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Assessing the distribution of algal biodiversity across the shelf zones of the Gulf of Mexico and adjacent waters

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ABSTRACT

Algae constitute a group of autotrophic organisms that play a critical role in the functional structure of the oceans. However, research on their biodiversity distribution at a community level, considering a biogeographic scale, has been scarce in some regions, such as the Gulf of Mexico. Thus, this study aims to address this gap by analyzing the continental shelf algae of the Gulf of Mexico. Information was compiled from the GBIF, OBIS, and SNIB-CONABIO databases. Biodiversity distribution patterns were assessed by estimating the expected richness using a rarefaction method, corrected weighted endemism index, and recognizing algal assemblages. Bias due to the unequal sampling effort was also assessed. The expected richness and endemism patterns were not influenced by the sampling effort. Expected richness was homogeneous across the study area, except on the Texas-Louisiana shelf, likely due to the accessibility of coastal environments and the exclusion of the historically understudied oceanic component. Otherwise, endemism was low throughout most of the study area, which may reflect the high dispersal rate of planktonic and drifting algae. Identifying distinct assemblages allowed us to recognize a spatially structured algal community, which matched previously proposed ecoregions in the area. Our findings provide valuable information on the distributional patterns of algae in the Gulf of Mexico and contribute to establishing a biogeographic baseline for the region. Future biogeographic perspectives in the Gulf include increasing the sampling effort, addressing algae's response to environmental variability at a regional scale, and corroborating the assemblages recognized by comparing them with other taxonomic groups.

1. Introduction

Algae constitute a group of eukaryotic and autotrophic organisms distributed in almost all marine and freshwater environments of the photic zone (Kerswell, 2006; Duarte et al., 2022). Based on their size, algae can be classified into two major groups, i.e., micro- and macroalgae, which has oriented their study (Wulff et al., 2009). Globally, algae play a fundamental role by producing 50–70 % of the atmospheric oxygen (Sekerci and Petrovskii, 2015). In the ocean, some macroalgae represent habitats for other organisms (e.g., kelp forests, pelagic *Sargassum* islands) (Bojorge-García and Cantoral-Uriza, 2016; Brodie et al., 2017) and actively participate in biogeochemical cycles by sequestering carbon and nitrogen from ecosystems (Battin et al., 2008). Hence, studying their distribution is fundamental to knowing their natural history, as well as ecological and biogeographic aspects that facilitate management planning for their conservation (Vilchis et al., 2018). The global biogeography of this group has been well-studied in recent years (e.g., Kerswell, 2006; Vieira et al., 2021; Rebelo et al., 2021). However, in some regions, such as the Gulf of Mexico (GoMx), its study has been spatially localized, providing a partial vision of its distribution patterns (e.g., Vilchis et al., 2018; Guinda et al., 2012; Correia et al., 2022).

The GoMx is a semi-closed basin of the Atlantic Ocean with high biodiversity owing to a complex geological and oceanographic history (Galloway, 2011). The continental shelf of the GoMx is one of its most important geological features, due to its large extent, karstic composition, and several reefs in the Yucatán and Florida peninsulas (Davis, 2017). In the rest of the region, the continental shelf becomes narrower

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and consists of terrigenous sediments derived from rivers and highly productive ecosystems (Chanton et al., 2019). The continental slope of the GoMx is characterized by a sharp bathymetric change towards the oceanic region, where the environmental characteristics are more homogeneous (Roberts, 2011). Therefore, biotic differentiation between shelf and oceanic communities is expected in response to their abiotic differences (Ahuatzin-Hernández et al., 2023; Oliveira et al., 2024). Environmental features are also fundamental to understanding species distribution in the region. For instance, the northern Gulf is characterized by warm-temperate waters, while the southern zone has tropical waters, resulting in the convergence of two historically differentiated biotas (Neigel, 2009; Ahuatzin-Hernández et al., 2023). Unfortunately, studies testing these hypotheses in the region are null, and those analyzing the distributional patterns of shelf biotas are spatially local (e.g., Espinosa-Fuentes and Flores-Coto, 2004; King et al., 2013; Vilchis et al., 2018). Few studies have addressed the distribution patterns of biotas across the continental shelf of the entire GoMx (Murawski et al., 2018; Ahuatzin-Hernández et al., 2023), but no one has intended to assess them considering algae as a taxonomic group and at a regional scale, which represents a gap in the biogeographic knowledge of the region for a future regionalization.

