



**UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO**  
**POSGRADO EN CIENCIAS DEL MAR Y LIMNOLOGÍA**  
**(BIOLOGÍA MARINA)**

RECONSTRUCCIÓN DEL REGISTRO SEDIMENTARIO Y CAMBIOS EN LA  
COMUNIDAD DE MOLUSCOS EN UNA LAGUNA HIPERSALINA DE LA PENÍNSULA DE  
YUCATÁN

TESIS  
QUE PARA OPTAR POR EL GRADO DE:  
DOCTOR EN CIENCIAS

PRESENTA:  
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**MÉXICO, CD. MX., JUNIO, 2023**



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## Resumen

Los moluscos bentónicos poseen distintas características que permiten su aplicación en estudios paleoecológicos y en la caracterización de las condiciones históricas de las lagunas costeras. Los vacíos en el conocimiento sobre los cambios históricos y modernos en los ecosistemas acuáticos, se dan en parte, debido a la escasez de información de su fauna y los óptimos ecológicos. Las comunidades de moluscos en la laguna de Río Lagartos, México, se estudiaron espacial y temporalmente utilizando dos enfoques: 1) En 2017 y 2018, se muestrearon moluscos modernos (con partes blandas) en 24 estaciones a lo largo de la laguna costera, abarcando tres épocas del año (sequía, Nortes y lluvias). En cada estación se determinó la salinidad en la columna del agua, el porcentaje de cobertura vegetal y la distribución del tamaño de sedimentos; y 2) Se estudiaron los moluscos en el registro sedimentario de la laguna costera mediante la recolección de tres núcleos de sedimento en el 2017. Los moluscos en los sedimentos fechados con  $^{210}\text{Pb}$  se relacionaron con acontecimientos antropogénicos, ambientales y climáticos que ocurrieron en la laguna y en zonas cercanas a esta durante el último siglo. Posteriormente, se probó si la hipótesis del disturbio intermedio explicaba los cambios temporales en la fauna de moluscos. En los núcleos de sedimento, se identificaron 18799 especímenes, 65 especies (20 Bivalvia y 45 Gastropoda), 48 géneros y 32 familias. Estos resultados se compararon con los moluscos modernos que correspondieron a 2598 especímenes, 39 especies, 34 géneros y 23 familias. Ambos estudios reportaron las mismas especies comunes (e.g., *Anomalocardia puella*, *Bittium varium* y *Acteocina canaliculata*) y los mismos hábitos de alimentación. Alrededor del doble de especies fueron encontradas en los núcleos de sedimentos que en los muestreos modernos. Se reportaron diferencias en la abundancia de moluscos, así como en la composición taxonómica espacial y temporalmente. No hubo una respuesta de la comunidad a los acontecimientos considerados en el estudio (i.e., huracanes, aumento de la población, construcciones y transformación del hábitat), pero las tendencias temporales en moluscos se relacionaron con cambios en la salinidad del cuerpo de agua, mediadas por el recambio de agua desde las entradas. Este tipo de estudios sirven como base para esfuerzos de conservación en la laguna costera. A pesar de esto, se evidenciaron vacíos en el conocimiento de la fauna de moluscos. Para algunas especies, se desconocen los valores óptimos y tolerancias ambientales. Dicha información debe complementarse con estudios ecofisiológicos, monitoreos de la fauna y registros de eventos ambientales, lo cual mejorará las interpretaciones y la capacidad en el uso de moluscos como bioindicadores ambientales.

## Summary

Benthic molluscs have different characteristics that allow their application in paleoecological studies and can be used to characterize past conditions in coastal lagoons. Knowledge gaps about past and ongoing aquatic ecosystem changes occur, in part, because of a paucity of information about fauna and ecological optima. Mollusc communities in the Río Lagartos Lagoon, Mexico, were studied in spatial and through time using two approaches: 1) In 2017 and 2018, modern molluscs with intact soft parts were sampled at 24 stations along the coastal lagoon, covering in three seasons (dry, Nortes, and rainy). Salinity in the water column, percent vegetation cover and sediment particle size distribution were determined at each sampling site; and 2) molluscs in the lagoon sediment record were studied by collecting three cores in 2017. Mollusc assemblages in sediments were dated with  $^{210}\text{Pb}$  and were related to human-mediated, environmental and climatic events that occurred around the coastal lagoon during the last century. We then tested whether the intermediate disturbance hypothesis explains temporal changes in the mollusc fauna. A total of 18,799 specimens, representing 65 species (20 Bivalvia and 45 Gastropoda), 48 genera, and belonging to 32 families, were identified in the sediment cores. Mollusc remains in the sediments were compared with modern mollusc samples, which were represented by 2,598 specimens from 39 species, 34 genera, and 23 families. Both surveys registered the same common species (e.g., *Anomalocardia puella*, *Bittium varium*, and *Acteocina canaliculata*), which display the same feeding habits. About twice as many species were identified in the sediment cores as in the modern assemblages. We assessed differences in molluscan abundance, as well as in spatial and temporal taxonomic composition, were reported. There was no community response to disturbance events (i.e., hurricanes, human population increase, construction, and habitat transformation), but temporal trends in mollusc assemblages were related to changes in salinity of the water body, mediated by water exchange at the inlets. This type of study can serve as the basis for conservation efforts in the lagoon. Nevertheless, there were obvious gaps in our knowledge of the mollusc fauna ecology. For some species, we still need optima and tolerance environmental. Such information should be supplemented with ecophysiological studies, faunal monitoring, and records of environmental perturbations, all of which will enhance using such benthic molluscs as environmental bioindicators.



## Introducción general

En las últimas décadas, los hábitats costeros se han visto afectados por distintos sucesos tanto climáticos como actividades antropogénicas. Estas últimas han aumentado desde la revolución industrial e implican actividades como la deforestación, combustión de hidrocarburos, cambios en el uso del suelo, eutrofización, infraestructura entre otros. Por consiguiente, es necesario rastrear la duración y la frecuencia de esta serie de sucesos, así como comprender la variabilidad temporal de la fauna.

En particular, las lagunas costeras se encuentran entre los sistemas marinos más productivos, pero son los más impactados en la Tierra, principalmente por el crecimiento poblacional (Kennish & Paerl 2010). En 2015, la población mundial era de alrededor 7.3 billones de personas (UN 2015), y en el año 2017, el 40% de estas, habitaban en zonas costeras (ONU 2017). La diversidad de las lagunas costeras ha impulsado el desarrollo de distintas actividades humanas, pero en contraste, se han reducido los servicios ambientales (e.g., hábitats para la reproducción, cría, refugio, alimento, ciclo de nutrientes, amortiguadores de sucesos adversos y calidad del agua etc.) (Pérez-Ruzafa *et al.* 2011) que proporcionan las mismas.

### Las lagunas costeras

Las lagunas costeras contribuyen significativamente al bienestar económico, ecológico y social, y por estas características, se hace importante comprender los distintos procesos históricos en estas áreas, en particular. Desde un enfoque hidrodinámico, estos ecosistemas acuáticos son controlados por distintos factores como los intercambios con el mar (principalmente con las mareas), el viento, las descargas continentales, los flujos de calor y de agua con la atmósfera, que actúan a diferentes escalas temporales (Casares-Salazar & Mariño-Tapia 2016).

En la Península de Yucatán, las lagunas costeras presentan una variabilidad hidrológica intra-laguna tanto espacial como temporalmente, resultado de la conectividad, diferencias en los aportes de agua dulce y marina, intensidad de corrientes y amplitud de las mareas (Herrera-Silveira 2006; Valle-Levinson *et al.* 2022). Además, los hábitats costeros de la Península de Yucatán son consideradas zonas de alto riesgo, por encontrarse en la zona

de influencia de tormentas tropicales y huracanes que se originan tanto en el Caribe como en el Atlántico. Otro fenómeno meteorológico son los Nortes o vientos del norte, que son sistemas atmosféricos fríos y de alta presión atmosférica, que modifican la dirección del viento, la temperatura y el clima en general durante un período aproximado de 2 a 5 días (Quesadas-Rojas *et al.* 2021). En algunas ocasiones, estos vientos se presenta con fuertes lluvias y oleaje, que provocan inundaciones y abren bocas a través de la duna costera (Carabias-Lillo *et al.* 1999).

La laguna costera de Río Lagartos se caracteriza por 1) ser un sistema hiperhalino resultado de un exceso de evaporación sobre la precipitación y un bajo aporte de descargas continentales; 2) presentar un gradiente espacial de salinidad con valores más altos en la zona interior (>87 unidades prácticas de salinidad) y que gradualmente disminuye a valores marinos (~36 UPS) (Peralta-Meixueiro & Vega-Cendejas 2011); 3) estar rodeada de manglares y pastos marinos. Debido a su importancia biológica, es considerada Refugio Nacional de Vida Silvestre y se encuentra en la lista de humedales de importancia internacional y es una Reserva protegida de la biosfera (Carabias-Lillo *et al.* 1999). Además, la laguna costera de Río Lagartos presta distintos servicios ambientales y económicos, de ellos destacan actividades turísticas, pesquerías; además, sirven de sitios de crianza de muchas especies, entre moluscos, peces y crustáceos.

La elección de esta laguna para el presente estudio se debe principalmente a la intención de analizar, desde una perspectiva paleoecológica, cómo los eventos tanto antropogénicos y climáticos, afectan a los moluscos en el tiempo.

#### Reconstrucciones históricas y fechado con $^{210}\text{Pb}$

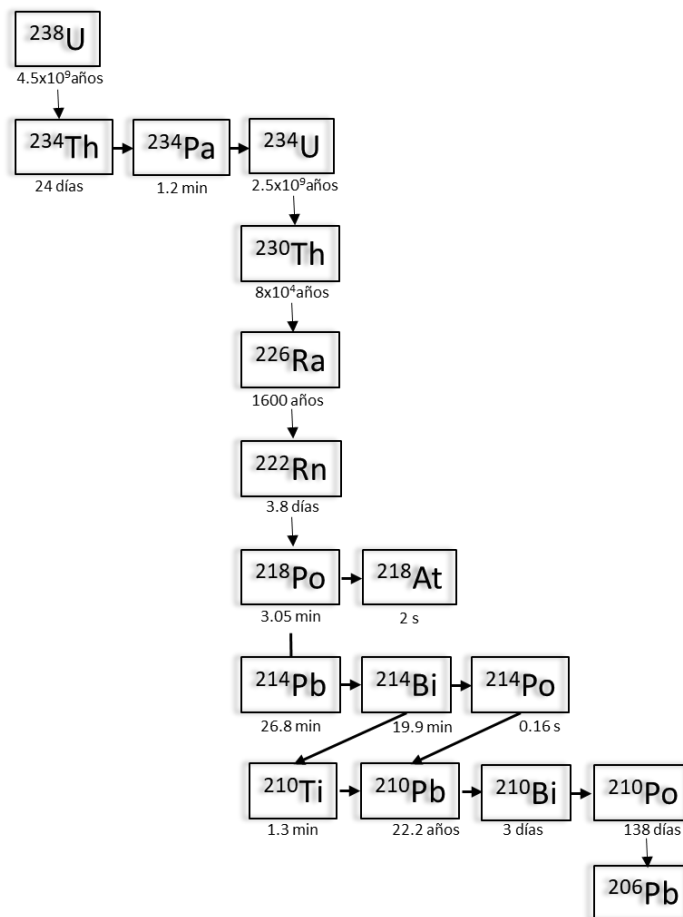
Los distintos efectos del cambio global se han acumulado con el tiempo, lo que ha generado la necesidad de conocer los legados históricos con el fin de mejorar la comprensión de los cambios en la diversidad (Lara-Lara *et al.* 2008; Essl *et al.* 2015) ante los impactos antropogénicos y ambientales (Armenteros *et al.* 2012). A través del análisis de núcleos de sedimentos, se puede obtener una perspectiva de las condiciones históricas de la variabilidad de la diversidad y la respuesta de los ecosistemas a cambios en el tiempo. Con los núcleos se puede acceder a los archivos naturales que se producen con la

sedimentación y los depósitos de animales (Swetnam *et al.* 1999; Kidwell & Tomasovych 2013).

Comúnmente las inferencias de las condiciones anteriores se han estudiado a partir de indicadores físicos, químicos y biológicos (e.g., corales, algas coralinas, moluscos, entre otros). Toda la información derivada de estos indicadores en los registros sedimentarios es utilizada para reconstruir las condiciones que se produjeron en el pasado. Los estudios paleoecológicos se han realizado de forma exclusiva con aquellos organismos con estructuras mineralizadas. En las reconstrucciones históricas, es fundamental establecer una cronología de sucesos mediante el fechado de las muestras que se depositan, para esto, se utilizan relojes radiométricos como el Plomo-210.

#### El Plomo-210

El  $^{210}\text{Pb}$  es un radionúclido natural utilizado para fechar sedimentos recientes entre 0 y 150 años, con una vida media de  $22.3 \pm 0.12$  años (DDEP: Data Decay Evaluation Project 2010). El  $^{210}\text{Pb}$  pertenece a la cadena radioactiva del  $^{238}\text{U}$  (radioisótopo primario o padre, con una edad de 4500 millones de años) (Sanchez-Cabeza *et al.* 2012; Brenner & Kenney 2013) (Figura 1). El  $^{210}\text{Pb}$  está presente en la atmósfera, la litósfera y la hidrósfera. Ha sido ampliamente utilizado en distintos estudios, como biogeoquímicos, depósito atmosférico, procesos sedimentarios y geocronología de sedimentos.



**Figura 1.** Cadena de desintegración de  $^{238}\text{U}$ .

Las fuentes de  $^{210}\text{Pb}$

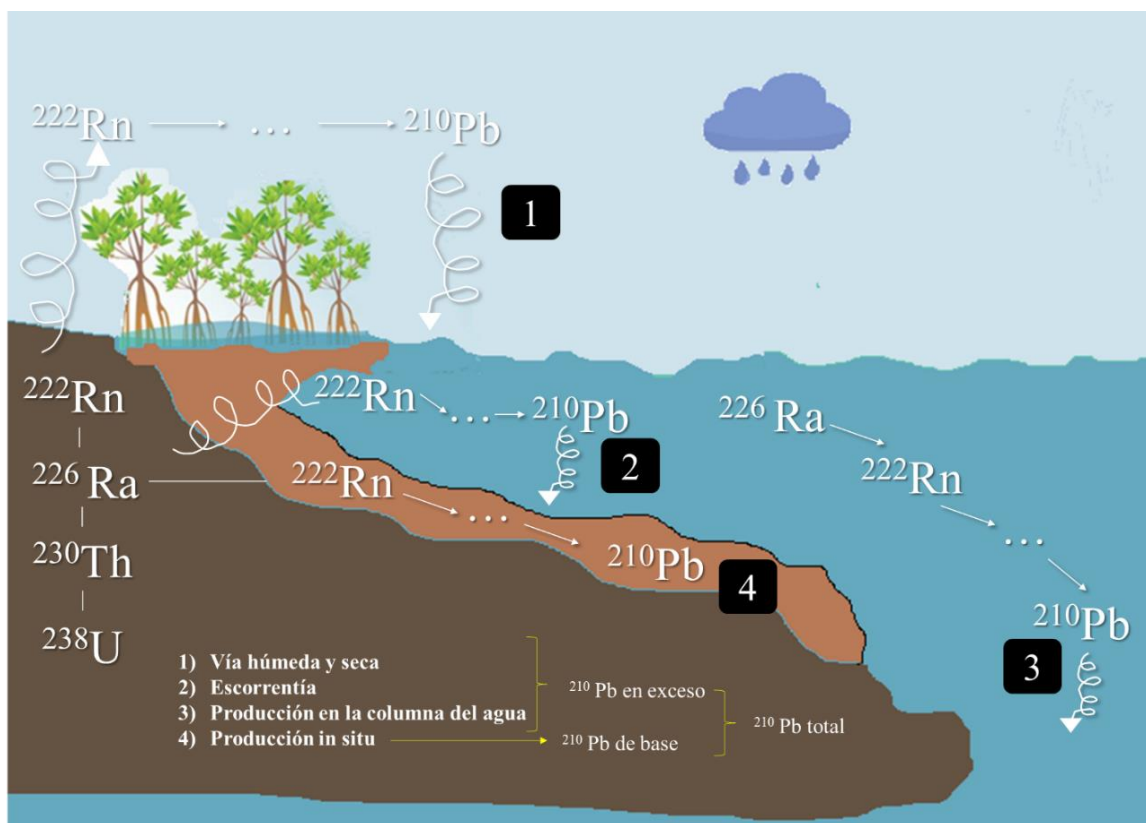
El Plomo-210 es miembro de la cadena de decaimiento del Uranio-238 que se encuentra en los océanos y en los materiales geológicos. Por su propiedad de radioisótopo, sufre una serie de desintegraciones para producir el  $^{226}\text{Ra}$ . El Radio-226 (vida media 1600 años), se desintegra a su vez en  $^{222}\text{Rn}$ . El Radón-222 es un gas (vida media 3.8 días) que se distribuye ampliamente por la atmósfera y desintegra a través de varios radioisótopos "hijos" que tienen una vida media corta. Estos producen partículas de  $^{210}\text{Pb}$  que finalmente se depositan por vía húmeda y seca (tiempo de residencia en la atmósfera de aproximadamente 10 días). Una pequeña cantidad del  $^{210}\text{Pb}$  en los cuerpos de agua someros puede originarse a partir de partículas que contienen  $^{226}\text{Ra}$ , transportadas a través de escorrentía y ríos. En aguas profundas (>100 m aproximadamente), una fracción del

$^{210}\text{Pb}$  procede del  $^{226}\text{Ra}$  disuelto en el agua de mar. El  $^{210}\text{Pb}$  también puede proceder de la descomposición de  $^{226}\text{Ra}$  que se encuentra en el sedimento. Los sedimentos resultan teniendo  $^{210}\text{Pb}$  producido *in situ* por la desintegración  $^{226}\text{Ra}$  ( $^{210}\text{Pb}$  base "supported") y el que procede de la columna del agua ( $^{210}\text{Pb}$  exceso "unsupported") que finalmente termina depositándose en el sedimento (Sanchez-Cabeza *et al.* 2012; Brenner & Kenney 2013) (Figura 2).

La actividad total del  $^{210}\text{Pb}$  en sedimentos tiene dos componentes:  $^{210}\text{Pb}$  base ( $^{226}\text{Ra}$ ) y  $^{210}\text{Pb}$  exceso. El Plomo base o soportado generalmente está en equilibrio radioactivo con  $^{226}\text{Ra}$ . El  $^{210}\text{Pb}$  exceso se estima con la diferencia entre el  $^{210}\text{Pb}$  total y  $^{226}\text{Ra}$ , llamado  $^{210}\text{Pb}$  base.

$$^{210}\text{Pb}_{\text{exceso}} = ^{210}\text{Pb}_{\text{total}} - ^{226}\text{Ra}$$

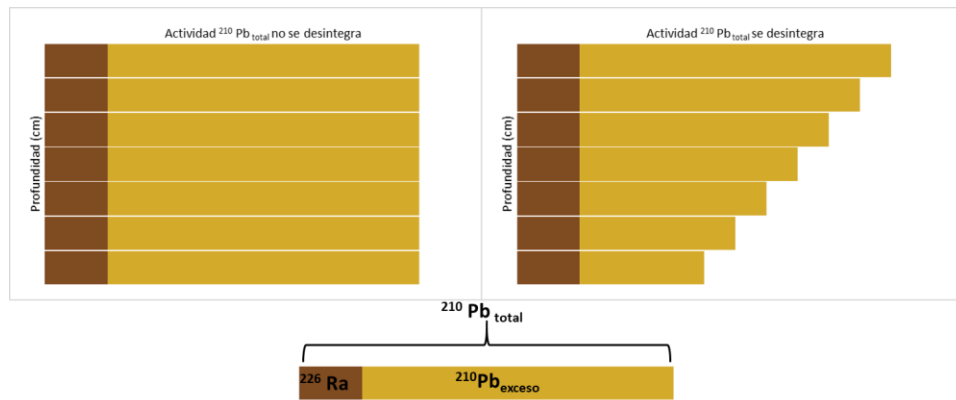
El Plomo en exceso, es el que se utiliza para datar los sedimentos, por lo tanto, es necesario distinguir cuál es el Plomo base y cuál es el exceso en un núcleo de sedimento.



**Figura 2.** Ciclo geoquímico del  $^{210}\text{Pb}$ , modificado de Sanchez-Cabeza *et al.* (2012).

Para la datación de sedimentos a partir del Plomo en exceso, usando el modelo de tasa constante de suministro, es necesario tener en cuenta algunos requerimientos (Sanchez-Cabeza *et al.* 2012):

- El Plomo se deposita de manera constante en los sedimentos.
- Se espera que, en la capa superficial, se encuentre el depósito más reciente y mayor concentración de  $^{210}\text{Pb}$  y que los estratos inferiores tengan un perfil decreciente debido a la desintegración del mismo en el tiempo (Figura 3).



**Figura 3.** Perfil "ideal" de la actividad de  $^{210}\text{Pb}$  en los sedimentos. El  $^{226}\text{Ra}$  ( $^{210}\text{Pb}$  base) permanece en menor proporción y se desintegra en un período mayor (1600 años). El  $^{210}\text{Pb}$  deberá tener una mayor concentración y se desintegra a una vida media de 22.2 años. Tomado y modificado de (Rodríguez Vegas *et al.* 2013).

## Moluscos

Los moluscos son un grupo susceptible para la caracterización de los cambios de la biodiversidad, los impactos antropogénicos y los cambios ambientales (Wanamaker *et al.* 2011; Yan *et al.* 2014; Fortunato 2015; Armenteros *et al.* 2016). Se consideran entre los organismos más prometedores del bentos para investigaciones históricas, principalmente porque: 1) la mayoría de los moluscos presentan conchas carbonatadas que se preservan en los sedimentos después de muertos (Parkhaev 2007; Fortunato 2015); 2) poseen una alta diversidad taxonómica y funcional en los ecosistemas, ofreciendo directa o indirectamente una gran cantidad de información de los cambios en la comunidad (Brusca & Brusca 2002); 3) la taxonomía está bien consolidada y es de fácil acceso; 4) existe una amplia red de malacólogos y colecciones biológicas con especies conservadas tanto nacionales, como internacionales; y 5) su presencia a través de gradientes latitudinales

permite su uso como biosensores para estudiar cambios ambientales (Brewster-Wingard & Ishman 1999; Gaiser *et al.* 2006; Vereycken & Aldridge 2022). Tanto los depósitos como las agregaciones de moluscos los hacen ser considerados importantes ingenieros del ecosistema en zonas costeras, estuarios y el mar profundo. Aunque existen otros grupos como los foraminíferos, que también se ha demostrado son buenos indicadores, los moluscos están mejor correlacionados con el tipo de sustrato (Ferguson 2008).

## **Objetivos**

El objetivo general de este estudio es describir los cambios históricos en las especies de moluscos a una escala local grabados en los registros sedimentarios de una laguna hipersalina en la Península de Yucatán, Golfo de México, con el desarrollo de los siguientes objetivos particulares:

- Datar y describir la geoquímica de los estratos en los núcleos 4A, 4B y 6A de la laguna costera de Río Lagartos.
- Determinar la composición taxonómica de moluscos, analizar los grupos tróficos y la disposición en el sustrato de cada una de las especies encontradas.
- Analizar la relación de la edad del sedimento, con la composición de las especies de moluscos.
- Describir y comparar el inventario de moluscos modernos a lo largo de la laguna con aquellos moluscos que se acumularon en el tiempo en los registros sedimentarios.

## **Estructura del trabajo de tesis**

La tesis está compuesta por cinco capítulos. El capítulo 1 reúne los acontecimientos climáticos y antropogénicos ocurridos en la laguna costera de Río Lagartos en el último siglo, para poner en contexto los posibles acontecimientos que pudieron influir en la fauna de moluscos.

El capítulo 2 contiene el análisis de los acontecimientos encontrados en el capítulo 1 y se hace una clasificación considerando los niveles de disturbio. Estos se correlacionaron con la abundancia y el número de especies de moluscos depositados en los núcleos de sedimento para explicar los cambios en la fauna de moluscos en el último siglo.

El capítulo 3 ha sido publicado en una revista científica y el capítulo 4 está sometido para su publicación. Debido a esto, se presentan en inglés. Se adjuntan los resúmenes en español. En el capítulo 3, se explican las relaciones entre los moluscos modernos encontrados en la laguna costera de Río Lagartos y las variables ambientales.

El capítulo 4 retoma los resultados del capítulo 2 y 3 con el fin de comparar los moluscos en los núcleos de sedimento con las condiciones ambientales en las que se recolectaron los moluscos modernos. Esto se realizó para obtener una aproximación de las condiciones ambientales pasadas a las que estuvieron sometidos los moluscos, y explicar si los cambios faunísticos responden a cambios ambientales.

Finalmente, el capítulo 5 incluye conclusiones generales e integrativas de todo el documento.



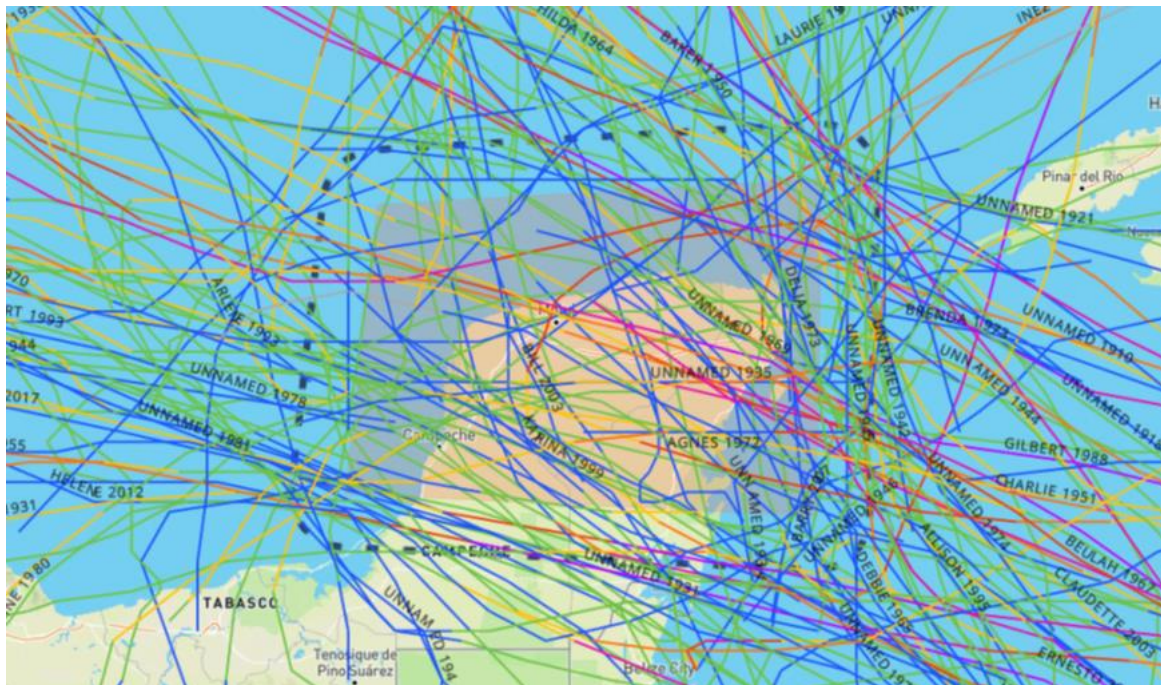
# Capítulo 1. Revisión histórica del contexto ambiental y antropogénico en la laguna de Río Lagartos

## Huracanes en la laguna costera de Río Lagartos

La Reserva de Ría Lagartos se encuentra en la zona de afectación de tormentas tropicales y huracanes que se originan en el Caribe y en el Atlántico oriental, es por esto que es considerada como zona de alto riesgo. Se han registrado un total de 107 tormentas en Yucatán entre 1851 a 2000 (149 años) (Figura 1). El 73% de las tormentas han sido huracanes (categoría 1 y 2), mientras que el 27% fueron huracanes intensos ( $\geq$  categoría 3) (Boose *et al.* 2002). La distribución de lluvias durante el paso de los ciclones tropicales se ha registrado en México desde 1950 con eventos cercanos a la laguna de Río Lagartos desde 1956 hasta 2016 (CONAGUA 2021).

Los huracanes se miden según la velocidad sostenida de los vientos con la escala de Saffir-Simpson (clasificación de 1 a 5). Tanto los huracanes como las tormentas proveen efectos positivos en el planeta tierra, como el enfriamiento de los océanos, circulación oceánica, recarga de los mantos freáticos a través de las lluvias, aireación de la columna de agua, además favorecen el transporte de sedimentos, nutrientes y materia orgánica (Michener *et al.* 1997; Trenberth *et al.* 2007, 2018; Bianucci *et al.* 2018). Sin embargo, también se consideran una amenaza global para los recursos costeros, ya que pueden destruir parte de los ecosistemas (e.g., manglares, zonas de barrera, playas), la infraestructura y provocar pérdidas humanas (Lin *et al.* 2014). Estos efectos negativos se deben a la acción de los vientos intensos, oleaje de gran altura e intensidad (Salazar-Vallejo 2002).

