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Cover picture: The opalescent nudibranch, *Hermissenda opalescens*, shines like a living jewel in an underwater dreamscape of multicolored algae. (Photo: Roberto Calderón).

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Rates and socioecological drivers of mangrove forest cover loss in Honduras: a systematic review

Marco Herminio Osorto-Nuñez[1]*

CORRESPONDING AUTHOR
* E-mail: mh.osorto@ucenm.net

[1] Universidad Cristiana Evangélica Nuevo Milenio, Centro Regional Choluteca, 504-51101 Choluteca, Honduras.

ABSTRACT. In Honduras, mangrove forests have experienced considerable decline, and to date, there is no synthesis addressing forest cover loss at the national level and its drivers. The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines were used to conduct a systematic review to analyze forest cover loss in Honduran mangroves and the socioecological drivers that have influenced it over time. The literature review revealed that a total of 68,766.34 ha of mangrove forest cover were lost between 1965 and 2024. The areas most affected by deforestation were the Pacific coast of Honduras (PCH), with a loss of 54,409.75 ha and an annual rate of 1.51%, followed by the Atlantic coast of Honduras (ACH), particularly the departments of Cortés (loss: 1,377.83 ha; annual rate: 2.62%) and Gracias a Dios (loss: 10,260.23 ha; annual rate: 1.39%). Aquaculture and agriculture emerged as the main drivers, especially in the PCH (Gulf of Fonseca). On the other hand, urban development and industrialization played a predominant role in the ACH. Furthermore, the effects of climate change, particularly sea level rise, emerged as key drivers resulting in considerable mangrove losses in Cortés. The findings of this review highlight the importance of investigating national and regional variations in mangrove loss in Honduras and its underlying causes. With this information, more effective conservation measures tailored to the specific circumstances of each area can be designed to safeguard the sustainability of these valuable ecosystems.

Key words: aquaculture, agriculture, climate change, coastal development, drivers, coastal wetlands.

INTRODUCTION

Mangroves provide a unique connection between terrestrial and marine ecosystems and host a rich biodiversity of flora and fauna species that are critical to the livelihood of millions of people due to their ecological and economic importance (McKee et al. 2007, Bhowmik et al. 2022, Moore et al. 2022, Hamza et al. 2024). These coastal environments provide ecological and social benefits along tropical and subtropical coasts (Lee et al. 2014, Canty et al. 2022, Moore et al. 2022). Despite their crucial role in maintaining coastal biodiversity and providing essential ecosystem services, mangroves have suffered an alarming global loss, with estimates of at least 35% since the 1960s, due to their natural fragility and the impacts of human activity (Valiela et al. 2001, Bryan-Brown et al. 2020, Moore et al. 2022). The loss of cover and resulting fragmentation have also substantially affected the provision of ecosystem services (Feller et al. 2017).

Mangroves worldwide face diverse threats ranging from natural, such as climate change encompassing sea level rise and hurricanes (Schaeffer-Novelli et al. 2016), to anthropogenic drivers such as the expansion of aquaculture and agriculture, overlogging, salt extraction, human settlements, and coastal development (Valiela et al. 2001, Canty et al. 2018). These drivers have the potential to exacerbate the rate of mangrove deforestation, which results in the loss of critical functions such as nutrient cycling, coastal protection, and habitat provision for biodiversity, as well as the release of large amounts of CO2 into the atmosphere due to the decomposition of organic matter (Lovelock et al. 2017, Alongi 2018).

Between 1980 and 2005, approximately 3.6 million ha of mangroves were lost worldwide, representing 20% of global cover (FAO 2007). Current mangrove cover is estimated at 147,359 km² across 108 countries, with net losses of around 3.5% between 1996 and 2020 (Spalding and Leal 2021, Bunting et al. 2022). Specifically, Honduras has

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suffered one of the highest losses of mangrove cover (more than 20,000 ha; Carrasco and Caviedes 2014). On the Atlantic coast of Honduras (ACH), the main drivers of mangrove deforestation have been hurricanes, agriculture, urban expansion, and tourism infrastructure (Cahoon et al. 2003, Fickert and Grüninger 2010, Recio et al. 2016, Flores-Marin 2017, Tuholske et al. 2017, ICF 2022). On the Pacific coast of Honduras (PCH), aquaculture has been the main driver, as well as logging and salt production (Stanley 1998, Chen et al. 2013, ICF 2022).

The destruction of mangroves in Honduras has had serious consequences, such as altered drainage patterns, increased saline intrusion, and depletion of fish populations in the PCH and ACH (Thornton et al. 2003, Recio et al. 2016, Maya-Jariego et al. 2023). Ultimately, this loss has exposed the coast to erosion, flooding, and damage from extreme events. For example, mangrove responses to hurricanes on the Honduran islands of Roatán and Guanaja resulted in the disturbance and alteration of regeneration patterns (Cahoon et al. 2003; Fickert 2018, 2020). On the other hand, reports indicate that the presence of pollutants affects the soil of mangrove ecosystems and limits their development (Burgos-Bennett 2011, Davila-Chuga 2021). This phenomenon has been observed in fields of the African oil palm (*Elaeis guineensis*), which contribute chemical compounds with phosphorus and nitrogen to the environment. Furthermore, the arrival of cruise ships to Caribbean islands leads to the discharge of pollutants, which disrupt mangrove ecosystems (Burgos-Bennett 2011, Doiron and Weissenberger 2014, Canty et al. 2018).

In the Gulf of Fonseca, the expansion of shrimp farming has increased land use changes and land conflicts, which have led to socioecological problems, such as deterioration of water quality, degradation of land, disappearance of seasonal lagoons, and decline in fish populations (Dewalt et al. 1996, Stanley 1998, Stonich 1992, Acharya 2002). Shrimp farming, along with demographic development, has indirectly affected mangroves through hydrological alterations caused by road construction, which modified mixing of fresh and salt water (Dewalt et al. 1996). In this regard, the objectives of this study were to identify the main drivers of mangrove deforestation in Honduras based on the scientific literature, analyze changes in historical forest cover, and assess the current status of mangrove forests.

Materials and methods

Protocol and information sources

To conduct this review, we used the guidelines established in the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) for documenting systematic literature reviews (Moher et al. 2009). The main sources used for the search were Web of Science; Scopus; Directory of Open Access Journals (DOAJ); *Red de Revistas Científicas de América Latina y el Caribe, España y Portugal* (REDALYC) (REDALYC); and Scientific Electronic Library Online (SCIELO). In addition, Google Scholar was used to collect gray literature, such as theses, technical reports, and management plans, which were incorporated into the review. Following the recommendation of Pullin and Stewart (2006), the inclusion of this type of document in systematic reviews helps reduce publication bias. The search period was from 1 January 1980 to 30 July 2024, with the objective of covering the largest amount of available evidence on the drivers of mangrove deforestation in Honduras. During this period, original articles, commentaries, books, book chapters, reports, and management plans relevant to the study were collected.

Eligibility criteria

The drivers of mangrove deforestation in Honduras were categorized using a systematic process based on a comprehensive analysis of the available scientific literature. This methodological approach allowed us to identify and classify the drivers that determine mangrove cover loss, using predefined criteria and thematic sets of keywords. The main classification criteria considered the intrinsic nature of the drivers, differentiating between those of natural origin and those of anthropogenic origin.

The initial bibliographic selection process identified 105 relevant sources, which were further filtered by applying 2 specific sets of keywords. These keyword sets were based on classifications defined by Bhowmik et al. (2022) and Hagger et al. (2022) and based on a priori knowledge of the main drivers of mangrove deforestation in Honduras.

In this sense, the identification of the main groups of drivers was based on a systemic approach that considered 2 broad categories: natural and anthropogenic drivers. The group of natural drivers refers to drivers originating in the natural environment, although they can be influenced by human activities. Conversely, anthropogenic drivers originate from human and socioeconomic actions and processes.

The first set of words included natural drivers classified into 2 main categories: "Climate Change," characterized by variations in sea level, precipitation patterns, and temperature patterns; and "Tropical Cyclones," characterized by abrupt natural disturbances, such as hurricanes, that occur mostly in the PCH region. The second set of words included anthropogenic drivers, categorized through a hierarchical process into 4 main groups: (1) aquaculture and agriculture (shrimp farming, African oil palm cultivation, and saltpeter works); (2) urbanization and development (settlement expansion, tourism infrastructure, and logging); (3) industrialization and pollution; and (4) water flow modification (water diversion, sedimentation, and hydroelectric dam construction).

In addition, the keyword set used both Spanish and English terms such as "mangroves" or "coastal wetlands," combined with location terms such as "Honduras," "Gulf of Fonseca," "Pacific," "Caribbean," "Gracias a Dios," "Colón," "Cortés," "Cayos Cochinos," "Bay Islands," and "Atlantis," as well as specific location names such as “Útila,” “Roatán,” “Guanaja,” “La Mosquitia,” “Jeannette Kawas National Park,” “Barra de Cuero y Salado,” “Bacalar Lagoon,” “Cuyamel-Omoa,” “Guaimoreto Lagoon,” “Punta Izopo,” and “Karataska Lagoon.”

Studies and datasets containing information on the main drivers of mangrove deforestation in Honduras, as well as data on historical and current mangrove cover loss, were incorporated. Articles or documents that did not meet any of the selection criteria were excluded from further analysis. Specifically, documents that were unavailable or inaccessible, as well as those that were not relevant to the research objectives, were discarded. After the manual selection process, 92 documents that met the established criteria were included and considered for detailed analysis (Fig. 1).

Regarding the above, a thorough qualitative analysis of all bibliographic documentation was conducted. However, for the quantitative analysis of mangrove cover, only 41 documents provided spatially explicit and methodologically consistent data for ACH and PCH. The number of studies reporting each of the identified drivers of change, as well as their distribution by driver group, was quantified in the seven locations where the mangrove ecosystems are located.

Data analysis process

Changes in the Honduran mangrove cover between 1965 and 2024 were analyzed, based on 41 studies reporting cover in the PCH and ACH (Fig. 1). Forest area values were compared, and changes in cover were calculated, determining losses at the national level. The average annual mangrove deforestation rate was calculated using the model proposed by the Food and Agriculture Organization of the United Nations (FAO 1996), which quantifies the annual percentage change in mangrove cover at the beginning of each period analyzed. This methodology is widely used in studies of forest ecosystem dynamics and is expressed in the following equation:

$$\mathit{Annual\ rate}\,(\%) = 1-\left(\frac{S_2^{1/t}}{S_1}\right)100\,, \qquad (1)$$

where t is the time period analyzed, S_1 is the initial mangrove surface (older) and S_2 is the final mangrove surface (more recent).

The time periods analyzed were determined through an exhaustive review of the available scientific literature, directly extracting data reported in previous studies. For the PCH, the study period spanned from 1965 to 2024 (59 years); for the ACH, the study period spanned from 1985 and 2024 (39 years). This chronological selection was based on the availability of consistent and comparable data, thus ensuring the reliability of the temporal analyses performed. The disparity in the length of the periods between the 2 regions reflects differences in the historical coverage of mangrove studies in each area.

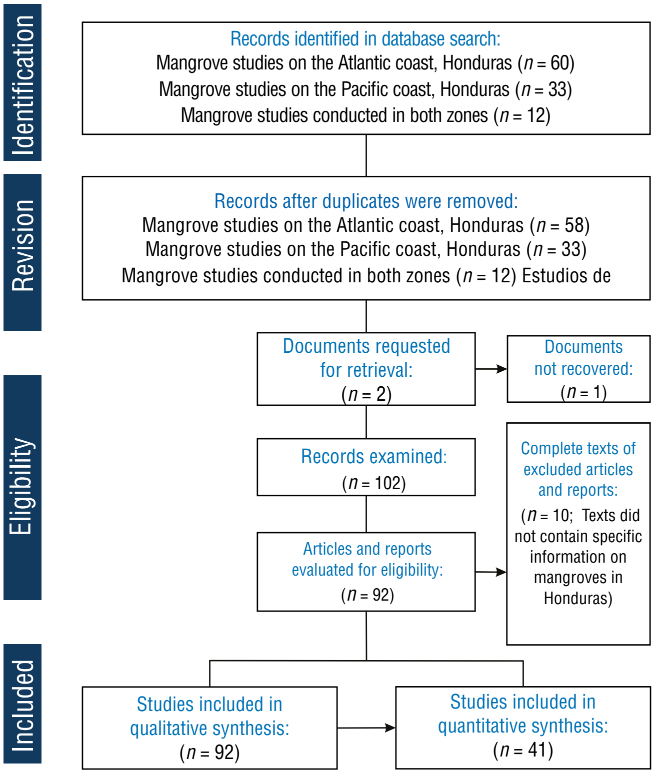

Figure 1. Flowchart based on the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines for the literature selection process in the systematic review to identify forest cover loss and its drivers in Honduran mangroves. Studies that included quantitative analyses were selected from the initial set of qualitative reviews.