Biogeographical regionalization is essential to understanding the evolutionary history of biotas and for management planning and conservation decision-making (Costello et al., 2017). One of the first steps in biogeographical regionalization is to identify patterns of biodiversity distribution. This task has been performed with different taxa in the GoMx (e.g., Engle and Summers, 2000; Vilchis et al., 2018; Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023; Hernández-Zaltrón et al., 2025). Even different area schemes have been proposed, recognizing two main regions, the northern and the southern (Spalding et al., 2007; Wilkinson et al., 2009). However, these schemes do not necessarily reflect the distribution patterns and endemism of the taxa, so an approach with these characteristics is needed (Ahuatzin-Hernández et al., 2023). For algae, the sampling effort across the continental shelf of the GoMx is relatively homogeneous (Cardoso et al., 2024); however, biogeographic studies have been punctual (e.g., Garduño-Solórzano et al., 2005; Vilchis et al., 2018; Hernández et al., 2021), leading to a gap in the biodiversity distribution knowledge of the region. Consequently, the objective of this study was to assess the distribution of algal biodiversity across the continental shelf of the GoMx by analyzing species richness and endemism, as well as recognizing biotic assemblages.

2. Material and methods

2.1. Data acquisition and cleaning process

In order to compile the geographic information, we retrieved occurrence records of the phyla/division Chlorophyta, Heterokontophyta, Rhodophyta, and Prasinodermatophyta from the online databases Global Biodiversity Information Facility (GBIF.org, 2023; GBIF.org, 2024a; GBIF.org, 2024b), the Ocean Biodiversity Information System (OBIS.org, 2023; OBIS.org, 2024a; OBIS.org, 2024b) and the Sistema Nacional de Información sobre Biodiversidad (SNIB-CONABIO, Gallegos Martínez et al., 2018). We also integrated the database of Castillo et al. (2024), which is partnered with GBIF. Only records at the species level, with geographic coordinates and from 'preserved specimen' and 'material citation', were considered. Duplicated records and those falling on land were removed with the CoordinateCleaner package (Zizka et al., 2019). Typos, invalid species, and synonyms were checked against the World Register of Marine Species (WoRMS). The accuracy of the dataset was then validated by manually verifying the distribution of each species against the distribution range provided by WoRMS (partnered with AlgaeBase) and peer-reviewed literature (Supplement 1). Subsequently, the 200 m isobath was implemented as a proxy for the continental shelf of the GoMx to remove all records outside its boundaries. The final database consisted of 21 792 records (Supplement 2), which were coded into two community matrices of species per quadrants (1° x 1°). The first matrix codified the number of records of each species in each quadrant and was used as a proxy to assess the sampling effort (records matrix) (Supplement 3). The second matrix coded '1' for the presence of each species in each quadrant and '0' for its absence (occurrence matrix) (Supplement 4).

2.2. Algal richness and endemicity

Species richness was calculated as the expected number of species in a sample of (*n*) randomly selected records from a sample with (*N*) records, (*S*) species, and *Ni* records of the *ith* species. This calculation was performed on the records matrix using the vegan package (Oksanen et al., 2022), considering 15 random subsamples (ES15), and the criteria of Hurlbert (1971) and Heck et al. (1975). This approach has proven useful in studies with large databases coming from online repositories, which are strongly influenced by unequal sampling effort (e.g., Arfianti and Costello, 2020; Pamungkas et al., 2021; Kohlenbach et al., 2023). The algal endemicity of the GoMx was addressed with the corrected weighted endemism (CWE) index. First, the weighted endemism index was calculated using the 'phyloregion' package (Daru et al., 2020) on the occurrence matrix. CWE was then estimated by dividing each weighted endemism value by the local species richness. Bias in the richness and endemism due to unequal sampling effort was assessed using Spearman's rank correlation coefficient, contrasting the sampling effort vector (number of records per quadrant) against the raw richness, expected richness, and CWE vectors. To account for the gaps in certain zones due to the lack of sampling, an inverse distance-weighted interpolation was performed on the number of records per quadrant (sampling effort), expected richness, and CWE, using QGIS v 3.32.3. This method explicitly assumes that things close together are more similar than things farther apart. To do this, the sampled points are weighted during the interpolation so that the influence of one point relative to another decreases with the distance to the unknown point to be created.

