diverse factors, such as (1) the distribution of researchers and marine research centers in different locations (e.g., in Mexican territory, only the Sistema Arrecifal Veracruzano, and the slope of the Yucatán Peninsula are comparable to the sampling effort conducted in US territory, such as the Florida Peninsula; Solís-Marín et al., 2013); (2) differences in investment in biodiversity projects among the three countries sharing the Gulf of Mexico waters (the US invests higher budget in biodiversity research than Latin America; Cardoso et al., 2024); (3) accessibility of sampling sites (zones with extensive coastal territory have a greater diversity of ecosystems such as lagoons, bays or estuaries, which are easier and cheaper to access). Direct estimation of biodiversity based on raw richness information is not recommended, as it is strongly biased by unequal sampling effort. In contrast, the rarefaction method and CWE seem to be more reliable approaches to estimating richness and endemism with this type of data, consistent with previous studies (Brown et al., 2016; Arfianti & Costello, 2020). However, other strategies need to be tested, such as considering other indices or different subsample sizes to reduce the correlation with sampling effort.

The number of echinoderm species reported in this study is greater than in the previous inventories for the region (see Pawson et al., 2009; Solís-Marín et al., 2013, 2014a), suggesting that knowledge of species richness has increased in recent years. It is worth mentioning that previous checklists considered only some of the regions dealt with in this study, either the Mexican Gulf and the Caribbean (Solís-Marín et al., 2013, 2014a) or excluded the Caribbean (Pawson et al., 2009), making it difficult to make a direct comparison. Moreover, this study considered subspecies, which are likely to have added taxa to the previously conducted inventories. This encourages further efforts to integrate knowledge of echinoderm biodiversity, as the Gulf of Mexico is highly connected to and shares many species with adjacent zones, such as the Mexican Caribbean, Cuba, and the eastern Florida Peninsula. The distribution pattern of the expected richness (ES15) across the continental slope suggests the conformation of an ecotone between shelf and oceanic biotas, which has been pointed out previously (Escobar-Briones, 2004) and supports the hypothesis that the Gulf of Mexico encompasses two main biotic components, one characteristic of oceanic zones and the other characteristic of shelf zones (Ahuatzin-Hernández et al., 2023; Oliveira et al., 2024). The pattern of endemism is consistent with previous studies, indicating the highest values of endemism for hydrozoans and amphipods in the Yucatán and Florida peninsulas (Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023). These facts suggest that the Gulf continental platform and slope are physical barriers between neritic and oceanic biotas, as well as fundamental components for understanding the biogeography of the region (Oliveira et al., 2024).

Echinoderm assemblages

The high turnover in the northern shelf areas of the study area is also reported with hydrozoans (Ahuatzin-Hernández et al., 2023). This has been associated with the presence of a transition zone in this area, where two different biotas overlap, one characteristic of tropical waters (part of the Florida Peninsula) and the other of warm-temperate waters (off Alabama and Texas). The 'Northern' assemblage is consistent with the Northern Gulf of Mexico ecoregion proposed by Wilkinson et al. (2009), which is characterized by a broad continental shelf and semi-tropical waters (Wilkinson et al., 2009), contributing to the conformation of a warm-temperate biota in this region. The western area of the 'Northern' assemblage is distinguished by numerous fluvial channels, muds, sands, relict reefs and knolls (Davis, 2017), while the eastern zone, delimited by the Florida Peninsula, constitutes a thick accumulation of limestone surface with scattered carbonate and terrigenous sediments (Davis, 2017). According to previous studies, in the northern Gulf of Mexico, some echinoderms are more dominant, showing a relationship with some substrates; for instance, in eastern Alabama and Northwest Florida, the most common species are *Astropecten articulatus* (Say, 1825), *Luidia clathrata* (Say, 1825), *Ophiolepis elegans* Lütken, 1859, *Clypeaster prostratus* Ravenel, 1848 (associated with quartz sand sheet, and relic carbonate sediments of biological origin), *Echinaster* (*Echinaster*) *modestus* Perrier, 1881, *Echinaster* (*Othilia*) *brasiliensis* Müller & Troschel, 1842, *Pawsonaster parvus* (Perrier, 1881), *Anthenoides peircei* Perrier, 1881, *Asteroporpa* (*Asteroporpa*) *annulata* Örsted & Lütken in Lütken, 1856, *Stylocidaris affinis* (Philippi, 1845), *Genocidaris maculata* A. Agassiz, 1869, *Psolus tuberculosus* Théel, 1886 (associated with relic algal nodules), and *C. ravenelii* (A. Agassiz, 1869) (associated with hard packed quartz sand sheet) (Hopkins et al., 1991). This supports the hypothesis that substrate preferences of some echinoderms contribute to understanding their distributional patterns in the region.

