Benthic mollusc communities across space and through time in a hypersaline coastal lagoon, Mexico

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ABSTRACT

The coast of the Yucatan Peninsula (Mexico) has undergone numerous changes over the last century as a result of population growth, shifts in land use, establishment of industries, and storm impacts. To understand how the mollusc fauna responded to these changes over time, paleoecological studies were conducted to compare historical and modern data, and to reveal information on past environmental conditions. We analyzed mollusc assemblages in sediment cores from Río Lagartos coastal lagoon, which span the last ~70 years. Mollusc assemblages in the sediment cores were compared to a modern inventory of Mollusca fauna, which was compiled to assess species distributions associated with multiple environmental variables. Mollusc assemblages from the sediment cores (17,089 specimens), which represent 19 bivalve and 43 gastropod species, and modern inventory datasets possess the same ubiquitous species and the same feeding guilds, i.e., groups that exploit the same food resources. Nearly twice as many species were identified in the sediment cores as in the modern inventory. This finding probably reflects the fact that the mollusc community changed through time at the core sites in response to shifting environmental conditions. Nevertheless, we encountered a number of taxa in the modern survey samples, which were absent from the sediment cores. This was probably a consequence of the limited spatial coverage of the cores and small diameter of the core barrels, which precluded sampling of large taxa. We report differences in mollusc abundance and taxonomic composition in the cores across space and time, which may be related to salinity changes in the lagoon and modifications of the nearby terrestrial environment.

1. Introduction

In recent decades, coastal habitats have been affected by natural (climate) and anthropogenic factors. The latter have increased since the Industrial Revolution and include activities such as deforestation and changes in land use, hydrocarbon combustion, eutrophication, infrastructure development, and discharge of contaminants (Abarca et al., 2021; Arcega-Cabrera et al., 2015; Fichez et al., 2017; Medina-Gómez and Herrera-Silveira, 2003; Quesadas-Rojas et al., 2021; Ruiz-Luna and Berlanga-Robles, 2003). Coastal lagoons are among the most productive but most impacted marine systems on Earth, mainly because of human population growth (Kennish and Paerl, 2010). In

2015, the world's human population was about 7.3 billion (UN, 2015), and in 2017, 40% of the global population lived in coastal areas (ONU, 2017). The diverse resources of coastal lagoons have driven development of multiple human activities. As a consequence, environmental conditions and ecological services provided by these coastal systems (e. g., habitats for reproduction, food provisioning, nutrient cycling, buffering against adverse climate events, water quality, etc.) (Pérez-Ruzafa et al., 2011), have been compromised .

Coastal lagoons contribute to economic, ecological, and social well-being. Given these societal benefits, it is important to understand the historical processes that have occurred in these areas. These coastal aquatic ecosystems are influenced by factors such as hydrologic exchanges with the sea (mainly associated with tides), wind, continental runoff, and heat and water interactions with the atmosphere, which act on different temporal scales (Casares-Salazar and Mariño-Tapia, 2016). Coastal lagoons on the Yucatan Peninsula are also affected by human activities such as residential development, agriculture and cattle ranching, and local groundwater can be contaminated with pollutants that accumulate because of slow water exchange (Herrera-Silveira and Morales-Ojeda, 2010; Quesadas-Rojas et al., 2021). In addition, the coastal margin of the Yucatan Peninsula is considered a high-risk area because of its vulnerability to tropical storms and hurricanes that originate in the Caribbean Sea and Atlantic Ocean (Mendoza et al., 2013).

Understanding the processes/mechanisms of change in ecosystems requires a historical (paleoecological) perspective (Armenteros et al., 2021; Estes and Vermeij, 2022). Paleoecological studies involve analyses of death assemblages (thanatocoenoses) that are composed of individuals which belonged to past generations of organisms that lived in the study area, either temporarily or permanently (Kidwell, 2013). Such death assemblages can be used to make inferences about past environmental conditions if modern optima and ranges of specific taxa are known, e.g., with respect to environmental variables such as temperature, salinity and substrate type (Kidwell, 2015; Wingard et al., 2017, 2022).

Comparison of fossil assemblages from sediment cores with modern communities is an approach that has been used in studies of different biotic remains, including molluscs (Brewster-Wingard and Ishman, 1999; Bush, 1988; Kusnerik et al., 2022; Wingard and Hudley, 2012), to understand past patterns of change in ecosystems. Gaps in our knowledge of historical biotic changes often stem from a paucity of information about species geographic distributions, community species richness and evenness, community structure, ecological interactions, and factors that caused past biotic shifts. Nevertheless, recent marine mollusc inventories have begun to expand our knowledge of the biota and environmental conditions in some regions, such as the Gulf of Mexico (García-Cubas and Reguero, 2004, 2007; Mikkelsen and Bieler, 2008; Moretzsohn et al., 2009; Ortigosa et al., 2018; Rosenberg et al., 2009; Turgeon et al., 2009; Vokes and Vokes, 1983; Wingard and Stackhouse, 2020a, 2020b; Wingard and Surge, 2017), and in Río Lagartos coastal lagoon (Gonzalez et al., 1991; Suárez-Mozo et al., 2023). Molluscs meet many of the criteria required for organisms to be good bioindicators. They are widespread and found across a range of environmental conditions, are taxonomically diverse, are capable of rapidly occupying new habitats, and respond quickly to environmental changes. Nevertheless, their utility as reliable bioindicators of past environmental changes requires that we improve our knowledge of their optima and tolerances with respect to specific environmental variables.

Paleoecological investigations, in combination with studies of the modern fauna, have the potential to enhance our understanding of how

and why the mollusc fauna in the region was established. This study had several objectives: 1) analyze historical mollusc assemblages in sediment cores from Río Lagartos coastal lagoon, 2) evaluate the environmental variables that are most important in shaping the mollusc community in the lagoon, using modern data, and 3) relate historical shifts in the mollusc community to known historical changes in the region.

Past studies of mollusc assemblages in sediment cores focused on stratigraphic changes in assemblages from dated late Pleistocene and Holocene profiles, which were then compared with modern assemblages collected across a range of selected environmental variables. In some cases, sedimentation events and eutrophication were shown to have affected mollusc assemblage diversity (Armenteros et al., 2021). Elsewhere, molluscs were utilized to explore the consequences of environmental restoration in South of Florida (Wingard et al., 2022; Wingard and Surge, 2017), direct and indirect human impacts on spring-fed Florida rivers (Kusnerik et al., 2022), transitions from mangrove stands to seagrass beds, as a consequence of sea level rise in Florida (Jones et al., 2019) and Cuba (Armenteros et al., 2021; Díaz-Asencio et al., 2020; Poirier et al., 2009), and environments affected by storms in Brazil (Pereira et al., 2021). In Tasmania, declines in populations of mollusc species were shown to have been caused by dredging for scallops (Edgar and Samson, 2004).