To assess changes in mangrove forest cover and the conservation status of species associated with this ecosystem, data from global reference platforms were systematically integrated and analyzed. Cover dynamics were assessed using records from Global Mangrove Watch (GMW 2025) and the geoportal of the *Instituto de Conservación Forestal de Honduras* (ICF 2024). In addition, to assess the distribution and conservation status of the characteristic species of this ecosystem, we consulted the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2025) and the native distribution dataset from Plants of the World Online (POWO 2025).

Mangrove ecosystems were mapped in 7 locations in Honduras, and natural and anthropogenic drivers of deforestation were identified and categorized. The thematic maps used in this study were created through a systematic classification process specifically designed for the objectives of the analysis. The cartographic databases used as the main input were obtained from the official geoportal of the *Instituto Nacional de Conservación Forestal* (ICF) using Quantum GIS v. 3.16.10. The number of research studies addressing each driver in the 7 locations with mangrove ecosystems was documented (Table 1), and the geographic zones in which these drivers interact were determined based on the literature. Finally, both natural and anthropogenic drivers were mapped at the national level using a chord dependency diagram.

RESULTS

Spatiotemporal distribution studies developed for the loss of mangrove forest cover in Honduras

Initially, 105 documents were identified according to the established search criteria. However, 10 of these documents were deemed unsuitable and were excluded from the final analysis. Furthermore, of the initial selection of 105 documents, 12 were subsequently excluded because they did not contain relevant information, and 1 document could not be retrieved because downloading was not permitted, which resulted in a total of 92 documents that met the requirements (Fig. 1). Data related to the loss of mangrove forest cover were found to be limited, especially in the ACH region (Cortés, Colón, Atlántida, Gracias a Dios, and Cayos Cochinos).

Regarding the research on the mangrove species in the 7 localities of Honduras and their current distribution, the bibliographic review enabled the documentation of the conservation status of 8 mangrove species and their differential distribution between the coasts of the country: 7 species in the PCH and 5 in the ACH (Table 2). Note that only 1 article mentioned the presence of Tea Mangrove (*Pelliciera rhizophorae*) in Honduras; most of the previous literature did not refer to the presence of this species in the ACH, because its presence in Honduran territory was unknown until 2018 (Sutherland and Pérez 2018).

According to IUCN criteria, 5 of these species were classified as species of "least concern." It is worth noting that, although not registered for Honduras in the IUCN database, the Red Mangrove (*Rhizophora racemosa*) was documented both in POWO and in previous scientific studies (Jiménez 1987, Lizano et al. 2001, Castañeda-Moya et al. 2006). On the other hand, the Zapatero or Caballero Mangrove (*Rhizophora harrisonii*) was not evaluated by the IUCN; however, its presence in the country was confirmed in POWO. Among the threatened species, 2 had a status of vulnerable: the Bicolor Mangrove (*Avicennia bicolor*) (in the PCH) (Sanchez-Paez 2000, Castañeda-Moya et al. 2006) and *P. rhizophorae* (in ACH) (Sutherland and Pérez 2018).

The detailed analysis of the geographic distribution, which focused on the drivers of mangrove deforestation, showed that the majority of research studies focused on 2 main areas: the Gulf of Fonseca ($n = 44$) in the PCH and the Bay Islands ($n = 33$) in the ACH. Research has primarily focused on the Gulf of Fonseca due to its location as the epicenter of anthropogenic mangrove deforestation in Honduras.

Studies in the Bay Islands have focused on land-use changes due to urbanization, coastal development, and the impacts of tourism. Abundant research has been conducted in this region due to the presence of the second-largest coral reef in the world, which is a UNESCO World Heritage Site (Tuholske et al. 2015). Diving activity, real estate development, and tourism infrastructure have been the subject of studies focused on understanding their effects on the

Table 1. Natural and anthropogenic drivers of mangrove deforestation on the Pacific coast of Honduras (PCH) and on the Atlantic coast of Honduras (ACH). Values refer to the number of documents reviewed.

	Anthropogenic drivers				Natural drivers	
Site	Aquaculture and agriculture	Urbanization and development	Industrialization and pollution	Flow modification	Climate change	Tropical cyclones
PCH						
Valley and Choluteca (Gulf of Fonseca)	44	11	7	8	3	6
ACH						
Cortés	12	13	8	7	5	5
Atlántida	12	12	7	9	6	5
Colón	6	9	8	7	4	5
Gracias a Dios	9	4	2	7	6	3
Bay Islands	2	17	10	17	8	14
Cayos Cochinos	1	5	3	4	6	5
Total	86	71	45	59	38	43

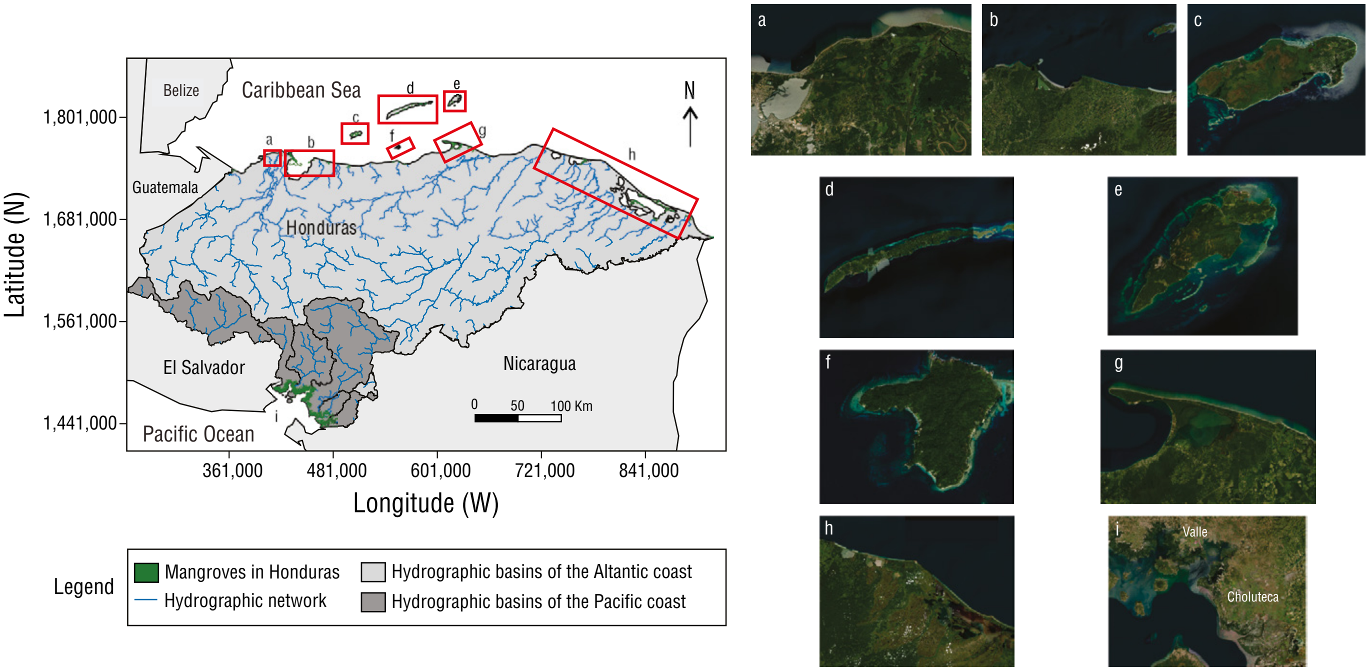

Figure 2. Distribution of mangroves in 7 locations along the Pacific coast of Honduras (PCH) and the Atlantic coast of Honduras (ACH): Cortés (**a**), Atlántida (**b**), Útila (**c**), Roatán (**d**), Guanaja (**e**), Cayos Cochinos (**f**), Colón (**g**), Gracias a Dios (**h**), and Gulf of Fonseca (**i**) (Monserrate 2017).

environment. This has highlighted the growing interest of the scientific community and policymakers in understanding the protective role that mangrove forests and reefs play in the face of the impacts of climate change and human activities (Cahoon et al. 2003; Lebigre et al. 2003; Canty 2007; McKee et al. 2007; Vanselow et al. 2007; Fickert and Grüninger 2010; Doiron and Weissenberger 2014; Tuholske et al. 2017; Fickert 2018, 2020). Regarding the distribution of studies in Honduras, 13% (n = 12) covered research in all locations where mangroves are found (Fig. 3).

Historical and current loss of mangrove forest cover in Honduras

In Honduras, the loss of mangrove forest cover has exceeded 20,000 ha, with annual deforestation rates of 1.27%. Approximately 52% of the mangroves that once existed in Honduras have disappeared. Marked variability in deforestation rates was recorded along the PCH, with a particularly high impact in the Gulf of Fonseca (Fig. 4; Table 3). In this region, the mangrove deforestation rate reached 1.51% per year, similar to the value observed in Gracias a Dios (1.39% per year), but lower than that recorded in Cortés (2.62% per year).

The main changes in land use that have led to mangrove replacement were identified based on the literature. In the PCH, shrimp farming and salt farms emerged as the most important land uses, as did the presence of other types of crops and urbanized areas. On the other hand, in the ACH, conversion to agriculture was important at the regional level. In Gracias a Dios, livestock and agricultural land and agroforestry occupied considerable areas. The towns of Atlántida, Colón, and Cortés, African palm fields covered large areas that, along with urban and industrial areas, dominated land use. It is important to mention that numerous hydroelectric plants were located in these towns, which have caused sediment retention and, consequently, coastal erosion (Carrasco and Caviedes 2014). In the Bay Islands, cultivated fields also occupied large areas, especially in Útila. Urbanized areas were larger in Roatán, where coastal development occurred as a result of the tourism industry (Figs. 5, 6).

Socioecological drivers of mangrove deforestation in Honduras

The spatial patterns of natural and anthropogenic drivers varied markedly between the ACH and PCH regions. In the Bay Islands, deforestation was primarily associated with coastal tourism development and hurricane disturbances (Fickert 2018, 2020); in the continental areas of the ACH and PCH, aquaculture, agriculture, and urban expansion predominated (Fig. 7). These findings were consistent with the reviewed literature, which identified human activities as the most significant drivers of mangrove loss. The interaction between natural and anthropogenic drivers suggests a negative feedback scenario, where environmental disturbances

Table 2. Number and distribution of mangrove species present on the Pacific coast of Honduras (PCH) and on the Atlantic coast of Honduras (ACH). The Valle and Choluteca sites together are considered the Gulf of Fonseca.

		PCH	ACH					
Family	Species	Valley and Choluteca (Gulf of Fonseca)	Gracias a Dios	Atlántida	Colón	Cortés	Bay Islands	Cayos Cochinos
Rhizophoraceae	*Rhizophora mangle*	x	x	x	x	x	x	x
	Rhizophora racemosa	x						
	Rhizophora harrisonii	x						
Combretaceae	*Laguncularia racemosa*	x	x	x	x	x	x	x
	Conocarpus erectus	x	x	x	x	x	x	x
Acanthaceae	*Avicennia germinans*	x	x	x	x	x	x	x
	Avicennia bicolor	x						
Tetrameristaceae	*Pelliciera rhizophorae*		x					

increase ecosystem susceptibility to anthropogenic pressures, thus accelerating its degradation.

DISCUSSION

Decrease in mangrove cover in Honduras

The literature on mangrove cover changes in Honduras (41 studies) spanned 5 decades for the PCH and 3 for the ACH, revealing a significant human footprint. Sixty-one percent of the mangroves were found in the PCH (Gulf of Fonseca) and the remaining 39% were distributed in the ACH (Cortés [1.19%], Atlántida [6.45%], Colón [5.12%], Gracias a Dios [22.42%], and Bay Islands [3.79%]). Of the literature reviewed, 62% studied ACH localities, which experienced a 38% loss of the national historical mangrove cover (Carrasco et al. 2013a, Carrasco et al. 2013b, Rivera-Monroy et al. 2013, Carrasco and Caviedes 2014, Flores-Marin 2017, Tuholske et al. 2017, Davila-Chuga 2021, Flores-Bueso 2022, ICF 2022). This is similar to what was reported for the PCH, which experienced the greatest loss of mangroves, with a 41% decrease of the historical cover, being the highest nationwide (Sanchez-Paez and Guevara-Mancera 2000, Wilburn-King 2008, Chen et al. 2013, Carrasco and Caviedes 2014, ICF 2022).