The area delimited by the 'Sigsbeean' assemblage partially matches the bathymetric zonation of the deep-sea macrofauna in this region (Wei et al., 2010), which is influenced by the Mississippi River plume (Shin et al., 1977; Williams et al., 2011; Yarbuh & Contreras, 2015). This area is distinguished by high relief and ridges (Shin et al., 1977; Buffler & Worzel, 1978), while the influence of the Mississippi River provides this area with soft sediments, organically enriched, which are favorable for filter feeders echinoderms, mainly holothurians and some echinoids. Therefore, a biota consisting predominantly of sea cucumbers and sea urchins is expected in this region (Khanna & Yadav, 2005; Carney, 2010; Pawson et al., 2015). Recent studies have evidenced a distinct composition of echinoids and holothurians in this zone, even describing new species and providing new records for the Gulf of Mexico, which support the conformation of the 'Sigsbeean' assemblage (Pawson et al., 2015). Additionally, the abrupt change in the bathymetry of the Sigsbee escarp (Roberts, 2011) and the characteristic relief of the zone likely represent a geographic barrier between neritic and oceanic biotas, contributing to its distinct echinoderm composition and low affinity with the remaining assemblages when $k=4$ (Fig. 2c) (Petović & Krpo-Ćetković, 2016). The 'Basin' assemblage includes an area distinguished by the Mexican Ridges Foldbelt and the Campeche Salt basin in its southern region and by part of the Port Isabel and Perdido Foldbelts in the northern (Yarbuh & Contreras, 2015). This assemblage supports the hypothesis of an oceanic biotic component in the basin Gulf when $k=6$ and 8 (Ahuatzin-Hernández et al., 2023, 2024).

The area delimited by the 'Southern' assemblage is characterized by coral reefs, e.g., Sistema Arrecifal Veracruzano (off the Coast of Veracruz), Campeche Bank Reefs (north of the Yucatán Peninsula), and Sistema Arrecifal Mesoamericano (Quintana Roo) (Rioja-Nieto et al., 2019; Turner & Rabalais, 2019). Coral development is a key factor in understanding the spatial patterns of echinoderm assemblages (González-Gándara et al., 2015; Hermosillo-Núñez et al., 2023; Sotelo-Casas et al., 2025) and allowed us to explain the conformation of the 'Southern' assemblage. Moreover, there is a large coverage of seagrasses and macroalgae in this area, which provides food and substrate availability for many species, mainly for grazer echinoids (Celaya-Hernández et al., 2008). The area delimited by this assemblage can be divided into two regions: the western region, characterized by the Tuxpan platform and the northern Chiapas basin, and the southeastern region, characterized by the extensive karst platform of the Yucatán Peninsula (Yarbuh & Contreras, 2015). The affinity of the 'Southern' assemblage with the 'Northern' is consistent with previous studies (Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023), being explained by the similarity between the Yucatán and Florida Peninsulas, the influence of the Loop Current (Davis, 2017; Rioja-Nieto et al., 2019; Turner & Rabalais, 2019), and the ancient connection between the Yucatán and Florida Platforms (~ 140–160 Ma) (see Bird et al., 2011). In addition, this assemblage is consistent with three areas of endemism and different generalized tracks identified with irregular echinoids and gelatinous zooplankton, which supports its recognition as a biogeographic area (Martínez-Melo et al., 2015; Caballero-Ochoa et al., 2017; Ahuatzin-Hernández et al., 2024).

The 'Caribbean' assemblage suggests the presence of a distinct open-ocean echinoderm component. In this region, Ophiuroidea has been reported as the richest class, followed by Asteroidea (Pérez-Ruzafa et al., 2013). Due to the strong current system of the Caribbean, a great diversity of suspensive filter-feeder echinoderms is expected, such as crinoids and some holothurians (Meyer, 1973; Hendler et al., 1995). Previous studies have assessed biogeographic patterns in the Caribbean Sea, considering echinoderms, shorefishes, and azooxanthellate corals (Dawson, 2002; Alvarado, 2011; Robertson & Cramer, 2014). However, as these studies considered larger geographic units, a direct comparison with the area characterized by the 'Caribbean' assemblage is not possible. Given its affinity with the 'Transitional' assemblage and its geographic location, it is likely that the 'Caribbean' represents an assemblage composed of deep-water echinoderms. Building on this, in the Caribbean, the class Ophiuroidea is reported as predominant at depths between 1000 and 2000 m, while Asteroidea and Holothuroidea are predominant at depths between 2000 and 6000 m (Pérez-Ruzafa et al., 2013).