2. Study area

The E-W-oriented Río Lagartos coastal lagoon, on the north coast of the Yucatan Peninsula (Fig. 1), is connected to the Gulf of Mexico at its western end. The coastal lagoon is part of the Ría Lagartos Biosphere Reserve, a protected area created in 1979. The region includes multiple terrestrial and aquatic ecosystems such as sand dunes, inland freshwater wetlands, low-stature tropical dry forests, and mangroves forests, the latter dominated by red (*Rhizophora mangle*) and black (*Avicennia germinans*) mangrove species. The lagoon is hypersaline, with a gradient from the head near El Cuyo (>70 PSU) to the western, seaward region near the town of Río Lagartos (33–38 PSU) (Dávila-Jiménez et al., 2019; Herrera-Silveira and Ramírez-Ramírez, 1998; Suárez-Mozo et al., 2023). Hypersalinity is the result of low rainfall (<500 mm/year), high evaporation (~2000 mm/year), absence of freshwater inputs, long water residence times, and other characteristics (Peralta-Meixueiro and Vega-Cendejas, 2011; Valdes and Real, 2004). The lagoon bottom is covered by an algae mat of *Udotea flabellum* and *Halimeda incrassata* (Vega-Cendejas and Hernández De Santillana, 2004; Wojtarowski et al., 2021) and the distribution of seagrass throughout the lagoon is limited by hypersaline conditions in the interior eastern region (Herrera-Silveira and Ramírez-Ramírez, 2017). The reserve extends over a length of 74 km, ~20% of the total shoreline of the state of Yucatan (Wojtarowski et al., 2021). The lagoon is characterized by water depths between 0.4 and 0.8 m, but channels reach depths of ~3.5 m in some places (Valle-Levinson et al., 2022). Fishing is the most important activity in the area, followed by tourism. Salt extraction has been practiced in this area intermittently since Colonial times (Audefroy and Sánchez, 2017), and there is currently a large, industrial salt works on the north side of the lagoon. The climate is characterized by two seasons, a dry season that extends from January to late May, and a rainy season from late May to December. Some have described the period from November to February as the windy "*Nortes*" season (Vega-Cendejas and Hernández De Santillana, 2004). Diurnal tides pre-dominate and semidiurnal tides occur during neap tides (Cuevas-Jiménez and Euán-Ávila, 2009). The tidal

Table 1
Core designations, core site coordinates, water salinity and depth at the core sites, core lengths and section intervals in cores from Río Lagartos coastal lagoon, Mexico.

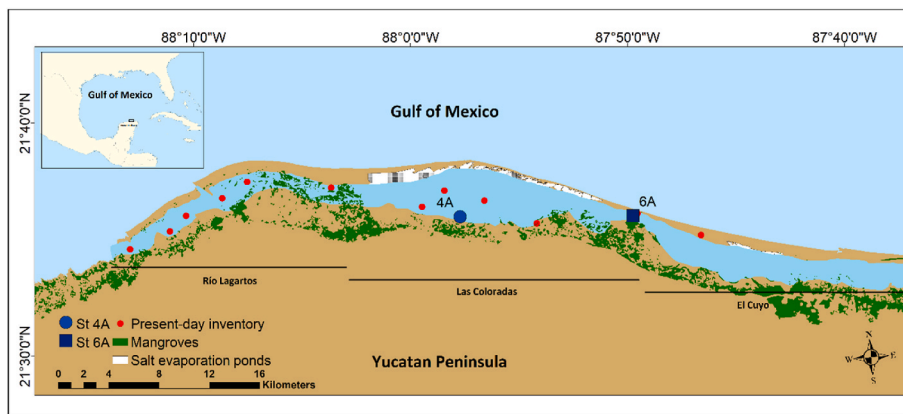| Core	Latitude	Longitude	Water salinity (UPS)	Water depth (cm)	Core length (cm)	Sectioned intervals (cm)
Core 4A	21°34′12.3′′N	87°58′28.6′′W	45	100	22	1
Core 6A	21°33′31.1′′N	87°50′30.9′′W	62	70	13	1

Fig. 1. Map of Río Lagartos coastal lagoon on the northern Yucatán Peninsula, Mexico, with the locations of sediment cores: core 4A (blue dot) and core 6A (blue square). Locations of present-day ecological inventory monitoring sampling sites (modern observations) are indicated by red dots. Mangroves are indicated by the green areas and salt extraction ponds on the barrier island are shown in white. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

signal is attenuated by the lagoon entrance and the tide range is between 0.6 and 1.0 m (Valle-Levinson et al., 2022).

3. Materials and methods

3.1. Core collection

Temporal changes in Río Lagartos coastal lagoon were studied using mollusc assemblages in sediment cores. Cores were collected at sites with low physical disturbance (Casares-Salazar and Mariño-Tapia, 2016; Rey et al., 2018; Valle-Levinson et al., 2011). Cores were taken with a hand-driven piston-corer that used 3.7" ID (9.4 cm), transparent polycarbonate core barrels. Cores from two sites were analyzed: core 4A was located in the coastal lagoon, south of the salt production ponds, whereas core 6A was collected farther east in the channel, near the El Cuyo Basin (see Table 1). Sediment sampling took place on 25–27 July 2017. Each sediment core was sectioned vertically at ~1-cm intervals. The mass of volumetric sediment sections was recorded, and samples were later lyophilized with a freeze dryer in the laboratory. Sediments for dating were ground to a powder with a mortar and pestle and sent to the University of Florida for ^{210}Pb analysis.

3.2. Chronology

We used ^{210}Pb dating to establish a chronology for recent sediments. We used well-type, low-background gamma detectors to measure total ^{210}Pb, supported ^{210}Pb (^{226}Ra) and ^{137}Cs activities (Schelske et al., 1994). Age-depth models for the sediment cores were established using the Plum package (Aquino-López et al., 2018). The primary distinction between Plum and other dating models is that Plum is a Bayesian model whose inputs include the total ^{210}Pb and ^{226}Ra activities. Age can be estimated at any depth where excess ^{210}Pb was detected. The model was implemented using R version 4.2.1 and the rPlum package (Blaauw et al., 2020). This approach provides a robust age model for the period of recent environmental history, i.e., about the last century (Blaauw et al., 2020).

3.3. Mollusc assemblages in the core sediments

Mollusc shells were sampled from the two short sediment cores collected from Río Lagartos coastal lagoon. All sediment samples were sieved through a 1-mm mesh and observed under a stereomicroscope (Amscope and Nikon-SMZ800). Mollusc shells were enumerated using the following criteria: 1) presence of the hinge in the case of bivalves, 2) presence of more than half of the shell and the aperture and apex for gastropods. In the case of bivalves were counted as a single individual. Mollusc shells were assigned to their taxonomic class (Bivalvia or Gastropoda), habitat, feeding guilds and ecological preferences.

Information about geographic distribution and specimen numbers for each taxon appears in Supplementary Material 1 and the dataset can be found in the Ocean Biodiversity Information System (OBIS). We used the GrapherTM (version 21) from Golden software, LLC (www.golden-software.com) (Golden software, 2023) to generate stratigraphic diagrams for the mollusc assemblages. To compare mollusc assemblages in the core sediments with modern mollusc assemblages, and infer past environmental conditions, we used the recent inventories of Gonzalez et al. (1991) and Suárez-Mozo et al. (2023) in the Río Lagartos coastal lagoon.