The results revealed a 52.9% loss of Honduran mangroves in recent decades (~68,766 ha), with an average annual rate of 1.27% (~1,166 ha·y^{-1}). These figures exceed the global average of annual mangrove loss (0.16–0.39%; Hamilton and Casey 2016), highlighting Honduras as a deforestation hotspot. Of the 52.9% mangrove loss, 79% corresponds to the Gulf of Fonseca mangroves in the PCH and the remaining 21% to the ACH mangroves (Table 3). At the national level, mangrove cover was reduced by 54,409.75 ha in the PCH at a rate of 922.19 ha·y^{-1} and 14,356.59 ha in the ACH at a rate of 368.11 ha·y^{-1} (Table 3).

The loss of mangroves in Honduras reflects a more accelerated environmental crisis than in other tropical countries. For example, mangrove deforestation in the Colombian Pacific was estimated at a loss of 14% between 1984 and 2020 (Murillo-Sandoval et al. 2022), whereas in Honduras the loss was 52.9%. This discrepancy could be explained by the lack of effective conservation policies, such as those implemented in Brazil, where the establishment of protected areas has mitigated the pressures causing mangrove deforestation (Figueiroa et al. 2016, Medeiros et al. 2023). The data from Gracias a Dios (1.39% annually) are also worrying, as this region is home to the second largest mangrove area in the country. Here, mangrove degradation has been attributed to illegal logging and the expansion of livestock ranching (Burgos-Bennett 2011, Davila-Chuga 2021), which are recurring problems in areas with poor environmental governance (Supplementary Material Figure S7).

In general, the main drivers of mangrove loss in Honduras are anthropogenic: aquaculture in the PCH and agriculture

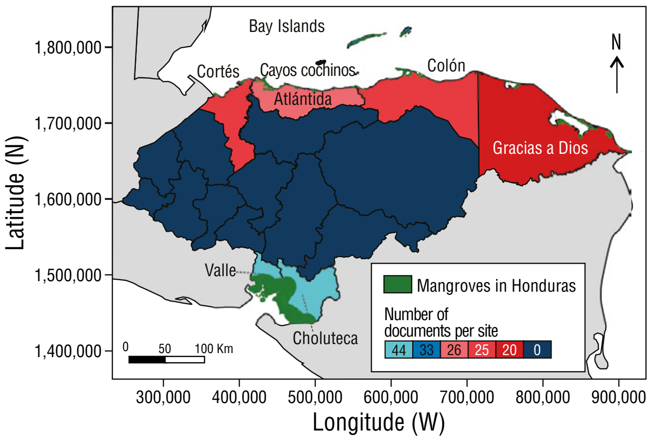

Figure 3. Geographic distribution of research studies of Honduran mangroves associated at the locality level.

and infrastructure in the ACH. Climate change and extreme events are also important factors, especially in Cortés and the Bay Islands (Cahoon and Hensel 2002, Vanselow et al. 2007, Fickert and Grüninger 2010, Fickert 2018, Fickert 2020). The loss of mangrove area due to human activities implies a reduction in ecosystem services specific to each location. If deforestation continues at an accelerated rate, the negative impacts on biodiversity and the provision of environmental services will be more evident.

Environmental drivers

Climate change

Of the literature reviewed, 9% identified environmental factors as drivers of mangrove decline in Honduras, including coastal erosion, increased salinity, ocean acidification, temperature changes, rising sea levels, and variations in precipitation (Table 3). These factors, associated with climate change, affect the hydroperiod, regeneration, growth, composition, and spatial distribution of mangroves (Field 1995). For example, rising temperatures have been found to increase water vapor deficits, reducing mangrove growth and survival (Adame et al. 2021). Furthermore, rising sea levels have caused flooding and erosion, which increases mangrove vulnerability. On the other hand, reduced precipitation has been observed to decrease photosynthesis, productivity, and reproduction, whereas high rainfall causes flooding that deposits sediments, suffocating mangroves. These changes in sedimentation, turbidity, and salinity significantly influence the growth and distribution of mangroves, which highlights the complex interaction between climatic factors and the health of these ecosystems (Friess et al. 2022).

Sea level rise has been identified as the primary threat to mangroves in Honduras. Studies in Puerto Cortés and Puerto Castilla revealed increases of 8.9 mm·y^{-1} and 3.2 mm·y^{-1}, respectively, between 1940 and 1970 (Aubrey et al. 1988, Ellison and Farnsworth 1996). A USAID study (2012) confirmed these data, showing increases of 9.2 mm·y^{-1} in Puerto Cortés (1945–1975) and 3.1 mm·y^{-1} in Puerto Castilla (1954–1970). In Cuyamel-Omoa, mangrove cover showed an 80% decrease as a result of the impact of waves (ICF 2012). The most affected areas were Trujillo (Colón), Brus Laguna (Gracias a Dios), and the Bay Islands, with increased coastal erosion, except in the Bay Islands (USAID 2012, Carrasco et al. 2013a, b).

These locations, with the exception of the Bay Islands, have shown an increased coastal erosion (Carrasco and Caviedes 2014). In the Gulf of Fonseca, sea level has risen approximately 50 cm, leaving the coast vulnerable due to mangrove deforestation (Fig. 8) (Del Cid-Gómez and Cáceres 2017). Although mangrove loss due to climate change in Honduras has not been quantified, it is likely significant, which creates the need for further research in this area.

Tropical cyclones

Honduran mangroves are particularly vulnerable to tropical cyclones due to their geographic location. These events affect mangroves through sediment deposition, wind damage, and submersion (Krauss and Osland 2020). Ten percent of the literature mentioned the impact of hurricanes, especially in the Bay Islands. Historically, 101 tropical storms and hurricanes have affected Honduras. Hurricane Mitch in 1998 was particularly devastating, causing significant losses in the mangroves of Trujillo, Colón. In the Bay Islands, especially Roatán and Guanaja, stands of mangrove trees with high mortality have been observed as a result of substrate collapse from the breakdown of mangrove peat (Doyle et al. 2002, Cahoon et al. 2003). Hurricane Mitch reduced mangrove forests by 37% in Roatán and by 97% in Guanaja, demonstrating the

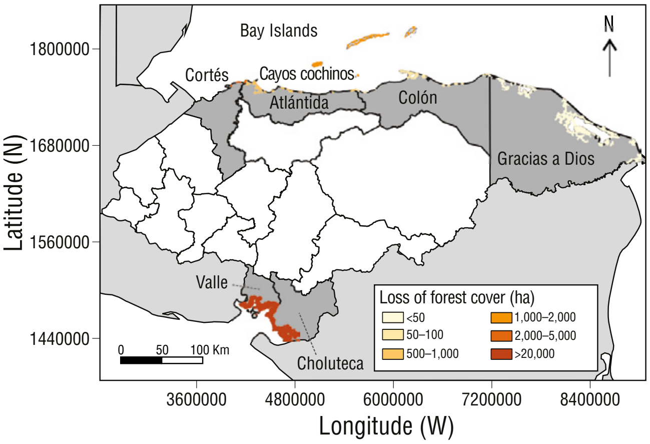

Figure 4. Historical loss of the forest cover of Honduran mangroves by locality. Together, the localities of Valle and Choluteca are considered the Gulf of Fonseca.

Table 3. Rates of forest cover loss of mangrove forests on the Atlantic coast of Honduras (ACH) (1985–2024) and Pacific coast of Honduras (PCH) (1965–2024).

Coast	Region	Historical surface (ha)	Current surface (ha)	Area of lost mangrove (ha)	Annual deforestation rate
PCH	Valle y Choluteca (Golfo de Fonseca)	91,800.00	37,390.25	54,409.75	1.51%
ACH	Islas de la Bahía	2,874.00	2,318.72	555.28	0.54%
	Gracias a Dios	23,995.00	13,735.00	10,260.23	1.39%
	Atlántida	4,464.91	3,950.11	514.80	0.31%
	Colón	4,782.00	3,134.00	1,648.45	1.05%
	Cortés	2,104.00	726.17	1,377.83	2.62%
	Total	130,019.91	61,253.57	68,766.34	1.27%

*For the mangroves of Cayos Cochinos, there are no historical or current estimates of forest cover. Only a density of 1,140 trees per hectare has been estimated (García-Salgado et al. 2006) (Supplementary Material, Figure S6).

severe impact of these events on mangrove ecosystems (Supplementary Material Fig. S1) (Cahoon et al. 2003; Fickert 2018, 2020; Canty et al. 2022).

Although Hurricane Mitch did not directly impact the Gulf of Fonseca, mangroves were affected by debris flows and sediment accumulation (McKee and McGinnis 2003). Some were buried under layers of sediment up to 100 cm deep, carried by river floods from the upper basin (Cahoon and Hensel 2002). In the central Gulf, there was massive tree mortality, canopy damage, and changes in elevation and soil properties (Cahoon et al. 2003, Hensel and Proffitt 2003, McKee and McGinnis 2003). In the southern region, a storm surge caused flooding and sediment deposition (Rivera-Monroy et al. 2002). In general, little attention has been paid to the consequences of hurricanes on mangroves, and the reduction in forest cover in ACH and PCH has not been quantified. The increased frequency of these events could limit the recovery time of mangroves, increasing the risk of permanent loss.

Anthropogenic drivers

Aquaculture and agriculture

Aquaculture and agriculture are the main drivers of mangrove deforestation, with aquaculture accounting for 47% of global mangrove loss in the 20th century (Friess et al. 2019, Goldberg et al. 2020, Bhowmik et al. 2022). In the PCH, the expansion of shrimp farming and saltpeter works has been the main cause of mangrove loss since 1965. In 1973, the expansion of shrimp farms resulted in the loss of 2,132.5 ha of dense forests (Dewalt et al. 1996). Between 1982 and 1992, shrimp farming occupied 11,515 ha, including 4,307 ha of mature, stressed, or dwarf mangroves (Ramirez 1994, Páez-Osuna 2001). Wilburn-King (2008) reported a loss of 3,733 ha of mangroves between 1989 and 1998 due to the production of salt and shrimp. Chen et al. (2013) reported that approximately 11.9% of mangroves were lost between 1985 and 2013, primarily due to shrimp farming (Supplementary Material Fig. S2) (Recio et al. 2016, Son et al. 2017). These data demonstrate the significant impact that human activities, such as shrimp farming, have had on the decline of mangrove forests over time in the PCH. Furthermore, sites in this area are considered to be particularly susceptible to the effects of climate change and human activities (Bhomia et al. 2016, Maya-Jariego et al. 2023).

Agricultural intensification has contributed to mangrove loss in the ACH. In particular, the main threats included the development of African palm plantations, land use change to pasture, and agriculture, which occupy approximately 140,000 ha, much of which used to be wetlands (Carrasco and Caviedes 2014, Flores-Marin 2017, Davila-Chuga 2021). A notable case is La Másica, Atlántida, where around 12 km² of forested wetlands, including mangroves, were lost (Carrasco et al. 2013c). In the same area, socioeconomic activities have