Uno de los acontecimientos climáticos más fuertes en la Reserva de Ría Lagartos fue el producido por el huracán Beulah de categoría 4, el cual afectó la zona al ingresar a tierras yucatecas el 17 de septiembre de 1967 con vientos superiores a los 300 km/h. Otro huracán que también afectó la reserva fue Gilberto, el cual tocó tierra peninsular en Cozumel antes de pasar por Cancún el 14 de septiembre de 1988, causando graves daños a la infraestructura de la planta salinera en la laguna costera de Río Lagartos disminuyendo su capacidad de producción de sal. El mismo huracán destruyó el muelle de embarque de la industria salinera de Yucatán, que posteriormente fue reconstruido en 1996. En 2002, el huracán Isidoro alcanzó la categoría de 4 y golpeó con intensidad a la Península de Yucatán (Aguirre-Macedo *et al.* 2011; Audefroy & Sánchez 2017).



**Figura 1.** Trayectoria de depresiones tropicales (línea azul), tormentas tropicales (línea verde), huracanes (H5 línea morada, H4 línea fucsia, H3 línea roja, H2 línea naranja, H1 línea amarilla) que han pasado por la Península de Yucatán en el periodo del 1910 hasta el 2017. Zona de amortiguamiento de 60 km (línea negra punteada). Datos provistos por la NOAA “historical hurricane tracks” (NOAA 2022).

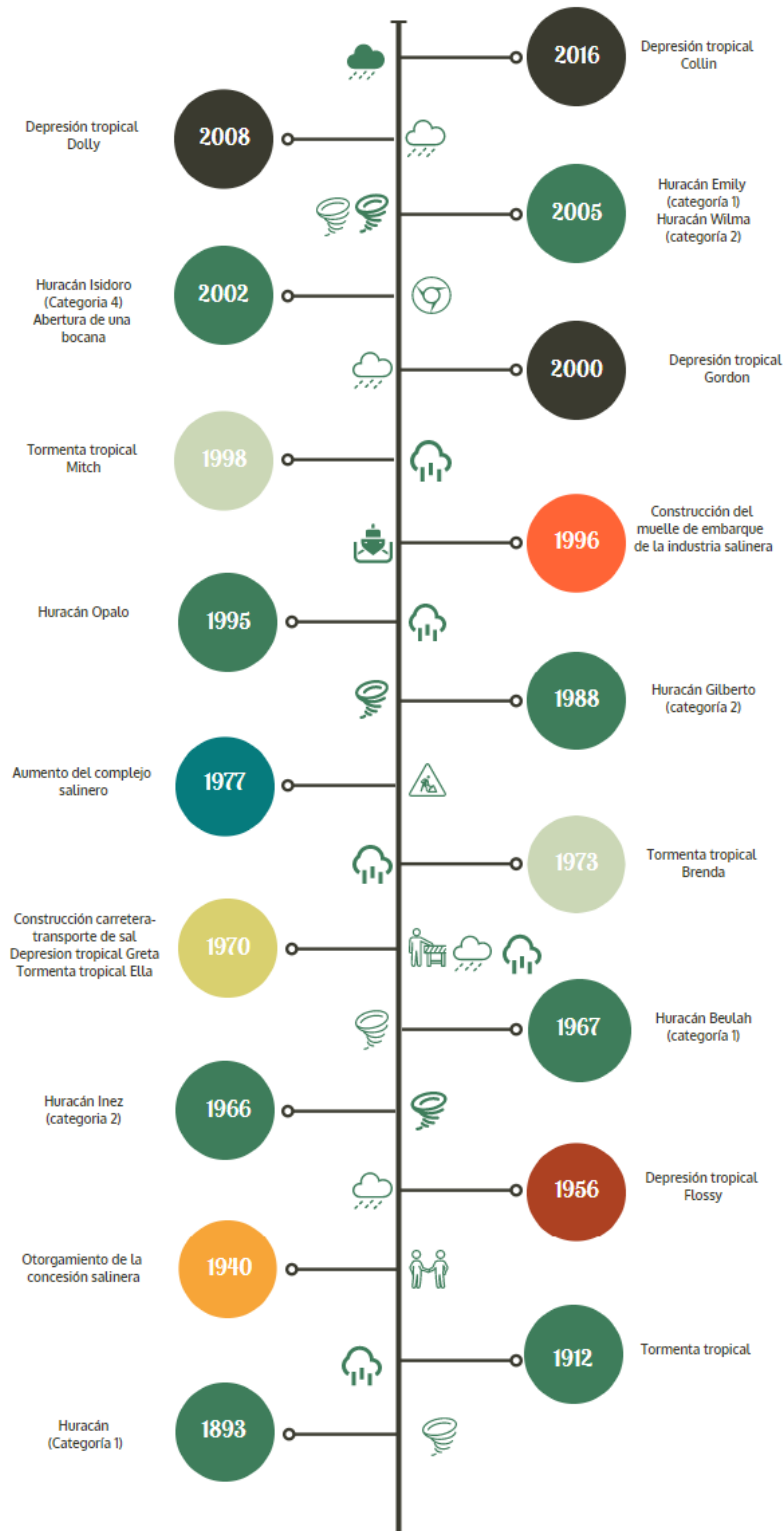
**Fragmentación y transformación del hábitat**

Una de las principales amenazas en la Reserva de Ría Lagartos es la tala y desmonte de grandes extensiones para utilizar el terreno en la ganadería. También se ha modificado el hábitat por la construcción de escolleras, diques y caminos. Por ejemplo, las construcciones en la entrada de los pueblos San Felipe, Río Lagartos, Las Coloradas y El Cuyo han modificado el flujo de agua en la laguna costera y en las zonas de manglar (Carabias-Lillo *et al.* 1999). Un estudio en la zona reveló la dinámica espacio temporal de la cubierta vegetal por medio de imágenes de satélite de distintas décadas, pudiendo determinar la tasa de transformación del hábitat (Carranza Sánchez & Molina Islas 2003). Las principales actividades que han transformado la cobertura vegetal en la Reserva de Ría Lagartos son la ganadería, a través de pastizales cultivados, y la industria salinera.

La principal actividad económica de la población en la laguna de Río Lagartos es la Industria Salinera de Yucatán S. A. (ISYSA). La concesión para esta industria fue otorgada por el

gobierno federal en 1940, convirtiéndose en la segunda producción de sal en México después de Guerrero Negro, Baja California Sur (Díaz Yarto 2010). Esta salina se ha explotado intermitentemente desde el periodo colonial y ha tenido un aumento en su área: en 1945, el área de estanques cubría cerca de 20 ha, y para 1977, el complejo aumentó a 1700 ha. Además, en 1970, fue inaugurada una vía terrestre para facilitar el transporte de sal de las coloradas hasta al sur y centro de la república mexicana. En la actualidad, se calcula el área de ~2,800 ha, con un área concesionada total de 5,000 ha aproximadamente (Carabias-Lillo *et al.* 1999).

La laguna de Río Lagartos se ha enfrentado a distintos acontecimientos históricos, como eventos climáticos, desarrollo económico e industrial, entre otros. A continuación, se presenta una línea de tiempo que resume los acontecimientos ocurridos desde 1893 hasta 2016 (Figura 2).



**Figura 2.** Línea de tiempo de acontecimientos ocurridos en la Reserva de Ría Lagartos de 1893 hasta 2016, teniendo en cuenta que los muestreos históricos abarcan hasta el año 2017 (Carabias-Lillo *et al.* 1999; NOAA 2022).

## **Capítulo 2. Respuesta de la comunidad de moluscos bentónicos a los cambios ambientales del último siglo en la laguna costera de Río Lagartos**

## Resumen

Las zonas costeras se enfrentan a distintos agentes que pueden causar daños a los ecosistemas (e.g., manglares, pastos marinos, islas de barrera) y a la fauna que ahí habita. Los niveles de disturbio, en cuanto a su intensidad y frecuencia, fueron evaluados por Connell (1978) con la hipótesis del disturbio intermedio. Para probar si los disturbios históricos tenían relación con las tendencias en la comunidad de moluscos en la laguna de Río Lagartos, se enlistaron los posibles disturbios y se clasificaron por niveles (1-bajo, 2-moderado, 3-intermedio y 4-alto). Se estimó el grado de correlación para identificar los posibles mecanismos responsables de los cambios en la comunidad de moluscos. Aunque la abundancia, riqueza de especies y hábitos alimenticios de los moluscos cambiaron a lo largo del tiempo, la prueba de hipótesis reveló que los cambios no fueron respuesta a los acontecimientos considerados en el estudio, sino que pudo deberse a la respuesta de los moluscos a acontecimientos de pequeña escala o acontecimientos indirectos que no fueron contemplados en el estudio. Convirtiéndose la comprensión de la respuesta de los ecosistemas ante los disturbios en escalas espaciales y temporales en un desafío que requiere un mayor estudio y profundización.

## Introducción

Los análisis paleoecológicos con moluscos pueden proporcionar información detallada sobre el entorno pasado de un ecosistema y sus cambios en el tiempo (Cerrato *et al.* 2013). Combinados con análisis geoquímicos, registros de temperatura, salinidad, contaminantes, entre otros, mejoran la interpretación de los análisis de las comunidades y sus cambios en el tiempo. Las comparaciones a largo plazo, en una sola área marina, son escasas, y en el Golfo de México, los trabajos se han concentrado en estudios con conchas de ostras, concentración de sedimentos y en regiones específicas como Cuba, Florida, Celestún y Río Lagartos (Surge *et al.* 2003; Aragón-Moreno *et al.* 2012; Armenteros *et al.* 2012, 2016; Wingard & Surge 2017; Carnero-Bravo *et al.* 2018; De Jesús-Carrillo *et al.* 2021).

Las lagunas costeras de la Península de Yucatán, se encuentran influenciadas por la agricultura y la ganadería. Específicamente, la laguna costera de Río Lagartos han sido impactada por la extracción de sal y el arribo de huracanes (Herrera-Silveira & Morales-Ojeda 2010). Algunas actividades que han transformado la cobertura vegetal en la Reserva

de Ría Lagartos es la ganadería, a través de pastizales cultivados, la destrucción de la vegetación para el desarrollo de superficies urbanas y la industria salinera (Díaz Yarto 2010). También ha sido sometida a distintos acontecimientos climáticos, con varios huracanes que tocaron tierra en la región en el último siglo. El huracán Beulah de categoría 4, afectó la reserva de Ría Lagartos al ingresar a tierras yucatecas el 17 de septiembre de 1967, con vientos superiores a los 300 km/h. El huracán Gilberto tocó tierra peninsular en Cozumel el 14 de septiembre de 1988, causando graves daños a la infraestructura de la planta salinera en Río Lagartos; disminuyendo su capacidad de producción. El huracán Ópalo llegó a las costas yucatecas el 30 de septiembre de 1995 y el huracán Isidoro, alcanzó la categoría de 4 y golpeó con intensidad a la Península en 2002 (Carabias-Lillo *et al.* 1999; NOAA 2022).

El análisis de la composición de moluscos ha demostrado aportar información sobre los cambios en el tiempo sobre el nivel del mar, uso de la tierra, las alteraciones antropogénicas, la salinidad y los cambios en el hábitat (Wingard & Surge 2017). Los trabajos paleoecológicos que han estudiado a los moluscos con respecto a acontecimientos meteorológicos (e.g., tormentas tropicales, depresiones tropicales y huracanes) registran al bivalvo *Anomalocardia auberiana* (d'Orbigny, 1853) y los gasterópodos de la familia Cerithidae como indicadores, debido al cambio de la salinidad durante y después de la llegada de tormentas en las lagunas de Belice (Adomat & Gischler 2017). En Cuba, también se ha demostrado que los huracanes pueden tener un fuerte impacto sobre la comunidad de moluscos (Armenteros *et al.* 2021); pero aunque la comunidad puede verse afectada por el paso de un huracán, esta puede tener un rápido retorno a las condiciones que tenían antes del huracán (Jackson 1972), y también los cambios en la composición de moluscos se han asociado con actividades de pesquería de arrastre (Edgar & Samson 2004).

Los moluscos se han utilizado para predecir cambios espaciales y temporales. Por ejemplo, se ha estudiado su respuesta a cambios en la salinidad (Wingard & Ishman 1999), cambios en los gremios tróficos de moluscos y presencia de especies (e.g., *Nuculana acuta* (Conrad, 1831) y *Finella dubia* (d'Orbigny, 1840)) durante eventos de alta sedimentación (Armenteros *et al.* 2016). El aumento del nivel del mar durante el Holoceno (Poirier *et al.* 2009) produjo un cambio en la composición de moluscos por la transgresión marina, con la transición de especies de agua dulce a salobre hasta comunidades marinas (Zinke *et al.* 2005).

Teniendo en consideración lo anterior, se propuso abordar los siguientes interrogantes: 1) ¿La comunidad de moluscos en la laguna costera de Río Lagartos ha sido influenciada por



los disturbios ambientales y/o antropogénicos que han ocurrido en la región en el último siglo? 2) ¿Las correlaciones entre los disturbios recopilados históricamente y los patrones espaciales y temporales de la diversidad de moluscos en la laguna costera durante el último siglo, respaldan la hipótesis del disturbio intermedio?

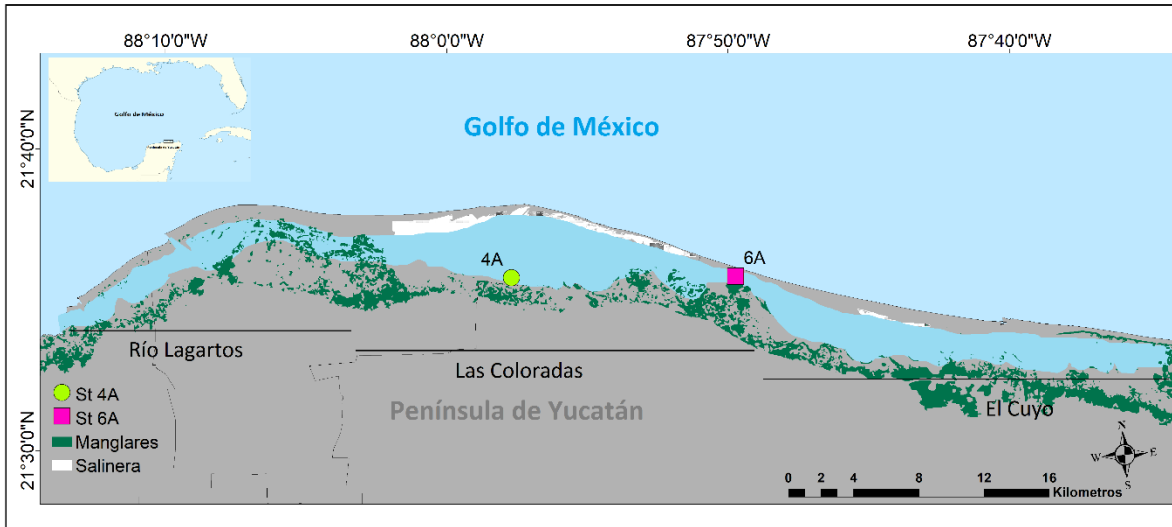
## **Materiales y métodos**

### Área de estudio

El área de estudio es la laguna costera de Río Lagartos (Figura 1), la cual tiene una longitud de 74 kilómetros de longitud y se encuentra ubicada en la Reserva de la Biósfera de Ría Lagartos en la provincia fisiográfica denominada Región Peninsular Yucateca y en la subprovincia de la llanura Cárstica. Se caracteriza por una plataforma de caliza (rocas sedimentarias porosas formadas mayoritariamente por carbonatos) compuesta por rocas sedimentarias del Pleistoceno y Holoceno. Los suelos de la reserva derivan del intemperismo de la roca caliza, procesos climáticos y sedimentación marina. El borde norte está formado por una isla de barrera por la sedimentación de arena. Además, debido a su restringida comunicación con el mar, la laguna costera tiene escasa renovación de aguas internas (~450 días) (Herrera-Silveira & Morales-Ojeda 2010).

La laguna se conecta con el Golfo de México a través de dos ensenadas ubicadas en la parte occidental. El régimen mareal es mixto, predominando la marea diurna y la marea semidiurna durante mareas muertas. El intervalo mareal varía de 0.1 y 0.8 metros (Cuevas-Jiménez & Euán-Ávila 2009). Debido al escaso intercambio con el mar y a que la evaporación supera la precipitación, ocasiona aumentos en la salinidad. En la zona de El Cuyo, por ejemplo, la salinidad alcanza valores superiores 100 ppm. La época de lluvias es de junio a octubre, representando el mes de septiembre las mayores precipitaciones y en el mes de octubre una recarga pronunciada del acuífero (Quesadas-Rojas *et al.* 2021). Los Nortes se presentan de noviembre a febrero; existiendo un mayor flujo de aguas menos salinas, lo que permite una mayor oxigenación, un enfriamiento y aumento de los niveles de agua en la laguna en el mes de diciembre y enero (Carabias-Lillo *et al.* 1999; Quesadas-Rojas *et al.* 2021). La época de sequía comprende los meses de diciembre a mayo.

En el sur de la laguna costera hay influencia de la agricultura y la ganadería. Además, se han observado signos de eutrofización y contaminación. Por otra parte, la laguna se encuentra rodeada de vegetación en dunas costeras y manglares que han sido afectados por la extracción por parte de la industria salinera, tala y por los huracanes (Herrera-Silveira & Morales-Ojeda 2010).

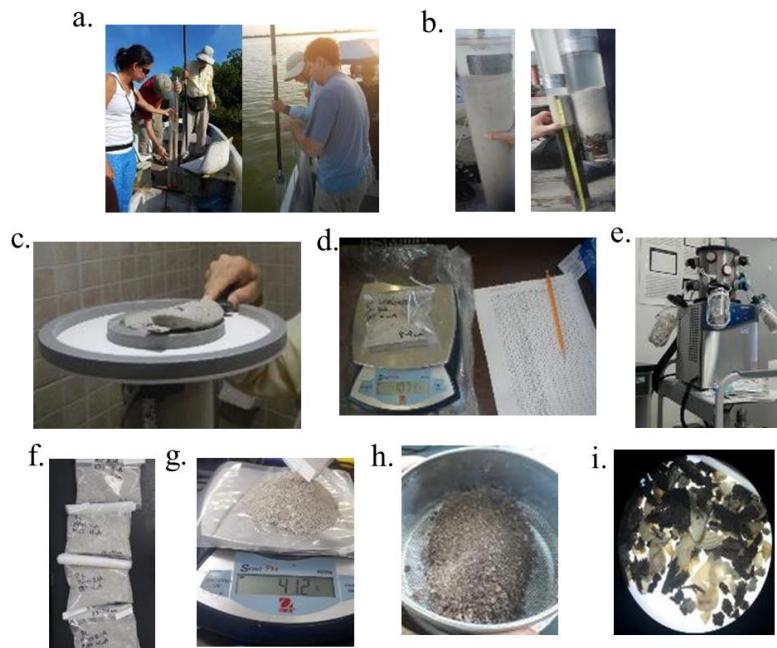


**Figura 1.** Ubicación de la laguna costera de Río Lagartos en la Península de Yucatán México, se muestran la ubicación de los núcleos de sedimento, núcleo 4A (círculo azul), y núcleo 6A (cuadrado naranja), se detallan las zonas de manglar y las salineras.

#### Núcleos de sedimento y datación

Para conocer los cambios espaciales y temporales ocurridos en la laguna costera de Río Lagartos, se extrajeron núcleos de sedimentos en lugares con baja perturbación física y mezcla de sedimentos, en tres sitios en la laguna. Para la selección de los sitios, se tuvo en cuenta la información disponible en la literatura (Valle-Levinson *et al.* 2011; Quesadas-Rojas *et al.* 2021). El muestreo en Río Lagartos se realizó del 25 al 27 de julio de 2017. Cada núcleo se cortó en secciones de ~1 cm (núcleos 4A y 6A) de espesor, para una mejor resolución de las tendencias de cambio que fueron grabadas en el sedimento. En el laboratorio, cada una de las secciones fue congelada y secada por liofilización. Posteriormente, se almacenaron en bolsas de plástico y se subdividieron en dos fracciones: una fracción para análisis geoquímicos (fechado) y la otra fracción para la identificación de moluscos (Figura 2).

La cronología se basó en el modelo de datación del  $^{210}\text{Pb}$ . Para esto, los sedimentos secados en la liofilizadora correspondientes a los núcleos 4A y 6A recolectados en Río Lagartos fueron molidos en un mortero y enviados al laboratorio del Instituto de investigación Paleoambiental de la Universidad de Florida. Allí, siguieron los métodos para datación empleados en Schelske *et al.* (1994) y Brenner & Kenney (2013). Una vez medidas las actividades de  $^{210}\text{Pb}_{\text{total}}$ ,  $^{226}\text{Ra}$ , se procedió a determinar el  $^{210}\text{Pb}_{\text{exceso}}$ . Este se calculó como la diferencia entre  $^{210}\text{Pb}_{\text{total}}$  y el  $^{226}\text{Ra}$  (i.e., Plomo-210 soportado) para cada sección de los núcleos. Teniendo en cuenta que la concentración determinada en cada capa es el resultado de dos procesos: el flujo de  $^{210}\text{Pb}_{\text{exceso}}$  a la superficie del sedimento y el flujo de la masa o tasa de acumulación sedimentaria (cm/año) (SAR, Sediment Accumulation Rate), que también puede ser vista como la tasa de acumulación másica ( $\text{g cm}^{-2} \text{año}^{-1}$ ) (MAR, Mass Accumulation Rate).



**Figura 2.** a. Trabajo de campo en Río Lagartos, extracción de los núcleos de sedimento. b. Núcleos de sedimento recolectados. c. Corte de los estratos de los sedimentos. d. Pesado de los sedimentos en húmedo. e. Secado de las muestras en una liofilizadora. f. Muestras de sedimento secas. g. Pesado de los sedimentos secos. h. Tamizaje de la muestra de sedimento. i. Vista de la muestra de sedimento y moluscos en un estereoscopio.

## Clasificación de acontecimientos

Los distintos acontecimientos ambientales y antropogénicos ocurridos entre 1950 y 2017 se clasificaron en cuatro niveles (1-bajo, 2-moderado, 3-intermedio y 4-alto) según su intensidad y su capacidad para modificar las condiciones ambientales en la laguna costera (Tabla 1).

Tabla 1. Nivel de disturbio de los acontecimientos ocurridos en la laguna costera de Río Lagartos por décadas, incluyendo el año de muestreo de los núcleos (2017), nivel de categoría: 1-bajo, 2-moderado, 3-intermedio y 4-alto. Acontecimientos antropogénicos se clasificaron en: incremento de la población (INEGI 2020), construcción, fragmentación y transformación del hábitat (Carranza Sánchez & Molina Islas 2003), acontecimientos ambientales fueron clasificados en huracanes (H1-H6), tormentas (TS) y depresiones tropicales (DT) (NOAA 2022).

Décadas	Antropogénicos			Ambientales				Nivel de disturbio
	Incremento de la población (N°Ind)	Construcciones	Fragmentación y transformación del hábitat %	H6,H5,H4	H1,H2,H3	TS	DT	
2010	4,936					Rina, Don, Karen, Colin, Nate		3
2000	4,668		24	Isidoro, Emily	Wilma, Ida	Claudette, Alberto, Dolly	Gordon, Bonie, Cindy, Olga, Barry	4
1990	3,321	Construcción del muelle	19.7			Mitch, Ópalo, Alberto	Katrina	3
1980	2,652		16.2	Gilberto, Allen		Keit	Danny, Albert	4
1970	1,981	Carretera de la salinera	11.8			Ella, Brenda, Eloise	Greta, Henri, Caroline, Delia	2
1960	1,264				Beulah, Inez, Carla		Debbie	2
1950	920				Hilda, Charlie		Flossy, How	1

## Muestras de moluscos

La fracción de sedimentos que no se utilizó para los análisis geoquímicos se tamizó a través de una malla de 1 mm para eliminar las partículas finas. Las muestras de moluscos fueron observadas en los microscopios estereoscópicos marca Amscope y Nikon-SMZ800. Todas las conchas de moluscos que tuvieran estructuras suficientes para su identificación fueron consideradas, la charnela en el caso de bivalvos y apertura y ápice para gasterópodos, además la presencia de más de la mitad de la concha. En el caso de los bivalvos, las valvas articuladas y desarticuladas que coincidían se contaron como un solo individuo. Las especies recolectadas se identificaron con base a caracteres morfológicos y se guardaron en viales de plástico en la colección seca de moluscos “Colección de Moluscos de la Península de Yucatán” (CMPY), ubicada en la Unidad Multidisciplinaria de Docencia e Investigación Campus Sisal, Universidad Nacional Autónoma de México, México.

Para la identificación taxonómica de las especies de moluscos recolectados se tomó en cuenta las especies incluidas en la colección de moluscos de la Península de Yucatán (CMPY) y referencias bibliográficas. La clasificación taxonómica siguió a Bouchet *et al.* (2010) para la clase Bivalvia y Bouchet *et al.* (2017) para la clase Gastropoda, los moluscos fueron identificados usando múltiples literatura (García-Cubas & Reguero 2004, 2007; Mikkelsen & Bieler 2008; Tunnell *et al.* 2010; Espinosa *et al.* 2012; Redfern 2013).

## Análisis de datos

### Composición y características de la fauna de moluscos

Todas las especies fueron cuantificadas y clasificadas por especie, gremio trófico (consumidores de depósito, carnívoros, ramoneadores y suspensívoros) y disposición en el sustrato (infaunal y epifaunal). Para probar si existía cambios en la composición de especies entre núcleos se realizó un análisis de similitud (ANOSIM) (Sommerfield *et al.* 2021). El factor utilizado fue el núcleo de sedimento.

## Respuesta de los moluscos a perturbaciones

1. Se evaluaron los cambios estratigráficos en los núcleos de sedimento, con la matriz dispuesta por estratos (muestras) y las especies de moluscos como variables. Esta matriz se transformó en raíz cuarta para reducir el efecto de las especies abundantes en relación con las especies raras. Posteriormente, se estimó el coeficiente de similitud de Bray-Curtis entre todos los pares de muestras en los núcleos, a partir de lo cual se generó una matriz triangular que se utilizó para los análisis estadísticos. Los patrones de similitud de cada núcleo se estimaron y se visualizaron con el escalamiento multidimensional no métrico (nMDS, por sus siglas en inglés) Todos los análisis se realizaron utilizando el programa PRIMERV7 & PERMANOVA (Clarke *et al.* 2014).
2. Se correlacionó la abundancia de los moluscos con el nivel de perturbación. Para esto se probó la hipótesis nula que la abundancia no está correlacionada con el nivel de perturbación acumulado en el tiempo. Se construyó una matriz modelo usando la matriz de Bray-Curtis y el nivel de perturbación para cada uno de los núcleos de sedimento (i.e., 6A y 4A). Luego se realizó la prueba “RELATE” para poner a prueba esta asociación. La prueba se realizó utilizando 999 permutaciones y el método de correlación de Spearman (Clarke & Gorley 2015).
3. Se evaluó la relación entre la  $\alpha$ -diversidad y el nivel de perturbación. Para esto se probó la hipótesis nula que el número de especies no está asociado con los niveles de perturbación registrados en el tiempo. Luego se realizó el análisis utilizando la matriz modelo, el número de especies y la prueba “RELATE” para poner a prueba esta asociación (Clarke & Gorley 2015).