3.4. Classification of molluscs

Taxonomic classification for all molluscs followed Bouchet et al. (2010) for Bivalvia and Bouchet et al. (2017) for Gastropoda. Molluscs were identified to the lowest possible taxonomic level, using multiple sources (Espinosa et al., 2012; García-Cubas and Reguero, 2004, 2007; Mikkelsen and Bieler, 2008; Redfern, 2013; Tunnell et al., 2010; Vokes and Vokes, 1983). Species were classified and assigned to their taxonomic class (Bivalvia or Gastropoda), habitat (infaunal or epifaunal) and feeding guilds (suspension feeders, carnivores, deposit consumers or grazers) (Wingard et al., 2012). Each specimen was assigned a catalog number (Supplementary Material 1) and deposited in the "Colección de Moluscos de la Península de Yucatán" (CMPY), Unidad Multidisciplinaria de Docencia e Investigación Campus Sisal, Universidad Nacional Autónoma de México, Mexico.

3.5. Statistical analysis

We used coverage-based rarefaction and extrapolation methods (Chao and Jost, 2012) to compare the species richness between sediment cores 4A and 6A. For each depth interval, the richness at a sample coverage of 0.99 was estimated using individual-based rarefaction and extrapolation (Hsieh et al., 2016). This analysis was performed using the iNEXT package (Hsieh et al., 2016) in the R program (R Development Core Team, 2013).

To assess structure of the assemblages from the sediment cores, counts of each species were arranged in a matrix that included the number of samples and raw abundance count data for each species. The matrix was 4th-root-transformed to down weight the effect of highly abundant species and a Bray-Curtis dissimilarity coefficient matrix was generated between every pair of samples. For each core, we tested whether the structure and composition of mollusc assemblages changed through time. Specifically, we assessed assemblages in every interval of each core. The data were evaluated using two statistical methods: 1) spatial patterns (if any) were visualized using Principal Coordinates Analysis (PCoA) (Gower, 1966), and 2) to represent temporal patterns in species composition and structure with depth intervals, we constructed a

canonical correlation analysis (CCA) based on principal coordinates (Anderson and Willis, 2003). The hypothesis of no correlation between the multivariate structure and the depth intervals was evaluated using 999 permutations. All analyses were done using the software PRIMER v7 & PERMANOVA (Clarke et al., 2014).

4. Results

4.1. Chronology

In both core, the unsupported ^{210}Pb activity (total ^{210}Pb activity minus supported ^{210}Pb activity [^{226}Ra activity]), showed a general decline with increasing sediment depth (Supplementary Material 2). In core 4A, total ^{210}Pb activity displayed a maximum value of 7.0 dpm/g near the surface and a minimum of 2.9 dpm/g at 22 cm, the depth at which there was no remaining unsupported ^{210}Pb. According to the Plum model, the date at 22 cm in the core is about 1938 CE (common Era), and it thus spans ~79 years of sediment accumulation. In core 6A, total ^{210}Pb activity displayed a maximum value of 7.2 dpm/g near the surface, which declined to 0.7 dpm/g in the section at 20 cm, where

there was no more excess ^{210}Pb. The age model indicates the core spans ~122 years of sedimentation, with a basal age of *ca.* 1894 CE. The Cesium-137 activities were low to undetectable in both cores and could not be used to corroborate the ^{210}Pb age models.

4.2. Taxonomic composition of mollusc assemblages in cores

A total of 17,089 mollusc specimens, representing 19 bivalve species and 43 gastropod species, which belong to 32 families and 46 genera, were identified in sediments from the two cores taken in Río Lagartos coastal lagoon. The 62 species, except for *Bulla occidentalis* were photographed (Figs. 2–6) and represent the first visual compilation of molluscs that inhabited Río Lagartos coastal lagoon throughout the last century. Shells were generally well preserved, enabling identification in most cases. The most abundant species in the core assemblages were *Anomalocardia puella* (Philippi, 1846) (=*Anomalocardia auberiana* (d'Orbigny, 1853)) (16,875 ind), *Bittiolum varium* (L. Pfeiffer, 1840) (717 ind) and *Acteocina canaliculata* (Say, 1826) (171 ind). Bivalves in the family Lucinidae, as well as *Tampaella tampaensis* (Conrad, 1866), *Dosinia* sp., *Dallocardia muricata* (Linnaeus, 1758), *Angulus* sp., and
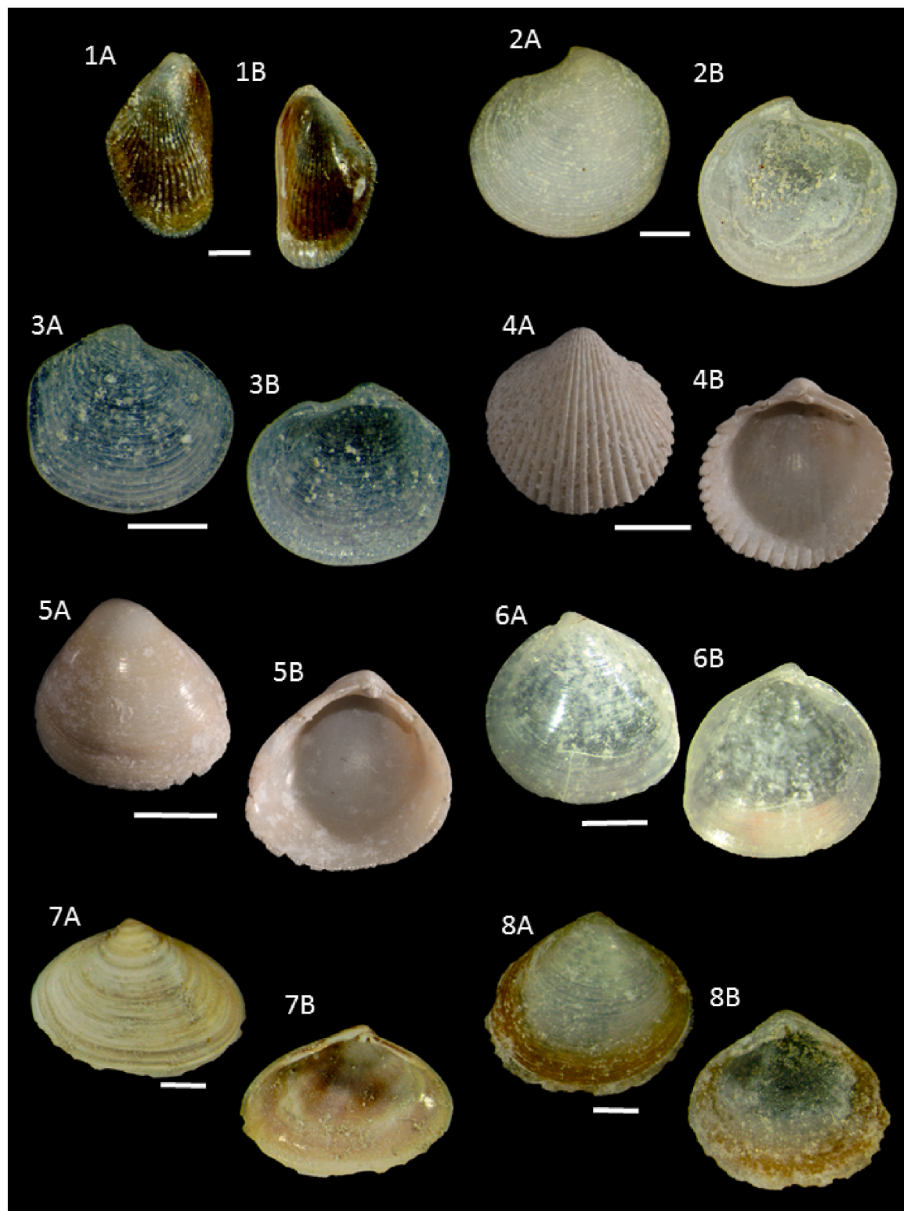
Fig. 2. Historical mollusc assemblages from sediment cores organized by species and their respective families. **Mytilidae** 1. *Brachidontes exustus* (Linnaeus, 1758) (CMPY-006486) Scale bar = 1 mm. **Lucinidae** 2. Lucinidae sp. (CMPY-006120) Scale bar = 1 mm. 3. *Parvilucina crenella* (Dall, 1901) (CMPY-006251) Scale bar = 1 mm. 4. *Dallocardia muricata* (Linnaeus, 1758) (CMPY-006409) Scale bar = 5 mm. **Cardiidae** 5. *Laevicardium serratum* (Linnaeus, 1758) (CMPY-006314) Scale bar = 5 mm. 6. *Laevicardium mortoni* (Conrad, 1831) (CMPY-006183) Scale bar = 1 mm. **Cyrenidae** 7. *Polymesoda floridana* (Conrad, 1846) (CMPY-006121) Scale bar = 1 mm. 8. *Polymesoda* sp. (CMPY-006389) Scale bar = 1 mm.