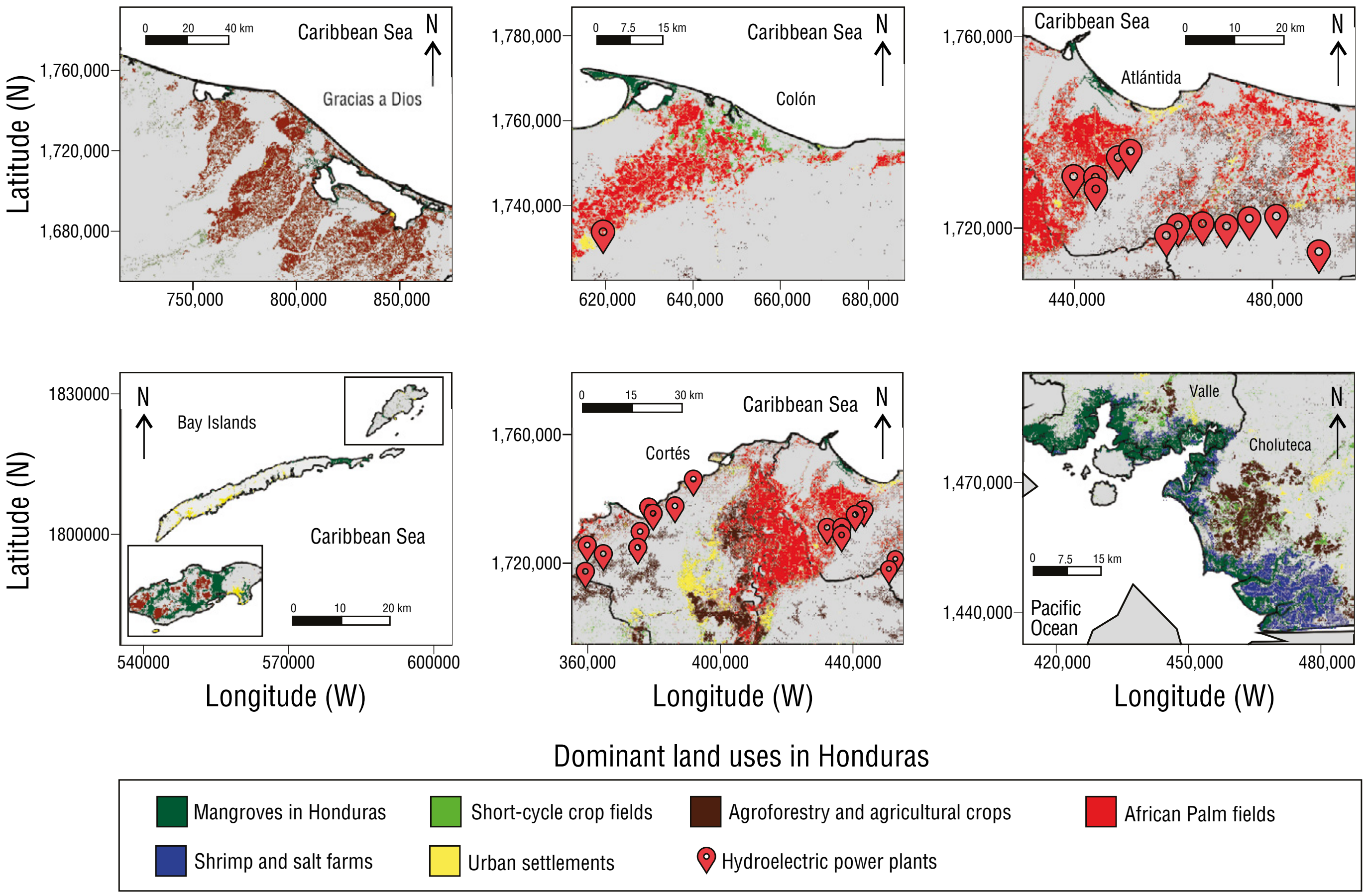

Figure 5. Dominant land uses that have affected mangrove areas on the Pacific coast of Honduras (PCH) and the Atlantic coast of Honduras (ACH) in 2024.

destroyed more than 500 hectares of mangroves. In Colón, the expansion of the African palm has led to the reduction of these forest areas; in Gracias a Dios and Cortés, livestock farming and technological agriculture have also had a negative impact (Burgos-Bennett 2011, Davila-Chuga 2021). In contrast, these activities have caused less damage in the PCH, although agriculture and aquaculture in the middle and upper basins produce pollutants that affect the development of mangrove ecosystems (Osorto-Nuñez 2022, Osorto-Nuñez et al. 2023).

Industrialization and pollution

Industrialization and pollution are key factors in the loss of mangrove cover (Zhang et al. 2014). Since 1995, organochlorine pesticides (e.g., carbofuran and propiconazole) have been detected in the Choluteca River, which flows into the Gulf of Fonseca, evidencing the damage that chemical pollutants cause to mangroves (Kammerbauer and Moncada 1998, Meyer 1999, Osorto-Nuñez 2022, Maya-Jariego et al. 2023). In the Bay Islands, discharges of organic matter from industrial waters have promoted the growth of calcareous green algae, which threaten these ecosystems. Furthermore, the cruise ships that arrive in this region have also contributed to pollution (Canty 2007, Carrasco et al. 2013d, Doiron and Weissenberger 2014). In Colón, the mining industry has caused mangrove destruction due to excessive sedimentation and the presence of heavy metals in the water and soil (Burgos-Bennett 2011). In the Sula Valley, approximately 150 of the 380 industries have produced problematic effluents that contaminate the Ulúa and Chamelecón rivers with mercury, lead, and arsenic (Marin and Hernandez 2002). Unfortunately, the accumulation of metals, such as copper and zinc, has become a global driver of mangrove deforestation (Sruthi et al. 2016, Bhowmik et al. 2022).

Urbanization and development

Of the studies reviewed, 37% indicated that urbanization and development are key drivers of mangrove deforestation in Honduras. Activities such as logging and the construction of settlements, roads, and tourism infrastructure have significantly reduced forest cover. In Roatán, between 1985 and 2015, the development of hotel infrastructure and the expansion of the airport increased the urban area by 982.8 ha, with 224.1 ha of mangroves converted to urban areas (Supplementary Material Fig. S3) (Carrasco et al. 2013d, Doiron and Weissenberger 2014, Tuholske et al. 2015, Tuholske et al. 2017). In Útila, the urban area grew from 118 ha in 2014 to 231 ha in 2021, affecting the southern mangroves (Flores-Bueso 2022). In Tela, Atlántida, tourism development has put additional pressure on mangroves (Stovall 2015). In addition, population growth and hotel infrastructure have fragmented wetlands and altered the hydrological regime, exacerbating the loss of these vital ecosystems.

The extraction of mangrove wood has had an important impact on the loss of forest cover, especially in the Gulf of Fonseca, where wood and bark are used as energy sources (Alfaro-Trejos 2011, Maya-Jariego et al. 2023). Between 1983 and 1986, the use of mangrove wood for fuel exceeded 80,000 $m^3 \cdot y^{-1}$ to 120,000 $m^3 \cdot y^{-1}$ (Jiménez 1992). From 1983 to 1989, 34,200 m^3 of firewood and 5,340 m^3 of timber were extracted, and consumption increased from 3,644 $m^3 \cdot y^{-1}$ to 4,212 $m^3 \cdot y^{-1}$ between 1986 and 1995 (Jiménez 1999, Sanchez-Paez and Guevara-Mancera 2000, CONGESA 2001). According to Dewalt et al. (1996), this represented the use of 250 to 350 ha of mangroves annually. In the Gulf of Fonseca, 85% of households relied on wood for energy and construction of housing (Supplementary Material Fig. S4). In addition, industries such as bakeries and brickyards also use wood as a primary resource. In Roatán, logging has reduced the frequency of the Buttonwood Mangrove (*Conocarpus erectus*); this activity is also carried out in Cuyamel-Omoa for domestic and commercial purposes, highlighting the impact of timber extraction on these ecosystems (ICF 2012, Carrasco and Caviedes 2014).

The expansion of human settlements and urbanization have significantly impacted mangroves in Honduras, especially in Útila (Supplementary Material Fig. S5). As observed in Atlántida, water pollution is a critical problem in Útila, where sewage contributes phosphorus to the mangroves (Carrasco et al. 2013d). In Colón, the accumulation of garbage and solid waste has severely affected these ecosystems (Burgos-Bennett 2011). In the Gulf of Fonseca, sewage discharges and solid waste accumulation have negatively impacted mangroves (Supplementary Material Fig. S4) (Maya-Jariego et al. 2023). In Cortés, settlements near Los Micos Lagoon have contaminated the soil and surface water (Carrasco et al. 2013b). Similarly, in the Bay Islands, especially in Útila, mangrove loss has been caused by sewage, logging, and the accumulation of waste from urban expansion (Carrasco et al. 2013d, Carrasco and Caviedes 2014). In Gracias a Dios, urbanization has contributed to logging and soil erosion, posing threats to mangroves (Davila-Chuga 2021). These factors highlight how urbanization has jeopardized the integrity of Honduran mangroves.

Flux modification

The modification of the water flux in the upper basin has been shown to decrease mangrove productivity (Bhowmik et al. 2022). According to projections based on previous scientific literature, dam construction in Honduras has had negative impacts on mangrove forests and has altered their ecological balance. The main consequences include sediment and nutrient retention, increased salinity in coastal areas, and the intensification of erosion processes (Morais and Pinheiro 2011). For example, in Balfate, Colón, a dam has altered the morphology and hydrodynamics of the river, which resulted in sediment retention (Carrasco and Caviedes 2014). In the Barra de Cuero and Salado Wildlife Refuge, hydroelectric projects are planned for 11 rivers, which could modify the natural hydrological regime and decrease the primary productivity of mangroves (Carrasco et al. 2013c). The Patuca III hydroelectric dam, in Gracias a Dios, could increase the salinity of the lagoons by reducing the contribution of water and sediment from the Patuca River, putting the mangroves at

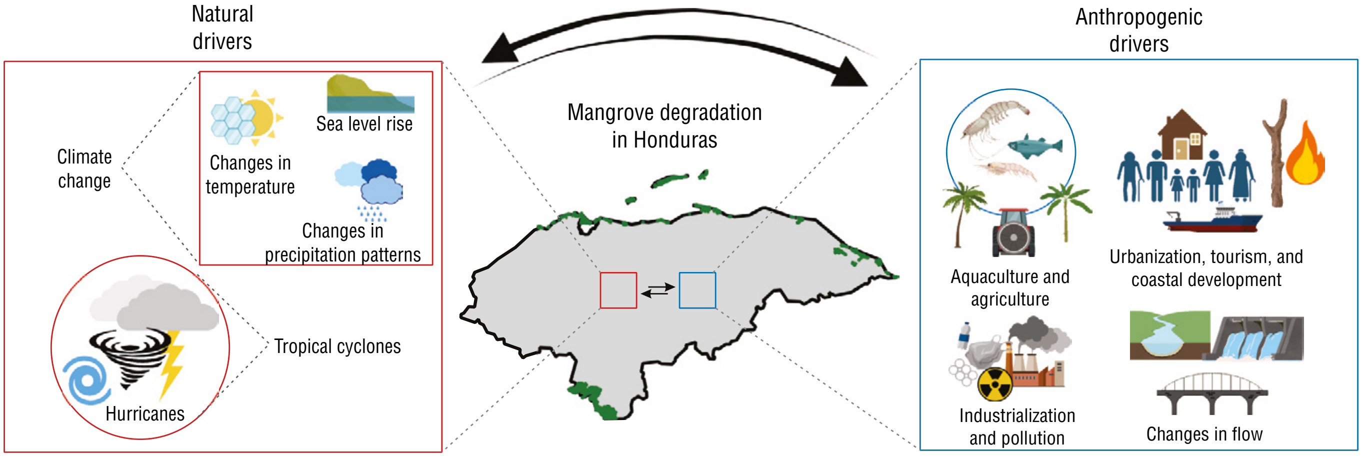

Figure 6. Group of identified natural and anthropogenic drivers of mangrove deforestation in Honduras.

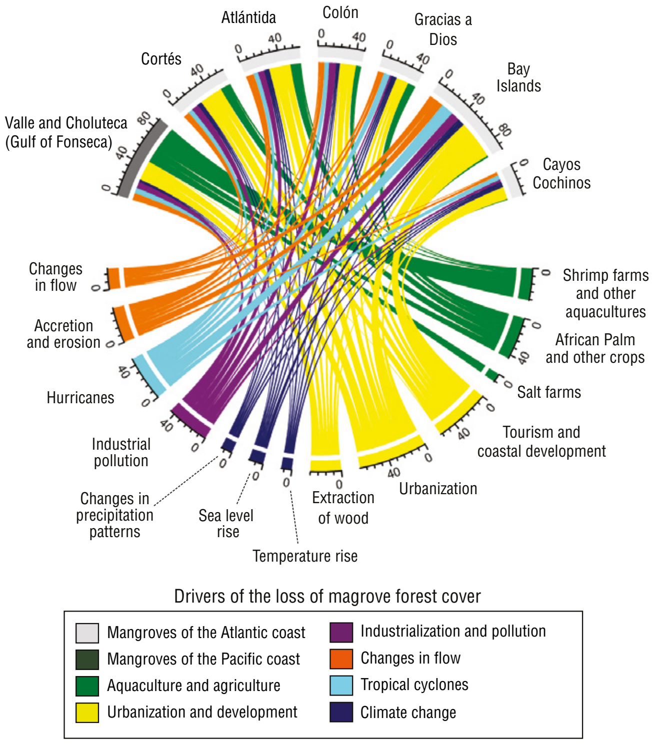

Figure 7. Chord dependency diagram among the groups and subgroups of drivers of mangrove deforestation in Honduras. The scale shows the number of studies that indicate the interaction between the driver and the location.

risk (Carrasco and Colindres 2011, Carrasco et al. 2013a). In Jeannette Kawas National Park, the hydrological regime has changed by 80% due to the channeling and draining of several rivers, highlighting the importance of considering these effects when planning hydroelectric projects to preserve these coastal ecosystems.