2.3. Algal assemblages

Algal assemblages were identified by evaluating beta diversity. Thus, the form $D[ik] = sqrt((b+c) / (a+b+c))$ of the Jaccard index was estimated with the adespatial package (Dray et al., 2022), where i and k denote two rows of the matrix Y, $D[ik]$ 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. This formula provides a dissimilarity matrix with Euclidean properties, which is handy in subsequent ordination analyzes that depend on this property (Legendre and De Cáceres, 2013). A hierarchical clustering with contiguity constraint was then performed using the grouping criterion of Ward (1963) and considering three different cut-off levels (k = 4, k = 5, k = 6). Finally, principal coordinates analysis (PCoA) was conducted using the previously obtained dissimilarity matrix and considering the recognized assemblages in each cut-off level. The combination of classification and ordination methods considering different dissimilarity levels is useful since it allows us to analyze the dynamism of assemblages, spatial gradients, and biological affinities, all of which are fundamental for the recognition of biogeographically important areas, such as transition zones (Kreft and Jetz, 2010; Vilhena and Antonelli, 2015).

3. Results

3.1. Algal richness and endemicity

A total of 765 species were recorded in the study area. The number of records shows a homogeneous distribution across the continental shelf of the GoMx, except for reef zones and the Texas-Louisiana shelf (Fig. 1A-B). Raw species richness values were strongly correlated with