Fig. 3. Historical mollusc assemblages from sediment cores organized by species and their respective families. **Tellinidae** 1. *Tampaella tampaensis* (Conrad, 1866) (CMPY-006218) Scale bar = 5 mm. 2. *Angulus paramerus* (Boss, 1964) (CMPY-006170) Scale bar = 1 mm. 3. *Angulus* sp. (CMPY-006493) Scale bar = 5 mm. 4. *Macoploma extenuata* (Dall, 1900) (CMPY-006288) Scale Bar = 1 mm. 5. *Serratina martinicensis* (d'Orbigny, 1853) (CMPY-006118) Scale bar = 1 mm. **Semelidae** 6. *Cumingia* cf. *tellinoides* (CMPY-006613) Scale bar = 1 mm. **Veneridae** 7. *Anomalocardia puella* (Philippi, 1846) (CMPY-006696) Scale bar = 5 mm. 8. Veneridae sp. (CMPY-006563) Scale bar = 5 mm. 9. *Dosinia* sp. (CMPY-006227) Scale bar = 1 mm. 10. *Parastarte triquetra* (Conrad, 1846) (CMPY-006309) Scale bar = 1 mm. 11. *Gouldia cerina* (C. B. Adams, 1845) (CMPY-006313) Scale bar = 1 mm.

Cumingia cf. *tellinoides* were all rare, each represented by only a single individual.

Among the gastropods, 20 were also rare, with several taxa represented by only a single individual, e.g., *Bulla occidentalis* Bruguière, 1792, *Astyris lunata* (Say, 1826), *Schwartziella catesbyana* (d'Orbigny, 1842) and *Crepidula convexa* (Say, 1822). Based on their occurrences in the core samples, the most ubiquitous species were *Anomalocardia puella* (38 intervals), *Bittiolum varium* (36 intervals) and *Acteocina canaliculata* (30 intervals). Eighteen species (28%) were carnivores, 18 species (28%) were suspension feeders, five (7%) were deposit consumers and 24 species (37%) were grazers (Supplementary Material 1). Species found in the core assemblages were dominated by epifaunal organisms, with a high number of species belonging to Gastropoda, followed by infaunal organisms, dominated by Bivalvia