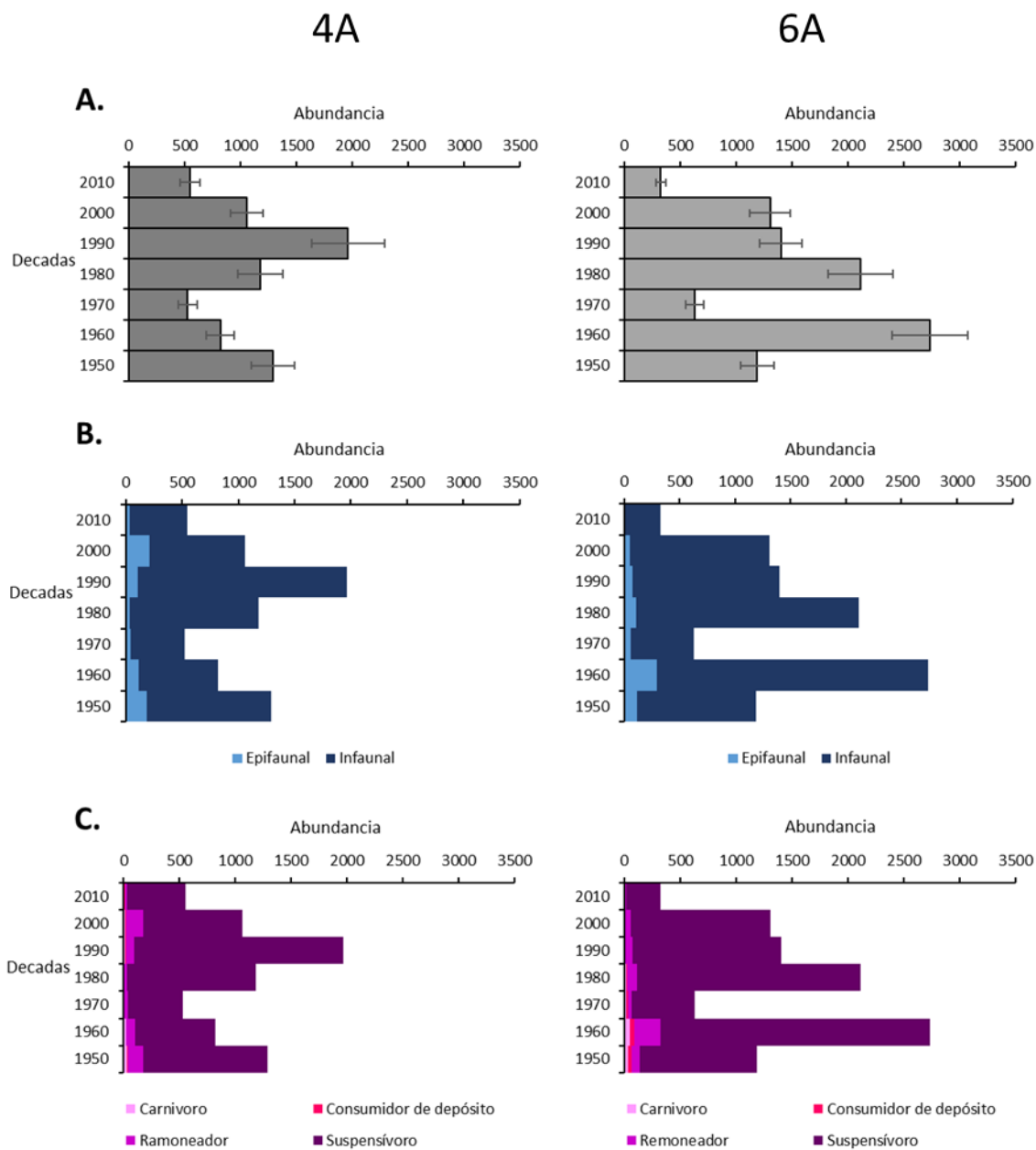
## Resultados

### Estructura y composición de la fauna de moluscos

En los núcleos de sedimento 4A y 6A se identificaron 65 especies de moluscos, representadas por 20 especies de la clase Bivalvia y 45 de la clase Gastropoda, pertenecientes a 32 familias, 8 géneros y 17089 individuos. Las especies más frecuentes fueron los bivalvos *Anomalocardia auberiana* [= *Anomalocardia puella* (Philippi, 1846)] y

*Brachidontes exustus* (Linnaeus, 1758) y los gasterópodos *Bittium varium* (L. Pfeiffer, 1840) y *Acteocina canaliculata* (Say, 1826). La mayoría de las especies (32 especies) eran raras y solo aparecieron una vez.

Todos los estratos de sedimento en el núcleo 4A contenían más de 500 individuos (Figura 3A). Las muestras del núcleo 6A contenían también más de 500 individuos, solo una capa de la década de 2010 contenía menos de 500 individuos. Ambos núcleos mostraron fluctuaciones estratigráficas en la abundancia. En general, hubo más individuos infaunales que epifaunales (Figura 3B). Hubo representantes de los cuatro gremios tróficos en ambos núcleos (Figura 3C), pero no se encontraron representantes en todos los estratos (décadas). En el núcleo 4A, los consumidores de depósito y carnívoros presentaron una menor abundancia con respecto a los ramoneadores y suspensívoros. Además, los consumidores de depósito estuvieron ausentes en la década de 1970. En el núcleo 6A, también los consumidores de depósito y los carnívoros presentaron una menor abundancia con respecto a los ramoneadores y suspensívoros. Además, los carnívoros estuvieron ausentes en la década de 2010.



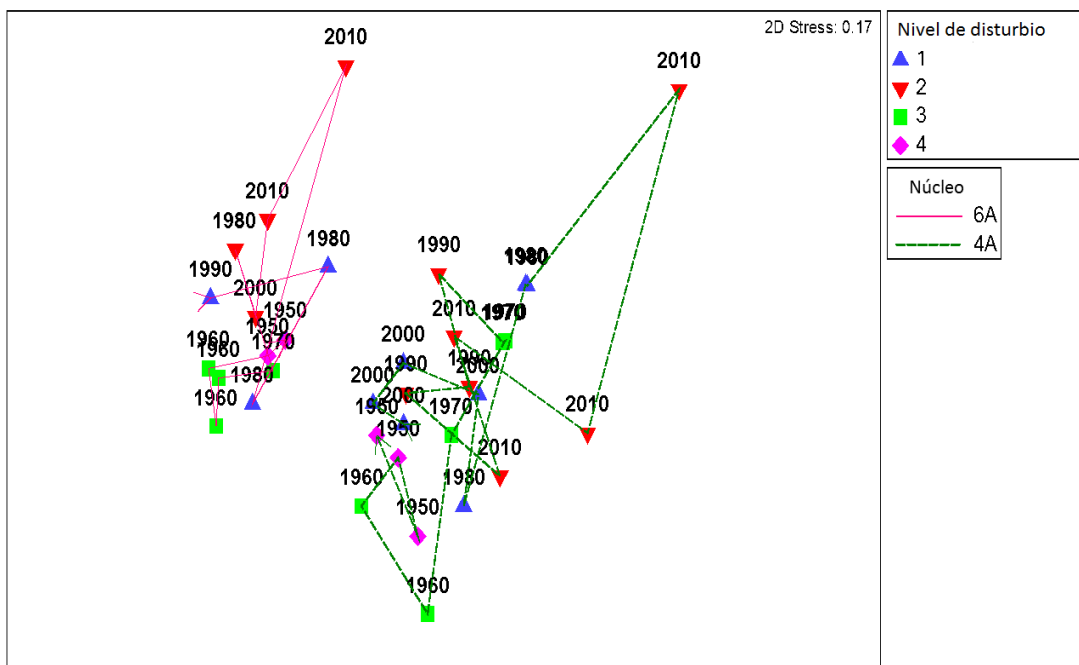
**Figura 3.** Abundancia de individuos, disposición en el sustrato y gremios tróficos por décadas para los núcleos 4A y 6A recolectados en la laguna costera de Río Lagartos.

#### Nivel de perturbación

La composición de especies observadas en el núcleo 6A difiere del núcleo 4A (ANOSIN pruebas pareadas de los núcleos, 6A VS. 4A  $R=0.527$ ,  $p=0.001$ ). Las muestras representadas en el nMDS mostraron una distribución a lo largo de las décadas y se



observó una agrupación por núcleos 4A (Figura 4). Desde una perspectiva cualitativa, las trayectorias temporales mostraron cambios en diferentes direcciones, indicando un cambio en la composición de especies. La prueba RELATE demostró que la abundancia de moluscos en el núcleo 4A no estaba relacionada con los acontecimientos que ocurrieron en la laguna ( $Rho = -0.005$ ;  $p > 0.01$ ). De manera similar, no hubo una relación significativa entre la abundancia y los acontecimientos en el núcleo 6A ( $Rho = 0.168$ ;  $p > 0.01$ ). La riqueza de especies ( $\alpha$ -diversidad) en el núcleo 4A no estaba relacionada con los acontecimientos históricos en la laguna costera ( $Rho = 0.058$ ;  $p > 0.01$ ). Del mismo modo, en el núcleo 6A las dos variables no estuvieron relacionadas ( $Rho = -0.123$ ;  $p > 0.01$ ).



**Figura 4.** Escalamiento multidimensional no métrico (nMDS, por sus siglas en inglés) de cada uno de los estratos para los distintos núcleos: núcleo 4A (línea punteada verde) y núcleo 6A (línea fucsia) en la laguna de Río Lagartos. La abundancia de especies se transformó a raíz cuarta, el coeficiente de disimilitud utilizado fue Bray-Curtis. Los números sobre cada símbolo representan las décadas por estrato, y los triángulos los cuatro niveles de disturbio. Las líneas unen las décadas (estratos) sucesivos para cada núcleo.

## Discusión

Este estudio representa la síntesis de los acontecimientos ambientales y antropogénicos ocurridos a lo largo del último siglo en la laguna de Río Lagartos, con el fin de probar la

hipótesis del disturbio intermedio (Connell 1978) en este contexto. La abundancia, riqueza de especies, disposición en el sustrato y los gremios tróficos de los moluscos cambiaron a lo largo del tiempo, pero el análisis reveló que los cambios no fueron como respuesta a los acontecimientos considerados en el estudio (vistos como niveles de perturbación; Tabla 1) para la laguna de Río Lagartos.

Los acontecimientos considerados en el estudio, como los sucesos climáticos pueden actuar a pequeña y gran escala, y pueden causar cambios a corto o largo plazo dependiendo de su intensidad y proximidad al ecosistema. Por ejemplo, en una laguna costera como Río Lagartos el aumento del nivel del agua producto de los vientos pudo contribuir a empujar el agua y los sedimentos desde las entradas hasta el interior de la laguna, modificando a su vez las concentraciones de oxígeno y salinidad (Patrick *et al.* 2020; Valle-Levinson *et al.* 2022), e influir en los cambios en la composición de moluscos de la laguna.

Otro de los acontecimientos considerados en el estudio, fueron las actividades humanas. Se evidenció un aumento de la población humana que habitó en la laguna a lo largo del tiempo (Tabla 1) (INEGI, 2020). Este acontecimiento pudo estar contribuyendo a la contaminación por lixiviados y aguas residuales, sumado al aumento en el turismo (Arenas Castillo *et al.* 2015; SEFOTUR 2020) y la construcción de carreteras.

Se sabe que la respuesta a los disturbios en moluscos está relacionada con la combinación de varios factores bióticos (e.g., competencia, depredación) y abióticos (e.g., salinidad, temperatura) (Armenteros *et al.* 2016; Gallmetzer *et al.* 2017; Wingard & Surge 2017). Pero no sabemos qué factores estresantes pudieron haber afectado a la comunidad de moluscos después de los acontecimientos en la laguna de Río Lagartos. Se ha demostrado que los factores estresantes influyen en la salud, abundancia y la distribución de especies (Przeslawski *et al.* 2015; Ellis *et al.* 2017; Vilas-Boas *et al.* 2021). En este estudio paleoecológico, no pudimos realizar un análisis de la respuesta de la comunidad inmediatamente después de que ocurriera una perturbación, los cambios que se detectaron en los núcleos reflejan respuestas a los disturbios que se promediaron durante períodos de años a décadas.

Los disturbios generan cambios en los ecosistemas que influyen en las comunidades (Castañeda-Moya *et al.* 2020). El concepto de disturbio a distintas frecuencias e intensidades y su relación con la diversidad fue establecido por Connell (1978), quien

estableció que la riqueza de especies es alta en niveles de perturbaciones intermedias. Cuando el disturbio era intenso y frecuente, se excluía a la mayoría de las especies, dejando solamente aquellas especies más resistentes. Cuando el disturbio era raro o de baja intensidad, había baja diversidad. La comprensión de la respuesta de los ecosistemas ante los disturbios en escalas espaciales y temporales resulta ser un desafío. Por ejemplo, en Río Lagartos los huracanes propiciaron la entrada de agua, lo que produjo una disminución en la salinidad del cuerpo de agua, mientras que en Florida, los huracanes Wilma e Irma depositaron sedimentos en la zona de los manglares, promoviendo la distribución de sedimentos y nutrientes (Castañeda-Moya *et al.* 2020). En la Laguna de Términos, la intrusión marina entre los 1980 y finales de 1990 contribuyó a la erosión costera y la acumulación de carbono orgánico en las praderas de pastos marinos (Ruiz-Fernández *et al.* 2020).

El estudio del cambio de la composición de moluscos debido a los acontecimientos se ha estudiado en otras regiones, pero los procesos implican niveles de disturbio alto, que han contribuido a la disminución de las comunidades. Sin embargo, en Cuba no se encontraron señales claras respecto a que los cambios en la comunidad en moluscos hubiesen sido por huracanes. En cambio, se han identificado otros acontecimientos, como la eutrofización, cambios en el uso del suelo y contaminación por mercurio (Armenteros *et al.* 2016). En el norte del Mar Adriático, la disminución de moluscos se debió a altas tasas de sedimentación y concentraciones elevadas de metales (Gallmetzer *et al.* 2017). En la laguna de Río Lagartos, existe un cambio en la composición de especies a lo largo del tiempo (Figura 4), pero estos cambios no estuvieron relacionados con los acontecimientos que se enlistaron en el estudio. Por lo tanto, es necesario identificar, para estudios posteriores, las condiciones bióticas y abióticas que intervienen en la fauna de moluscos. Resultaría interesante medir la susceptibilidad de las especies al disturbio y si esta depende de la madurez de la comunidad. Algunos modelos donde se simuló el disturbio y se midió la capacidad de recuperación de los ecosistemas, se encontraron que hay una relación inversa entre ecosistemas maduros y estabilidad (Pérez-España & Arreguín-Sánchez 2001). Pero, también existen opiniones contradictorias, donde consideran que los ecosistemas maduros son más estables (Lenz *et al.* 2004).

## Capítulo 3. Molluscs along a salinity gradient in a hypersaline coastal lagoon, southern Gulf of Mexico

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## Resumen

Los moluscos son un filo diverso en las lagunas costeras debido a que muestran amplios intervalos de tolerancia y preferencias óptimas con respecto a las condiciones ambientales. Reportamos la composición taxonómica, preferencias de hábitat y gremios alimenticios de moluscos de la laguna costera de Río Lagartos, México. Los moluscos fueron recolectados en la temporada de lluvias (septiembre/octubre 2017), durante la temporada de invierno (Nortes) (febrero 2018) y al final de la temporada seca (mayo 2018). Las muestras se tomaron usando una draga Ponar, un núcleo cilíndrico de PVC o una red de cerco de playa. Se analizaron las características abióticas (distribución del tamaño del grano del sedimento, abundancia de vegetación acuática sumergida y salinidad) para explorar las diferencias en la composición de moluscos a través del gradiente de salinidad que caracteriza a la laguna costera (~30-78 PSU). Se encontraron 39 especies, 34 géneros, 23 familias y dos clases de moluscos. Las especies estenohalinas fueron más numerosas que las eurihalinas, pero su presencia en las muestras fue baja (<20% de las muestras). Los taxones estenohalinos vivían principalmente en entornos caracterizados por la salinidad marina, y pocos se encontraron en condiciones hipersalinas. Se recolectaron un menor número de especies que en los estudios realizados en la laguna hace más de 35 años. Las curvas de acumulación de especies revelaron que no se capturó toda la riqueza de especies. Los ambientes euhalinos mostraron una mayor riqueza de especies de moluscos y tenían una mayor proporción de vegetación acuática sumergida. En los ambientes hipersalinos, la riqueza de especies puede verse favorecida por la menor dominancia de arenas. Los suspensívoros fueron el grupo más diverso tanto en los ambientes euhalinos como en los hiperhalinos.

## Abstract

Molluscs are a diverse phylum in coastal lagoons because the numerous taxa collectively display broad ranges of optima and tolerance with respect to ambient conditions. We report on the taxonomic composition, habitat preferences and feeding guilds of molluscs from Río Lagartos coastal lagoon, Mexico. Molluscs were collected in the rainy season (September/October 2017), during the winter (Nortes) season (February 2018) and at the end of the warm, dry season (May 2018). Samples were taken using a Ponar dredge, a cylindrical PVC core barrel, or a beach seine. We studied the abiotic characteristics (sediment grain-size distributions, submersed aquatic vegetation abundance and salinity) to explore assemblage differences across the broad salinity gradient that characterizes the system (~30–78 PSU). Molluscs were represented by 39 species, 34 genera, 23 families and two classes. Stenohaline species were more numerous overall than euryhaline species, but their occurrence in samples was low (<20% of the samples). Stenohaline taxa lived primarily in environments characterized by marine salinity, and few were found under hypersaline conditions. We collected a smaller number of species than did studies carried out in the lagoon >35 years ago. Species accumulation curves revealed that the full species richness was not captured in our study. Euhaline environments displayed greater mollusc species richness and had a larger proportion of amount (mass) of submersed aquatic vegetation. In the hypersaline environments, species richness may be favoured by the lower dominance of sands. Suspension feeders were the most diverse group in both the euhaline and hyperhaline environments.

## Introduction

Mexico has approximately 1,567,300 ha of coastal wetlands, of which about 674,500 ha (43%) lie along the Gulf of Mexico (GoM) (including the Atlantic Ocean and the Caribbean Sea) (Contreras-Espinosa & Warner 2004). These are represented by about 149 geomorphological forms, of which 59% are coastal lagoons (De La Lanza Espino *et al.* 2013). Coastal lagoons are shallow, enclosed or semi-enclosed coastal wetlands, which are ephemeral or permanently flooded, and usually separated from the sea by a sand barrier (Lankford 1977; Kjerfve 1994). Coastal lagoons are often characterized by strong spatial salinity gradients (Lampton & Armah 2008) and temporal variations in salinity at different

time scales, the latter related to intra-annual fluctuations in the precipitation-evaporation balance, tidal forces and wind stress, all of which regulate the hydrologic balance (Kjerfve & Magill 1989). Such lagoons are often highly productive aquatic systems that contain many habitat types (Herrera-Silveira & Morales-Ojeda 2010) and therefore support numerous invertebrate phyla (Hernández-Guevara *et al.* 2008).

Molluscs are an abundant and diverse phylum in coastal lagoons because the numerous taxa collectively display a broad range of optima with respect to ambient conditions, e.g. salinity and temperature, and some individual species display a broad tolerance with respect to those variables (Wingard & Surge 2017). Temperature is perhaps the most important environmental variable that determines large-scale geographic distributions of marine organisms, whereas salinity exerts greater control at the local level (Lamprey & Armah 2008; Tunnell *et al.* 2010; Selly *et al.* 2018; De Jesús-Carrillo *et al.* 2020, 2021). In addition to temperature and salinity, other environmental factors affect benthic mollusc distributions, such as water circulation (Tunnell *et al.* 2010; Grenz *et al.* 2017), substrate type (Abdelhady *et al.* 2019), habitat complexity (Duarte *et al.* 2020) and oxygen concentration (De Jesús-Carrillo *et al.* 2020).

Benthic mollusc taxa occupy many positions in the food web. Most bivalves are suspension feeders, whereas gastropods, which display infaunal and epifaunal benthic life habits, are primarily grazers, predators or scavengers (De Lucena *et al.* 2012; Wingard & Surge 2017). Molluscs are also a preferred food source for many other organisms (Arceo-Carranza *et al.* 2013; Chi-Espínola & Vega-Cendejas 2013; Hinojosa-Garro *et al.* 2013).

Several investigations yielded lists of molluscs from the coastal GoM (Vokes & Vokes 1983; García-Cubas & Reguero 2004, 2007). For coastal lagoons, a great deal of information from the western and southern GoM was generated from the 1970s to 2000. It consists of taxonomic inventories, as well as studies on community structure and ecology (García-Cubas 1970; García-Cubas 1971, 1981; Reguero & García-Cubas 1989, 1991b, 1993, 1994; García-Cubas *et al.* 1990, 1992, 1999). Recently, the assemblage structure and functional ecology of molluscs was addressed in Mecoacan Lagoon, also in the southern GoM (De Jesús-Carrillo *et al.* 2020, 2021). An exhaustive evaluation of the malacological diversity associated with different habitats was performed in Los Petenes Biosphere Reserve, Campeche (Mexico), and in a suite of coastal lagoons along the western and southeastern Mexican GoM (Lagunas Mandinga, Sontecomapan, Carmen-Machona, Mecoacán, Tupilco-Ostión, Terminos, Atasta, Santa Anita, and Sabancuy) (Gonzalez *et al.*

2018). Nevertheless, studies of molluscs in the eastern GoM (i.e., the Yucatán Peninsula and Caribbean coastal wetlands) are few. The geographic distribution patterns and species richness of bivalves and gastropods from 33 localities along the shoreline (including some coastal wetlands) and corals reefs of the Yucatán Peninsula were studied about 20 years ago, using specimens collected during the 1980s (Gonzalez *et al.* 1991). In the last decade, a study addressing the entire macrobenthic fauna community in the Río Lagartos coastal lagoon, northern Yucatán Peninsula, yielded information on the presence, patterns of distribution, and physical-chemical controls on the dominant molluscs (Kuk-Dzul *et al.* 2012). Aside from those studies, however, we lack critical information, such as functional traits, updated inventories, or ecological preferences, about molluscs in coastal lagoons of the eastern GoM (Yucatán Peninsula).

The coastal zone of the Yucatán Peninsula is often recognized as a characteristic unit, with two subregions that have very different oceanographic characteristics: (i) the northern and western parts of the Yucatán Peninsula, which are part of the Gulf of Mexico, and (ii) the eastern coast of the Peninsula, which is part of the Caribbean Sea (Herrera-Silveira *et al.* 2013 and references cited therein). The first subregion, also called the “Campeche Bank” is an extension of the Peninsula that is a vast and shallow continental shelf, which, like the terrestrial portion of the Yucatán Peninsula is composed of porous, Karst limestone of high permeability. This enables direct communication between continental and marine waters (Valle-Levinson *et al.* 2011). The shallow environment of this subregion promotes important heat gain and evaporation, which in the coastal lagoons and along the coastal environment in general, contributes to the development of warm and very saline waters that enter the GoM (Enriquez *et al.* 2013). Also, being part of the GoM, tides of this subregion are predominantly diurnal (Tenorio-Fernandez *et al.*, 2016), with maximum tidal ranges that reach 0.6 m during tropical tides, and minimum ranges of only 0.1 m during equatorial tides, when the tide can be semi-diurnal, as long as it does not coincide with neap tides (Valle-Levinson *et al.* 2022). The second subregion is different, as the water depth increases abruptly very close to the coast, where the intense oceanic Yucatán Current flows northward through the Yucatán Channel into the GoM. Tides in this subregion are semi-diurnal and also micro-tidal (<0.6 m range). Both regions are greatly influenced by the dominant Trade Winds (easterlies) and by substantial continental submarine fresh groundwater discharges. The northeastern corner of the Yucatán Peninsula is a peculiar transition zone, which is influenced by both the Caribbean Sea and GoM. The region receives nutrient-rich upwelling water that arises from the Yucatán Current and moves onto the shallow Yucatán Shelf,

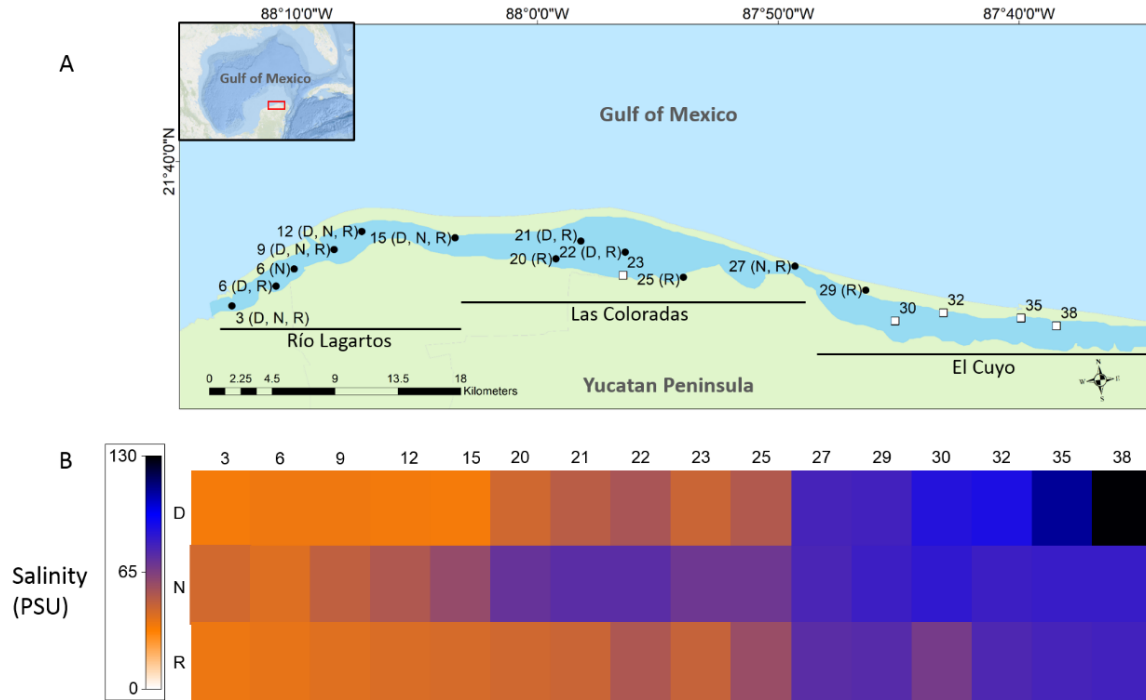


interacting with the continental border (western boundary current) (Enriquez et al., 2010; Reyes-Mendoza et al., 2016). Linked to this transitional character are particular biological communities, including molluscs, which are observed in the northern Yucatán Peninsula near-coastal areas, including the coastal lagoons. Those communities differ from communities in the southern GoM to the west and in the Caribbean Sea to the east (Gonzalez *et al.* 1991; Herrera-Silveira *et al.* 2013; Aguilar-Medrano & Vega-Cendejas 2021).

Given the distinctive geographic characteristics of the northern Yucatán Peninsula and the paucity of mollusc research in the area, we undertook this study to evaluate mollusc community composition in the second largest coastal lagoon on the northern Yucatán Peninsula, i.e. the Río Lagartos coastal lagoon. Considering the marked spatial salinity gradient in this system, we also explored how mollusc species and functional groups are distributed with respect to salinity.

#### Study area

The Río Lagartos coastal lagoon is located on the north-east coast of the Yucatán Peninsula (21°26'–21°38'N 87°30'–88°5'W), Mexico, and is part of the Ría Lagartos Biosphere Reserve. This east–west-oriented lagoon is ~80 km long and has a total surface area of ~98 km<sup>2</sup>. The lagoon is divided into three hydrologically connected basins: Río Lagartos basin [mouth], Las Coloradas basin [middle] and El Cuyo basin (head [interior]) (Quesadas-Rojas *et al.* 2021) (Figure 1A). It is generally shallow (~0.4–1.0 m) (Valdes & Real 2004; Quesadas-Rojas *et al.* 2021), with some deeper locations, up to 3.5 m in channels or between zones (Quesadas-Rojas *et al.* 2021). The lagoon is hypersaline throughout much of its length, with a gradient from the head near El Cuyo (>70) to the seaward region near Río Lagartos (33–38) (Herrera-Silveira & Ramírez-Ramírez 1998) (Figure 1B). Hypersaline conditions are a consequence of low rainfall (<500 mm/year), high evaporation (~2000 mm/year), absence of overland freshwater inputs, long residence times, and physical/geomorphological characteristics (Valdes & Real 2004; Peralta-Meixueiro & Vega-Cendejas 2011).



**Figure 1.** (A) Location of the Río Lagartos coastal lagoon on the northern Yucatán Peninsula, Mexico. The extents of the three main basins of the system are shown (Río Lagartos basin (mouth), Las Coloradas basin (middle) and El Cuyo basin (head)). Black dots indicate sites where molluscs were collected, open squares indicate sites without molluscs and letters denote the season when molluscs were collected (N: cool Nortes season (February sampling), R: rainy season (September/October sampling), D: warm and dry season (late May sampling)). (B) Heat map of the salinity values per station (shown at the top) and season (D: warm and dry, N: cool Nortes, R: rainy) (shown on the left).