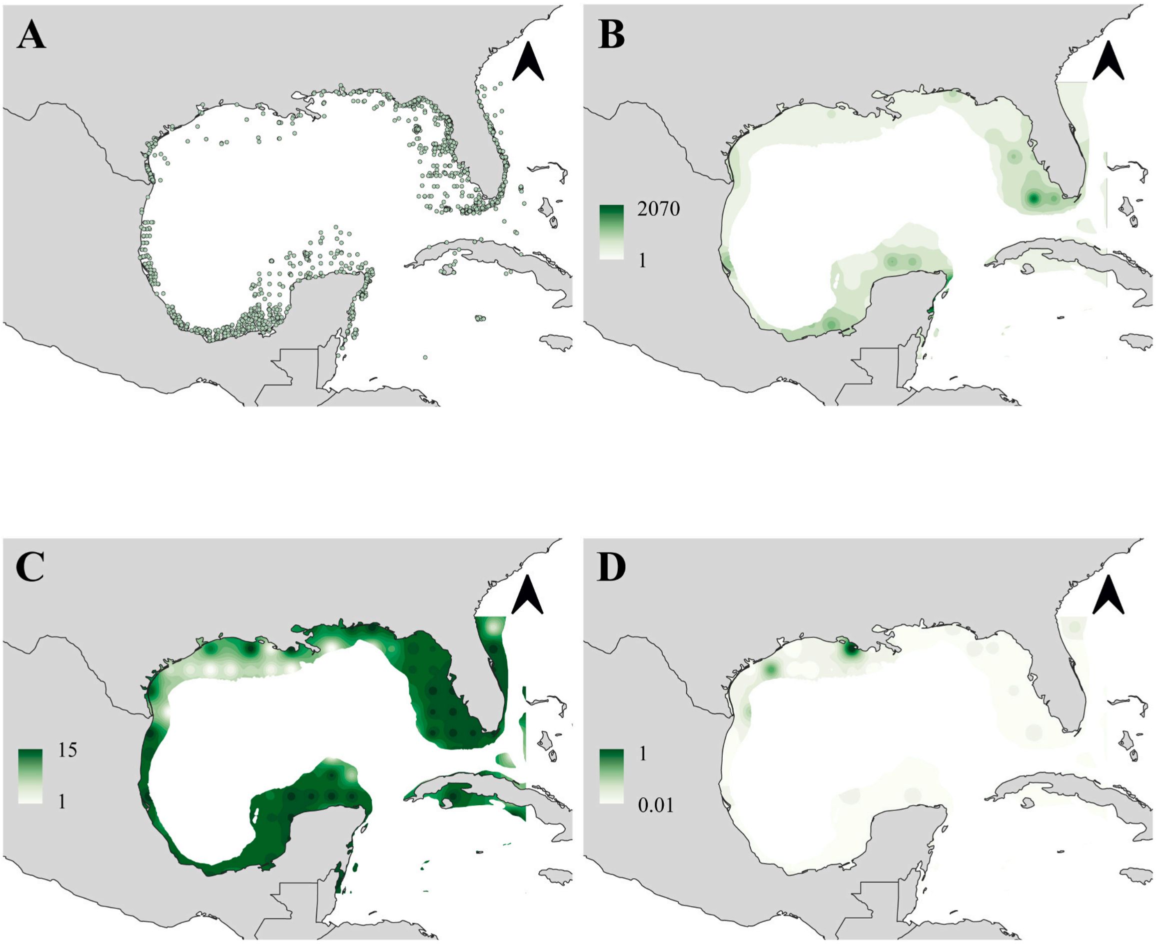

Fig. 1. Distribution patterns of algal biodiversity across the continental shelf of the Gulf of Mexico and adjacent waters. A) Distribution of algae records in the study area. B) Sampling effort distribution. C) Expected richness distribution. D) Corrected Weighted Endemism (CWE) distribution.

the sampling effort (Spearman rho = 0.96; $p < 0.0001$). In contrast, the expected richness distribution was homogeneous throughout the study area and did not correlate with the sampling effort (Spearman rho = 0.65; $p < 0.0001$) (Fig. 1C). Algal endemicity was low across the study area, except at two sites located off Louisiana and Texas (Fig. 1D) and proved to be not influenced by unequal sampling effort (Spearman rho = 0.44; $p < 0.0001$).

3.2. Algal assemblages

When k = 4, the 'Yucatanian' assemblage characterizes the Yucatán Peninsula and part of the western peninsula, off the states of Tabasco and Veracruz. The 'Veracruzanian' assemblage is distributed along the coast of Veracruz, in front of Tabasco and Campeche, having a distinct algal composition that shows no affinity with other assemblages. The 'Floridan' assemblage is restricted to the Florida Peninsula, mainly to its southern part, and shows affinity with the 'Yucatanian' assemblage. The 'Transitional' assemblage shows a discontinuous distribution, being distributed from the eastern side of the northern Florida Peninsula, including escarpment zones of the western Florida platform and the Texas-Louisiana shelf to the coasts of Tamaulipas. In the southern zone, it characterizes the Campeche and Yucatán escarpments (Fig. 2A-C). When k = 5, the 'Transitional' assemblage splits and emerges the 'Tamaulipan' assemblage in the northwestern Gulf, off the coasts of Tamaulipas and Texas. This assemblage showed an affinity with the 'Floridan', 'Yucatanian', and 'Transitional' assemblages. Finally, when k = 6, the 'Transitional' assemblage splits again, emerging the 'Texan' assemblage, which characterizes the Texas-Louisiana shelf and some points of the northern Yucatán shelf escarpment. This assemblage evidences a distinct algal composition that is only related to the 'Transitional' assemblage (Fig. 2A-C).

4. Discussion

4.1. Algal richness and endemicity

The homogenous distribution of the sampling effort across the study area contrasts with previous studies where a bias between shelf and oceanic zones was observed (Miloslavich et al., 2010; Ahuatzin-Hernández et al., 2024). This can be explained by excluding the oceanic component, which has historically been less studied in the region (Cardoso et al., 2024). For instance, neritic zones have a greater variety of ecosystems, such as lagoons, bays, and estuaries, which are easier and cheaper to access, enabling a more constant effort (Hernández-Zaltrón et al., 2025). In contrast, sampling the different strata of oceanic zones requires specialized gear, which is expensive, resulting in a clear distinction in the available information on neritic and oceanic environments. This fact allows us to understand the homogenous distribution of richness, which is likely due to different punctual efforts across the continental shelf, while the variety of substrates (e.g., karst, silt, sand), together with the influence of rivers and upwellings, explains the high values of richness in almost all the study area (Garduño-Solórzano et al., 2005; Hernández et al., 2021). The low richness of the Texas-Louisiana shelf matches the low sampling effort in the zone (Fig. 1B-C). This pattern is likely due to the high sedimentation rate, low salinity, and turbidity, which creates a dead zone where it is difficult for