4.3. Molluscs as proxies for environmental changes in the Río Lagartos coastal lagoon

The inventory of modern mollusc assemblages from hypersaline Río Lagartos coastal lagoon showed that species are distributed across a broad salinity gradient and represent euhaline to hypersaline taxa. Some species encountered in the modern inventory were not recorded in the cores, including: *Mitrella antares*, *Cardites floridanus*, *Cerithium atratum*, *Cerithium lutosum*, *Chione cancellata*, *Lucinisca nassula*, *Macoma cerina*, Vermetidae sp., *Ameritella sybaritica*, *Anodontia alba*, Cerithiidae sp., *Crassinella* sp., *Ctena orbiculata*, *Eulithidium adamsi*, *Henrya henryi*, Lasaeidae sp., *Lyonsia* sp., *Merisca* sp., *Phrontis vibex*, *Odostomia laevigata* and *Zebina browniana* (Supplementary Material 3). Nevertheless, many species identified in the sediment core assemblages were not found in the modern inventory, including: *Acteocina canaliculata*, *Angulus* sp., *Dallocardia muricata*, *Dendropoma* sp., *Dosinia* sp., *Gouldia cerina*, *Henrya* sp. 1, *Laevicardium mortoni*, *Laevicardium serratum*, Lucinidae sp., *Serratina martinicensis*, Olivellidae sp., *Pedipes* sp., *Polymesoda floridana*, *Sayella* sp., *Schwartziella catesbyana*, *Truncatella pulchella*, Veneridae sp., *Vitrinella* sp., *Angustassiminea succinea*, *Astyris lunata*, *Bittiolum varium*, *Blauneria heteroclita*, *Caecum* cf. *floridanum*, *Caecum* cf. *textile*, *Caecum pulchellum*, *Cerithidea* sp., *Cerithium muscarum*, Cochliopidae sp, *Crepidula* sp., *Cumingia* cf. *tellinoides*, Ellobiidae sp., *Elachisina floridana*, *Eulithidium* sp., *Evalea* sp., *Japonactaeon punctostriatus*, *Melampus* sp. 1, *Melampus* sp. 2, *Melongena corona*, *Nassarius* sp., *Odostomia*
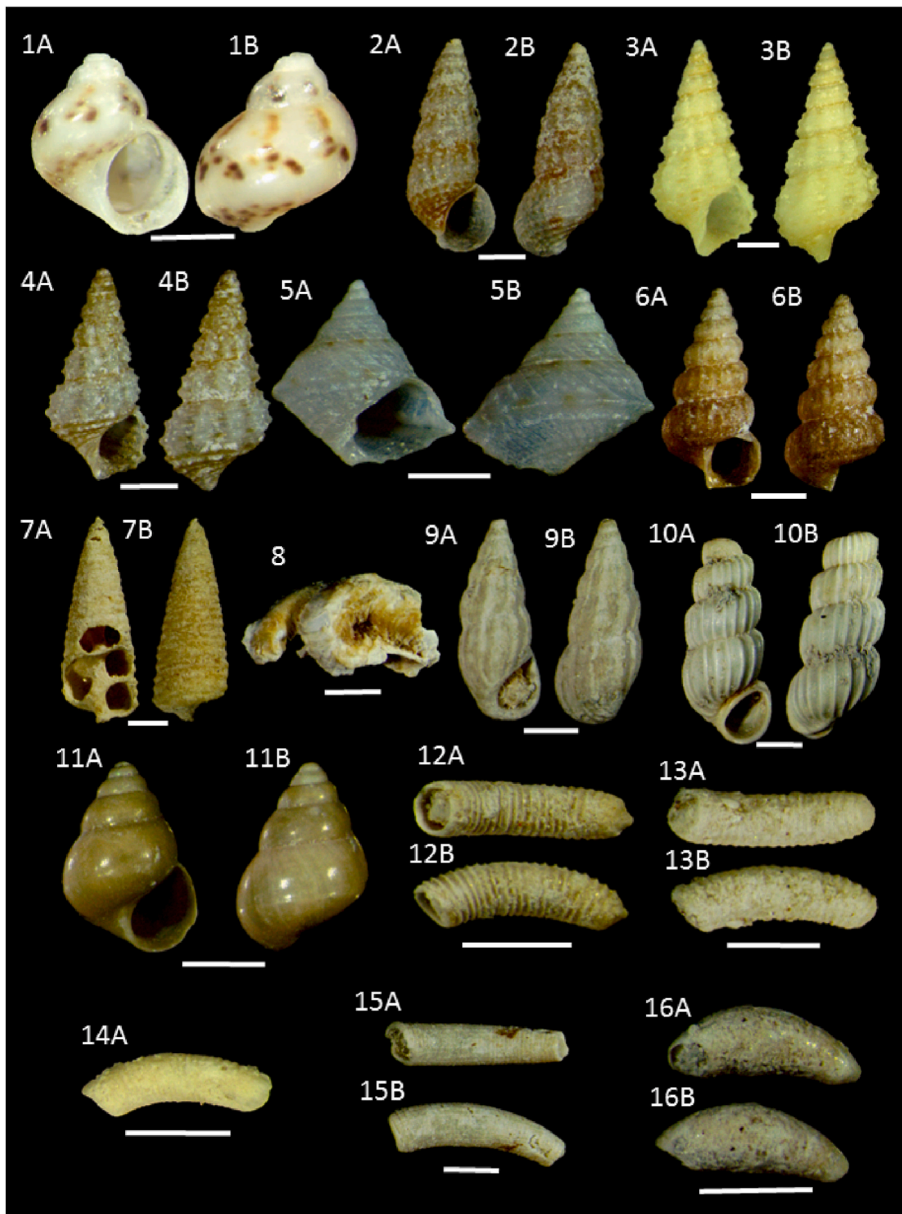
Fig. 4. Historical mollusc assemblages from sediment cores organized by species and their respective families. **Phasianellidae** 1. *Eulithidium* sp. (CMPY-006581) Scale bar = 1 mm. **Cerithiidae** 2. *Bittiolum varium* (L. Pfeiffer, 1840) (CMPY-006210) Scale bar = 1 mm. 3. *Cerithium eburneum* Bruguière, 1792 (CMPY-006588) Scale bar = 1 mm. 4. *Cerithium muscarum* Say, 1832 (CMPY-006177) Scale bar = 1 mm. **Modulidae** 5. *Modulus modulus* (Linnaeus, 1758) (CMPY-006176) Scale bar = 1 mm. **Potamididae** 6. *Cerithideopsis* sp. (CMPY-006167) Scale bar = 1 mm. **Cerithiopsidae** 7. *Seila* sp. (CMPY-006415) Scale bar = 1 mm. **Vermetidae** 8. *Dendropoma* sp. (CMPY-006328) Scale bar = 1 mm. **Zebinidae** 9. *Schwartziella catesbyana* (d'Orbigny, 1842) (CMPY-006331) Scale bar = 1 mm. **Truncatellidae** 10. *Truncatella pulchella* L. Pfeiffer, 1839 (CMPY-006204) Scale bar = 1 mm. **Assimineidae** 11. *Angustassiminea succinea* (L. Pfeiffer, 1840) (CMPY-006213) Scale bar = 1 mm. **Caecidae** 12. *Caecum donmoorei* Mitchell-Tapping, 1979 (CMPY-006431) Scale bar = 1 mm. 13. *Caecum* cf. *floridanum* (CMPY-006308) Scale bar = 1 mm. 14. *Caecum pulchellum* Stimpson, 1851 (CMPY-006375) Scale bar = 1 mm. 15. *Caecum* cf. *textile* (CMPY-006326) Scale bar = 1 mm. 16. *Meioceras nitidum* (Stimpson, 1851) (CMPY-006307) Scale bar = 1 mm.

pocahontasae, *Odostomia* sp., *Olivella minuta*, *Polymesoda* sp., Pyramidellidae sp.1, and *Seila* sp. (Supplementary Material 3).

Taxa encountered in the sediment core assemblages were divided into three groups based on their environmental preferences, according to either the modern inventory or comparisons with environmental conditions where they were encountered in other lagoon localities (Fig. 7). Living *Anomalocardia puella* and *Brachidontes exutus* were encountered across a wide range of salinity and were placed in the euryhaline group; *Bulla occidentalis* and *Parastarte triquetra* were encountered in a narrow range of salinity and were placed in the stenohaline group (Fig. 7). Species of *Melampus* and *Polymesoda* were encountered in other coastal lagoons, where they showed a preference for nearshore, brackish and mangrove localities. In core 4A the numbers of individuals of *Anomalocardia puella*, *Brachidontes exustus*, *Acteocina canaliculata* and *Bittiolum varium* were greater in the decades of the ~1950s and ~1980s and lower in the ~1970s and ~2010s, a pattern also seen in core 6A. The nearshore species increased in the ~1960s and *Melampus* sp. appeared in the ~1970s. In all the cores, the taxa displayed fluctuations in abundance during the last few decades.

The estimated species richness sample coverage for cores 4A and 6A

was calculated to be 0.99 (Fig. 8). A summary of abundance data estimators and more detailed information is provided in Supplementary Material 4. The estimated richness shows a similar pattern across decades, but the magnitude varied. In the 1950s, the estimated richness values in core 4A ranged from 7.9 to 12.6, with confidence levels from 4.3 to 20.8. In core 6A, the estimated richness values ranged from 10.8 to 13.8, with confidence levels from 7.3 to 16.8. During the 1950s and 1960s, there was an increase in estimated richness in both cores, consistent with the observed richness. However, in the 1970s and 1980s, there was a decrease in estimated richness. In core 4A, values ranged from 2.7 to 6.6, while in core 6A, values ranged from 10.7 to 14.7. From the 1990s–2010s, there was a decrease in estimated richness in both cores, although there was a high value in the 1-2-cm interval of core 6A. The broad confidence levels are primarily a consequence of the dominance of *Anomalocardia puella* relative to the rare species found in each interval.