## Materials and methods

### Field sampling and data collection

Sampling strategy: samples were collected in the Río Lagartos coastal lagoon system (Figure 1A) as part of the Salinity Gradient Energy project of the Centro Mexicano de Innovación en Energía Océano (CEMIE Océano). Samples were obtained from 16 stations distributed along the lagoon, in the three main basins of the system: Río Lagartos basin to the mouth, in the west (stations: 3, 6, 9, 12, 15), Las Coloradas basin, in the middle (stations: 20, 21, 22, 23, 25) and El Cuyo basin to the head of the lagoon, in the east (stations: 27, 29, 30, 32, 35, 38) (Figure 1A; Table 1). Spatial distribution of the stations was based on

previous studies of abiotic and biotic variables, which indicated that the three basins can be considered environmentally and biologically distinct (Ortegón-Aznar *et al.* 2001; Valdes & Real 2004; Vega-Cendejas & Hernández De Santillana 2004; Peralta-Meixueiro & Vega-Cendejas 2011; Dávila-Jiménez *et al.* 2019). The lagoon was sampled during three periods that coincided with the end of the three seasons in the region: the rainy season (September/October 2017), the cool Nortes season (February 2018) and the warm, dry season (May 2018) (Table 1). This was done to capture seasonal differences in the mollusc fauna throughout the year. Samples were collected at water depths ranging from 0.5–1.5 m.

Table 1. Sampling locations where molluscs were collected in the hypersaline Río Lagartos coastal lagoon, Yucatán Peninsula, Mexico. Survey letters ‘RL’ indicate Río Lagartos and survey numbers indicate the year of sampling and month when the sampling survey started. Site numbers are as indicated in Figure 1A and locations are designated by latitude (north) and longitude (west). Date is collection date (year-month-day). Season of collection is indicated by R: rainy season (September/October sampling), N: cool Nortes season (February sampling), and D: warm and dry season (late May sampling). Basin of the lagoon system (RL: Río Lagartos (mouth), CO: Las Coloradas (middle), CU: El Cuyo (head)), and value of salinity in Practical Salinity Units (PSU) also indicated.

Survey code	Site	Latitude N	Longitude W	Date of collection	Season	Basin	Salinity (PSU)
RL1709	3	21.574	-88.231	2017-10-03	R	RL	36.7
RL1709	6	21.581	-88.199	2017-10-03	R	RL	38.2
RL1709	12	21.608	-88.135	2017-10-03	R	RL	41.6
RL1709	15	21.596	-88.071	2017-10-04	R	RL	42.5
RL1709	20	21.575	-88.003	2017-10-04	R	CO	44.1
RL1709	21	21.592	-87.985	2017-10-04	R	CO	45.8
RL1709	22	21.581	-87.955	2017-10-05	R	CO	53.0
RL1709	25	21.563	-87.916	2017-10-05	R	CO	58.1
RL1709	27	21.560	-87.838	2017-10-02	R	CU	74.0
RL1709	29	21.535	-87.791	2017-10-02	R	CU	75.0
RL1709	9c1	21.603	-88.156	2017-09-29	R	RL	40.0

RL1709	9c2	21.603	-88.156	2017-09-29	R	RL	40.0
RL1709	9c3	21.603	-88.156	2017-09-29	R	RL	37.7
RL1709	9c4	21.603	-88.156	2017-09-30	R	RL	40.0
RL1802	3	21.574	-88.230	2018-02-27	N	RL	43.5
RL1802	6	21.592	-88.185	2018-02-27	N	RL	40.5
RL1802	12	21.608	-88.136	2018-02-27	N	RL	52.3
RL1802	15	21.596	-88.071	2018-02-28	N	RL	58.9
RL1802	27	21.560	-87.838	2018-02-23	N	CU	78.0
RL1802	9c2	21.603	-88.156	2018-02-26	N	RL	37.2
RL1802	9c3	21.603	-88.156	2018-02-26	N	RL	36.9
RL1805	3	21.574	-88.230	2018-05-19	D	RL	34.5
RL1805	6	21.580	-88.198	2018-05-19	D	RL	36.0
RL1805	12	21.608	-88.135	2018-05-19	D	RL	35.2
RL1805	15	21.596	-88.071	2018-05-19	D	RL	34.3
RL1805	21	21.592	-87.985	2018-05-21	D	CO	49.8
RL1805	22	21.581	-87.955	2018-05-20	D	CO	53.8
RL1805	9c1	21.603	-88.156	2018-05-17	D	RL	36.2
RL1805	9c2	21.603	-88.156	2018-05-17	D	RL	37.2
RL1805	9c3	21.603	-88.156	2018-05-18	D	RL	35.4
RL1805	9c4	21.603	-88.156	2018-05-18	D	RL	35.3

Mollusc sampling: molluscs were collected using three methods. Samples of macrobenthic molluscs were obtained using a standard Ponar dredge (9" × 9" or 22.9 × 22.9 cm; 0.052 m<sup>2</sup> sampling area), or a cylindrical PVC core tube (6" diameter; 0.018 m<sup>2</sup> sampling area), the latter in the event that the substrate was too hard and the dredge did not penetrate the sediment. Duplicate samples were obtained at each station, and sediments were sieved through a 500-µm mesh to separate the macrofauna. Megabenthic molluscs were collected

using a 40-m-long and 1-m-high beach seine with half-inch mesh size, covering an area of 400 m<sup>2</sup>. Molluscs on the roots of red mangrove (*Rhizophora mangle* Linnaeus, 1753) were also obtained in some cases, by gently scraping them from the root surface over a 20 × 20 cm<sup>2</sup> area, at mid-depth in the water column. Details about the sampling locations and gear used are found in Supplementary Material 1. Specimens from one replicate at each station were initially anaesthetized with magnesium chloride, and then preserved in 4% formaldehyde. The other replicate was frozen for future chemical analyses. In the laboratory, the formaldehyde samples were transferred to 70% ethanol, after which all molluscs were sorted and identified, usually to species level, under a stereo- or a compound microscope.

Taxonomic classification largely followed Bouchet et al. (2010) for Bivalvia, and Bouchet et al. (2017) for Gastropoda, though some classifications were updated using Mikkelsen & Bieler (2008), Redfern (2013) and Tunnell *et al.* (2010). Molluscs were identified to the lowest possible taxonomic level, using multiple sources (García-Cubas 1981; García-Cubas & Reguero 2007; Mikkelsen & Bieler 2008; Tunnell *et al.* 2010; Espinosa *et al.* 2012; Redfern 2013), and photographed. The term specimen generally refers to live-collected animals with soft parts intact. Bivalve shells are described as “paired,” and only articulated individuals were photographed. Only for the species of gastropod *Cerithium atratum*, photographs were obtained from a dead specimen with a sipunculid worm inside, but for numerical analyses, only live animals were considered. Each specimen was assigned a catalog number 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.

Salinity measurement: At each station, salinity was measured in the water column at depths between 0.15 and 0.35 m, using a multiparameter Aquaprobe AP-5000. A refractometer was used to measure salinity when values exceeded 60, and a Baume hydrometer was used when salinity was >80.

Sediment sampling: Sediments were sampled with the same dredge or PVC core barrel used for biological sampling and collected material was stored at -20 °C for grain-size analysis. In the laboratory, sediments were dried at 60 °C to a constant weight, and later, proportions of gravel (>2 mm), sand (0.063-2 mm) and silt/clay (<0.063 mm) (Wentworth 1922) were obtained by sieving sediments with a sieve agitator for 20 minutes.

Submersed vegetation: The macroscopic vegetation collected in each macrobenthos sample was separated from the sediment after thorough inspection under the microscope to separate the organisms. Wet weights of the vegetation and sediments were obtained after drying with blotting paper, and the gravimetric contribution of vegetation (macroalgae and seagrasses) to the whole sample (i.e., vegetation and sediments) was calculated as a proxy for the amount of vegetation in the sample.

## Data analysis

### Community composition analysis

A sample presence-absence matrix was constructed. Presence of the species in each basin and during each sampling period was examined and the total number of species was obtained. Organisms were classified according to their taxonomic class (Bivalvia or Gastropoda), habitat (infaunal or epifaunal) and feeding guild (suspension feeders, carnivores, deposit consumers or grazers), following the classification scheme of García-Cubas (1981) and García-Cubas & Reguero (2007), and the number of species in each group was determined. These three classifications were related in an alluvial diagram with the online software Raw graphs 2.0.

### Species vs. salinity analysis

Samples were classified into two groups based on salinity (euhaline [30-40] and hyperhaline [ $>40$ ]), following the classification of Wingard et al. (2012), and the salinity range occupied by each species was explored. Next, species were classified into two groups based on salinity tolerance, i.e. stenohaline (occurring in  $<20\%$  of the total salinity range in the lagoon) and euryhaline (occurring in  $>20\%$  of the total salinity range in the lagoon). The percent contribution to the total number of species and the frequency of occurrence ( $FO\% = \text{number of samples in which a class was present} / \text{total number of samples} \times 100$ ) of each taxonomic class, habitat group, and feeding guild were calculated for the euhaline and hyperhaline environments. Mean values and standard deviations of the different sediment grain-size

classes and of the submersed vegetation gravimetric percentages were also estimated for both environments.

Species accumulation curves were constructed for each salinity environment with interpolation-extrapolation of Hill Numbers of order  $q$ : species number ( $q=0$ ) to compute diversity estimates and the associated 95% (0.95) confidence intervals for the two groups, based on salinity. Analyses were performed using the online package iNEXT (Chao *et al.* 2016). A data summary is provided in Supplementary Material 2.

## Results

### Taxonomic composition

A total of 2598 mollusc specimens from the Río Lagartos coastal lagoon, representing 39 species (Table 2), 34 genera, 23 families (Figures 2–5), and two classes, were enumerated. Molluscs were found at seven stations in the dry season, six stations in the cold (Nortes) season and 11 stations in the rainy season. Species *Carditamera floridana*, *Meioceras nitidum*, *Modulus modulus* and *Crepidula convexa* were present during all three seasons (Table 2). Nine species were collected during the cold season, 22 species in the rainy season and 28 species in the warm dry season. Thirty-seven species were collected in the Río Lagartos basin (mouth) (RL), six species in the Las Coloradas basin (middle) (CO) and five species in the El Cuyo basin (head) (CU) (Table 2). The most ubiquitous species were *Prunum apicinum* (Menke, 1828), encountered at 14 stations, *Anomalocardia auberiana*, encountered at nine stations, and *Meioceras nitidum* (Stimpson, 1851), *Angulus paramerus* (Boss, 1964), *Modulus modulus* (Linnaeus, 1758), *Crepidula convexa* (Say, 1822) and *Carditamera floridana* (Conrad, 1838), encountered at eight stations. Thirty-three species were collected with the dredge, 12 species with the beach seine and four species with the cylindrical PVC tube. Twenty species (51%) belonged to the class Gastropoda, and 19 (49%) to the Bivalvia (Figure 6). Twenty-two species (56%) were epifaunal and 17 (44%) were infaunal (Table 2, Figure 6). Nine species (23%) were carnivores, 14 (36%) were suspension feeders, seven (18%) were deposit consumers and nine (23%) grazers (Table 2, Figure 6).

Table 2. Species presence by season (N: cool and dry Nortes season (February sampling), R: rainy season (September/October sampling), D: warm and dry season (late May sampling)), basin (RL – Río Lagartos (mouth), CO – Las Coloradas (middle), CU – El Cuyo (head)), and sampler used (dredge, beach seine and PVC tube). Feeding guild (SF: suspension feeder, DC: deposit consumers, G: grazer, C: carnivore) and habitat (E: epifaunal, I: infaunal) of each species also indicated.

N°	Species	Season			Basin			Sampler			Feeding guild	Habitat
		N	R	D	RL	CO	CU	Dredge	Beach seine	PVC Tube		
<b>Bivalvia</b>												
1	<i>Brachidontes exustus</i>		x		x	x		x		x	SF	E
2	<i>Musculus lateralis</i>			x	x			x			SF	E
3	<i>Anodontia alba</i>		x	x	x			x			SF	I
4	<i>Ctena orbiculata</i>	x			x			x			SF	I
5	<i>Luciniscia nassula</i>		x	x	x			x			SF	I
6	<i>Parvilucina crenella</i>			x	x			x			SF	I
7	<i>Carditamera floridana</i>	x	x	x	x			x	x		SF	I
8	<i>Crassinella</i> sp.			x	x			x			SF	I
9	<i>Lasaeidae</i> sp.			x	x			x			SF	I
10	<i>Angulus merus</i>		x		x			x			DC	I
11	<i>Angulus paramerus</i>		x	x	x	x		x			DC	I
12	<i>Angulus sybariticus</i>			x	x			x			DC	I
13	<i>Macoma cerina</i>			x	x			x			DC	I
14	<i>Macoma tenta</i>		x				x	x			DC	I
15	<i>Merisca</i> sp.			x	x			x			DC	I
16	<i>Anomalocardia auberiana</i>		x	x	x	x		x	x		SF	I
17	<i>Chione cancellata</i>		x	x	x			x			SF	I
18	<i>Parastarte triquetra</i>		x		x	x		x			SF	I
19	<i>Lyonsia</i> sp.			x	x			x			SF	I
<b>Gastropoda</b>												
20	<i>Eulithidium adamsi</i>	x			x				x		G	E
21	<i>Cerithiidae</i> sp.		x		x			x			G	E
22	<i>Cerithium atratum</i>	x		x	x				x		G	E
23	<i>Cerithium eburneum</i>		x	x	x			x	x		G	E
24	<i>Cerithium lutosum</i>		x		x					x	G	E
25	<i>Modulus modulus</i>	x	x	x	x			x	x		G	E
26	<i>Vermetidae</i> sp.		x	x	x			x		x	DC	E
27	<i>Caecum donmoorei</i>			x	x			x			G	E
28	<i>Meioceras nitidum</i>	x	x	x	x		x	x		x	G	E
29	<i>Zebina browniana</i>		x		x			x			G	E
30	<i>Crepidula convexa</i>	x	x	x	x			x	x		SF	E
31	<i>Granulina</i> sp.			x	x			x			C	E
32	<i>Prunum apicinum</i>		x	x	x	x		x	x		C	E
33	<i>Astyris antares</i>			x	x			x			C	E
34	<i>Melongena corona</i>	x		x	x	x	x		x		C	E
35	<i>Nassarius vibex</i>		x		x				x		C	E
36	<i>Henrya henryi</i>		x				x	x			C	E
37	<i>Bulla occidentalis</i>		x	x	x				x		C	E
38	<i>Haminoea succinea</i>			x	x			x	x		C	E
39	<i>Odostomia laevigata</i>	x		x	x		x	x			C	E
Total species		9	22	28	37	6	5	33	12	4		

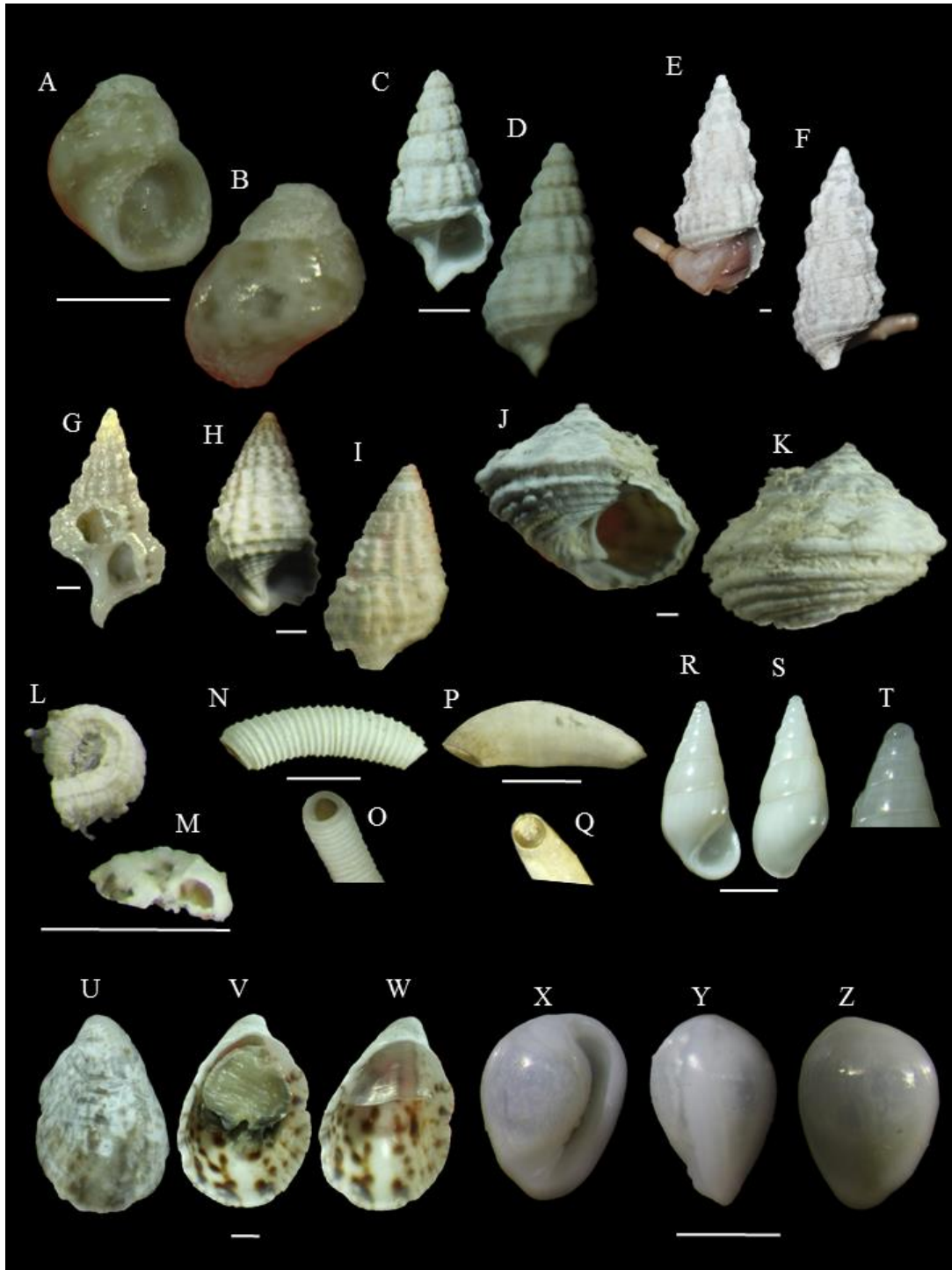




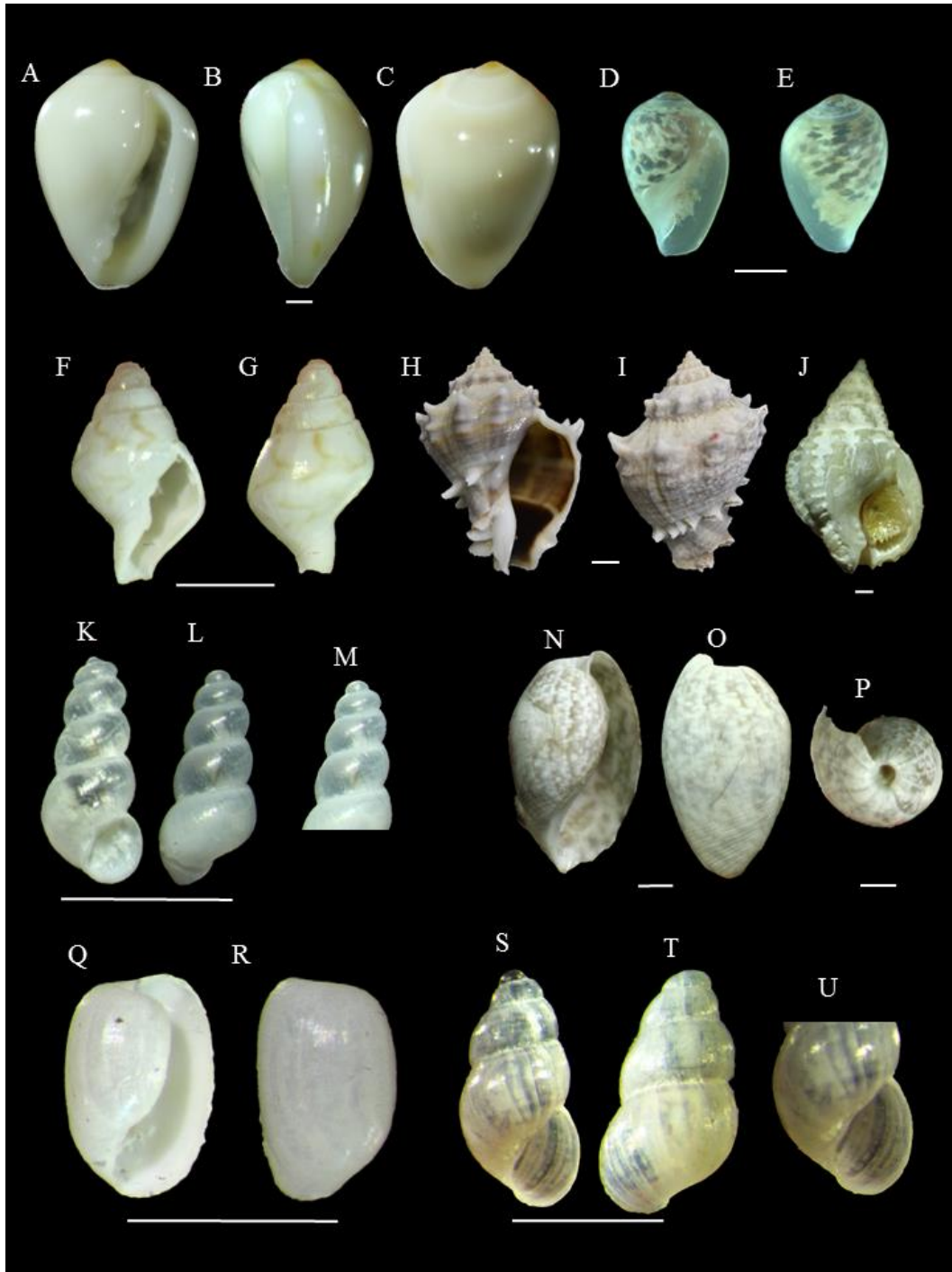
**Figure 2. Mytilidae:** *Brachidontes exustus*: (A-B). *Musculus lateralis*: (C-D). **Lucinidae:** *Anodontia alba*: (E-G). *Ctena orbiculata*: (H-J). *Lucinisca nassula*: (K-M). *Parvilucina crenella*: (N-P). **Carditidae:** *Carditamera floridana*: (Q-S). **Crassatellidae:** *Crassinella* sp.: (T). **Lasaeidae:** *Lasaeidae* sp.: (U-V). **Tellinidae:** *Angulus merus*: (W-Y) Scale bars = 1 mm.



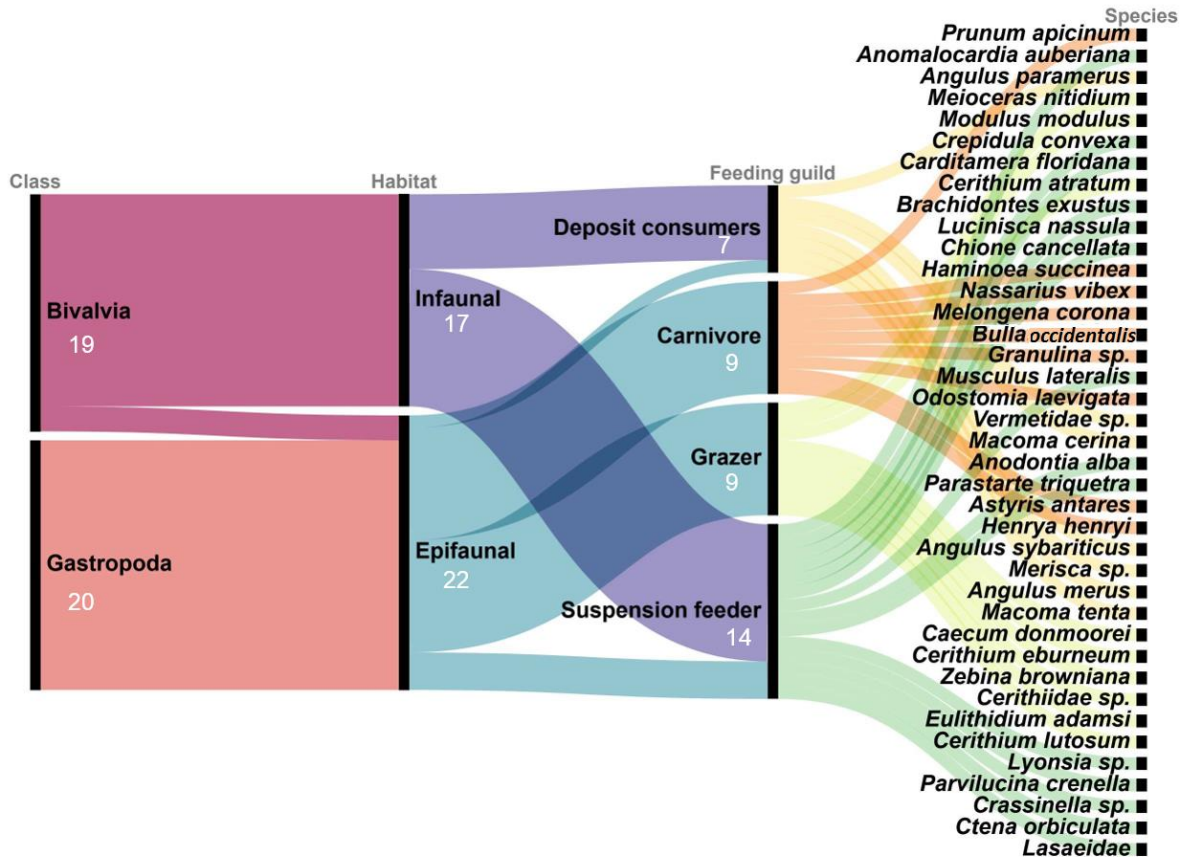
**Figure 3. Tellinidae:** *Angulus paramerus*: (A-B). *Angulus sybariticus*: (C). *Macoma cerina*: (D-E). *Macoma tenta*: (F-H). *Merisca* sp.: (I-K). **Veneridae:** *Anomalocardia auberiana*: (L-M). *Chione cancellata*: (N-O). *Parastarte triquetra*: (P-Q). **Lyonsiidae:** *Lyonsia* sp.: (R). Scale bars = 1 mm.



**Figure 4. Phasianellidae:** *Eulithidium adamsi*: (A-B). **Cerithiidae:** Cerithiidae sp.: (C-D). *Cerithium atratum*: (E-F) (with Sipuncula). *Cerithium eburneum*: (G). *Cerithium lutosum*: (H-I). **Modulidae:** *Modulus modulus*: (J-K). **Vermetidae:** Vermetidae sp.: (L-M). **Caecidae:** *Caecum donmoorei*: (N-O). *Meioceras nitidum*: (P-Q). **Zebinidae:** *Zebina browniana*: (R-T). **Calyptraeidae:** *Crepidula convexa*: (U-W). **Marginellidae:** *Granulina* sp.: (X-Z). Scale bars = 1 mm.