In general, our study, based on a synthesis of scientific literature, shows an intermediate value. The differences could reflect variations in the reference years, since the studies are not completely simultaneous, or in the spatial delimitation of the areas assessed. For example, the ICF (2024) could have incorporated recent restoration areas not accounted for in the GMW, whose version 3.0 dates from 2022. Likewise, the heterogeneity in the operational definitions of "mangrove" such as the inclusion or exclusion of associated salt marshes introduces variability.

Discrepancies in the current mangrove cover (61,253.57 ha) compared to that of the GMW (60,564 ha) and the ICF (61,639 ha) can also be attributed to methodological, technological, and temporal factors. First, the *Sistema de Información para la Gestión y Monitoreo Forestal* (SIGMOF 2024) reports that forest cover for 2024 was estimated with a declared accuracy of 92% and a margin of error of 8%, using multi-source data from the Sentinel-1 (radar) and Sentinel-2 (optical) satellites. This approach, which combines optical and radar sensors, has enabled a more robust classification in the face of adverse weather conditions (e.g., cloud cover), which could explain its slightly higher estimate.

The GMW, on the other hand, uses L-band Synthetic Aperture Radar (SAR) data, developed under the Kyoto & Carbon initiative of JAXA. This technology is notable for its sensitivity to woody biomass and its ability to monitor mangroves in areas with frequent cloud cover (Lucas et al. 2014). However, as mentioned by Bunting et al. (2018), this technology has inherent limitations in discriminating mangroves from other woody vegetation covers (especially terrestrial forests and crop fields) on continental margins, which can lead to classification errors. Furthermore, the GMW uses a canopy cover threshold of 10% to define "mangrove," whereas the ICF could apply more inclusive criteria, such as including areas undergoing regeneration.

GMW version 2.0 (Bunting et al. 2019), currently considered the global reference standard due to its spatial resolution (25 m) and temporal update, optimized its methodology by integrating Landsat optical data to improve the accuracy in the delimitation of mangrove extent. However, as demonstrated by Thomas et al. (2014, 2018), L-band SAR sensors, while optimal for detecting temporal changes, have limited capabilities for accurately classifying absolute extent, particularly in regions with complex ecotonal gradients. This technical limitation adds to the global challenges documented in mangrove datasets, which include: (1) unmapped areas due to sensor failures (e.g., scan line error in Landsat 7 ETM+), (2) uneven temporal availability of images, and (3) interference from persistent cloud cover (Spalding 2010, Giri et al. 2011, Bunting et al. 2018).

The discrepancy in the results, although showing little difference in cover compared to GMW v. 2.0 (2020) and ICF (2024), could be attributed to differences in classification algorithms and variability in the quality of input data used by the various studies found in this research. This uncertainty underscores the need to implement standardized protocols that integrate complementary technologies to improve accuracy at local scales. The findings presented in this study emphasize that, while GMW represents a significant advance in global mangrove monitoring, its application to national-scale studies requires in situ validation and specific methodological adjustments that consider the biogeographical characteristics of each region.

Conclusions

This review provides a synthesis of the drivers of mangrove forest cover loss in Honduras. The 52.9% decline in mangrove cover in Honduras over the past few decades significantly exceeded the global average rate of deforestation, positioning the country as a hotspot for mangrove loss. This severe decline, with an average annual rate of 1.27%, has been driven by a complex interplay of factors, with anthropogenic pressures emerging as the primary catalysts on both coasts. Specifically, the expansion of aquaculture in the PCH (Gulf of

Figure 8. Impact of sea level rise on the coastal infrastructure of Cedeño, Pacific coast of Honduras (PCH). Submerged infrastructure due to sea level rise (**a**) and coastal erosion labeled in red and local businesses destroyed by sea level rise (**b**).

Fonseca) and, in parallel, tropical cyclones, agricultural intensification and infrastructure development in the ACH, represent the most important threats.

It is essential to implement strict monitoring and conservation measures, focusing on the most affected areas, while prioritizing comprehensive research in data-deficient regions, such as Gracias a Dios and Cayos Cochinos, to establish an accurate baseline of the extent and condition of their mangroves. This initial synthesis quantifies loss rates and elucidates the socio-ecological drivers of deforestation, laying the groundwork for future research employing advanced remote sensing methodologies and predictive models. Combined with high-resolution multispectral remote sensing and systematic field sampling, these approaches, which enable more precise and dynamic monitoring of mangrove cover, will reduce current margins of error and generate the robust information needed for the sustainable management of these critical ecosystems. Ultimately, integrating robust conservation policies with effective environmental governance will be fundamental to mitigate anthropogenic and natural impacts and ensure the resilience and continued provision of ecosystem services that these critical ecosystems provide to coastal communities and the biodiversity of the country.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3534/420421226.

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Conflict of interest

The author declares no conflict of interest.

Data availability

Data for this study can be obtained from the corresponding author upon reasonable request.

Author contributions

Conceptualization: MHON; Data curation: MHON; Data analysis: MHON; Funding acquisition: MHON; Investigation: MHON; Methodology: MHON; Project management: MHON; Resources: MHON; Software: MHON; Supervision: MHON; Validation: MHON; Visualization: MHON;

Writing—original: MHON; Writing—review and editing: MHON.

Use of AI tools

The author did not employ any AI tools in this work.

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Ciencias Marinas (2025), 51:e3541 **Review Article**

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The use of acoustic and satellite telemetry to study elasmobranchs in Latin America: past efforts and future directions

Claudia I Vázquez-Aguilar[1], Omar Santana-Morales[2], León F Álvarez-Sánchez[3], Luis Malpica-Cruz[1,2]*

Abstract. The study of marine animal movements is crucial for understanding the diversity of oceanic ecosystems and the fundamental role of each species. Today, acoustic and satellite telemetry are non-invasive methods that is widely used to track marine animals, including elasmobranchs (sharks and rays). Despite its importance, there is no systematic review assessing the use of telemetry in elasmobranch studies in Latin America. We conducted a literature review and analyzed 106 publications, of which the majority pertained to elasmobranch studies in Mexico (*n* = 60), Brazil (*n* =16), and Ecuador (*n* = 13). The predominant focus among studies was habitat use (*n* = 94). Pop-off satellite archival transmitting (PAT or PSAT) tags and smart position and temperature (SPOT) tags were primarily used for large spatial scale studies (i.e., migration). Acoustic telemetry was better suited for tracking long-term behavior over comparatively smaller spatial scales (e.g., regional movements). While successful cases exist in the literature, challenges remain due to the high financial costs, effort to maintain collaborative equipment, and limited research output in Latin America. Our findings highlight the need to enhance the application of telemetry data for effective elasmobranch management and conservation and reflect the importance of connecting research outcomes to practical actions amid ongoing management and conservation challenges.

Key words: telemetry, habitat use, movement ecology, shark, ray, elasmobranch, management, conservation.

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Corresponding author
* E-mail: lmalpica@uabc.edu.mx

[1] Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, 22860 Ensenada, Baja California, Mexico.
[2] ECOCIMATI, A.C., 22880 Ensenada, Baja California, Mexico.
[3] Unidad de Informática Marina, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, 04510 Coyoacán, Mexico City, Mexico.

Introduction

The study of animal movement and habitat use arises from the need to understand the vast biodiversity within marine ecosystems and the fundamental role each species plays in these complex systems. Telemetry is a key tool for this purpose, as it enables detailed tracking of the movements and behaviors of animals in their natural habitats via satellite tags, depth sensors, and radio frequency systems (Hussey et al. 2015). This tool provides precise data on migration, habitat use, intra- and interspecific interactions (Lahoz-Monfort and Magrath 2021). Additionally, telemetry offers valuable information to support fisheries management, conservation, and assessments of human impacts on marine ecosystems, thereby contributing to efforts to protect animals and preserve their habitats (Crossin et al. 2017, Brownscombe et al. 2022).

The history of telemetry in aquatic animal studies dates to 1653, when Izaak Walton first reported attaching ribbon tags to the tails of juvenile Atlantic Salmon (*Salmo salar*) to track their migration following the marine phase of development. While the exact materials Walton used are unknown, it is presumed that these ribbon tags were simple and flexible labels made from paper or cloth that were designed to be visible above the water to aid in identification when the fish were recaptured (McFarlane et al. 1990, Walton and Cotton 1898). The first underwater telemetry study was conducted by Trefethen (1956), who also focused on salmonids, specifically Pacific salmon (*Oncorhynchus* spp.), and aimed to study their migration patterns and behaviors (Hockersmith and Beeman 2012). Since then, tagging methods have evolved from natural marks to spaghetti tags (McFarlane et al. 1990, Kohler and Turner 2001) and from passive synthetic tags to electronic

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tags that rely on radio telemetry, which involves recording and transmitting instrument readings (Rodgers 2001). Satellite tags have been developed to suit the unique morphological and behavioral traits of animal carriers, including fish, marine mammals, birds, and reptiles (Hussey et al. 2015).

Chondrichthyes is a class of cartilaginous fish that includes sharks, skates, and rays (96%), as well as chimeras (4%) (Bigelow 1953, Hamlet 1999). These species typically exhibit low population growth rates due to their longevity, late sexual maturity, long gestation periods, and low fecundity, making them highly susceptible to anthropogenic impacts (Hamlet 1999, Barría and Colmenero 2019). Elasmobranchs encompass a large number of predatory species, from the small rocky-reef dwelling Horn Shark (*Heterodontus francisci*) to the large-bodied, wide-ranging, migratory White Shark (*Carcharodon carcharias*). As meso- or top predators of the ecosystems they inhabit, they are natural regulators of trophic dynamics (Young et al. 2015) and important indicators of the health and productivity of marine ecosystems (Graham and Largier 1997, Croll et al. 2005, Wingfield et al. 2011). However, elasmobranchs are difficult to study given their broad habitat ranges, life cycles, and mobility that can span oceanic basins (Llopiz and Cowen 2008, Llopiz et al. 2010, Catalán et al. 2011, Llopiz and Hobday 2015).

Elasmobranch telemetry studies, which began in 1965, have provided basic information on diel patterns of movement and space utilization, depth distributions, body temperatures, swimming speeds, and physiological parameters, offering valuable insights into population status, distribution patterns, habitat use, and behavior (Stevens 1999, Hammerschlag 2011, Matley 2022, Renshaw 2023). Satellite telemetry tools, such as smart position and temperature transmitting (SPOT) tags and pop-off satellite-linked archival transmitting (PAT or PSAT) tags, have since been developed to track elasmobranch movements over large spatial scales (Weng et al. 2005, Rigby et al. 2019, Hart et al. 2021, Hicks and Lobel 2024). Smart position and temperature transmitting and PSAT tags, which are attached externally (Weng et al. 2005, Hart et al. 2021, Hicks and Lobel 2024), can provide unique and valuable information about the migratory behavior of elasmobranchs (Bonfil and O'Brien 2015) (Table 1).

Smart position and temperature transmitting tags track movement by sending a geographic message to a satellite every time a tagged fin breaks the surface of the water, along with depth and temperature data (Welch and Eveson 1999, Jewell et al. 2011, Rigby et al. 2019). However, they do not archive or transmit data when the animal is submerged, which may result in data gaps depending on surfacing behavior. Smart position and temperature transmitting tags provide relatively accurate position data (<250 m to 5 km), depending on the number of satellite connections, with a lower number of connections resulting in higher position error.

Pop-off satellite-linked archival transmitting tags are programmed to automatically release from an animal on a predetermined date or when exposed to specific depth (pressure) conditions; once released, the tags float to the surface. At the surface, the exposed antenna transmits summary data to a satellite. A full, detailed data archive can be downloaded if a tag is physically recovered. Pop-off satellite-linked archival transmitting tags record light (Welch and Eveson 1999), depth, and temperature data. Geolocation information can be estimated using the recorded light levels (dawn and dusk) based on the latitudinal position of the individual carrying the tag. However, geolocation estimates can carry errors of 60–80 km (Seitz et al. 2003). Therefore, PSAT tags are mainly used to study large-scale movements and temperature and depth preferences (Jewell et al. 2011, Rigby et al. 2019).