4.4. Mollusc assemblages through time

Analysis of the multivariate ordination plot showed that species

Fig. 5. Historical mollusc assemblages from sediment cores organized by species and their respective families. **Cochliopidae** 1. Cochliopidae sp. (CMPY-006130) Scale bar = 1 mm. **Vitrinellidae** 2. *Vitrinella* sp. (CMPY-006335) Scale bar = 1 mm. **Calyptraeidae** 3. *Crepidula convexa* Say, 1822 (CMPY-006297) Scale bar = 1 mm. 4. *Crepidula* sp. (CMPY-006287) Scale bar = 1 mm. 5. *Prunum apicinum* (Menke, 1828) (CMPY-006223) Scale bar = 5 mm. **Granulinidae** 6. *Granulina* sp. (CMPY-006324) Scale bar = 1 mm. **Columbellidae** 7. *Astyris lunata* (Say, 1826) (CMPY-006507) Scale bar = 1 mm. **Melongenidae** 8. *Melongena corona* (juvenile) (Gmelin, 1791) (CMPY-006281) Scale bar = 1 mm. **Nassariidae** 9. *Nassarius* sp. (CMPY-006401) Scale bar = 1 mm. **Olividae** 10. *Olivella minuta* (Link, 1807) (CMPY-006381) Scale bar = 1 mm. 11. *Olivella* sp. (CMPY-006246) Scale bar = 1 mm. **Murchisonellidae** 12. *Henrya* sp. (CMPY-006332) Scale bar = 1 mm. **Acteonidae** 13. *Japonactaeon punctostriatus* (C. B. Adams, 1840) (CMPY-006565) Scale bar = 1 mm.

composition was different between cores 4A and 6A (Fig. 9A). Core 4A differed from core 6A by 56.81%, caused in part by the presence of several species in the latter, for example *Angustassiminea succinea*, *Anomalocardia puella* and *Truncatella pulchella*, but absent from the former. A Canonical analysis of principal coordinates showed assemblage changes over time (intervals) [Correlation = 0.8465, P: 0.001, number of permutations used: 999] (Fig. 9B). Both cores showed this separation of intervals, indicating that the taxonomic composition and structure of assemblages changed over time in both cores, but that those changes were different at the two core sites in the coastal lagoon.

5. Discussion

5.1. Taxonomic composition in sediment cores

Mollusc taxa encountered in Río Lagartos coastal lagoon total 150 species, a value that includes individuals collected in modern samples (Gonzalez et al., 1991; Suárez-Mozo et al., 2023) and in cores from this study. The historical and modern inventory datasets (Suárez-Mozo et al., 2023) possess the same feeding guilds and ubiquitous species: *Prunum*

apicinum, *Meioceras nitidum*, *Anomalocardia puella* (=*Anomalocardia auberiana*), *Modulus modulus* and *Crepidula convexa*, indicating their persistent role as dominant species in this heterogeneous environment. Sixty-seven of the species found by Gonzalez et al. (1991) did not appear in the sediment core assemblages (Supplementary Material 3). There may be several reasons for the absence of so many taxa from the sediment records. First, our cores sampled a limited portion of the environmentally heterogeneous lagoon. Furthermore, it is likely that our relatively small-diameter core barrel simply missed larger species (e.g., *Macrostrombus costatus*). Compared to our inventory study of modern molluscs in the lagoon, which yielded 39 species (Suárez-Mozo et al., 2023), we found almost double the number of species in the sediment cores (62 species), which reveals the importance of studying assemblages across time (Kidwell, 2013) if one hopes to get a true sense of species richness in a locality. There were methodological differences between the Suárez-Mozo et al. (2023) and Gonzalez et al. (1991) modern inventory studies, which were addressed by Suárez-Mozo et al. (2023). They included differences in the timing of sampling (seasons), types of samplers deployed, and condition of organisms, i.e., inclusion of both live animals and empty shells in the inventory of Gonzalez et al.

Fig. 6. Historical mollusc assemblages from sediment cores organized by species and their respective families. **Tornatinidae** 1. *Acteocina atrata* P. S. Mikkelsen & P. M. Mikkelsen, 1984 (CMPY-006208) Scale bar = 1 mm. 2. *Acteocina canaliculata* (Say, 1826) (CMPY-006245) Scale bar = 1 mm. 3. *Acteocina* cf. *recta* (CMPY-006350) Scale bar = 1 mm. **Haminoeidae** 4. *Haminoea succinea* (CMPY-006642) Scale bar = 1 mm. **Pyramidellidae** 5. Pyramidellidae sp.1 (CMPY-006188) Scale bar = 1 mm. 6. *Evalea* sp. (CMPY-006261) Scale bar = 1 mm. 7. *Odostomia pocahontasae* Henderson and Bartsch, 1914 (CMPY-006182) Scale bar = 1 mm. 8. *Odostomia* sp. (CMPY-006382) Scale bar = 1 mm. 9. *Sayella* sp. (CMPY-006209) Scale bar = 1 mm. **Ellobiidae** 10. *Blauneria heteroclita* (Montagu, 1808) (CMPY-006372) Scale bar = 1 mm. 11. Ellobiidae sp. (CMPY-006291) Scale bar = 1 mm. 12. *Pedipes* sp. (CMPY-006300) Scale bar = 1 mm. 13. *Melampus* sp. 1. (CMPY-006207) Scale bar = 1 mm. 14. *Melampus* sp. 2. (CMPY-006306) Scale bar = 1 mm.

(1991). But differences between modern and sedimented mollusc assemblages suggest that molluscs were likely influenced by multiple environmental factors (Suárez-Mozo et al., 2023), such as salinity (the number of species found was greater in euhaline compared to hypersaline conditions) and vegetation cover, which predominated in euhaline conditions and probably shifted throughout the lagoon over time. Thus, taxa with diverse optima and broad tolerances for environmental variables were encountered in the sediment core assemblages, which reflect changes in both time and space.