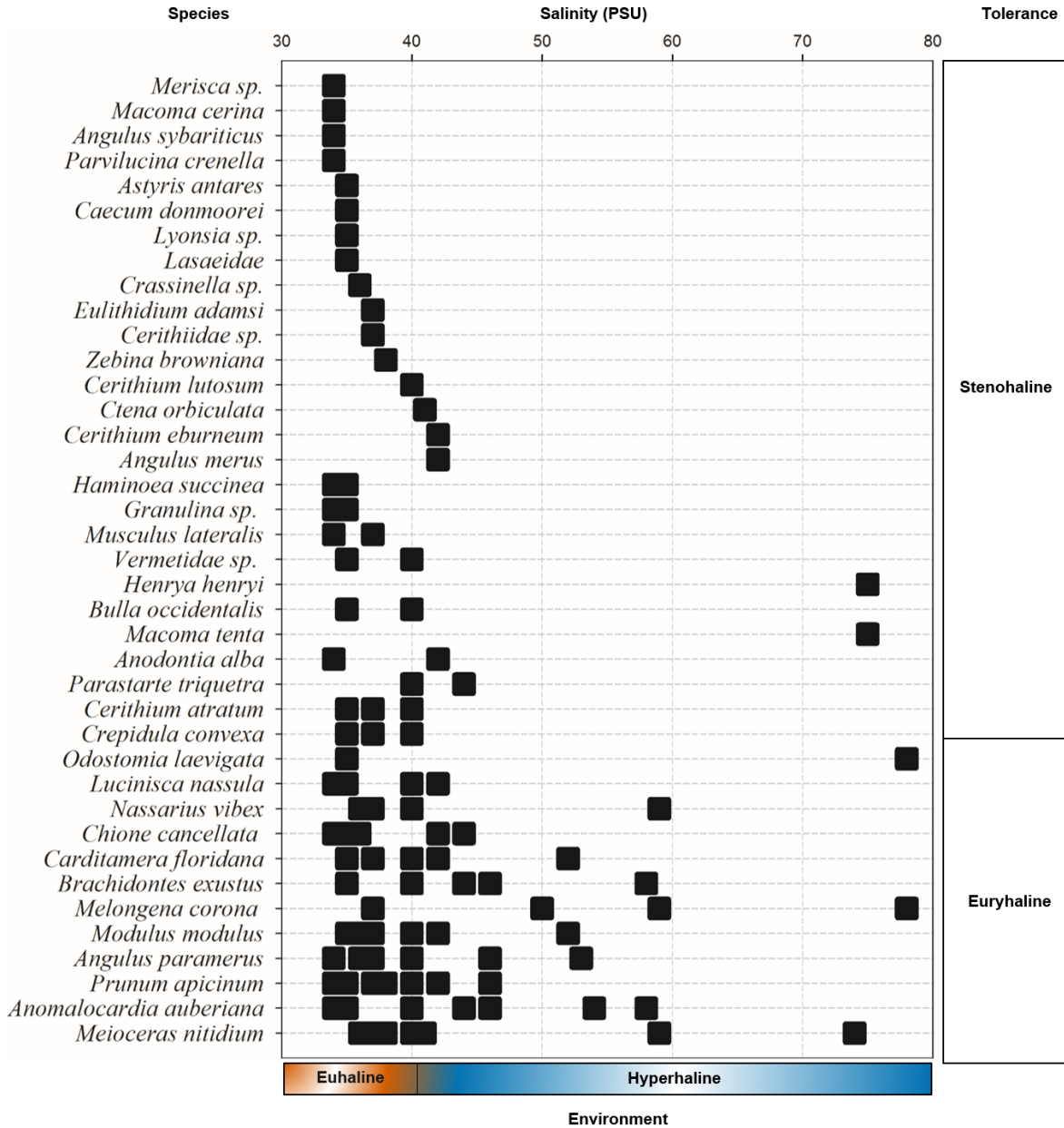
**Figure 5.** Marginellidae: *Prunum apicinum*: (A-E). Columbellidae: *Astyris antares*: (F-G). Melongenidae: *Melongena corona* (H-I) (scale bar = 5 mm). Nassariidae: *Nassarius vibex*: (J). Murchisonellidae: *Henrya henryi*: (K-M). Bullidae: *Bulla occidentalis*: (N-P). Haminoeidae: *Haminoea succinea*: (Q-R). Pyramidellidae: *Odostomia laevigata*: (S-U). Scale bars = 1 mm.



**Figure 6.** Alluvial plot depicting the relationship between classes and species for two different functional traits: habitat and feeding guild. The species numbers are provided for each category.

#### Molluscs and salinity in Río Lagartos coastal lagoon

The Río Lagartos coastal lagoon is inhabited by both stenohaline (27 species; 69%) and euryhaline (12 species; 31%) species (Figure 7). Stenohaline species displayed lower occurrence (<20%), and some species were collected exclusively under euhaline (15 species) or hypersaline conditions (6 species). Twelve species tolerate a broad salinity range (euryhaline). The species distributed in the largest salinity range were: *Melongena corona* (37–78), *Anomalocardia auberiana* (34–58), *Meioceras nitidum* (36–74) and *Odostomia laevigata*, which was collected at only two stations with very different salinity (35 and 78).



**Figure 7.** Occurrence of mollusc species vs salinity. Ranges for euhaline (marine, 30-40 PSU) and hyperhaline environments (40-80 PSU) are indicated at the bottom of the figure. Salinity tolerance groups, i.e., stenohaline and euryhaline, are shown on the right. Terminology follows Wingard *et al.* (2012).

Abiotic characteristics and fauna composition differed between the two salinity environments (Table 3). In the euhaline sites, sediments were mostly sandy, and gravel and silt/clay were notably scarce (<10%) (Table 3). Percent submersed vegetation was  $15.25 \pm 29\%$ . Thirty-five species were collected in euhaline sites. Gastropoda and epifaunal molluscs occurred in all stations (FO = 100%). With respect to feeding guild, suspension feeders and grazers (FO = 79%) and carnivores (FO = 68%) appeared in more than half the samples. Suspension feeders were the most diverse group (40% of the species), followed by carnivores and grazers, each representing 23% of the species. In the hyperhaline sites, sediments were again mostly sandy, but the percentage contributions of gravel (7.8%) and silt/clay (11.3%) were greater than in the euhaline sites, and the sediments were more variable (Table 3). The percentage of submersed vegetation was lower ( $4.9 \pm 7.9\%$ ). We found 22 species associated with hyperhaline sites, and of those, infauna (FO = 79%) and the class Bivalvia (FO = 79%) were distributed extensively in the samples. With respect to feeding guilds, suspension feeders appeared in more than half of the samples (FO = 64%), and the rest of the guilds were distributed in <50% of the samples. The most diverse groups in the hypersaline environments were suspension feeders (36% of the species) and carnivores (32% of the species).

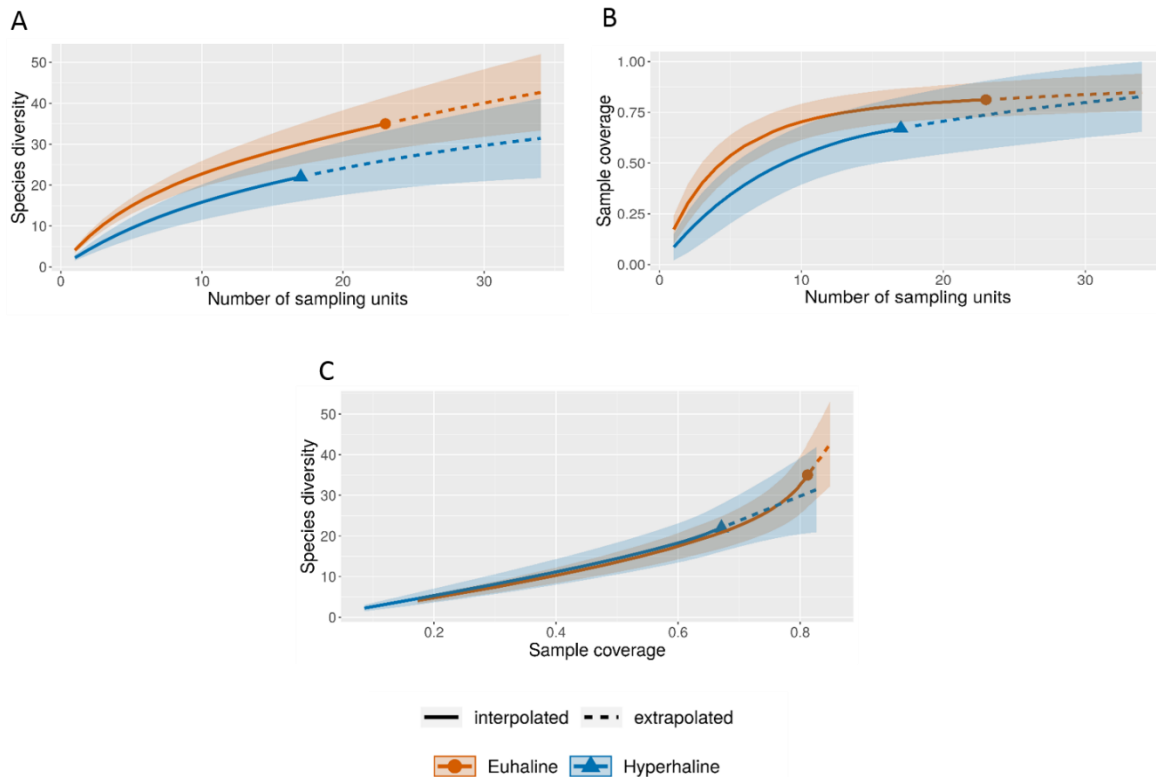
Table 3. Salinity ranges, number of sites (including samples in each season), proportions of sediment size-classes (gravel, sand, silt/clay) and submersed vegetation gravimetric contribution to the surface sediment samples (mean value  $\pm$  SD). The total number of species (S) per environment and species number range per site (in parenthesis) in the environment also shown. The percentage contribution to the total number of species (S) and frequency of occurrence (FO% = number of samples in which a class was present/total number of samples  $\times$  100) in the mollusc groups by class (Gastropoda and Bivalvia), habitat (epifauna and infauna), or feeding guild (suspension feeders, carnivores, deposit consumers and grazers) in the euhaline and hyperhaline environments of the Río Lagartos coastal lagoon are on the bottom

	Euhaline		Hyperhaline	
<b>Abiotic characteristics</b>				
Salinity (PSU)	30-40		>40 $\leq$ 78	
Number of sites	19		14	
Mean gravel %	6.3 $\pm$ 4.5		7.8 $\pm$ 10.5	
Mean sand %	90.8 $\pm$ 6.4		80.8 $\pm$ 21.2	
Mean silt/clay %	2.9 $\pm$ 5.2		11.3 $\pm$ 16.5	
Mean vegetation %	15.25 $\pm$ 29		4.9 $\pm$ 7.9	
<b>Fauna composition</b>				
Species number (S)	35 (1-9)		22 (1-8)	
	<b>S (%)</b>	<b>FO (%)</b>	<b>S (%)</b>	<b>FO (%)</b>
<b>Class</b>				
Bivalvia %	49	63	55	79
Gastropoda %	51	100	45	64
<b>Habitat</b>				
Epifauna %	57	100	55	79
Infauna %	43	58	45	79
<b>Feeding guild</b>				
Suspension feeders	40		36	
%		79		64
Carnivores %	23	68	32	43
Deposit consumers	14		18	
%		37		36
Grazers %	23	79	14	36

For comparison of diversity between the euhaline and hyperhaline environments, sample-size-based sampling curves were constructed, using reference sample sizes of 33 and 24 (considering each replicate), respectively. Extrapolation was carried out to >40 samples in both cases (Figure 8A). In all cases, sample completeness was <1 (0.8 for the hyperhaline environment and 0.7 for the euhaline environment) (Figure 8B), which indicates a deficit in the detection of species of about 20%. Comparisons of coverage-based sampling curves,



up to a base coverage, revealed higher diversity than expected in euhaline environments (Figure 8C).



**Figure 8.** Interpolation and extrapolation curves of mollusc species in samples from the Río Lagartos coastal lagoon under euhaline (red line) and hyperhaline (blue lines) conditions. (A) Species accumulation curves based on the occurrence of species. (B) Sample-coverage accumulation curve. (C) Sample completeness curves, linking curve 8A and 8B. The solid lines represent interpolation, whereas the dashed lines depict extrapolation.

## Discussion

### Taxonomic composition

This work updates and expands upon previous mollusc studies in the Río Lagartos coastal lagoon. We encountered 37 species in the Río Lagartos basin (mouth), six in the Las Coloradas basin (middle) and five in the El Cuyo basin (head). The numbers differ substantially from those obtained by Gonzalez *et al.* (1991), who reported the presence of 71 species in the Río Lagartos basin, four in the Las Coloradas basin, and one in the El Cuyo basin. Furthermore, only nine of the species found in this study overlap with those

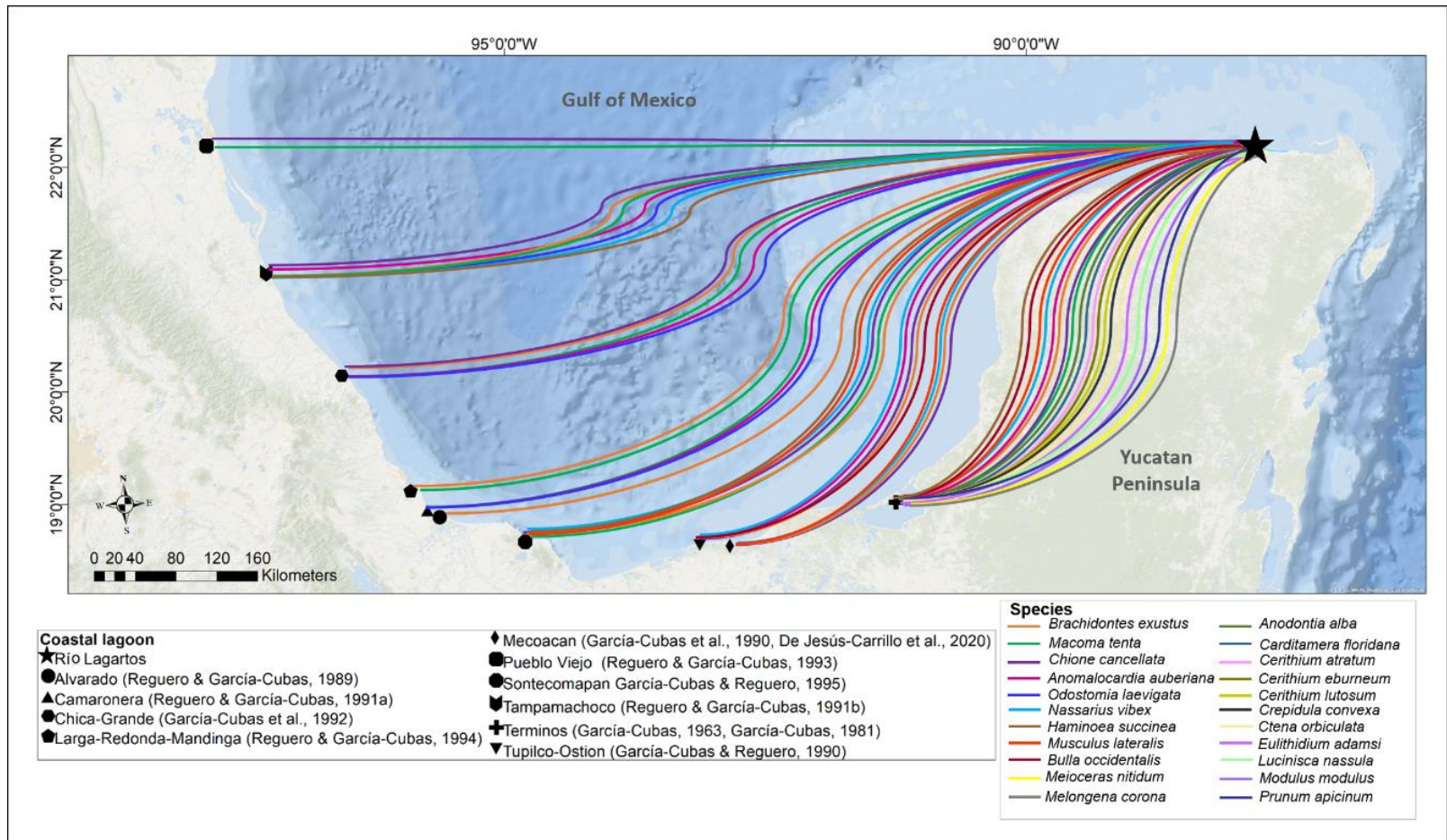
reported by Gonzalez *et al.* (1991) (*Anodontia alba*, *Carditamera floridana*, *Chione cancellata*, *Anomalocardia auberiana*, *Modulus modulus*, *Cerithium atratum*, *C. eburneum*, *Melongena corona* and *Bulla occidentalis*), all of which were collected from the Río Lagartos basin, only one from the Las Coloradas basin (*Melongena corona*) and none from the El Cuyo basin.

The difference in number and composition of species between the two studies may be a consequence of several factors, some related to changes in the environmental conditions, and others related to sampling and sample-processing methods. Regarding the environment, it is unlikely that the effects of recent climate change, which have been detected on the Yucatán Peninsula during the last 60 years (Carnero-Bravo *et al.* 2018; Andrade-Velázquez *et al.* 2021), affected the mollusc community composition inside the lagoon, as detected long-term variations are small compared with short-term (diel, fortnightly or seasonal) variations that occur in the waterbody. For instance, no directional change in lagoon salinity has been detected during the last 40 years (Wojtarowski *et al.* 2021). Given the rapid population growth and increased human activities around the lagoon during that same period, it is more plausible that the differences in faunal composition between the two studies are related to greater recent anthropogenic activities. For example, microplastics have been found in large quantities in recent lagoon sediments, and have been linked to human activity in the area (Quesadas-Rojas *et al.* 2021). Nevertheless, interannual differences in abiotic conditions related to, for example, changes in precipitation or impacts of individual extreme events such as tropical storms and hurricanes (De la Barreda *et al.* 2020), or longer-term climate variations (e.g., El Niño–Southern Oscillation; Fichez *et al.*, 2017), may also be responsible for such fauna differences between the two studies. Although all these explanations are plausible, we cannot rule out the possibility that differences between the two studies are attributable to sampling and sample-processing differences. Those methodological differences relate to: (1) the timing of sampling during the year, as suggested by the seasonal changes in species richness detected in our results, with the highest number of species (28) found in the dry season; (2) the types of samplers used, as the selectivity of each sampler is related to the net mesh size and the mode of operation (Raz-Guzman & Grizzle 2001) - in this study, the dredge retained more species (33) than did the other samplers (Supplementary Material 3); and (3) the use of both empty shells and live specimens in counts in the previous study. Determination of the true cause(s) of long-term temporal patterns in mollusc fauna composition in the lagoon would require regular monitoring and use of standardized methods, which are expensive and difficult to

sustain. Such large-scale efforts, which use standardized protocols (MBON Pole to Pole 2019; Obst *et al.* 2020; Ashton *et al.* 2022), can be employed to detect shifts in community composition going forward. Such programmes, however, cannot shed light on past community changes. To document such past changes, it will be necessary to undertake palaeoecological studies, like those that have been done to examine changes in marine fauna communities during the last century, in both coastal (Armenteros *et al.* 2016) and open-ocean contexts (Cartes *et al.* 2017, 2022).

In any case, the large disparity in the diversity between the two studies, together with the revealed deficit in the detection of species in this study, as seen in the species accumulation curves, reinforces the idea that, despite the great sampling effort, the Río Lagartos coastal lagoon has greater mollusc diversity, and likely spatio-temporal heterogeneity, than reported in this or previous studies. This highlights the lack of information from the region that will be necessary to achieve solid ecological baseline knowledge (Guerra-Castro *et al.* 2020).

All the species found in the Río Lagartos coastal lagoon have been reported previously from other lagoons around the Gulf of Mexico (Figure 9) and 22 species were reported earlier from the Caribbean (García-Cubas & Reguero 2004, 2007; Rosenberg *et al.* 2009; Turgeon *et al.* 2009). The high number of shared species between the Gulf of Mexico and the Caribbean is attributable to the dispersal of larvae by the Yucatán Current. Larvae may be carried from the Caribbean onto the continental shelf, particularly by upwelling events that occur seasonally, typically from April to September (Sanvicente-Añorve *et al.* 2014; Reyes-Mendoza *et al.* 2016; Kurczyn *et al.* 2021). Once in the northern coastal region of the Yucatán Shelf, the main current is directed westward along the coast mainly by winds, and enhanced by westward pulses of the Yucatán Current, which flows to the north (Enriquez *et al.* 2013). The Trade Winds (easterlies) are locally deflected southward by intense diurnal onshore breezes, which keep the westward-flowing waters close to the coast. This transport favours connectivity among populations (Herrera-Silveira *et al.* 2013).



**Figure 9.** Comparison of molluscs recorded in the Río Lagartos coastal lagoon (present study) and in other coastal lagoons around the Gulf of Mexico, Mexico (García-Cubas 1963, 1981; Reguero & García-Cubas 1993, 1994, 1989, 1991b, 1991a; García-Cubas & Reguero 1990, 1995; García-Cubas et al. 1990, 1992; De Jesús-Carrillo et al. 2020).

## Abiotic and biotic patterns

This study demonstrates that mollusc species richness in the Río Lagartos coastal lagoon is influenced by salinity. Species richness was higher under euhaline than hypersaline conditions, and no animals were collected at salinities >78. A decrease in species richness above hypersaline values in aquatic environments is common (Deaton 2019) and in the Río Lagartos coastal lagoon it is reflected by the substantially lower numbers of species in the Las Coloradas (middle) and El Cuyo (head) basins. Such a pattern was also detected by Gonzalez *et al.* (1991), and, in fact, the authors reported that the Las Coloradas and El Cuyo basins behaved as entities independent from the Río Lagartos basin, in terms of species richness.

Experimental studies on salinity tolerances of mollusc species and the mechanisms that underlie salinity limitation are notably scarce and mainly limited to species of economic interest (Calabrese & Davis 1970; Nell & Gibbs 1986; Deaton *et al.* 1989; Yang *et al.* 2018), and a few others (Berger & Kharazova 1997; Przeslawski 2004). Most of those studies considered salinities less than hypersaline, and little or nothing is yet known about the osmoregulatory physiology of hypersaline molluscs (Berger & Kharazova 1997; Deaton 2019). Khlebovich & Kondratenkov (1973) reported the high-salinity acclimation threshold for the snail *Hydrobia ulvae* at values between 75 and 80, and for other macrobenthic invertebrates such as polychaetes, survival was restricted to salinity values <70. Thus, absence of molluscs at salinities >78 may indicate that is a threshold value for this taxonomic group. Below 78, bivalves were more diverse and widespread under hypersaline conditions than were gastropods, the latter of which prevailed under euhaline conditions. Bivalves can withstand stressful conditions and respond to changes in environmental salinity by closing their shells (Vlašić *et al.* 2018). In the case of gastropods, extreme values of salinity and temperature slow development and/or increase embryonic mortality (Przeslawski 2004). On the other hand, the low incidence of gastropods could be a consequence of a low availability of food and reduced feeding activity under stressful conditions.

The bivalve *Anomalocardia auberiana* and the gastropods *Meioceras nitidum* and *Melongena corona* were the species distributed across the largest salinity ranges and the first two were among the most ubiquitous species in the Río Lagartos coastal lagoon. The large salinity tolerance ranges and the capacity to live under very high salinities, up to 58 for *A. auberiana*, 74 for *M. nitidum*, and 78 for *M. corona*, explains their widespread distribution

in the lagoon. Tolerance of hypersaline conditions was reported for *A. auberiana* in the Baffin Bay estuary (south Texas, USA) (Rubio *et al.* 2018), and *Melongena* spp. inhabit different ecosystems (i.e. shallow, low-energy embayments, lagoons, salt marshes, mangrove swamps and oyster bars) (Hayes 2003), which suggests a wide salinity tolerance of the genus. Instead, *M. nitidum* has usually been found in shallow habitats where the salinity is close to that of the ocean (Lester-Coll 2017). This suggests strong physiological plasticity and may point to high capacity for acclimation, as reported for other marine snails (Berger & Kharazova 1997). A similar yet less marked tolerance for high salinity (to 50 PSU) caused by exposure to high salinity values, can be deduced for the most frequently encountered mollusc species in the Río Lagartos coastal lagoon, the gastropod *Prunum apicinum*. This species was previously found inhabiting environments with salinity up to 40, with a preferred range of about 15-25 (Cain 1972; Roessler & Tabb 1974; Tampa Bay Water & Janicki Environmental Inc 2003; Jiménez-Ramos & Acosta-Balbás 2020). The very high and unstable salinity conditions that prevail in the Río Lagartos coastal lagoon probably favor the adaptation of species, which represents an adaptive advantage, given the predicted salinity increase associated with ongoing climate change (Curry *et al.* 2003; Boyer *et al.* 2005). This is especially relevant in this type of lagoon, where limited freshwater inputs and high evaporation rates drive salinity increases.

Salinity may not be the only factor responsible for the spatial distribution patterns of molluscs. Rather, substrate type, sediment grain size, hydrodynamics and salinity likely interact to create such patterns. Furthermore, the effects of salinity on molluscs may be direct, by acting on their osmotic and ionic equilibrium, or indirect, by affecting the distribution of other factors that in turn regulate mollusc distribution. For example, in the Río Lagartos coastal lagoon, the distribution of submersed vegetation, which serves as habitat or a food source for many macrobenthic taxa, is strongly influenced by salinity (Ortegón-Aznar *et al.* 2001). In this sense, higher species richness and frequency of occurrence of gastropods in the euhaline environment may be associated with the greater amount of submersed vegetation. The macrophytes provide a range of habitat types for epifaunal organisms and food for grazers, both functional groups being represented by gastropods in the Río Lagartos coastal lagoon. Accordingly, the widespread distribution of *Meioceras nitidum*, an epifaunal grazer, is enhanced by both its euryhaline character and a considerable capacity to inhabit a diverse array of substrates, as live specimens have been found on mangrove roots, algae from the intertidal to subtidal zone, and seagrass beds (Tunnell *et al.* 2010; Redfern 2013; Pereira Costa *et al.* 2021). Conversely, higher occurrence and diversity of bivalves, which

are predominantly infaunal, in the hypersaline environments, may be favoured by lower amounts of vegetation on the bottom, and the presence of a broader array of sediment grain sizes that are suitable for a large number of burrowing species (Alexander *et al.* 1993), or for suspension and deposit feeders.

Complex hydrodynamics and geomorphology of the lagoon favour high sediment heterogeneity. This may explain the presence of large denuded areas, even in the euhaline sites, which may trigger the spread of *A. auberiana*, an opportunistic species with a high capacity to rapidly invade newly available habitat, and soon after appear in large numbers (Grizzle 1984; Kuk-Dzul *et al.* 2012). Although tides have little influence throughout the entire lagoon, except near the mouth of the Río Lagartos basin, the local dynamics are important in the middle and upper basins because of their sizes, depths and processes therein. Possessing vast shallow areas, these basins are subject to the effects of wind and waves, which mix the whole water column and enhance resuspension of sediment particles throughout the area, providing food for the suspension feeders that dominate the lagoon's mollusc community.

Most of the stenohaline species in this study were rare, having been captured at only one or two stations. Although the sampling limitations mentioned previously cannot be ruled out as having caused the low recovery of these species (Lyons *et al.* 2005), low salinity tolerance, together with impaired dispersal or colonizing ability linked to the small-scale environmental heterogeneity of the system also seems a plausible explanation (Cao *et al.* 2001). For example, *Parastarte triquetra* was found at only two stations and in a narrow salinity range, consistent with the very localized distribution of the species recorded in other systems (Grizzle 1984; Morelos-Villegas *et al.* 2018). This species has been correlated with high values of trichlorobenzene in the Yucatán Peninsula coastal lagoons, and in this study it appeared at stations where high levels of pollution were reported previously (Kuk-Dzul *et al.* 2012).

This work revealed that the current state of knowledge regarding the abiotic and biotic controls on mollusc distributions in the eastern GoM is poor. Information from this study serves as a starting point ('baseline') for studies of future impacts on the Río Lagartos coastal lagoon, for example, changes in salinity regime and consequent redistribution of organisms. Our study also raises an important question: what factor or factors account for the lower (45.1%) number of mollusc species found in this study, relative to the number encountered in a similar study carried out almost four decades ago? The relative roles of

natural variation and anthropogenic activities on mollusc diversity changes remain to be distinguished and are crucial to understand the potential effects of ongoing global change on mollusc diversity. This question needs to be addressed cautiously, as factors independent from environmental variables, such as the types of samplers used, sampling intensity and time of the year, and high numbers of rare species, can all affect the number of species collected. We encourage colleagues who undertake similar future studies to collaborate with large-scale networks that use standardized protocols (MBON Pole to Pole 2019; Obst *et al.* 2020; Ashton *et al.* 2022). In addition, to better understand past changes and effects on the fauna since the 'Great Acceleration' of human impacts, we propose palaeoecological studies be undertaken. Such investigations can provide a historical perspective on changing mollusc species diversity in coastal lagoons over the last century or more. Lastly, to fully understand the drivers of recent shifts in mollusc community composition, knowledge of the environmental optima and tolerances for each taxon is required.



## Capítulo 4. Benthic mollusc communities across space and through time in a hypersaline coastal lagoon, México

Este capítulo es parte del manuscrito: Suárez-Mozo, N.Y., Brenner, M., Kenney, W.F., Díaz Asencio, M., Curtis, J.H., Aquino-Lopez, M.A., Guerra-Castro, E., & Simões, N. Benthic mollusc communities across space and through time in a hypersaline coastal lagoon, México. *Estuarine, Coastal and Shelf Science* (sometido)

## Resumen

Los estudios paleoecológicos proporcionan datos a largo plazo sobre los cambios históricos de los ecosistemas, a diferencia de los estudios de monitoreo, que suelen ser en su mayoría a corto plazo y de alcance geográfico limitado. Los enfoques paleoecológicos utilizan restos bióticos para proporcionar información sobre las condiciones ambientales del pasado. Un total de 18,779 especímenes de moluscos fueron recolectados y representan 20 especies de bivalvos y 45 especies de gasterópodos, pertenecientes a 32 familias y 48 géneros, fueron identificados en tres núcleos de sedimentos cortos recolectados en 2017 en la laguna costera de Río Lagartos, México. Los moluscos se compararon con un inventario actual que se había recolectado a lo largo de un gradiente de salinidad en 2017 y 2018 para evaluar las distribuciones de especies asociadas con las variables ambientales. Los moluscos de los núcleos de sedimentos y los moluscos modernos poseen las mismas especies frecuentes y los mismos gremios de alimentación, es decir, grupos que explotan los mismos recursos alimenticios. Sin embargo, se identificaron casi el doble de especies en los núcleos sedimentarios que en el inventario moderno. Se han observado diferencias en la abundancia y composición taxonómica de los moluscos en los núcleos de sedimento a lo largo del tiempo y el espacio, que pueden estar relacionadas con los cambios de salinidad en la laguna y las modificaciones del entorno terrestre cercano.