The 'Texan' assemblage coincides with a previously recognized hydrozoan assemblage, supporting a differentiated biotic composition from the rest of the study area (Ahuatzin-Hernández et al., 2023). The area delimitated by this assemblage has low relief, although it does have some reefs, relict knolls, and barrier islands (Holmes, 2011). Off the Coast of Texas, there are also diverse wetlands and associated environments, such as bays and estuaries, which harbor biotas adapted to their environmental features (Fautin et al., 2010; Williams et al., 2011; Davis, 2017), contributing to the endemism and regionalization of the area. The 'Floridan' assemblage supports the hypothesis that the Florida Platform constitutes a biogeographic area (Spalding et al., 2007; Paz-Ríos et al., 2021; Oliveira et al., 2024), as its distribution matches previous studies (Coppard & Lessios, 2017; Hancock et al., 2019; Oliveira et al., 2024), part of the geological boundaries of the Florida Platform and physiographic provinces of the region (Yarbuh & Contreras, 2015; Davis, 2017). The Florida Peninsula is distinguished by diverse habitats, many of which are favorable for the settlement and development of echinoderm communities. For instance, this area has extensive seagrass and macroalgae coverage, which are characteristic habitats for ophiuroids and sea urchins (Hendler et al., 1995; Muzaki et al. 2019; Czaja Jr & Pomory, 2022). Meanwhile, the mussel- and mud-rich sediments of the mangrove channels and nearby areas provide suitable habitats for brittle stars and suspension-feeding sea cucumbers (Hendler et al., 1995). These characteristics, together with historical and geological factors such as the karstic composition of the peninsula, the influence of the Mississippi River, episodic sedimentation events, and multiple range contractions and extinction events, allowed us to explain its diverse and distinct echinoderm fauna (Coppard & Lessios, 2017; Hancock et al., 2019).

The 'Northern-slope' assemblage matches the distribution of hydrozoans (Ahuatzin-Hernández et al., 2023) and partially matches the distribution of the Northern Gulf of Mexico Slope ecoregion, proposed by Wilkinson et al. (2009). The echinoderm fauna associated with the slope of the Gulf of Mexico is distinguished to present high abundance, endemism, and richness, especially in asteroids, ophiuroids, and holothuroids (Carney, 2010). In addition, the structure of the echinoderm community changes with depth in this area. For example, holothuroids of the superfamily Elasipodida become dominant at greater depths, asteroids are larger in size than in shallow waters, while ophiuroids are smaller than holothuroids and asteroids (Carney, 2010). This supports the hypothesis that the continental slope not only constitutes a barrier between shelf and oceanic biotas but also encompasses a distinct echinoderm composition, likely due to the convergence between two different regions. The affinity between the 'Northern-slope' and the 'Southern' assemblages may reflect their slope nature, both sharing oceanic and shelf taxa.

Conclusion

The assessment of the sampling effort bias is crucial for biodiversity studies based on species records from online databases. Conducting analyses that take this issue into account is fundamental to generating reliable estimates of the spatial patterns of biodiversity in light of this bias, especially at biogeographic scales (Cardoso et al., 2024). In this sense, rarefaction methods, CWE, and beta diversity estimated with the Jaccard index demonstrated to be good strategies in the face of these challenges.

The echinoderm diversity in the Gulf of Mexico and adjacent waters exhibits spatially structured patterns that coincide with previously proposed ecoregions and biogeographic areas. Likely, these patterns correspond to the selectivity of each echinoderm group for different substrates. According to Pérez-Ruzafa et al. (2013), the most common substrates for echinoderms are rocky, rubble, reef, sand, and seagrass habitats. This is a crucial aspect when evaluating the ecology and the distributional patterns of the group, as well as understanding the distribution of the assemblages identified in this study. Unfortunately, our analyses did not allow us to identify the affinity of each taxonomic group (i.e., Asteroidea, Ophiuroidea, Crinoidea, Echinoidea, Holothuroidea) with the different substrates that characterized the areas delimited by the assemblages (species are lost when estimating the distance matrix for beta diversity). Hence, this is a pending task for future studies, as it is a key point to understanding the biogeography of this and other benthic groups of the region.

The study of echinoderms in the Gulf of Mexico has been intermittent and uneven across the different jurisdictions that comprise the region (Pawson et al., 2009; Solís-Marín et al. 2013, 2014a), providing a partial picture of the group diversity; thus, more efforts are needed in this sense. Finally, this study contributes to the biogeographical baseline of the Gulf of Mexico. Future perspectives for the echinoderm biogeography in the region include: (1) generating a more homogeneous sampling effort, especially regarding oceanic zones; (2) implementing integrative taxonomic approaches that clarify the identity of cryptic groups (if taxonomic identity changes, the distributional pattern will also change); and (3) validating the assemblages identified in this study by comparing them with assemblages identified with other taxonomic groups and by implementing cladistic biogeographic analyses.

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Data availability All data supporting the findings of this study are available within the paper and its Supplementary Information.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest and non-financial interests.

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