5.2. Historical changes in mollusc assemblages

It is likely that both natural and human-mediated environmental changes caused the stratigraphic (temporal) shifts in mollusc species assemblage composition in the sediment cores, as has been documented in other parts of the world (Bianchette et al., 2022; Fortunato, 2015; Kusnerik et al., 2022; Weber and Zuschin, 2013; Wingard and Ishman, 1999). This pattern is most evident in the stratigraphic shifts in abundances of *Anomalocardia puella*, *Brachidontes exustus* and *Bittiolum varium* (Fig. 7), which may reflect salinity changes, or in the case of nearshore

species, may represent greater connection with the terrestrial environment. Furthermore, the estimated magnitudes of richness for each core demonstrate differences throughout the decades (Fig. 8), with a meaningful, statistically reliable and objective comparison (Chao and Jost, 2012). It is highly unlikely that any species is an indicator of freshwater inflow because the lagoon has no overland stream inputs and spring flow is low (Herrera-Silveira et al., 1998). Biotic changes driven by shifts in salinity could, however, be a consequence of hydrologic contributions from the Gulf of Mexico, which has lower salinity. Such inputs may be driven by hurricanes (Gilbert, 1988), along with associated high wind velocities and geomorphologic transformations (Mendoza et al., 2013; Valle-Levinson et al., 2022). Despite our limited understanding of the optima and tolerances of Mollusca taxa in Río Lagartos, with respect to environmental variables, and a paucity of physiological information about the species, our results provide an historical perspective on the mollusc community, reveal information on baseline environmental conditions and provide insights into past faunal assemblages and ecosystem dynamics (Fig. 9).

Species of molluscs that have been used in paleoecology to infer past salinity include: *Polymesoda* spp., *Cerithidea* spp., *Laevicardium mortoni*,
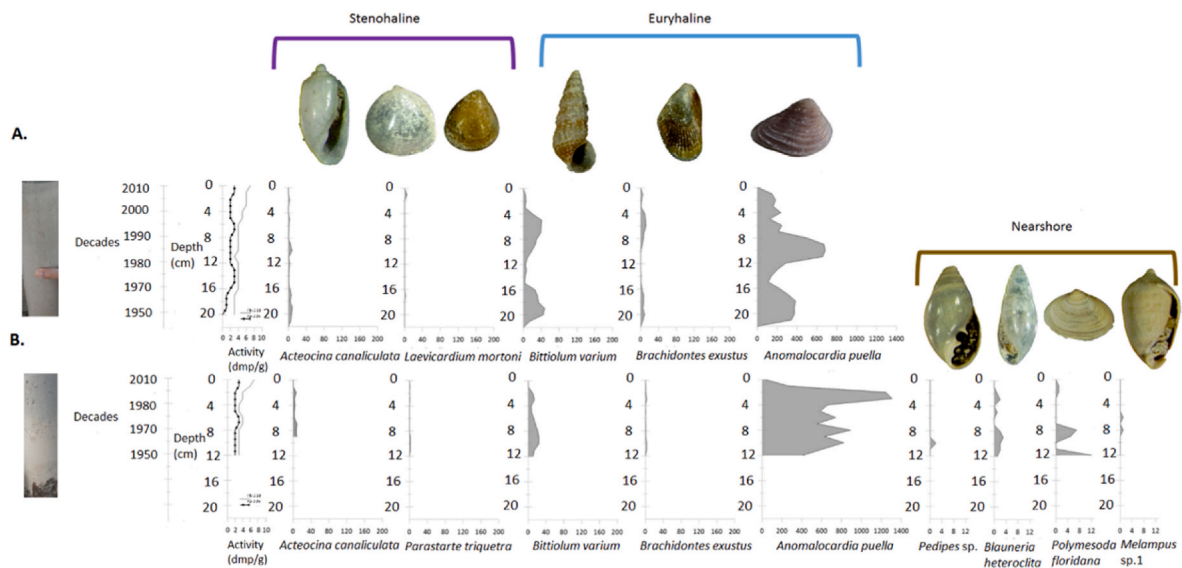
Fig. 7. Absolute abundances of selected mollusc species in sediment cores 4A (A) and 6A (B) from Río Lagartos coastal lagoon, Mexico, plotted by decade and core depth (cm). ^{210}Pb and ^{226}Ra activities (dpm/g) and photographs of cores are shown on the left. Species were classified into three indicator groups: stenohaline, euryhaline and nearshore.
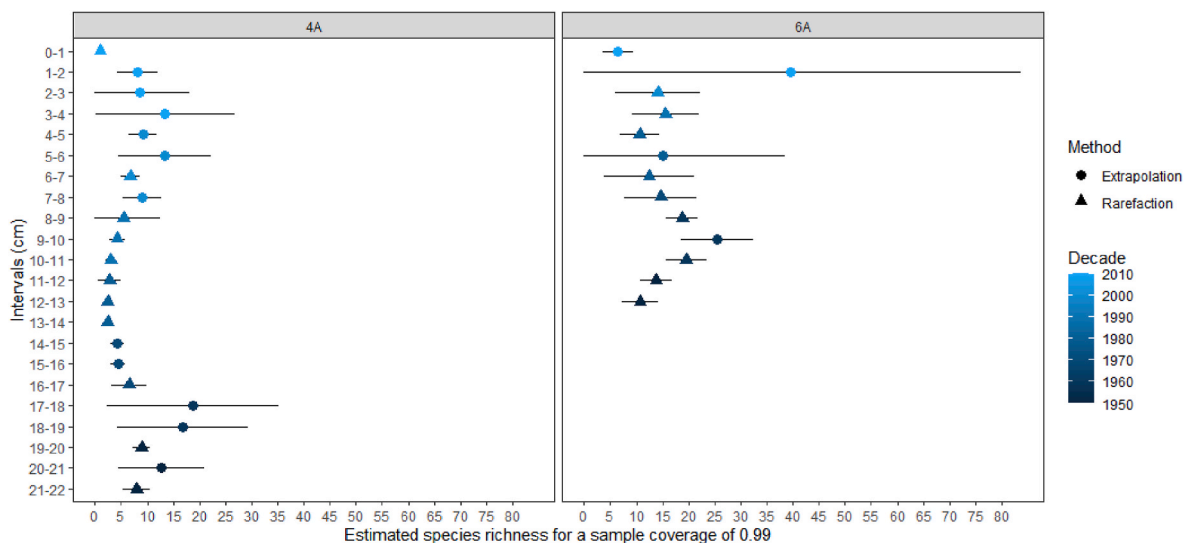

Fig. 8. Depth intervals and associated time intervals (decades) with respect to estimated sample coverage of 0.99 for cores 4A and 6A from Río Lagartos coastal lagoon. Bars represent the lower and upper confidence limits. The method used, interpolated (dot) or extrapolated (triangle), depended on the sample size within each interval.