## Abstract

Paleoecological studies provide long-term data on historical ecosystem change, in contrast to recent monitoring efforts, which have typically been short-term and geographically limited in scope. Paleoecological approaches have been used in previous studies of biotic remains to provide information on past environmental conditions. A total of 18,779 mollusc specimens, representing 20 bivalves and 45 gastropods species, and belonging to 32 families and 48 genera, were identified in three short sediment cores collected in 2017 from Río Lagartos coastal lagoon, Mexico. Mollusc assemblages in the sediment cores were compared to a present-day inventory of Mollusca fauna from the lagoon, which had been collected along a salinity gradient in 2017 and 2018 to assess species distributions associated with environmental variables. Mollusc assemblages from the sediment cores and present-day inventory datasets possess the same ubiquitous species and the same feeding guilds, i.e., groups that exploit the same food resources. Nevertheless, nearly twice as many species were identified in the sediment cores as in the present-day inventory. 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.

Keywords: Mollusca, Paleoecology,  $^{210}\text{Pb}$  dating, Río lagartos, Sediment, Yucatan.

## Introduction

Biotic monitoring efforts in the tropics have generally been restricted to recent and thus short time spans, and have been geographically limited (Baldassarre & Arengo 2000; Zaldívar-Jiménez *et al.* 2010; Guerra-Castro *et al.* 2020). For these reasons, we know little about the magnitude and timing of historical environmental changes in low-latitude ecosystems (Smol 2019). Understanding the processes and mechanisms of change in ecosystems requires a long-term, historical perspective (Armenteros *et al.* 2021; Estes & Vermeij 2022). Paleoecological studies have been used to obtain long-term data and gain insights into past climate and environmental changes in the southern region of the Gulf of Mexico, e.g., changes in sea level (Carnero-Bravo *et al.* 2018) and periods of drought on the Yucatán Peninsula (Brenner *et al.* 2002; Evans *et al.* 2018). One component of paleoecological

studies involves analysis of death assemblages (thanatocoenoses), which are composed of individuals that 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). Given that long-term environmental monitoring data are frequently lacking, fossil assemblages serve as windows into historic biological diversity and long-term baselines, and can be interpreted in conjunction with data on live assemblages, i.e., biocenoses (Kidwell 2013). Calibration datasets developed from live assemblages (i.e., present-day) should be species-rich, cover a broad area, include an array of habitat types, and involve a broad range of environmental variables (Bush 1988).

Comparison of fossil assemblages from cores with modern analogs is an approach that has been used in studies of different biotic remains, including pollen grains (Aragón-Moreno *et al.* 2012; Bush *et al.* 2021), foraminifers (Dowsett & Robinson 1998), ostracods (Macario-González *et al.* 2018; Ozawa & Tanaka 2019) and molluscs (Bush 1988; Brewster-Wingard & Ishman 1999; Wingard & 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, e.g., climate and sea level change and human disturbances. 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 (Vokes & Vokes 1983; García-Cubas & Reguero 2004, 2007; Mikkelsen & Bieler 2008; Moretzsohn *et al.* 2009; Rosenberg *et al.* 2009; Turgeon *et al.* 2009; Wingard *et al.* 2017; Ortigosa *et al.* 2018; Wingard & Stackhouse 2020), and in Río Lagartos coastal lagoon (Gonzalez *et al.* 1991; Suárez-Mozo *et al.* 2023).

Studies of mollusc assemblages in sediment cores have focused on stratigraphic changes in assemblages from dated late Pleistocene and Holocene profiles, which were then compared with present-day 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

Florida (Wingard *et al.* 2022), the transitions from mangrove stands to seagrass beds, as a consequence of sea level rise in Florida (Jones *et al.* 2019) and Cuba (Poirier *et al.* 2009; Díaz-Asencio *et al.* 2020; Armenteros *et al.* 2021), and in 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 scallop dredging (Edgar & Samson 2004). Other examples of use of mollusc assemblages for inferring past environmental conditions were reviewed by Wingard *et al.* (2017).

Río Lagartos is a hypersaline, elongated, shallow coastal lagoon located on the north coast of the Yucatan Peninsula, Mexico. It is underlain by porous, karst limestone, which enables both surface and sub-surface hydrologic exchange between the continent and marine environment (Valle-Levinson *et al.* 2011). The marine environment north of the Yucatan Peninsula is a transition region, influenced by the Caribbean Sea and Gulf of Mexico (Enriquez *et al.*, 2010; Reyes-Mendoza *et al.*, 2016). The coastal lagoon system is affected by human activities such as residential development, agriculture and cattle ranching, and local groundwater can be contaminated with pollutants that accumulate because of low water exchange (Herrera-Silveira & Morales-Ojeda 2010). Mollusc taxa that inhabit Río Lagartos coastal lagoon tolerate euhaline and/or hypersaline conditions. More bivalves than gastropods were found under hypersaline conditions and no molluscs have been collected at salinities >78 (PSU) (Suárez-Mozo *et al.* 2023). We investigated mollusc assemblages in sediment cores from Río Lagartos coastal lagoon and compared them to present-day mollusc assemblages to gain insights into environmental changes that occurred in the lagoon throughout the last century.

## Study area

The E-W oriented Río Lagartos coastal lagoon, on the northern coast of the Yucatan Peninsula (Figure 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 mangrove 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) (Herrera-Silveira & Ramírez-Ramírez 1998). 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 (Valdes & Real 2004; Peralta-Meixueiro & Vega-Cendejas 2011). The lagoon bottom is covered by an algae mat of *Udotea flabellum* and *Halimeda incrassata* (Vega-Cendejas & 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 & 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 & 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 & Hernández De Santillana 2004). Diurnal tides predominate and semidiurnal tides occur during neap tides (Cuevas-Jiménez & Euán-Ávila 2009). The tidal signal is attenuated by the lagoon entrance and the tide range is between 0.6 and 1.0 m (Valle-Levinson *et al.* 2022).



**Figure 1.** Map of Río Lagartos coastal lagoon on the northern Yucatán Peninsula, Mexico, with the locations of the sediment cores: core 4A (blue dot), core 4B (blue triangle) 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.

## Materials and methods

### 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 and that represent typical sediment dynamics in the lagoon (Casares-Salazar & Mariño-Tapia 2016; Rey *et al.* 2018). Cores were taken with a hand-driven piston-corer that used transparent polycarbonate core barrels. Cores from three sites were analyzed: cores 4A and 4B were located in the lagoon, south of the salt production ponds, whereas core 6A was collected farther east in the channel, near the El Cuyo Basin (Table 1). Sediment sampling took place on 25-27 July 2017. Each sediment core was sectioned vertically at ~1-cm (cores 4A and 6A) or ~5-cm intervals (core 4B), the latter profile collected largely to assess whether sediment accumulation and mollusk assemblages were relatively consistent at nearby sites. The mass of volumetric sectioned sediment was recorded, and samples were later lyophilized with a freeze dryer in the laboratory. Sediments were ground to a powder with a mortar and pestle and sent to the University of Florida for  $^{210}\text{Pb}$  analysis.

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 4B	21°34'12.3"N	87°58'28.6"W	45	100	25	5
Core 6A	21°33'31.1"N	87°50'30.9"W	62	70	20	1

## Chronology

We used  $^{210}\text{Pb}$  dating to establish a chronology for recent sediments. We used well-type, low-background gamma detectors to measure  $^{210}\text{Pb}$ ,  $^{226}\text{Ra}$  and  $^{137}\text{Cs}$  activities (Schelske *et al.* 1994). The age-depth models for the sediments core 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  $^{210}\text{Pb}$  and  $^{226}\text{Ra}$  activity. As a result, age can be estimated at any depth where excess  $^{210}\text{Pb}$  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 last century (Blaauw *et al.* 2020).

## Mollusc assemblages in the core sediments

Mollusc shells were sampled from the three short sediment cores collected from Río Lagartos coastal lagoon and observed under a stereomicroscope. 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, “paired” articulated valves 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)- *Historical molluscs from Río Lagartos coastal lagoon, Mexico* (Suárez-Mozo *et al.* 2023). We used the Grapher V21 software package to generate stratigraphic diagrams for the mollusc assemblages.

## The modern mollusc inventory in Río Lagartos coastal lagoon

A dataset of mollusc species that currently live in Río Lagartos coastal lagoon was compiled as part of the Salinity Gradient Energy Project of the Centro Mexicano de Innovación en Energía Océano (CEMIE Océano). Samples were collected from 16 stations distributed throughout the lagoon (Figure 1). Molluscs were collected in the rainy season



(September/October 2017), during the windy (*nortes*) season (February 2018) and at the end of the warm, dry season (May 2018). Samples were taken using a Ponar dredge (9"x 9" or 22.9 x 22.9 cm; 0.052 m<sup>2</sup> sampling area), a sediment corer (6" diameter; 0.018 m<sup>2</sup> sampling area), or a beach seine (1-m-high beach seine with half-inch mesh size, covering an area of 400 m<sup>2</sup>). The dataset can be found in OBIS - *Macrobenthos composition from the Río Lagartos hyperhaline coastal lagoon system, Yucatan, Mexico* (Abarca-Avila *et al.* 2021). The present-day mollusc assemblages were studied in relation to abiotic characteristics in the lagoon (sediment grain sizes proportions, submersed aquatic vegetation cover, and salinity) to explore factors that account for biotic differences throughout the coastal lagoon (Suárez-Mozo *et al.* 2023).

### 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 (Vokes & Vokes 1983; García-Cubas & Reguero 2004, 2007; Mikkelsen & Bieler 2008; Tunnell *et al.* 2010; Espinosa *et al.* 2012; Redfern 2013). 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 at the "Colección de Moluscos de la Península de Yucatán" (CMPY), Unidad Multidisciplinaria de Docencia e Investigación Campus Sisal, Universidad Nacional Autónoma de México, México.

### Statistical analysis

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 4<sup>th</sup> 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), 2) to represent the temporal patterns in species composition and structure with depth intervals, a canonical correlation analysis (CCA) based on principal coordinates was constructed (Anderson & 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). Statistical analyses, for comparative purposes, were applied only to cores 4A and 6A, i.e., the two cores that were sectioned throughout at 1-cm intervals.

## Results

### Chronology

In all three cores dated using  $^{210}\text{Pb}$ , unsupported  $^{210}\text{Pb}$  activity (total  $^{210}\text{Pb}$  activity minus supported  $^{210}\text{Pb}$  [ $^{226}\text{Ra}$  activity]), showed a general decline with increasing sediment depth (Supplementary Material 2). In core 4A, total  $^{210}\text{Pb}$  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  $^{210}\text{Pb}$ . According to the Plum model, the date at 22 cm in the core is about 1938 CE (i.e., common era), and it thus spans ~79 years of sediment accumulation. In nearby core 4B, total  $^{210}\text{Pb}$  activity displayed a maximum value of 7.4 dpm/g in topmost deposits, and a low of 2.8 dpm/g in the bottom section (25 cm). The age model indicated a date of about 1921 CE at the base, implying a period of ~96 years of sediment accumulation. In core 6A, total  $^{210}\text{Pb}$  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  $^{210}\text{Pb}$ . 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 all three cores and could not be used to corroborate the  $^{210}\text{Pb}$  age models.

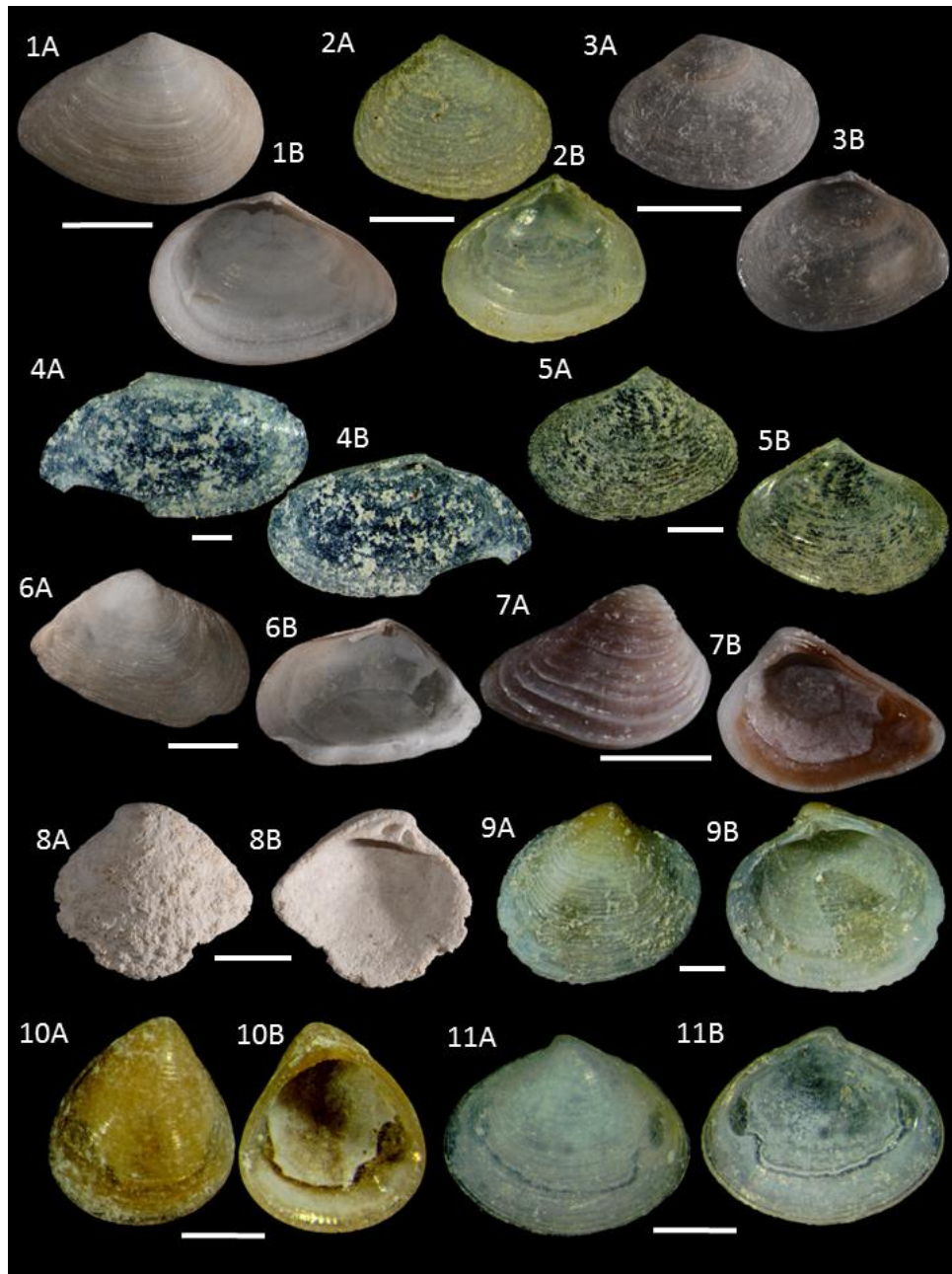
## Taxonomic composition of mollusc assemblages in cores

A total of 18,779 mollusc specimens, representing 20 bivalve species and 45 gastropod species, which belong to 32 families and 48 genera, were identified in sediments from the three cores taken in Río Lagartos coastal lagoon. The 65 species, except for *Bulla occidentalis* were photographed (Figures 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), *Bittium 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., *Dalocardia muricata* (Linnaeus, 1758), *Angulus* sp., *Cumingia* cf. *tellinoides* and *Musculus lateralis* (Say, 1822) 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), *Bittium 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 (Table 2). The historical and present-day inventory datasets possess the same ubiquitous species: *Prunum apicinum* (Menke, 1828), *Meioceras nitidum*, *Anomalocardia puella*, *Modulus modiolus* (Linnaeus, 1758) and *Crepidula convexa*, indicating their persistent role as dominant species in this heterogeneous environment.

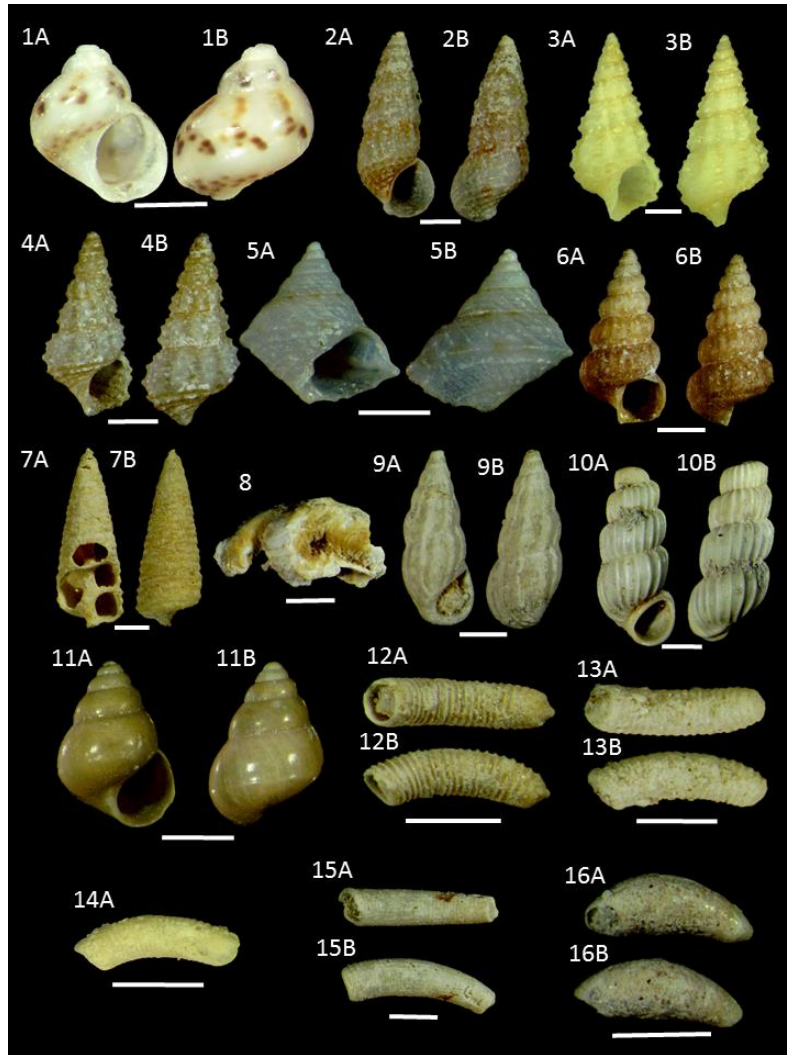
The same distributions of feeding guilds were found in the sediment core assemblages and present-day inventory datasets. The species classified as suspension feeders were predominant in both the historic and modern assemblages, and deposit feeders were less common. Species found in the core and modern assemblages were dominated by epifaunal organisms, with a high number of species belonging to Gastropoda, followed by infaunal organisms, dominated by Bivalvia.



**Figure 2.** Historical mollusc assemblages from sediment cores organized by species and their respective families. **Mytilidae** 1. *Brachidontes exustus* (Linnaeus, 1758) (CMPY-006486) Scale bar=1mm. 2. *Musculus lateralis* (Say, 1822) (CMPY-006672) Scale bar=1 mm. **Lucinidae** 3. Lucinidae sp. (CMPY-006120) Scale bar=1 mm. 4. *Parvilucina crenella* (Dall, 1901) (CMPY-006251) Scale bar=1 mm. 5. *Dallocardia muricata* (Linnaeus, 1758) (CMPY-006409) Scale bar=5 mm. **Cardiidae** 6. *Laevicardium serratum* (Linnaeus, 1758) (CMPY-006314) Scale bar=5 mm. 7. *Laevicardium mortoni* (Conrad, 1831) (CMPY-006183) Scale bar=1 mm. **Cyrenidae** 8. *Polymesoda floridana* (Conrad, 1846) (CMPY-006121) Scale bar=1 mm. 9. *Polymesoda* sp. (CMPY-006389) Scale bar=1 mm.



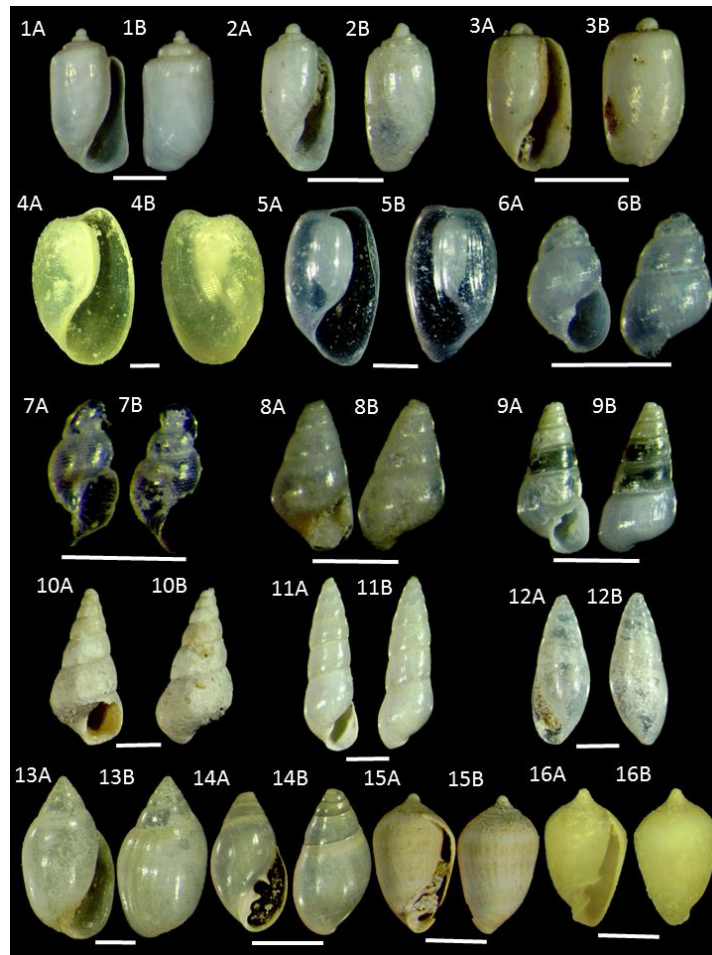
**Figure 3.** Historical mollusc assemblages from sediment cores organized by species and their respective families. **Tellinidae** 1. *Tampaella tampaensis* (Conrad, 1866) (CMPY-006218) Scale bar=5 mm. 2. *Angulus paramerus* (Boss, 1964) (CMPY-006170) Scale bar=1 mm. 3. *Angulus* sp. (CMPY-006493) Scale 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.



**Figure 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. *Bittiolium 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.



**Figure 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.



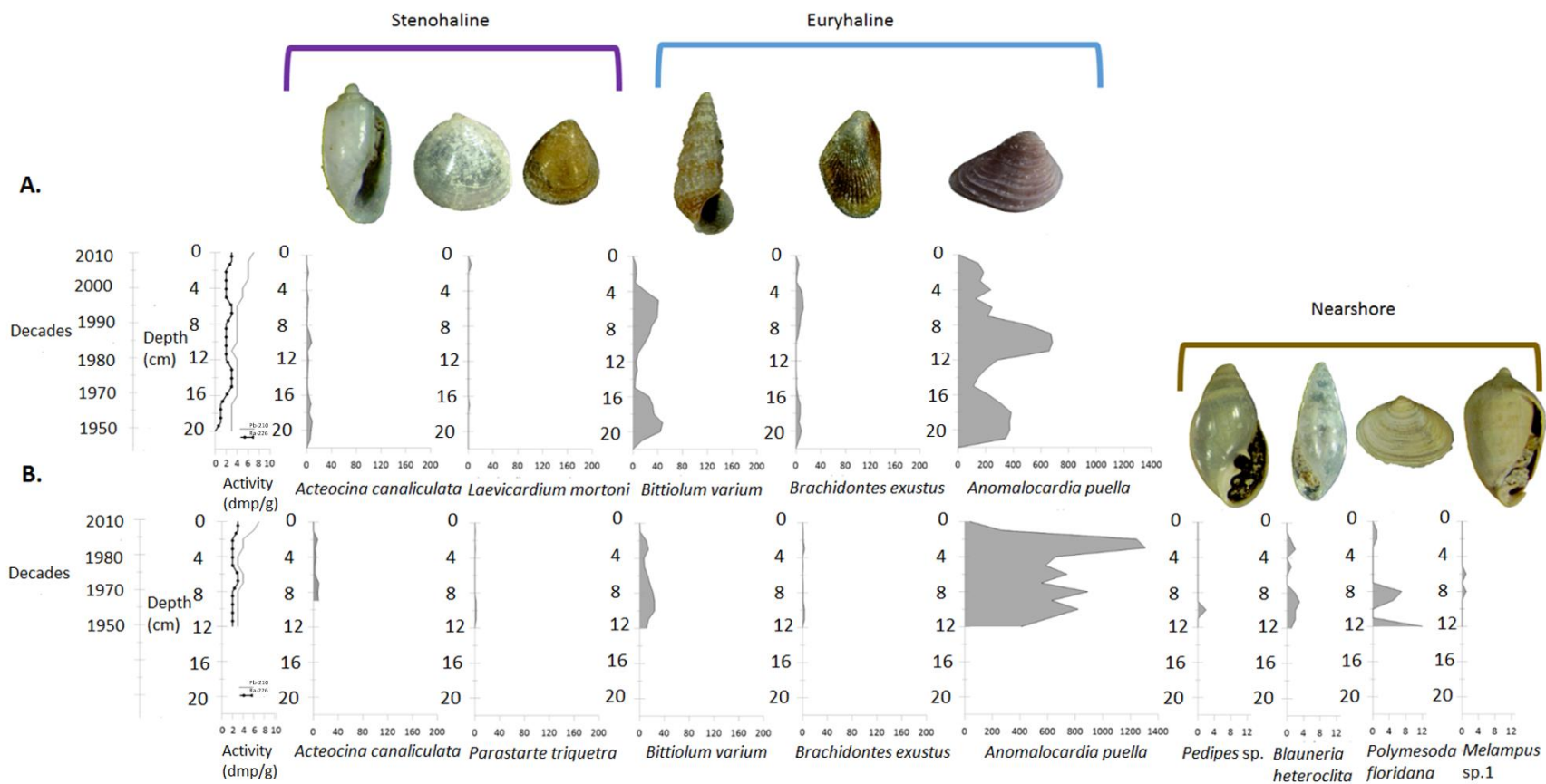
**Figure 6.** Historical mollusc assemblages from sediment cores organized by species and their respective families. **Tornatinidae** 1. *Acteocina atrata* P. S. Mikkelsen & P. M. Mikkelsen, 1984 (CMPY-006208) Scale bar=1 mm. 2. *Acteocina canaliculata* (Say, 1826) (CMPY-006245) Scale bar=1 mm. 3. *Acteocina* cf. *recta* (CMPY-006350) Scale bar=1 mm. **Haminoeidae** 4. *Haminoea* cf. *elegans* (CMPY-006669) Scale bar=1 mm. 5. *Haminoea succinea* (CMPY-006642) Scale bar=1 mm. **Pyramidellidae** 6. Pyramidellidae sp.1 (CMPY-006188) Scale bar=1 mm. 7. Pyramidellidae sp.2 (CMPY-006658) Scale bar=0.5 mm. 8. *Evalea* sp. (CMPY-006261) Scale bar=1 mm. 9. *Odostomia pocahontasae* Henderson & Bartsch, 1914 (CMPY-006182) Scale bar=1 mm. 10. *Odostomia* sp. (CMPY-006382) Scale bar= 1 mm. 11. *Sayella* sp. (CMPY-006209) Scale bar=1 mm. **Ellobiidae** 12. Ellobiidae sp. (CMPY-006291) Scale bar=1 mm. 13. *Blauneria heteroclita* (Montagu, 1808) (CMPY-006372) Scale bar=1 mm. 14. *Pedipes* sp. (CMPY-006300) Scale bar=1 mm. 15. *Melampus* sp. 1. (CMPY-006207) Scale bar= 1 mm. 16. *Melampus* sp. 2. (CMPY-006306) Scale bar=1 mm.