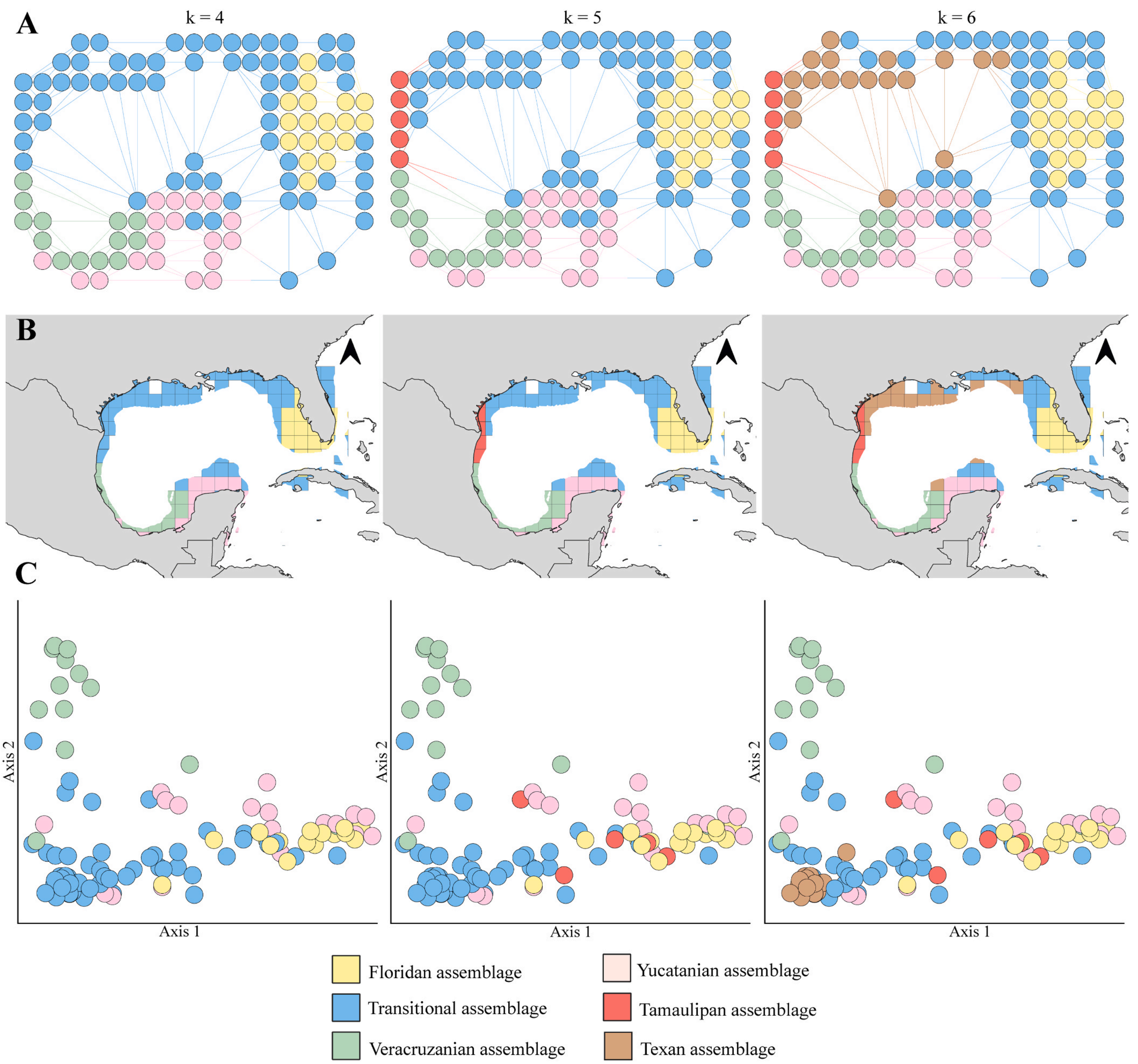

Fig. 2. Algal assemblages across the continental shelf of the Gulf of Mexico and adjacent waters. A) Hierarchical clustering with contiguity constraint (dotted lines represent edges with vertices in different clusters). B) Geographical distribution of algal assemblages. C) Principal Coordinates Analysis (PCoA) based on the dissimilarity matrix used to identify algal assemblages.

some organisms to develop (Rezak et al., 1990; Wilkinson et al., 2009; Hancock et al., 2019). The high endemism in the Texas-Louisiana shelf can be explained by the Atchafalaya River, which loads low salinity water with sediments and nutrients, causing dramatic effects on coastal habitats, disrupting the ranges of some coastal species and foresting a distinct environment (Neigel, 2009), additionally to the dead-zone effect due to the high sedimentation rate, low salinity, and turbidity of the zone (Rezak et al., 1990; Wilkinson et al., 2009; Hancock et al., 2019).