In recent years, acoustic telemetry has become essential to conservation efforts for endangered aquatic species (Cooke et al. 2008). It represents a useful alternative in deep, vertically stratified aquatic habitats, as acoustic telemetry allows signals to be transmitted and received even when the tagged animals are submerged (Hartog et al. 2009, Strickland et al. 2020). Acoustic telemetry, which employs tags from companies like InnovaSea (formerly VEMCO; Boston, USA), Wildlife Computers (Redmond, USA), or Lotek Wireless (Newmarket, Canada), is used mainly in elasmobranch studies to examine detailed behavior and movement patterns in specific areas. Acoustic tags are especially effective for long-term research, given that some tags (e.g., V16) can last up to 10 years, whereas most satellite tags have lifespans of <1 year. Acoustic telemetry has also been widely used to study elasmobranchs since the early 1980s (Klimley and Nelson 1984, Bessudo et al. 2011, Rodríguez-Arana-Favela 2018, Acosta-Pinzón 2023). This type of telemetry is considered a powerful tool for studying elasmobranch behavior and spatial ecology without disturbing natural activities. Once animals adapt to acoustic tags, stress is minimized (Zanella 2006), and the recorded behaviors are expected to reflect natural patterns (Digby et al. 2013, Kessel et al. 2014).

Active and passive strategies have been developed within the field of acoustic telemetry. Passive acoustic telemetry involves installing receivers in specific locations where tagged organisms are expected to pass; therefore, large-scale collaborative efforts are often needed to deploy receiver arrays with broad spatial coverage to maximize data collection (Lahoz-Monfort and Magrath 2021, Dwyer et al. 2023, Lennox et al. 2023). Active acoustic telemetry involves actively following a tagged organism from a boat using a hydrophone. Although it typically covers limited areas and temporal scales due to the logistical limitations of manual tracking, active acoustic telemetry offers the advantage of providing key information on the detailed movements of a few individuals (Bridges and Dorcas 2000, Heupel et al. 2006, Madalozzo et al. 2017).

Acoustic tagging methods have helped to assess short-term movement patterns and gather information on shark habitat use relative to environmental variables (e.g., depth and temperature). Nonetheless, employing these methods requires intensive effort and is limited globally, as it involves the in situ tracking of a single tagged animal at a time, which limits the number of animals that can be tagged and the duration of tracking efforts

Table 1. Comparisons between acoustic and satellite telemetry: primary uses and detection ranges.

Methodology	Description	Primary use	Detection range
Acoustic telemetry (active and passive)	Uses transmitters that emit sound signals detected and archived by receivers or hydrophones.	Studies of behavior and movement over short to medium time frames that are primarily focused on characterizing the movements of individuals in a detailed and specific manner within a given area.	Limited by the receiver network or receiver distance to the tagged organism, with distances typically spanning tens of kilometers.
Satellite telemetry	Uses transmitters that send data to satellites, allowing tracking over long distances.	Studies of long-term movements and migrations.	Global and limited only by battery life and satellite coverage.

and carries a high cost (e.g., boat, fuel, and personnel) (Curtis 2008, Kessel et al. 2014). Advances in transmitter miniaturization and battery life have enhanced the efficiency and longevity of passive and active acoustic methods. For instance, the smallest acoustic transmitters last a few days to weeks, while the largest can function from 3 to 10 years (Hellström 2022). Transmitter selection depends on factors such as the species of interest, the environment of the study site, and the research objectives (Baker et al. 2019) (Table 2).

Some countries, such as the United States, Australia, and South Africa, stand out for their research on the behavior and movement patterns of elasmobranchs using different types of telemetry (Heithaus et al. 2007, Yeiser et al. 2008, Jewell et al. 2011, Werry et al. 2012, Chapple et al. 2015, Hussey et al. 2015, Bruce et al. 2019). Previous studies have focused on the ecology, physiology, behavior, habitat use, and connectivity between oceanic and coastal systems of individual organisms (Heupel et al. 2006, Espinoza et al. 2011, Werry et al. 2012, Becker et al. 2015) and have aimed to integrate their findings into policy and management strategies, including the design of marine protected areas (MPAs) (Lombard et al. 2007). They have also been performed to observe the physical structure of the oceans of the world using the sensors embedded in acoustic tags (Pauthenet et al. 2018).

In Latin America, the earliest study using passive acoustic telemetry to track elasmobranchs was conducted by Klimley and Nelson (1984) and focused on evaluating the diel movement patterns of the Scalloped Hammerhead (*Sphyrna lewini*) at El Bajo Espíritu Santo in Mexico. In that study, the authors tracked the movements of 13 tagged sharks, revealing their consistent swimming along the seamount ridge during the day and their rhythmic departures and returns to the area. This approach highlights the advantages of using passive acoustic tracking as a remote monitoring method. In particular, animal behavior is undisturbed by the presence of researchers while the sampling effort is increased across time and space, thereby enhancing the probability of species detection (Madalozzo et al. 2017). Moreover, passive acoustic tracking permits organisms to be monitored at different times and over extended sampling periods, making it particularly useful for revealing activity patterns across daily and seasonal cycles (Digby et al. 2013).

Both satellite and acoustic telemetry have proven effective for studying animal movements and behavior, but each method has specific limitations. For instance, satellite tags may be expensive, have relatively low data resolution depending on the transmission frequency, and require the animal to surface (e.g., SPOT tags). In contrast, acoustic telemetry is constrained by its detection range and need for receiver infrastructure in situ, which limits its effectiveness in remote or deep-water habitats. Several authors have recommended using hybrid transmitters or combining multiple telemetry technologies within the same study to overcome these limitations and provide a more comprehensive understanding of animal movements and behavior (Brien et al. 2010, Calverley and Downs 2015, Baker et al. 2019).

Despite its importance, no systematic review has assessed the current use of telemetry in elasmobranch studies in Mexico and Latin America (Kohler et al. 2012). This review provides an overview of how telemetry has been used in elasmobranch studies in Latin America, highlights current issues surrounding its use and challenges to its broader implementation (e.g., costs, output, and focus), and examines the extent to which it has contributed to elasmobranch management and conservation.

Materials and methods

Systematic review

We conducted a literature review following the PRISMA (Preferred Reporting Items for Systematic Reviews and

Table 2. Differences between the most commonly used acoustic and satellite tags to track elasmobranchs in Mexico and Latin America.

Tag type	Smart position and temperature tags (SPOT)	Pop-off satellite archival transmitting tags (PAT or PSAT)	Acoustic tag
Location accuracy	Highly precise and provides accurate real-time locations every time the animal surfaces.	Less precise and more prone to error than SPOT and estimates location based on solar light.	Highly precise, depending on the density of the receiver network, and provides accurate locations when the animal is within the range of the hydrophones.
Battery life	Relatively short (weeks to months) due to high energy consumption from frequent data transmissions.	Relatively long (months to years) given that transmission occurs only when the tag is released and reaches the surface.	Long (several years) due to the low energy consumption of acoustic transmitters and infrequent transmissions.
Attachment method	Tags are drilled into the dorsal fin of the shark and remain fixed until the battery depletes.	Tags are attached to the animal and are released after a predefined period, with the collected data sent to the satellite once the tag reaches the surface.	Transmitters are attached to the animal, and receivers are deployed in the study area, typically on the seafloor or on buoys.
Transmission frequency	Frequent (every time the animal surfaces).	Transmits data only upon release or when breaking the surface of the water, thus conserving battery life.	Variable given that transmitters emit signals periodically, and receivers capture these signals when the animal is within range.

Meta-Analyses) guidelines (González-de-Dios et al. 2011), which involved following a standardized review protocol using specific search codes as eligibility criteria (e.g., elasmobranchs, Latin-American works, languages, or publication status) (Moraga and Cartes-Velásquez 2015). We looked for primary and gray literature of studies involving only elasmobranchs conducted in Latin America that were published in English, Spanish, or Portuguese. An electronic search code (elasmobranchs OR elasmobranchii AND acoustic telemetry OR acoustic tracking AND spot OR pat AND LATAM) was developed, and 34 databases and repositories were searched (Supplementary Material Table S1).

Data extraction

The information was manually downloaded and systematized in a spreadsheet, in which each article was assigned an identification code and details, such as author names, publication year, study location, tag, species, and approach, were recorded. Publications that did not specify the type of tagging method, species, or family of the specimen; those conducted outside Latin America; or those focused on fish other than elasmobranchs were excluded from the review. After including all documents in the spreadsheet, the studies were filtered by manually reviewing each criterion to ensure the quality of the information.

Classification of information

First, we classified the studies based on species, country, publication year, and the type of telemetry employed. Additionally, publications were classified based on whether they were gray or primary literature. Also, in studies that addressed more than one species, telemetry use was evaluated for each species individually. We also ensured no studies were repeated, given that some studies were first reported as gray literature and later published as primary literature. Lastly, the results from each article were analyzed by comparing their objectives, methods, and outcomes. The approach and objective of each article were synthesized into the following categories: habitat use, ethology, animal welfare, population dynamics, trophic ecology, tag effects, fisheries interactions, and management and conservation (Table 3).

The habitat use category was the predominant approach and encompassed a wide range of ecological and biological aspects, including distribution patterns and site fidelity. Kirk (2018) defined habitat use as "the way an animal uses or consumes a collection of physical and biological resources." Following this definition, most telemetry studies of elasmobranchs could reasonably be classified under the habitat use category. However, to avoid redundancy and better reflect the primary scientific contribution of each study, we categorized each article based on its primary objective or direct application, even if the study could be classified into secondary categories based on information in the title or text. For example, if a study on movement patterns aimed to analyze a specific behavior, such as hunting, feeding, or reproduction, it was classified under the ethology category rather than the habitat use category, as a behavioral interpretation was its core focus. More specifically, when movement data were used primarily to investigate feeding behavior or trophic position, the study was classified under the trophic ecology category, which we included to highlight the emerging use of telemetry in this ecological subfield.

A similar rationale was applied to the management and conservation category. Although most reviewed articles referred to conservation goals, in practice, only a few demonstrated direct applications of their findings to conservation policies or species management. Therefore, only studies whose results were clearly linked to concrete management actions were included in this category. For instance, the study by Santana-Morales et al. (2021) was the only one to demonstrate a direct application of telemetry data to the development or implementation of species management policies (Table 3). Data visualizations were created using the R package 'ggsankey' (Sjoberg 2021) in the R programming environment v. 3.2.4 (R Core Team 2018).

RESULTS

We analyzed a total of 106 scientific publications that used both acoustic and satellite telemetry to study elasmobranch populations. The publications included scientific articles from the primary literature (*n* = 79), as well as undergraduate theses, graduate theses, and technical reports of Natural Protected Areas from the gray literature (*n* = 27). Of these, 20 studies reported organisms that were tagged or tracked within the geographic boundaries of Southern California (*n* = 13); Florida (*n* = 5); temperate northeastern Atlantic, temperate northwestern Atlantic, and southwestern Atlantic (*n* = 1); and Indo-Pacific (*n* = 1), with some organism movements falling within Latin American seascapes (Weng et al. 2007, Domeier and Nasby-Lucas 2008, Medellín-Ortíz 2008, Jorgensen et al. 2012, Stewart 2016, Tyminski et al. 2015, Byrne et al. 2017, Coelho et al. 2017, Vaudo et al. 2017, Benson et al. 2018, Dewar et al. 2018, Byrne et al. 2019, Nasby-Lucas 2019, Rooker 2019, Nasby-Lucas 2020, Anderson et al. 2021, O'Sullivan 2022, Spurgeon 2022, Kanive et al. 2023, Logan et al. 2024).

Satellite telemetry comprised the method reported in most studies of the primary literature, followed by passive acoustic telemetry (Fig. 1, 2; Supplementary Material Table S2). Nine articles employed more than one type of telemetry (Bessudo et al. 2011, Afonso 2013, Afonso and Hazin 2014, Acuña-Marrero 2017, Chávez-Calderón 2017, Rosende-Pereiro and Corgos 2018, Ruíz-Sakamoto 2018, Salinas-de-León et al. 2022, Logan et al. 2024). Mexico (*n* = 31) had the highest number of studies that included satellite telemetry, followed by Brazil (*n* = 13).

A few articles combined active and passive acoustic telemetry (*n* = 3), whereas others (*n* = 6) integrated satellite telemetry and acoustic methods. A large proportion of the reports (*n* = 18) came from the gray literature stored in university libraries and repositories (Fig. 2). Of these, only 5 reports (4.59% of the total analyzed), namely 1 from Brazil, 1 from Argentina, and 3 from Mexico, were later published in the primary literature (Hoyos-Padilla et al. 2009, Afonso 2013, Nalesso 2014, De Wysiecki 2023, Beauvais 2024).