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

The inventory of modern mollusc assemblages from Río Lagartos hypersaline coastal lagoon showed that species are distributed across a broad salinity gradient and represent euhaline to hypersaline taxa. Some species encountered in the present-day inventory were not recorded in the cores, 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*, Pyramidellidae sp.2, *Bittium 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., *Haminoea* cf. *elegans*, *Japonactaeon punctostriatus*, *Melampus* sp. 1, *Melampus* sp. 2, *Melongena corona*, *Nassarius* sp., *Odostomia pocahontasae*, *Odostomia* sp., *Olivella minuta*, *Polymesoda* sp., Pyramidellidae sp.1, and *Seila* sp. (Supplementary Material 3).

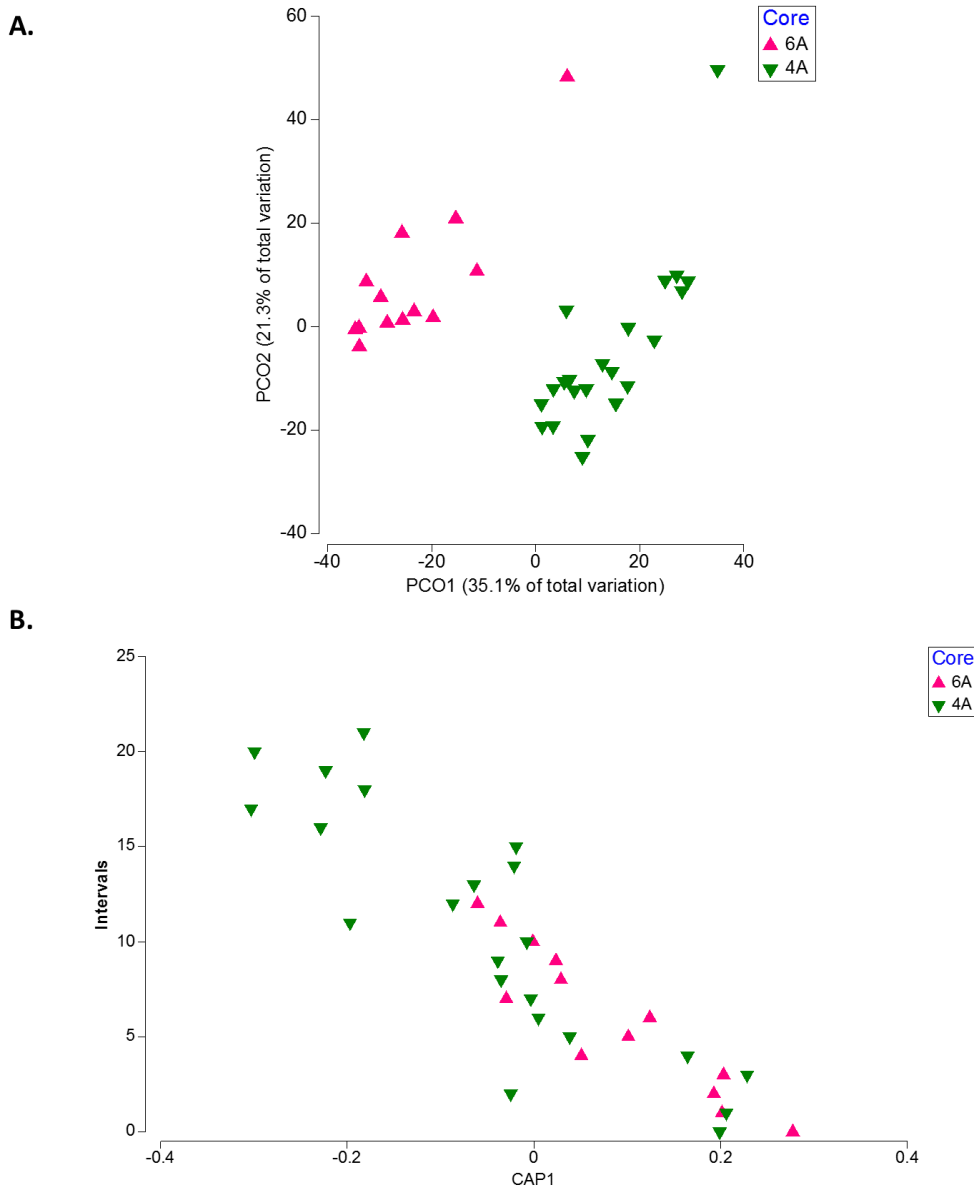
Taxa encountered in the sediment core assemblages were divided into three groups based on their environmental preferences according to either the present-day inventory or comparisons with environmental conditions where they were encountered in other lagoon localities (Figure 7). Living *Anomalocardia puella* and *Brachidontes exustus* were encountered across a wide range of salinity and were placed in the euryhaline group; *Bulla occidentalis* and *Parastarte triquetra* were encountered in narrow range of salinity and were placed in the stenohaline group (Figure 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 *Bittium 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.



**Figure 7.** Absolute abundance of mollusc species by decades and depth (cm) with the activities of  $^{210}\text{Pb}$  and  $^{226}\text{Ra}$  (dpm/g) in A) core 4A, and B) core 6A from Río Lagartos coastal lagoon, Mexico. Species were classified into three indicator groups: stenohaline, nearshore and euryhaline.

## Mollusc assemblages through time

Analysis of the multivariate ordination plot showed that species composition was different between cores 4A and 6A (Figure 8A). 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*. A Canonical analysis of principal coordinates showed assemblage changes over time (intervals) [Correlation=0.8465,  $P < 0.001$ , No. of permutations used=999] (Figure 8B). Both cores showed this separation of intervals, indicating that the taxonomic composition and structure of assemblages changed over time and that those changes were different at the two core sites in the coastal lagoon.



**Figure 8.** A. Principal coordinates ordination plot (PCO) based on Bray Curtis dissimilarities from 4<sup>th</sup> root abundances of molluscs. B. Canonical analysis of principal coordinates (CAP) plot generated from a resemblance matrix, using intervals as a factor. Green triangles=Core 4B and pink triangles= Core 6A.

## Discussion

### Taxonomic composition in sediments cores

Mollusc taxa encountered in Río Lagartos coastal lagoon total 153 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. Sixty-eight of the species found by in 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., *Atrina rigida*). Compared to our present-day mollusc inventory study in the same lagoon, which yielded 39 species, we found almost double the number of species in the sediment cores (65 species), which reveals the importance of studying time-averaged assemblages that derive from current and historical generations (Kidwell 2013) if one hopes to get a true sense of species richness in a locality. These differences between modern and sedimented mollusc assemblages suggest that the molluscs were likely influenced by multiple environmental factors, such as salinity, vegetation cover, and substrate type, which probably shifted dynamically throughout the lagoon over time. Thus, taxa with diverse optima and tolerances for environmental variables were encountered in the sediment core assemblages, which reflect changes in both time and space.

### Historical changes in molluscs assemblages

It is likely that both natural and human-mediated environmental changes caused the shift in mollusc species assemblage composition in the sediment cores, as has been documented in other parts of the world (Wingard & Ishman 1999; Weber & Zuschin 2013; Fortunato 2015; Bianchette *et al.* 2022; Kusnerik *et al.* 2022). This pattern is most evident in the stratigraphic shift in abundances of *Anomalocardia puella*, *Brachidontes exustus* and *Bittium varium* (Figure 7), which may reflect salinity changes, or in the case of nearshore species, may represent greater connection with the terrestrial environment. 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 that would 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 about the optima and tolerances of Mollusca taxa in Río Lagartos coastal lagoon, 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 ecosystem dynamics and faunal assemblages (Figure 8).

Species of molluscs that have been used in paleoecology to infer past salinity include: *Polymesoda* spp., *Cerithidea* spp., *Laevicardium mortoni*, *Crepidula* spp. *Anomalocardia auberiana*, *Cerithium muscarum* and *Brachidontes exustus* (Wingard & 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 (Wingard & Ishman 1999; Camargo Maia & Coutinho 2013). This is consistent with our findings because the sediment cores were collected near mangroves and agricultural areas (Figure 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 & Greenberg 1977). Species *Acteocina canaliculata*, *Bittium 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 present-day inventory 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 mussel *Brachidontes* dominates in areas of abundant sub-aquatic vegetation because the vegetation provide structure for bivalve attachment (via byssal threads), but it was difficult to determine the primary factor that controlled the species distribution (Wingard & Ishman 1999; Wingard *et al.* 2001). 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 *Meioceras nitidum*.

Our information is essential to understand ecological conditions that prevailed prior to human-mediated environmental impact (e.g., oil spills) (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. 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.

## **Conclusions**

Mollusc assemblages in sediment cores from Río Lagartos coastal lagoon revealed differences across space and through time. Stratigraphic shifts in mollusc assemblage composition in the last few decades were probably driven largely by changes in salinity, reflecting the limited tolerance of species to this environmental variable, and perhaps changes in the availability of resources to molluscs, which became limited by this environmental variable. The combination of a present-day and historical perspective enabled us to identify recent changes in the lagoon's mollusc community, understand trends in the lagoon's environmental conditions, and make additions to the lagoon's mollusc species list. This information will be of use for future management and conservation strategies in the biosphere reserve and should be supplemented with more ecophysiological studies of the species.

## Capítulo 5. Conclusiones generales integrativas



Existe la necesidad de comprender y conocer los distintos patrones temporales y espaciales de los ecosistemas acuáticos. Este trabajo describió desde lo taxonómico, ecológico y (paleo) limnológico las tendencias que ocurrieron en la laguna costera de Río Lagartos, con dos enfoques: 1) la fauna moderna de moluscos que se distribuye a lo largo de la laguna y 2) los moluscos que habitaron durante el último siglo y que se depositaron en el sedimento (Figura 1). Al realizar la línea base de los moluscos a lo largo de la laguna, se encontró un cambio en su distribución respondiendo a un control abiótico y biótico, desconociendo con exactitud la variable ambiental fue la que más contribuyó en este cambio, pero considerando estudios anteriores en la laguna costera, se estableció que la salinidad es una de las variables más importantes que ha limitado la distribución de las especies. Los moluscos encontrados en los núcleos de sedimento mostraron también un cambio en la composición y en las abundancias de moluscos, espacialmente y a lo largo del tiempo, pero no se pudo descubrir el impulsor principal que produjo este cambio. Al probar la hipótesis de disturbio intermedio y teniendo en cuenta los distintos acontecimientos que ocurrieron a lo largo de la laguna, los huracanes y las actividades antropogénicas pudieron desencadenar cambios en la laguna y, a su vez, en los moluscos. Al evaluar los distintos agentes que pudieron significar un disturbio (i.e. huracanes, aumento de la población humana, construcciones, modificación del suelo), no hubo un factor que mostrara una respuesta de los moluscos. Sin embargo, No se descarta que estos acontecimientos hayan podido afectar de manera a la fauna de moluscos que habitó en la laguna costera; como modificadores del hábitat, en la redistribución de sedimento, en el cambio hidrológico o modificando los niveles de salinidad.

El presente trabajo actualiza taxonómicamente los moluscos y presenta un aporte fotográfico de las conchas y especímenes de moluscos que habitaron en el último siglo. Después de analizar los moluscos que habitan en la laguna y aquellos que se depositaron a lo largo del tiempo, se recomienda establecer programas de monitoreo faunísticos y la medición de las variables ambientales a largo plazo, analizar los cambios en la fauna a distintas escalas, conocer las tolerancias de los organismos a las variables ambientales e incorporar en el análisis otros organismos, como diatomeas, ostrácodos y foraminíferos para corroborar si los cambios a lo largo del tiempo se evidencia en todos los habitantes de la laguna. Se sugiere recolectar más de un núcleo y sus réplicas para analizar la variabilidad de las muestras. Por último, es necesario tener un registro detallado de los acontecimientos que puedan impactar la laguna costera.



**Figura 1.** Gráfico resumen de los principales aportes del estudio en la laguna costera de Río Lagartos.

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### **Material complementario capítulo 3**

Supplementary Material 1. Data set of abundance of molluscs from the Río Lagartos coastal lagoon, including information about sample geographic location, abiotic variables, mollusc taxonomic and functional groups, and catalog numbers of each species deposited in the “Colección de Moluscos de la Península de Yucatán” (CMPY).

Specie/Stations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40								
<i>Angulus merus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
<i>Angulus paramerus</i>	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0				
<i>Angulus sybariticus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Anodontia alba</i>	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Anomalocardia auberiana</i>	0	0	0	0	0	0	0	2	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	10	32	54	0	0	454	574	0	0	0	0	0	0	0				
<i>Astyris antares</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
<i>Brachidontes exustus</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	2	0	0	0	0	0				
<i>Bulla occidentalis</i>	0	0	0	0	0	0	0	20	0	0	0	0	0	0	55	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Caecum donmoorei</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Carditamera floridana</i>	0	0	0	0	0	0	0	3	1	0	1	0	13	0	0	0	0	1	0	0	1	0	2	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Cerithiidae sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Cerithium atratum</i>	0	18	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	15	1	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cerithium eburneum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Cerithium lutosum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chione cancellata</i>	0	0	1	12	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Crassinella</i> sp.	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Crepidula convexa</i>	0	0	0	0	0	0	0	16	0	4	0	0	0	1	15	0	2	11	39	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ctena orbiculata</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Eulithidium adamsi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Granulina</i> sp.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0		

<i>Haminoea succinea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Henrya henryi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	
Lasaeidae	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lucinisca nassula</i>	0	0	0	14	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lyonsia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Macoma cerina</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Macoma tenta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1		
<i>Meioceras nitidum</i>	0	0	0	0	541	54	92	0	0	0	1	1	0	0	0	4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
<i>Melongena corona</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	
<i>Merisca</i> sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Modulus modulus</i>	0	0	0	0	0	0	0	13	0	0	0	0	0	0	28	0	1	22	10	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Musculus lateralis</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nassarius vibex</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Odostomia laevigata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<i>Parastarte triquetra</i>	0	0	0	0	0	0	0	0	0	0	0	0	122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parvilucina crenella</i>	0	0	0	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Prunum apicinum</i>	0	1	0	1	2	0	0	0	0	0	6	0	3	3	2	0	0	0	1	0	3	0	0	0	6	1	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Vermetidae sp.	0	0	0	0	0	0	0	0	44	0	0	0	0	0	0	58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Zebina browniana</i>	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

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Station name	Number
RL1709_3_Bent 1	1
RL1709_E3_Chin	2
RL1802_3_Bent 1	3
RL1805_3_Bent 1	4
RL1709_6_Bent 1	5
RL1805_6_Bent 1	6
RL1802_6_Bent 1	7
RL1709_E9c1_Chin 1	8
RL1805_9c4_Bent 1	9
RL1805_9c4_Bent-pas	10
RL1805_9c2_Bent 1	11
RL1709_9c3_Bent 1	12
RL1709_9c1_Bent 1	13
RL1709_9_C2_chin1	14
RL1709_E9_C2_chin1	15
RL1709_9c4_Epimangle 1	16
RL1802_9_C3_Chin1	17
RL1802_9_C2_Chin1	18
RL1805_E9_C4__Chin1	19
RL1805_E9_chinC4	20
RL1805_9_C3_Chin1	21
RL1805_9_Chin1	22
RL1802_12_Bent 1	23
RL1709_12_Bent 1	24
RL1709_E12_Chin1	25
RL1805_12_Bent 1	26
RL1709_15_Bent 1	27
RL1802_15_Bent 1	28



RL1802_15_Chin1	29
RL1805_15_Bent 1	30
RL1709_20_Bent 1	31
RL1709_21_Bent 1	32
RL1805_21_Chin1	33
RL1709_22_Bent 1	34
RL1805_22_Bent 1	35
RL1709_25_Bent 1	36
RL1709_27_Bent 1	37
RL1802_27_Bent 1	38
RL802_E27_Chin1	39
RL1709_29_Bent 1	40

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<b>St</b>	3	3	3	3	6	6	6	9c	9	9	9	9	9	9c	9c	9	9c	9c	9c	9c	9c	9c	12	12	12	1	15	15	15	1	20	21	21	22	22	25	27	27	27	29			
							1	c	c	c	c	c	c	2	2	c	3	2	4	4	3	1				2				5													
							4	4	2	3	1					4																											
<b>Lat</b>	2	21.	21	2	2	2	2	21.	2	2	2	2	2	21.	21.	2	21.	21.	21.	21.	21.	21.	21.	21.	2	21	21	21.	2	21	21	21.	21	21	21	21	21	21	21	21	21	21	
	1.	6	.6	1.	1.	1.	1.	6	1.	1.	1.	1.	1.	6	6	1.	6	6	6	6	6	6	6	6	1.	.6	.6	6	1.	.6	.6	6	.6	.6	.6	.6	.6	.6	.6	.6	.6	.6	.6
	6			6	6	6	6		6	6	6	6	6		6									6				6															
<b>Lon</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
	8	88.	88	8	8	8	8	88.	8	8	8	8	8	88.	88.	8	88.	88.	88.	88.	88.	88.	88.	88.	8	88	88	88.	8	88	88	88.	88	88	88	88	88	87	87	87	87.	87	
	8.	2	.2	8.	8.	8.	8.	2	8.	8.	8.	8.	8.	2	2	8.	2	2	2	2	2	2	2	2	8.	.1	.1	1	8.	.1	.1	1	8.	.0	.0	0	.0	.0	.9	.8	.8	8	.8
	2			2	2	2	2		2	2	2	2	2			2									1				1														
<b>Year</b>	2	20	20	2	2	2	2	20	2	2	2	2	2	20	20	2	20	20	20	20	20	20	20	2	20	20	20	2	20	20	20	20	20	20	20	20	20	20	20	20	20	20	
	0	17	18	0	0	0	0	17	0	0	0	0	0	17	17	0	18	18	18	18	18	18	18	0	17	18	18	0	17	17	18	17	18	17	18	17	18	17	18	18	18	17	
	1			1	1	1	1		1	1	1	1	1			1							1				1																
	7			8	7	8	8		8	8	8	7	7			7								8				8															
<b>Season</b>	R	R	N	D	R	D	N	R	D	D	D	R	R	R	R	R	N	N	D	D	D	D	N	R	R	D	R	N	N	D	R	R	D	R	D	R	R	N	N	R	R		
<b>Basin</b>	R	RL	RL	R	R	R	R	RL	R	R	R	R	R	RL	RL	R	RL	RL	RL	RL	RL	RL	RL	R	RL	RL	RL	R	C	C	C	C	C	C	C	C	C	C	C	C	C	C	
	L			L	L	L	L		L	L	L	L	L			L							L				L	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	
<b>Salinity</b>	E	Eu	Hy	E	E	E	E	Eu	E	E	E	E	E	Eu	Eu	E	Eu	Eu	Eu	Eu	Eu	Eu	Hy	Hy	Hy	E	Hy	Hy	Hy	E	Hy	Hy	Hy	Hy	Hy	Hy	Hy	Hy	Hy	Hy	Hy	Hy	Hy
<b>environmental</b>	u	hal	rh	u	u	u	u	hal	u	u	u	u	u	hal	hal	u	hal	hal	hal	hal	hal	hal	rh	rh	rh	u	rh	rh	rh	u	rh	rh	rh	rh	rh	rh	rh	rh	rh	rh	rh	rh	rh
<b>salinity</b>	al		ali	al	al	al	al		al	al	al	al	al			al						ali	ali	ali	al	ali	ali	ali	al	ali	ali	ali	ali	ali	ali	ali	ali	ali	ali	ali	ali	ali	ali
<b>salinity</b>	ine		ne	in	in	in	in	ine	in	in	in	in	in	ine	ine	in	ine	ine	ine	ine	ine	ine	ne	ne	ne	in	ne	ne	ne	in	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
<b>Salinity</b>	3	36.	43	3	3	3	4	40.	3	3	3	3	4	40.	40.	4	36.	37.	35.	35.	35.	36.	52	41	41.	3	42	58	58.	3	44	45	49.	53	53	58	74	78	78.	75	75		
	6.	7	.5	4.	8.	6.	0.	0	5.	5.	7.	7.	0.	0	0	0.	9	2	3	3	4	2	.3	.6	6	5.	.5	.9	9	4.	.1	.8	8	.0	.8	.1	.0	.0	0	.0	.0		
	7			5	2	0	5		3	3	2	7	0			0							2							3													
<b>Sampler</b>	D	Be	Dr	D	D	D	D	Be	D	D	D	D	D	Be	Be	S	Be	Be	Be	Be	Be	Be	Dr	Dr	Be	D	Dr	Dr	Be	D	Dr	Dr	Be	Dr	Dr	Dr	Dr	Dr	Dr	Dr	Be	Dr	
	re	ac	ed	re	re	re	re	ac	re	re	re	re	re	ac	ac	q	ac	ac	ac	ac	ac	ac	ed	ed	ac	re	ed	ed	ac	re	ed	ed	ac	ed	ed	ed	ed	ed	ed	ed	ed	ac	ed
	d	h	ge	d	d	d	d	h	d	d	d	d	d	h	h	u	h	h	h	h	h	h	ge	ge	h	d	ge	ge	h	d	ge	ge	h	ge	ge	ge	ge	ge	ge	ge	ge	h	ge
	g	sei		g	g	g	g	sei	g	g	g	g	g	sei	sei	ar	sei	sei	sei	sei	sei	sei			sei	g			sei	g											sei		
	e	ne		e	e	e	e	ne	e	e	e	e	e	ne	ne	e	ne	ne	ne	ne	ne	ne			ne	e			ne	e											ne		

<b>Vegetation Average %</b>	1		0.	6.	1	4	1.		0.	1		1.	1.		1.				28	13		2.	6.	5.		1.	3.		0.	0.	3.	0.	1.		0.					
	2.		0	6	0	0.	6		0	0		2	7		7				.2	.0		3	5	2		5	2		0	0	8	8	7		0					
	1				0.	5				0.																														
				0						0																														
<b>Gravel</b>	1	16.	1.	3.	4.	1.	4.	6.8	4.	4.	4.	6.	6.	6.8	6.8	6.	16.		4.0	4.0		2.8	2.	8.	8.6	6.	1.	0.	0.1	3.	4.	33	1.8	29	3.	3.	13	1.	1.6	3.
	6.	5	8	9	9	2	7		0	0	8	8	8			8	8					4	6		9	4	1		8	6	.2		.0	9	9	.6	6		6	
	5																																							
<b>Sand</b>	8	83.	94	9	7	9	9	89.	9	9	9	8	8	89.	89.	8	82.		94.	94.		95.	96	67	67.	9	43	98	98.	9	76	30	96.	70	95	93	84	97	97.	85
	3.	2	.9	5.	4.	6.	4.	0	4.	4.	4.	9.	9.	0	0	9.	7		7	7		6	.8	.6	6	2.	.9	.0	0	5.	.5	.8	5	.1	.9	.7	.2	.1	1	.8
	2			1	3	8	7		7	7	3	0	0			0										7				7										
<b>Clay</b>	0.	0.3	3.	1.	2	2.	0.	4.1	1.	1.	0.	4.	4.	4.1	4.1	4.	0.5		1.3	1.3		1.6	0.	23	23.	0.	54	2.	2.0	0.	18	36	1.6	0.	0.	2.	2.	1.	1.3	10
	3		2	0	0.	1	6		3	3	9	1	1			1						8	.8	8	3	.7	0		5	.9	.0		9	2	4	2	3		.7	
					8																																			

Supplementary Material 2. Summary of the iNEXT analysis of molluscs from the Río Lagartos coastal lagoon. Sheet 1. Basic data information. Sheet 2. Notes on the meaning of basic data information. Sheet 3. Rarefaction and Extrapolation. Sheet 4. Notes on the meaning of Rarefaction and Extrapolation.

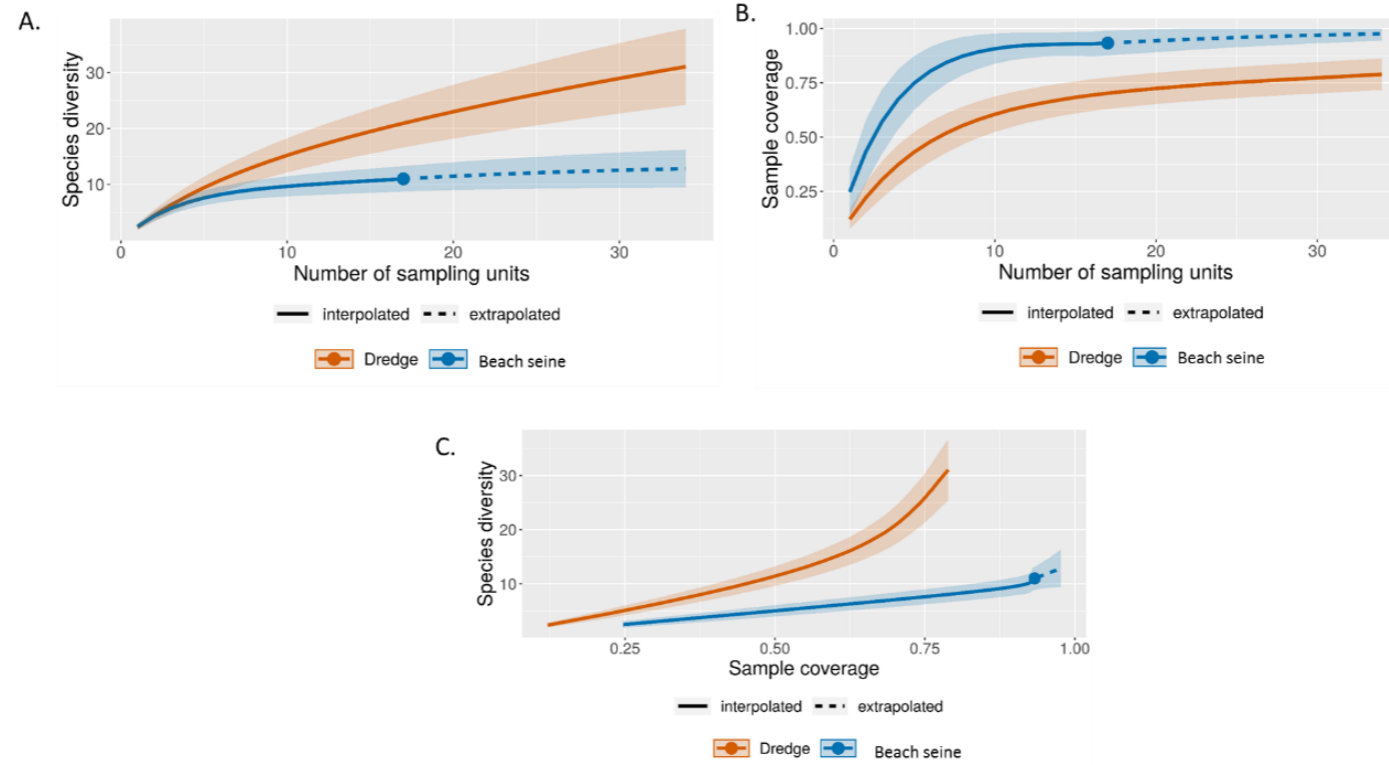
t	Method	Order	qD	qD.LC L	qD.UC L	SC	SC.LC L	SC.UC L	Site
1	interpolate d	0	3.121	2.521	3.722	0.142	0.094	0.19	Euhaline
2	interpolate d	0	5.799	4.733	6.865	0.252	0.181	0.324	Euhaline
4	interpolate d	0	10.192	8.412	11.971	0.412	0.322	0.502	Euhaline
6	interpolate d	0	13.679	11.344	16.015	0.521	0.427	0.614	Euhaline
7	interpolate d	0	15.175	12.595	17.756	0.563	0.47	0.656	Euhaline
9	interpolate d	0	17.789	14.759	20.819	0.631	0.541	0.721	Euhaline
11	interpolate d	0	20.007	16.565	23.448	0.682	0.597	0.768	Euhaline
13	interpolate d	0	21.924	18.1	25.748	0.722	0.641	0.802	Euhaline
14	interpolate d	0	22.793	18.786	26.799	0.738	0.66	0.816	Euhaline
16	interpolate d	0	24.387	20.034	28.741	0.764	0.69	0.838	Euhaline
18	interpolate d	0	25.827	21.148	30.505	0.784	0.715	0.854	Euhaline
19	interpolate d	0	26.499	21.666	31.333	0.793	0.725	0.861	Euhaline
21	interpolate d	0	27.768	22.64	32.897	0.807	0.742	0.873	Euhaline
23	interpolate d	0	28.951	23.547	34.356	0.819	0.756	0.882	Euhaline
25	interpolate d	0	30.065	24.401	35.728	0.829	0.768	0.89	Euhaline
26	interpolate d	0	30.599	24.812	36.386	0.833	0.773	0.894	Euhaline
28	interpolate d	0	31.627	25.604	37.649	0.841	0.781	0.901	Euhaline
30	interpolate d	0	32.607	26.364	38.851	0.848	0.789	0.908	Euhaline
32	interpolate d	0	33.545	27.094	39.997	0.854	0.795	0.914	Euhaline
33	observed	0	34	27.449	40.551	0.857	0.798	0.917	Euhaline
34	extrapolate d	0	34.445	27.798	41.093	0.86	0.8	0.92	Euhaline
34	extrapolate d	0	34.445	27.798	41.093	0.86	0.8	0.92	Euhaline
35	extrapolate d	0	34.881	28.139	41.624	0.863	0.803	0.923	Euhaline
36	extrapolate d	0	35.309	28.474	42.144	0.866	0.805	0.926	Euhaline
36	extrapolate d	0	35.309	28.474	42.144	0.866	0.805	0.926	Euhaline
37	extrapolate d	0	35.727	28.801	42.653	0.869	0.808	0.929	Euhaline
38	extrapolate d	0	36.137	29.122	43.153	0.871	0.81	0.932	Euhaline
39	extrapolate d	0	36.539	29.434	43.643	0.874	0.813	0.935	Euhaline