4.2. Algal assemblages

The 'Floridan' and 'Yucatanian' assemblages coincide with previous studies, indicating that the Yucatán and Florida peninsulas have distinct biological compositions with certain affinity between them. This pattern supports the hypothesis that both peninsulas can be recognized as biogeographic areas (Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023; Oliveira et al., 2024). Particularly, the 'Floridan' assemblage supports the biogeographic boundaries proposed by Walker et al. (2020) and Blank et al. (2022) for the region. The biological affinity between the Yucatán and Florida peninsulas has been noted with other taxonomic groups (Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023; Hernández-Zaltrón et al., 2025), being attributed to ecological and historical aspects such as their karstic composition, the influence of the Loop current and an ancient connection between the two peninsulas (Wilkinson et al., 2009; Bird et al., 2011; Paz-Ríos et al., 2021; Ahuatzin-Hernández et al., 2023). The 'Veracruzanian' assemblage is spatially consistent with different generalized tracks identified with macroalgae, echinoderms, members of the gelatinous zooplankton, and previous regionalizations of the shelf zones (Caballero-Ochoa et al., 2017; Vilchis et al., 2018; Ahuatzin-Hernández et al., 2024; Oliveira et al., 2024). The area delimited by 'Veracruzanian' is characterized by the influence of rivers, which play a crucial role in the distribution of algae, explaining its conformation and distinct algal composition that does not show affinity with other assemblages (Lara-Lara et al., 2008). The distribution of the 'Transitional' assemblage partially coincides with previous zonations of the northern GoMx coasts (Engle and Summers, 2000). Its discontinuous distribution and dynamism through different dissimilarity levels suggest the conformation of a transition zone in some of the regions that characterize it.

The 'Tamaulipan' assemblage matches the location of the Laguna Madre. This lagoon is characterized by its hypersaline conditions and long water exchange, either with the GoMx or other lagoons of the zone, creating a distinct physiographic and biological environment from those of the zone (Parker, 1959; Buskey et al., 1998). The affinity of 'Tamaulipan' with quadrants corresponding to the northern assemblages is supported by Aguilar-Medrano and Vega-Cendejas, (2019), who analyzed the biogeographic affinities of fishes and found that the Laguna Madre is more related to the northern provinces of the region. Additionally, this area has been indicated as a boundary between the northern and southern provinces (Oliveira et al., 2024), reflecting the gradual change between tropical and warm-temperate environments. The 'Texan' assemblage is spatially consistent with other assemblages identified with hydrozoans and echinoderms (Ahuatzin-Hernández et al., 2023; Hernández-Zaltrón et al., 2025), suggesting this zone to possess abiotic characteristics that allow a distinctive biological conformation. The area delimited by this assemblage is characterized by reefs, relict knolls, and barrier islands (Holmes, 2011). The discontinuous distribution pattern of this assemblage has been observed in other regionalizations (Oliveira et al., 2024), suggesting a biological connectivity between the Texas-Louisiana shelf and some points of the northern Yucatán shelf escarpment.

5. Conclusion

The present study contributes to establishing a biogeographic baseline of the GoMx and adjacent waters. In this sense, the algal diversity of the GoMx shelf zones showed spatially structured patterns, which are consistent with previously proposed biogeographic ecoregions that can be understood through oceanographic and geomorphological aspects. The exclusion of the oceanic algal component allowed us to homogenize the sampling effort, which has been a challenging task for this type of research, and it represents a good strategy for addressing biogeographic aspects of the region. The low endemism reflects the high dispersal rate of planktonic and drifting algae, due to the influence of the marine currents. Rarefaction and CWE proved to be good methods for assessing richness and endemism with datasets biased by unequal sampling effort. Future perspectives regarding the distribution of algae from the GoMx are 1) to increase the sampling effort across the study area, 2) to address macroecological aspects concerning the algae response to different environmental conditions, and 3) to implement techniques that corroborate the patterns found in this study.

CRediT authorship contribution statement

Ramón Emmanuel Gómez-Mendicuti: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Lorena Violeta León-Deniz:** Writing – review & editing, Writing – original draft, Validation, Supervision, Conceptualization. **José María Ahuatzin-Hernández:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Formal analysis, Conceptualization. **Verónica Michel Ojeda-Acosta:** Writing – review & editing, Writing – original draft, Data curation. **Duayner Said Pérez-López:** Writing – review & editing, Writing – original draft, Data curation. **Carlos Alberto Kao-Chicmul:** Writing – review & editing, Writing – original draft, Data curation.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2025.104543.

Data availability

All relevant data are within the manuscript and its Supporting information files

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