Of the total number of studies, most were conducted in Mexico (*n* = 60), primarily in the region of Baja California and Baja California Sur (*n* = 40) (Supplementary Material Table S2; Fig. 3), followed by Brazil (*n* = 16) and Ecuador (Galápagos Islands) (*n* = 13) (Fig. 3). The study species comprised different taxa and differed greatly in behavior, feeding habits, and distributions. The most studied species were the White Shark (*n* = 24), Scalloped Hammerhead (*n* = 23), Tiger Shark (*Galeocerdo cuvier*) (*n* = 14), and Whale Shark (*Rhincodon typus*) (*n* = 12; Supplementary Material Table S2; Fig. 3).

The most frequent approach category was habitat use (*n* = 94; Fig. 3). It was found that the White Shark was the only species used to study tagging effects (Domeier et al. 2012), in addition to aspects related to its management and conservation (Santana-Morales et al. 2021). Additionally, it is essential to highlight that only 11 (10.4%) of the 106 documents reviewed focused on rays (Oceanic Manta Ray [*Mobula birostris*], Sicklefin Devil Ray [*Mobula tarapacana*], Spinetail Devil Ray [*Mobula japonica*], Munk's Pygmy Devil Ray [*Mobula munkiana*], Yellownose Skate [*Dipturus chilensis*], and Ray [*Dipturus trachyderma*]), while 95 (89.6%) focused on sharks; no records were found for chimaeras (Supplementary Material Table S2).

DISCUSSION

The present literature review addressed the current application of acoustic and satellite telemetry to study elasmobranchs in Latin America. The first results from the use of this technology in the region emerged in 2006, and its use has increased ever since. Mexico stands out as the country that has used this technology most frequently. However, most reports and studies in institutional repositories constitute gray literature and are unavailable as primary literature, limiting the size of the audience and the impact of the studies. Additionally, the largest research focus was the ecology of the target species, mainly to elucidate habitat use. Only one study was found that focused.

Table 3. Criteria used to define the categories that classified the elasmobranch telemetry studies included in this review.

Category	General definition	Main inclusion criterion	Specific focus clarification
Habitat Use	Use or consumption of physical and biological resources by the animal (Kirk, 2018).	Studies with the primary objective of describing spatial patterns such as movements, migrations, site fidelity, or habitat use.	Although nearly all telemetry studies involve movement, only those where this was the main focus (not subordinated to another purpose) were included here.
Ethology	Study of animal behavior in its natural environment.	Studies using telemetry data to analyze specific behaviors such as reproduction, hunting, feeding, or social interactions.	If the main objective was to understand a particular behavior (e.g., feeding), then the study was categorized here, even if it used movement data.
Trophic Ecology	Study of trophic relationships and the position of the organism in the food web.	Studies investigating feeding behavior, trophic habits, or space use related to foraging.	If the behavior analyzed was specifically related to feeding, then the study was categorized here to highlight this emerging use of telemetry.
Animal Welfare	Assessment of the impact of tagging or tracking on the health, behavior, or physiology of the animal	Studies evaluating adverse effects of tagging, post-release survival rates, or stress related to handling.	Included methodological studies focused on the welfare of the tagged individual.
Population Dynamics	Processes affecting the size, structure, or spatial distribution of populations.	Studies focused on population connectivity, survival rates, recruitment, population structure, or dispersal	The main objective was to understand population-level processes rather than individual behaviors or movements.
Tag Effects	Impact of telemetry devices on animal performance or device performance.	Studies assessing tag performance, duration, accuracy, shedding rates, or mechanical/physiological impacts.	Differed from those focused on animal welfare in that the focus was more technical or methodological.
Fisheries Interactions	Interactions between elasmobranchs and fisheries.	Studies documenting bycatch, movements into fishing areas, or risks of interactions with fishing gears or efforts.	Included studies aimed at identifying the overlap with fishing activities.
Management & Conservation	Direct applications of results to species, habitat management, or conservation policies.	Only studies with findings that were explicitly used to develop, influence, or implement concrete management actions or policies.	Although many studies mentioned conservation as a general motivation, only those with documented management impacts were included (e.g., Santana-Morales et al. 2021).

Currently, global reviews, such as those by Renshaw et al. (2023) and Hammershlag et al. (2011), have focused on satellite tagging studies of sharks. The reviews by Kessel et al. (2014) and Matley et al. (2022) presented a comprehensive analysis of how the acoustic detection ranges of aquatic animals have been considered and assessed. However, no work has focused on evaluating different types of telemetry to study elasmobranchs, not only sharks or aquatic fauna, in Mexico or Latin America.

Improving tagging and tracking techniques is complicated due to high costs (Hebblewhite and Haydon 2010, Skupien et al. 2016), a lack of basic information (Thiem et al. 2010), and the limited number of comprehensive reviews focused specifically on the use of telemetry in marine fishes (Cooke et al. 2011). Given this context, many authors have suggested combining telemetry, hybrid transmitters, and other technologies within the same study to overcome the limitations inherent to each tracking technology (Brien et al. 2010, Calverley and Downs 2015, Baker et al. 2019).

Satellite telemetry

Across Latin America, studies using satellite telemetry have shed light on the relationships between the movements and behaviors of species, such as the Whale Shark and Blue Shark (*Prionace glauca*), their prey, and limiting oceanographic characteristics, such as the depth of the oxygen minimum zone in the water column (Oñate-González 2008, Mayorga-Martínez 2011).

Since the first transmitter-equipped shark was tracked in 1965, at least 26 shark species have been tracked, including demersal, pelagic, reef, and deep-sea species, as well as some of the largest species like the White Shark, Whale Shark, and Megamouth Shark (*Megachasma pelagios*) (Nelson et al. 1997). These findings have made notable contributions to improving management and conservation efforts. This review highlights the multiple applications of telemetry studies (Fig. 1).

In Brazil, Queiroz (2020) and other authors have utilized data from fishers, catch records, and video images alongside telemetry data to study the habitat use of the Galapagos Shark (*Carcharhinus galapagensis*). In the Gulf of Mexico, Ajemian et al. (2020) used telemetry to identify differences in Tiger Shark distribution patterns related to ontogeny and seasonality and evaluate variability in regional movement rates linked to sex. These wide-ranging applications of telemetry demonstrate its versatility in addressing diverse research objectives and offering critical insights into the ecology and behavior of different species.

Acoustic telemetry

While elucidating habitat use was the primary approach of most telemetry studies, some studies focused on understanding the ethology and trophic ecology of elasmobranchs, including the Tiger Shark, White shark, and other shark species (Papastamatiou et al. 2022, Salinas-de-León et al. 2022, Rangel 2023). Additionally, and more recently, while the primary goal of studies like those by Herrera et al. (2024) and Nalesso et al. (2019) was to understand the habitat use and movement patterns of sharks, these studies also showed a clear intention towards applying telemetry findings to more concrete and tangible management and conservation outcomes. For instance, the trophic ecology research by Rangel (2023) in Brazil integrated stable isotope analysis with telemetry data to inform conservation strategies tailored to species-specific dietary niches and energy requirements. Similarly, Salinas-de-León et al. (2019) combined satellite telemetry with trophic data to identify critical feeding grounds and ontogenetic shifts in the diet of the Tiger Shark in the Galapagos Marine Reserve, which contributed to refining protected area boundaries and zoning strategies that are still in use today. In another example, Afonso et al. (2014) examined trophic-mediated spatial partitioning among pelagic elasmobranchs, highlighting how interspecific dietary differences influence spatial use patterns, which has supported ecosystem-based fisheries management in the region.

These examples demonstrate how telemetry data can move beyond academic knowledge to shape practical, lasting management actions across Latin America when integrated with other approaches. Indeed, such efforts may serve as a model for the larger-scale protection of elasmobranchs and other endangered marine species. A better understanding of the ecology of shark movements is essential for designing effective protection strategies (Heupel 2015). Among the most effective and widely recommended measures is reducing interactions with fisheries, which directly decrease anthropogenic pressures on these vulnerable species.

In Mexico, most of the applications of active acoustic telemetry have focused on evaluating habitat use, with the White Shark being most frequently studied (Hoyos-Padilla 2009, Hoyos-Padilla 2016, Aquino-Baleytó et al. 2021, Santana-Morales 2021). To a lesser extent, there are also studies on the Scalloped Hammerhead, Oceanic Manta Ray, and Pacific Sharpnose Shark (*Rhizoprionodon longurio*) (Trejo-Ramírez 2017, Rosende-Pereiro 2018, Ruíz-Sakamoto 2018). In addition, the first records of active acoustic telemetry use in Latin America date back to Guadalupe Island, Mexico, in 2006 (Hoyos-Padilla 2009). The use of telemetry in this location has been crucial for improving our understanding of White Shark biology and ecology in Mexican waters and for informing conservation and management plans (Hoyos-Padilla 2016).

Baja California, Mexico, is a hotspot for telemetry

Due to its geographic proximity to the United States and collaborative work across institutions, Baja California stands out as the Latin American region with the highest number of publications using telemetry tracking technology. Some telemetry studies have reported that individuals marked off

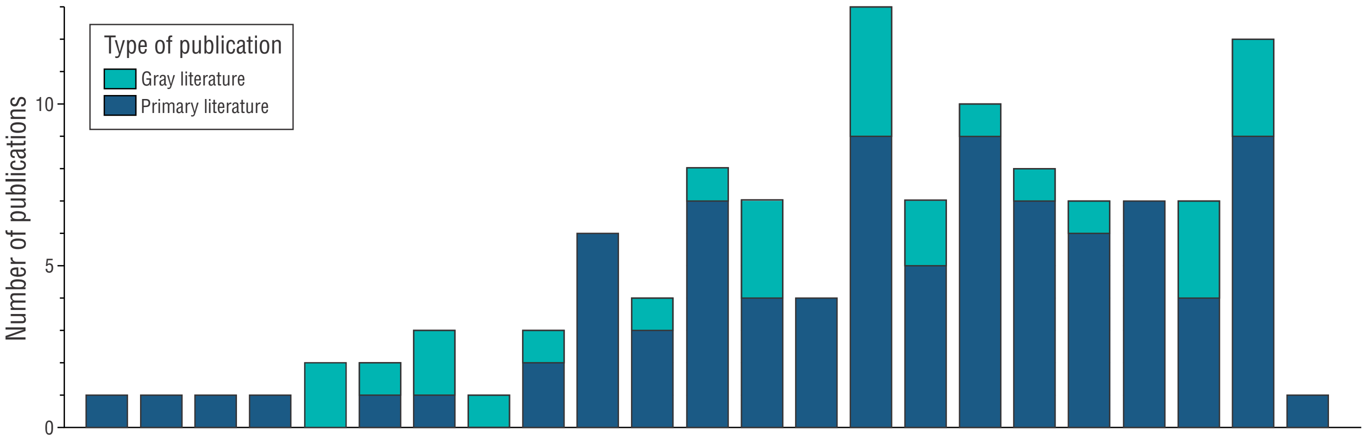

Figure 1. Number of scientific articles (primary literature) and gray literature published using telemetry by year in Latin America.

California, USA, crossed the border into the waters of Baja California, Mexico (Domeier et. al. 2012, Nasby-Lucas 2019, White et al. 2019, Anderson et al. 2021, Kanive et al. 2023). These studies support Baja California being the region with the most telemetry studies in this review and a geographical hotspot for which Renshaw et al. (2023) and Hussey et al. (2015) also reported a high number of satellite and acoustic telemetry applications, respectively.

Furthermore, among the binational studies included in this analysis, all (n = 18) but one employed telemetry to describe the movements of the Mako Shark (*Isurus oxyrinchus*) along the California and Baja California coasts (e.g., Medellín-Ortiz 2008) and correspond to the primary literature. This fact highlights the greater use of telemetry as a research tool in the region and the number of primary literature contributions compared to those of other regions in Latin America.

Mexico is the only country in Latin America in which studies have specifically addressed the effects of tagging (Domeier et al. 2012) and other aspects related to the management and conservation of elasmobranchs (Santana-Morales et al. 2021). Both lines of research focused on the White Shark in the Guadalupe Island Biosphere Reserve, which is located within the Exclusive Economic Zone of the Mexican Pacific. The reserve serves as one of the few known critical aggregation sites for the White Shark worldwide and potentially functions as a feeding, mating, or nursery ground (Domeier and Nasby-Lucas 2012, Malpica-Cruz et al. 2013, Hoyos-Padilla 2016). The ecological conditions of the reserve enabled the development of wildlife tourism in the form of cage diving, which was globally renowned and operated from the early 2000s until its official suspension in January 2023 by decree of the Mexican government (Meza-Arce et al. 2020, SEMARNAT 2023). Therefore, the combination of these geographical, ecological, and economic interests likely allowed Baja California to become one of the most extensively studied areas using telemetry in Latin America.