Crepidula spp. *Anomalocardia auberiana, Cerithium muscarum* and *Bra-chidontes exustus* (Wingard and Hudley, 2012). Other molluscs that have been used as paleoenvironmental indicators are Mytilidae sp., *Macoma* sp., *Acteocina* sp., and Pyramidellidae sp. (Martínez et al., 2013). Commonly, *Melampus* sp. and *Polymesoda* spp. are found together (Haas, 1940). *Melampus* sp. indicates the presence of a freshwater source and/or proximity to land (Camargo Maia and Coutinho, 2013; Wingard and Ishman, 1999). This is consistent with our findings because the sediment cores were collected near mangroves and agricultural areas (Fig. 1), but in the case of the mangroves, both salinity and water level fluctuate greatly. Although *Polymesoda* spp. have been associated with brackish environments, in laboratory conditions they tolerate 40 USP for up to 70 days, values greater than those in the natural environment (Gainey and Greenberg, 1977). Species *Acteocina canaliculata, Bittiolum varium, Laevicardium mortoni, L. serratum, Bulla occidentalis, Parastarte triquetra, Crepidula convexa,* and *Crepidula* sp. are encountered

commonly in open marine conditions, but at low relative abundances in the modern assemblages in Río Lagartos. Higher abundance of *Anomalocardia puella* has been associated with low salinities in Pass Key and Russel Bank (Florida, USA) (Wingard et al., 2001) and Biscayne Bay, south Florida (Wingard, 2004). Spatial differences in composition of the Polychaeta community were studied in the Río Lagartos coastal lagoon and the principal environmental drivers of distribution were salinity, vegetation cover and sediment grain size (Dávila-Jiménez et al., 2019). In Florida Bay, the bivalve *Brachidontes* dominates in areas of abundant sub-aquatic vegetation because the vegetation provides structure for bivalve attachment (via byssal threads), but it was difficult to determine the primary factor that controlled the species distribution (Wingard et al., 2001; Wingard and Ishman, 1999). A study near Cuba revealed the relationship between seagrass beds and species of molluscs (Armenteros et al., 2021), some of which occur in our sediment core samples: *Caecum* spp., *Cerithium eburneum, Eulithidium* sp., and *Meicoceras nitidum.*
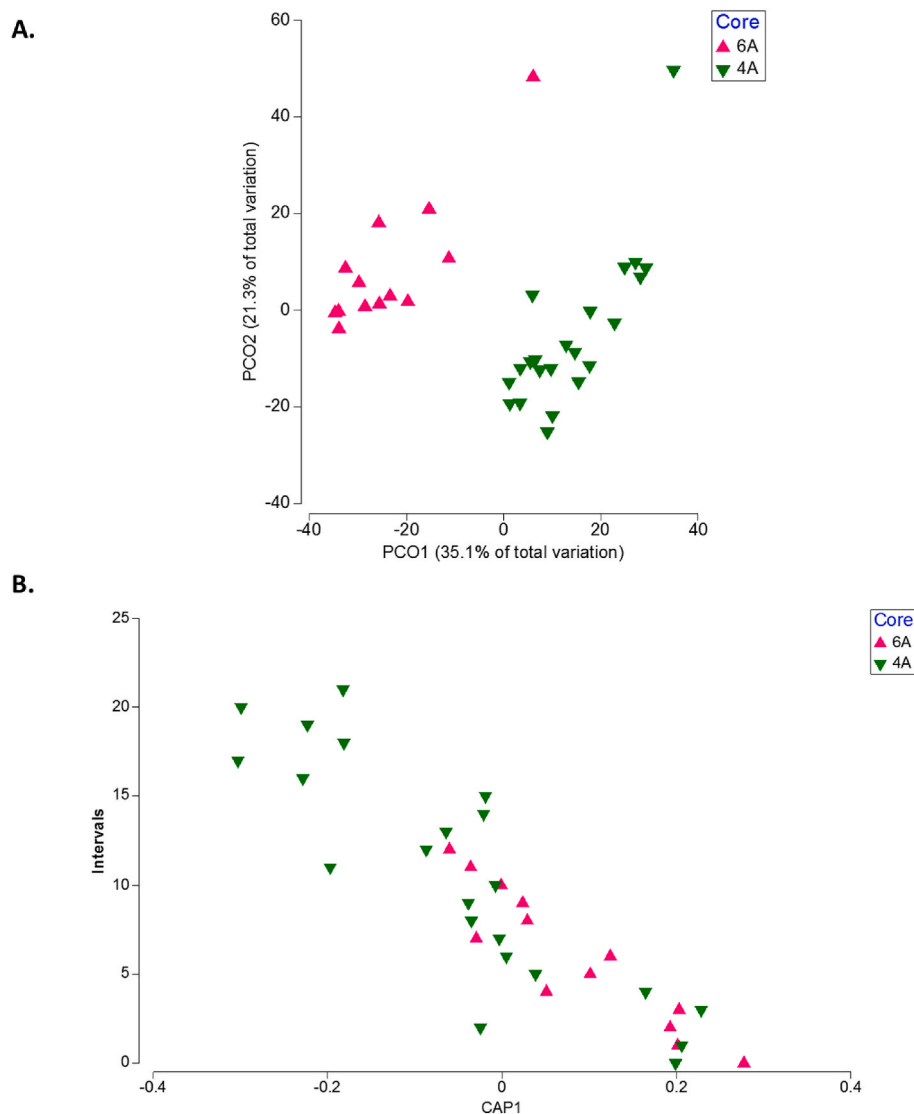
Fig. 9. A. Principal coordinates ordination plot (PCO) based on Bray Curtis dissimilarities from 4th-root abundances of molluscs. B. Canonical analysis of principal coordinates (CAP) plot generated from a similarity matrix, using intervals as a factor. Green triangles = Core 4A and pink triangles = Core 6A. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Our information is essential to understand ecological conditions that prevailed prior to human-mediated environmental impact (e.g., oil spills, land clearance) (Guerra-Castro et al., 2020), and to establish ecosystem restoration strategies (Marshall et al., 2014; Wingard et al., 2022). Our findings also illustrate the importance of understanding the ecological tolerances of species so that we can evaluate current environmental conditions with respect to multiple variables and manage ecosystems for conservation of organisms in light of ongoing human-mediated impacts, including climate change. Overall, our results demonstrate the utility of paleobiology studies as a first step toward understanding environmental and community change through time.

6. Conclusions

Mollusc assemblages in sediment cores from Río Lagartos coastal lagoon, Yucatan, Mexico, revealed differences across space and through time. We discovered almost twice as many taxa in the two sediment cores as in the modern monitoring samples, which likely reflects changes through time in the mollusc community, in response to shifts in environmental variables at the core sites. On the other hand, we encountered a number of taxa in modern samples that did not appear in the sediment

profiles. This was almost certainly a consequence of the limited cross-sectional area of the corer, which necessarily precluded capture of large species.

Stratigraphic shifts in mollusc assemblage composition in the last few decades were probably driven largely by changes in salinity, reflecting the limited tolerance of many species to this environmental variable, and perhaps changes in the availability of resources to molluscs (e.g., food), which became limited by shifts in salinity. The combination of modern and historical perspectives enabled us to identify recent changes in the lagoon's mollusc community, understand trends in the lagoon's environmental conditions, and add to the tally of the lagoon's mollusc species. This information will be of use for future management and conservation strategies in the biosphere reserve and should be supplemented with more eco-physiological studies of the species.

CRediT authorship contribution statement

Nancy Yolimar Suárez-Mozo: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Mark Brenner:** Writing – review & editing, Supervision, Conceptualization. **William F. Kenney:** Writing – review & editing, Methodology. **Misael Díaz Asencio:** Writing

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.ecss.2023.108413.

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