39	extrapolated	0	36.539	29.434	43.643	0.874	0.813	0.935	Euhaline
40	extrapolated	0	36.932	29.74	44.125	0.877	0.815	0.938	Euhaline
41	extrapolated	0	37.318	30.038	44.598	0.879	0.817	0.941	Euhaline
42	extrapolated	0	37.695	30.328	45.063	0.882	0.819	0.944	Euhaline
42	extrapolated	0	37.695	30.328	45.063	0.882	0.819	0.944	Euhaline
43	extrapolated	0	38.065	30.611	45.519	0.884	0.821	0.946	Euhaline
44	extrapolated	0	38.428	30.886	45.969	0.886	0.824	0.949	Euhaline
45	extrapolated	0	38.782	31.154	46.411	0.889	0.826	0.951	Euhaline
45	extrapolated	0	38.782	31.154	46.411	0.889	0.826	0.951	Euhaline
46	extrapolated	0	39.13	31.414	46.846	0.891	0.828	0.954	Euhaline
47	extrapolated	0	39.471	31.667	47.275	0.893	0.83	0.956	Euhaline
48	extrapolated	0	39.804	31.912	47.697	0.895	0.832	0.959	Euhaline
1	interpolated	0	1.417	0.949	1.885	0.059	0.009	0.109	Hyperhaline
2	interpolated	0	2.75	1.885	3.615	0.114	0.026	0.202	Hyperhaline
3	interpolated	0	4.005	2.796	5.214	0.166	0.05	0.282	Hyperhaline
4	interpolated	0	5.186	3.676	6.696	0.215	0.078	0.352	Hyperhaline
5	interpolated	0	6.298	4.52	8.077	0.261	0.108	0.413	Hyperhaline
7	interpolated	0	8.333	6.093	10.573	0.343	0.173	0.514	Hyperhaline
8	interpolated	0	9.264	6.821	11.706	0.38	0.205	0.556	Hyperhaline
9	interpolated	0	10.141	7.511	12.771	0.415	0.236	0.594	Hyperhaline
10	interpolated	0	10.97	8.166	13.774	0.447	0.266	0.628	Hyperhaline
12	interpolated	0	12.494	9.373	15.614	0.505	0.323	0.687	Hyperhaline
13	interpolated	0	13.195	9.93	16.46	0.531	0.349	0.713	Hyperhaline
14	interpolated	0	13.86	10.458	17.262	0.555	0.373	0.736	Hyperhaline
15	interpolated	0	14.491	10.958	18.024	0.577	0.396	0.758	Hyperhaline
16	interpolated	0	15.091	11.433	18.749	0.597	0.417	0.777	Hyperhaline
18	interpolated	0	16.206	12.311	20.101	0.634	0.456	0.812	Hyperhaline
19	interpolated	0	16.725	12.716	20.733	0.65	0.473	0.827	Hyperhaline
20	interpolated	0	17.22	13.101	21.34	0.665	0.489	0.841	Hyperhaline
21	interpolated	0	17.695	13.467	21.923	0.68	0.504	0.855	Hyperhaline
23	interpolated	0	18.583	14.141	23.026	0.706	0.532	0.88	Hyperhaline

24	observed	0	19	14.45	23.55	0.718	0.545	0.892	Hyperhaline
25	extrapolated	0	19.399	14.743	24.056	0.73	0.557	0.903	Hyperhaline
26	extrapolated	0	19.782	15.018	24.546	0.741	0.569	0.914	Hyperhaline
27	extrapolated	0	20.149	15.276	25.021	0.752	0.58	0.924	Hyperhaline
28	extrapolated	0	20.5	15.518	25.482	0.762	0.591	0.934	Hyperhaline
29	extrapolated	0	20.837	15.745	25.929	0.772	0.602	0.943	Hyperhaline
31	extrapolated	0	21.469	16.153	26.785	0.791	0.622	0.959	Hyperhaline
32	extrapolated	0	21.765	16.335	27.196	0.799	0.632	0.967	Hyperhaline
33	extrapolated	0	22.05	16.504	27.595	0.808	0.641	0.974	Hyperhaline
34	extrapolated	0	22.322	16.661	27.983	0.816	0.651	0.981	Hyperhaline
35	extrapolated	0	22.583	16.804	28.361	0.824	0.66	0.987	Hyperhaline
37	extrapolated	0	23.072	17.057	29.088	0.838	0.677	0.999	Hyperhaline
38	extrapolated	0	23.302	17.167	29.437	0.845	0.685	1	Hyperhaline
39	extrapolated	0	23.522	17.267	29.777	0.851	0.693	1	Hyperhaline
40	extrapolated	0	23.733	17.357	30.109	0.857	0.701	1	Hyperhaline
41	extrapolated	0	23.935	17.437	30.432	0.863	0.708	1	Hyperhaline
43	extrapolated	0	24.314	17.573	31.055	0.874	0.722	1	Hyperhaline
44	extrapolated	0	24.492	17.629	31.356	0.88	0.729	1	Hyperhaline
45	extrapolated	0	24.663	17.677	31.648	0.885	0.736	1	Hyperhaline
46	extrapolated	0	24.826	17.718	31.934	0.889	0.742	1	Hyperhaline
48	extrapolated	0	25.133	17.781	32.484	0.899	0.754	1	Hyperhaline

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Supplementary Material 3. Interpolation and extrapolation curves by sampler in the Río Lagartos coastal lagoon: dredge (red lines) and beach seine (blue lines). A. Species accumulation curve based on the occurrence of species. B. Sample-coverage accumulation curve based on sampler C. Sample completeness curves, linking curves A and B. The solid lines represent interpolation, whereas dashed lines represent extrapolation.



**Material complementario capítulo 4**

Supplementary Material 1. Taxonomic list of the identified species in the three sediments cores from Río Lagartos coastal lagoon. Information on distribution of Bivalvia is provided (Turgeon et al. 2009), (Tunnell et al. 2010) and for Gastropoda by (Rosenberg et al. 2009), (Redfern 2013) and (Ortigosa et al. 2018).

Species	Core 6A												Core 4A												Core 4B																						
	St 6A_0-	St 6A_1-	St 6A_2-	St 6A_3-	St 6A_4-	St 6A_5-	St 6A_6-	St 6A_7-	St 6A_8-	St 6A_9-	St 6A_10-	St 6A_11-	St 6A_12-	St 6A_13-	St 4A_0-	St 4A_1-	St 4A_2-	St 4A_3-	St 4A_4-	St 4A_5-	St 4A_6-	St 4A_7-	St 4A_8-	St 4A_9-	St 4A_10-	St 4A_11-	St 4A_12-	St 4A_13-	St 4A_14-	St 4A_15-	St 4A_16-	St 4A_17-	St 4A_18-	St 4A_19-	St 4A_20-	St 4A_21-	St 4A_22-	St 4B_0-	St 4B_5-	St 4B_10-							
<i>Acteocina canaliculata</i>			7	3	4	3	3	9	7	8	18	19	12				3																														
<i>Tampaella paramera</i>														1																											2						
<i>Angulus</i> sp.																									1																						
<i>Tampaella tampaensis</i>															1																																
<i>Anomalocardia puella</i>	38	26	12	13	66	58	74	55	89	63	821	614	409	5	14	18	16	23	12	24	21	49	67	684	658	287	204	145	111	223	312	385	373	375	343	16	52	829									
<i>Angustassiminea succinea</i>	1	1	19	15	7	6	14	10	27	17	20	20	3																													3	4				
<i>Astyris lunata</i>																																															
Pyramidellidae sp.2																																											1				
<i>Bittium varium</i>			1	11	14	7	8	13	17	22	24	24	14	11		5	6	4	21	41	40	39	30	26	18	9	5	7	4	3	26	32	34	48	44	15	7	60	27								
<i>Blauneria heteroclita</i>				1	2		1			2	3	2	2	1																																	
<i>Brachidontes exustus</i>		1	1	3		1		1	1	1	3	3			5	2	1	9	11	12	8	6	4				1	1	3	7	7	5	9	5	7	14	4										
<i>Bulla occidentalis</i>																																													1		
<i>Caecum</i> cf. <i>floridanum</i>				1	1	1								1	1																																
<i>Caecum textile</i>													1																																		
<i>Caecum donmoorei</i>																																															







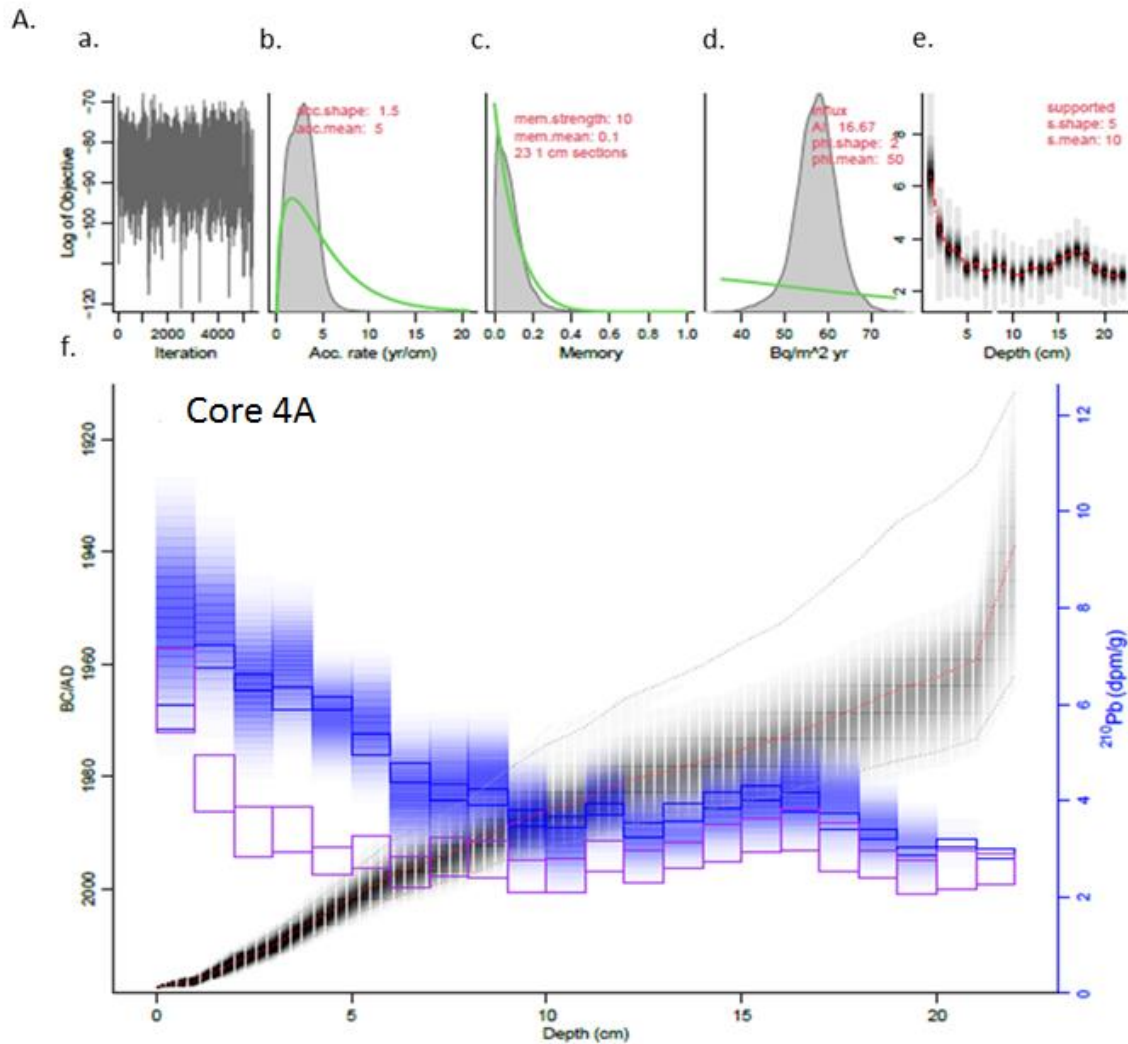
*Vitrinella* sp.

1

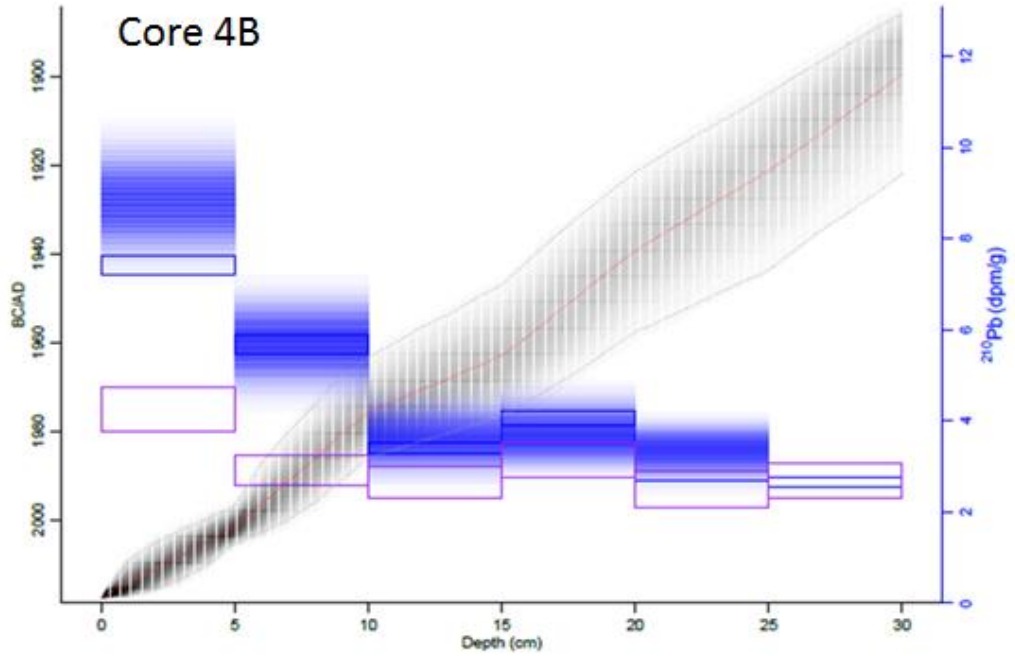
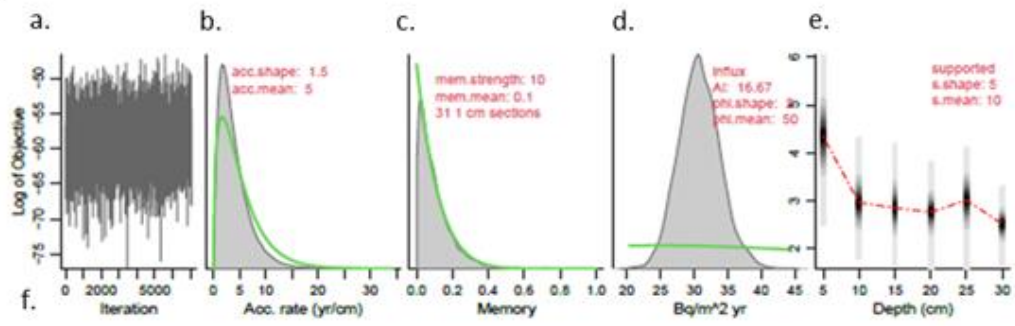
Core	6A	6A	6A	6A	6A	6A	6A	6A	6A	6A	6A	6A	6A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4A	4B	4B	4B				
Strat	0	1	2	3	4	5	6	7	8	9	10	11	12	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	0	5	10									
e																																															
Date	201	201	200	199	198	198	198	197	196	196	196	195	195	201	201	201	201	200	200	199	199	199	198	198	198	198	197	197	197	197	197	196	196	196	195	201	200	196									
S	8	1	3	5	7	3	0	5	9	5	1	8	4	8	7	3	0	6	2	8	5	2	9	6	4	1	9	7	5	3	1	8	4	2	9	8	2	3									
N	41	285	130	140	704	612	800	627	102	742	970	717	471	5	169	199	177	284	195	315	265	540	710	713	672	295	213	151	116	259	375	446	452	450	387	188	621	881									
			7	1																																											

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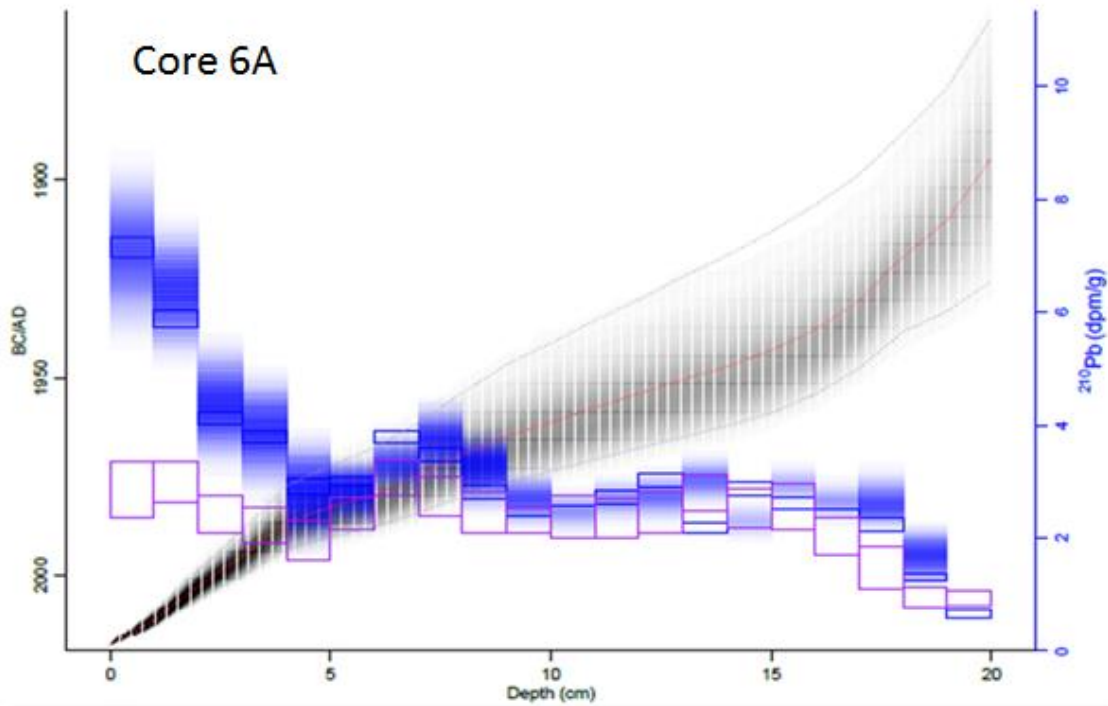
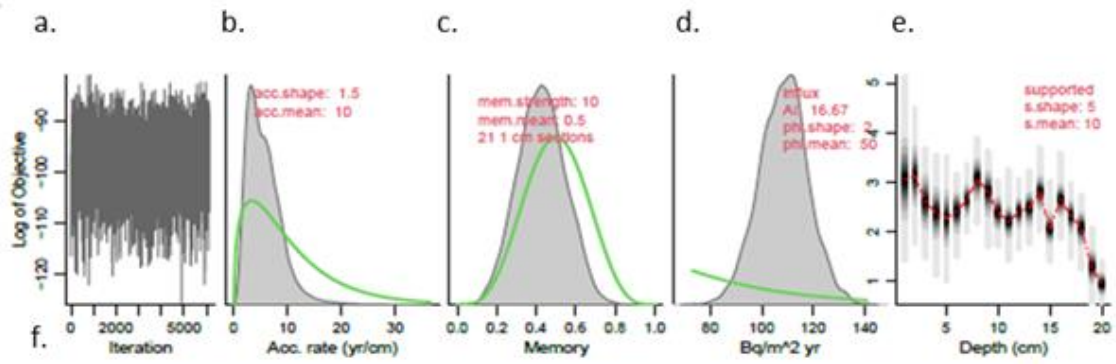
Supplementary Material 2. Age-depth model from Río Lagartos cores derived using Plum (rPlum). Figures A. Core 4A. Figures B. Core 4B and Figures C. Core 6A, a) log of objective to check the convergence of the method, panels b) c) and d) contain the model's parameters represented by their prior (in green) and posterior (in gray) distributions, b) accumulation rate, c) memory of the model, d. Influx of  $^{210}\text{Pb}$ , e. Supported activities of  $^{210}\text{Pb}$  (from  $^{226}\text{Ra}$  measurements), estimated by Plum, f. Resulting age-depth model with a red dashed line and its 95% confidence intervals. Blue bars are  $^{210}\text{Pb}$  and red bars are  $^{226}\text{Ra}$  profiles, which were used by Plum to infer the unsupported  $^{210}\text{Pb}$  in each sample.



B.



C.



Supplementary Material 3. Comparison of Molluscs fauna inventories between Gonzalez *et al.* (1991) and Suárez-Mozo *et al.* (2023) in Río Lagartos coastal lagoon.

ScientificName_accepted WoRMS	Gonzalez-Solis (1988) and (1991)	Present-day Suárez-Mozo et al. (2023)	Core historical assemblages
<i>Acteocina canaliculata</i>			1
<i>Ameritella sybaritica</i>		1	
<i>Anadara notabilis</i>	1		
<i>Anadara secernenda</i>	1		
<i>Anadara secticostata</i>	1		
<i>Anatina anatina</i>	1		
<i>Angulus</i> sp.			1
<i>Angustassiminea succinea</i>			1
<i>Anodontia alba</i>	1	1	
<i>Anomalocardia puella</i>	1	1	1
<i>Anomia simplex</i>	1		
<i>Arca zebra</i>	1		
<i>Argopecten gibbus</i>	1		
<i>Astyris lunata</i>			1
<i>Atrina rigida</i>	1		
Pyramidellidae sp.2			1
<i>Bittium varium</i>			1
<i>Blauneria heteroclita</i>			1
<i>Bostrycapulus aculeatus</i>	1		
<i>Brachidontes exustus</i>		1	1
<i>Brachidontes modiolus</i>	1		
<i>Bulla occidentalis</i>		1	1
<i>Bulla striata</i>	1		
<i>Caecum</i> cf. <i>floridanum</i>			1
<i>Caecum</i> cf. <i>textile</i>			1
<i>Caecum donmoorei</i>		1	1
<i>Caecum pulchellum</i>			1
<i>Calliostoma jujubinum</i>	1		
<i>Cardites floridanus</i>	1	1	
<i>Cerithidea</i> sp.			1
<i>Cerithideopsis pliculosa</i>	1		
<i>Cerithiidae</i> sp.		1	
<i>Cerithium atratum</i>	1	1	
<i>Cerithium eburneum</i>	1	1	1
<i>Cerithium lutosum</i>		1	
<i>Cerithium muscarum</i>	1		1
<i>Chama congregata</i>	1		
<i>Chicoreus florifer</i>	1		
<i>Chione cancellata</i>	1	1	
<i>Cochliopidae</i> sp.			1
<i>Columbella mercatoria</i>	1		
<i>Crassinella</i> sp.		1	

<i>Crepidula convexa</i>		1	1
<i>Crepidula plana</i>	1		
<i>Crepidula</i> sp.			1
<i>Crucibulum auricula</i>	1		
<i>Ctena orbiculata</i>		1	
<i>Cumingia sinuosa</i>			1
<i>Cymatium femorale</i>	1		
<i>Dallocardia muricata</i>	1		1
<i>Dendropoma</i> sp.			1
Ellobiidae sp.			1
<i>Dinocardium robustum</i>	1		
<i>Diodora cayenensis</i>	1		
<i>Dosinia concentrica</i>	1		
<i>Dosinia</i> sp.			1
<i>Elachisina floridana</i>			1
<i>Eulithidium adamsi</i>		1	
<i>Eulithidium</i> sp.			1
<i>Eurytellina alternata</i>	1		
<i>Eurytellina punicea</i>	1		
<i>Evalea</i> sp.			1
<i>Fasciolaria tulipa</i>	1		
<i>Ficus ficus</i>	1		
<i>Fulguropsis pyruloides</i>	1		
<i>Fulvia laevigata</i>	1		
<i>Gemma gemma</i>	1		
<i>Gouldia cerina</i>			1
<i>Granulina</i> sp.		1	1
<i>Haminoea</i> cf. <i>elegans</i>			1
<i>Haminoea succinea</i>		1	1
<i>Henrya henryi</i>		1	
<i>Henrya</i> sp. 1			1
<i>Japonactaeon punctostriatus</i>			1
<i>Laciolina magna</i>	1		
<i>Laevicardium mortoni</i>			1
<i>Laevicardium serratum</i>			1
<i>Lamarcka imbricata</i>	1		
<i>Lasaeidae</i> sp.		1	
<i>Linatella caudata</i>	1		
<i>Lindapecten muscosus</i>	1		
<i>Lithopoma phoebium</i>	1		
<i>Lucinidae</i> sp.			1
<i>Lucinisca nassula</i>		1	
<i>Lyonsia</i> sp.		1	
<i>Macoma cerina</i>		1	
<i>Macoploma extenuata</i>			1
<i>Macoploma tenta</i>		1	
<i>Macrostrombus costatus</i>	1		
<i>Mactrotoma fragilis</i>	1		
<i>Megapitaria maculata</i>	1		



<i>Meioceras nitidum</i>			1
<i>Meioceras nitidum</i>		1	
<i>Melampus coffea</i>	1		
<i>Melampus</i> sp. 1			1
<i>Melampus</i> sp. 2			1
<i>Melongena corona</i>	1	1	1
<i>Mercenaria</i> <i>campechiensis</i>	1		
<i>Mercenaria mercenaria</i>	1		
<i>Merisca</i> sp.		1	
<i>Mitrella antares</i>		1	
<i>Modiolus americanus</i>	1		
<i>Modiolus squamosus</i>	1		
<i>Modulus modulus</i>	1	1	1
<i>Musculus lateralis</i>		1	1
<i>Nassarius</i> sp.			1
<i>Nodipecten nodosus</i>	1		
<i>Odostomia laevigata</i>		1	
<i>Odostomia</i> <i>pocahontasae</i>			1
<i>Odostomia</i> sp.			1
<i>Olivella minuta</i>			1
<i>Olivellinae</i> sp.			1
<i>Parastarte triquetra</i>		1	1
<i>Parvilucina crenella</i>		1	1
<i>Pedipes</i> sp.			1
<i>Petalconchus erectus</i>	1		
<i>Phrontis vibex</i>		1	
<i>Phyllonotus pomum</i>	1		
<i>Pinctata imbricata</i>	1		
<i>Plicatula gibbosa</i>	1		
<i>Polymesoda floridana</i>	1		1
<i>Polymesoda</i> sp.			1
<i>Prunum apicinum</i>		1	1
<i>Prunum labiatum</i>	1		
<i>Pteria colymbus</i>	1		
<i>Ranularia cynocephala</i>	1		
Pyramidellidae sp.1			1
<i>Sayella</i> sp.			1
<i>Schwartziella</i> <i>catesbyana</i>			1
<i>Scissula similis</i>	1		
<i>Seila</i> sp.			1
<i>Semicassis granulata</i>	1		
<i>Serratina martinicensis</i>			1
<i>Sinistrofulgur</i> <i>contrarium</i>	1		
<i>Sinum perspectivum</i>	1		
<i>Tagelus plebeius</i>	1		
<i>Tampaella mera</i>		1	
<i>Tampaella paramera</i>		1	1

<i>Tampaella tampaensis</i>			1
<i>Tonna pennata</i>	1		
<i>Trachycardium egmontianum</i>	1		
<i>Trachycardium isocardia</i>	1		
<i>Trigonostoma tenerum</i>	1		
<i>Triplofusus giganteus</i>	1		
<i>Truncatella pulchella</i>			1
<i>Turbinella angulata</i>	1		
<i>Turbo castanea</i>	1		
<i>Veneridae</i> sp.			1
<i>Vermetidae</i> sp.		1	
<i>Vermicularia knorrii</i>	1		
<i>Vitrinella</i> sp.			1
<i>Zebina browniana</i>		1	
<b>Total</b>	<b>74</b>	<b>39</b>	<b>65</b>