Specific challenges to telemetry research and output in Latin America

Hellström et al. (2022) considered modern acoustic telemetry to be a low-cost, maintenance-free technology. However, its implementation in Latin America still faces logistical challenges, as costs often exceed local average research budgets and funding is typically directed toward charismatic species (Habib et al. 2014). Furthermore, the importance of selecting the most appropriate telemetry technology, based on factors like habitat type, target species, and research objectives, has been identified as limitation to researchers adopting these tools (Jacob and Rudran 2012, Skupien et al. 2016). These constraints, together with the regional economic context, limit the overall development of marine research and the specific implementation and advancement of telemetry studies focused on elasmobranchs and other marine species in Latin America.

Many authors, including Cooke et al. (2008), Obrist et al. (2010), and Dwyer et al. (2023), have considered acoustic tracking to be a useful, low-cost technology that reduces the overall monitoring cost. However, telemetry remains expensive for most Latin American countries with limited research budgets and in which the costs of acquiring new technology must be balanced with the need for more intensive, frequent, and detailed data collection (Zenteno-Savín 2007). In addition, transmitters and other items (e.g., antennas and signal receivers) increase the cost of this type of research.

In the case of satellite telemetry, GPS transmitters are considered the most expensive to acquire, and their use also involves satellite data transmission fees (Franklin et al. 2009, Skupien et al. 2016). Unlike acoustic telemetry, satellite telemetry is not limited by the spatial distribution of monitoring stations. Skupien et al. (2016) reported that each GPS logger used in their study cost approximately $1,225 (USD) while each VHF transmitter cost $183–300 (USD). These price differences can make satellite telemetry cost restrictive.

Additionally, the costs of field expeditions, such as fuel, salaries, repairs, duration, food for scientific personnel, and other logistics, can equal or even exceed the amount invested in the telemetry devices. For this reason, researchers using satellite telemetry often resort to smaller sample sizes, which can compromise the robustness of the study design and limit population-level inferences (Hebblewhite and Haydon 2010, Recio et al. 2011).

Technical aspects aside, from a historical perspective, researchers who are not native English speakers face greater difficulties in producing scientific publications (Ferguson and Pérez-Llantada 2011). Therefore, much of the scientific production from Latin America is published in low-impact, local journals in languages other than English (Ramírez-Castañeda 2020). Indeed, 22.6% of the documents reviewed in this study were theses or reports in Spanish or Portuguese, and 79.1% were not published as part of the English-language scientific literature, limiting their visibility and relevance. Some measures aimed to reduce this bias include the provision of review and translation services by international journals, the possibility of publishing in both English and the native language of the researcher (Meneghini and Packer 2007), and the promotion of free English writing courses at universities (Ferguson and Pérez-Llantada 2011).

In addition to language issues, the investment of Latin American governments in research directly influences academic production (Man et al. 2004). As such, budget constraints limit research and monitoring, and high publication fees cause valuable information to remain as gray literature or behind paywalls, thus limiting the audience. Lawson (2015) suggests that fee waivers should be offered to authors from low- or middle-income countries to boost the publication of high-quality scientific content from countries that host many species associated with conservation concerns. Our results showed that between 2006 and 2024, only some years included primary literature publications focused on elasmobranch telemetry while gray literature was generated in all years, reinforcing the conclusion that in Latin America, much scientific information (e.g., graduate theses) does not undergo peer review or publication in scientific journals (Man et al. 2004, Lawson 2015).

Habib et al. (2014) conducted a similar review to ours, focusing on telemetry technology applications in India and analyzing 82 studies that covered 47 species from four taxonomic classes. Most of these studies aimed to gather primary data, such as home range, migration patterns, movement behavior, and habitat preferences. These findings align with our review of Latin American telemetry studies. The reviews identified similar challenges for both regions that were also highlighted by Darras et al. (2016) and Kessel et al. (2014). Key issues included limited battery duration, the need for tag replacement, small sample sizes, premature tag release, difficulties in obtaining tagging permits or capturing animals, imprecise location data, challenges in data transmission, and limitations in the range of acoustic hydrophones (Tables 1 and 2).

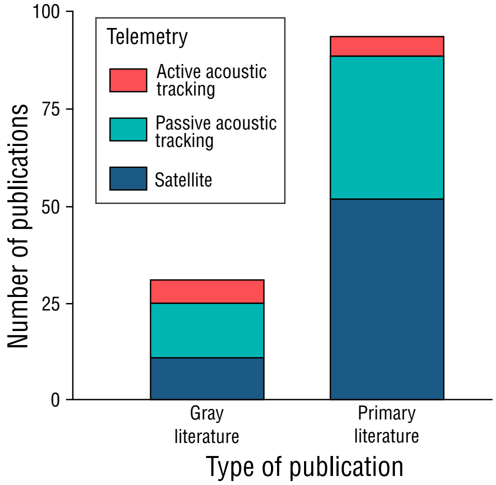

Figure 2. Number of scientific articles (primary literature) and gray literature that employed different types of telemetry in Latin America.

Telemetry for elasmobranch management and conservation

Assessing the application of results obtained from telemetry studies on elasmobranchs in Latin America is important. For example, while most of the published literature using telemetry on elasmobranchs claims conservation implications, the link between most of these studies and direct conservation and management actions is usually weak at best (Campbell et al. 2015, Jeffers and Godley 2016, Mitchell et al. 2023). However, many scientists affirm that more data will lead to better management and suggest evaluating the return on investment from research using animal-borne telemetry devices (Maxwell et al. 2015).

Indeed, telemetry provides valuable insights into the migratory behavior of elasmobranchs and can inform interactions with human activities. For example, the regional model developed by Salazar-Cervantes (2023) using satellite telemetry aimed to understand the biological and environmental factors that determine the distribution of the Silky Shark (*Carcharhinus falciformis*) and the overlap with fishing activities in the Mexican Pacific. The Silky Shark is not officially protected in Mexico; thus, focused management studies that build on these early results could improve fisheries management, reduce bycatch, and support the development of conservation strategies to ensure the survival of populations.

Even though the Official Mexican Standard NOM-059 (DOF 2010) protects species, such as the White Shark, Basking Shark (*Cetorhinus maximus*), and Whale Shark, and NOM-029-Pesca (DOF 2007) regulates the exploitation of sharks as fishing resources, evidence of elasmobranch overexploitation still exists (Mollet et al. 1996, Holts 1998, Castro 1999, Shivji et al. 2005, Smith et al. 2009, Cartamil 2011, Santana-Morales et al. 2020, Sosa-Nishizaki et al. 2020).

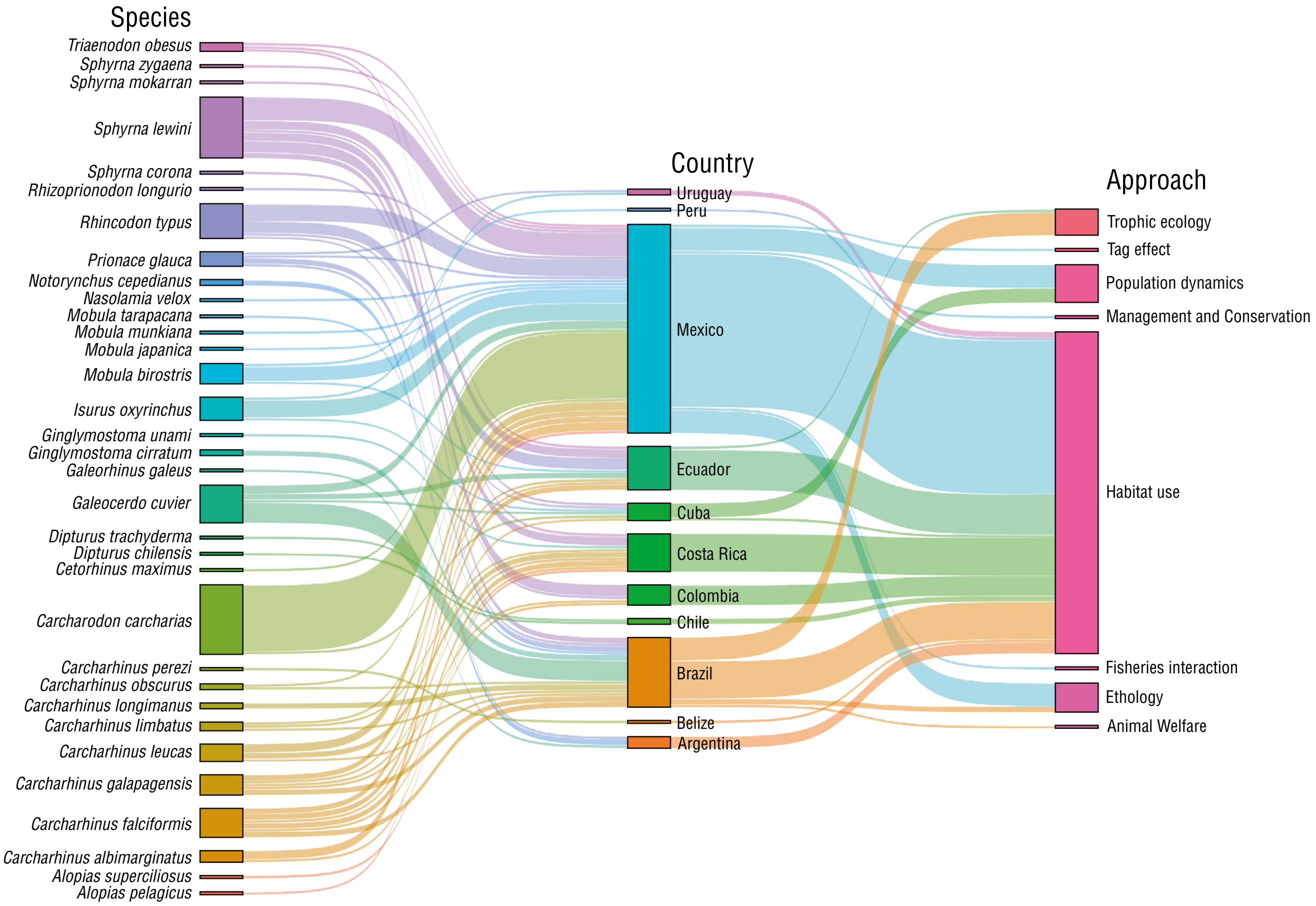

Figure 3. Relationships between species, research focus employing telemetry, and countries in Latin America.

Moreover, notable knowledge gaps remain regarding elasmobranch behavior, migration, and general ecology (Sundström et al. 2001, Heupel and Simpfendorfer 2008).

Elasmobranchs are the oldest living vertebrates on Earth (Edwards et al. 2019) and are usually K-selected species (Conrath and Musick 2012), which makes them particularly vulnerable to anthropogenic pressures and underscores the importance of filling knowledge gaps through telemetry. For example, for large-bodied offshore species, such as the Silky Shark that exhibits a low population renewal rate (Márquez-Farías et al. 2006) and faces overfishing and environmental threats, telemetry-based knowledge can prove critical for the design and implementation of appropriate management actions. For offshore species, a well-designed acoustic receiver array may be more appropriate to elucidate critical areas and migratory patterns (Lennox et al. 2023). Therefore, differences between coastal and offshore species, especially regarding spatial behavior and habitat use, can influence the effectiveness of acoustic telemetry, particularly regarding receiver placement and the detection range.

Given the potential of telemetry-derived data to inform resource management and conservation, and the high costs involved in collecting these data (e.g., the financial costs of equipment and salaries, potential for mortality, and reduction in reproduction output [Cooke et al. 2008, Brownscrombe et al. 2022]), it is essential to evaluate the benefits of telemetry for conservation. Also, researchers must be encouraged to utilize telemetry technology with an underlying conservation rationale to target their research towards gathering robust data to propel actions that maximize species survival and persistence and improve fisheries management (Liang et al. 2023).

Given the large investment and complex logistical needs of applying telemetry to studying elasmobranchs, careful planning is advised (e.g., Habib et al. 2014). Indeed, when study questions are carefully chosen and the study is well-designed, a single deployment of tags can yield notable insights. Telemetry data can also uncover unexpected information that can guide management efforts. For example, Bradley et al. (2018) revealed illegal shark fishing within a sanctuary when satellite tags were transmitted from a vessel, indicating illegal capture, transfer at sea, and transport to the Marshall Islands. Tolotti et al. (2015) used telemetry to assess the vulnerability of the Oceanic Whitetip Shark (*Carcharhinus longimanus*) to longline fisheries in Brazil. In addition, Aldana-Moreno et al. (2020) conducted telemetry-based monitoring in the Revillagigedo National Park, a no-take reserve and a World Heritage Site of the United Nations Educational, Scientific, and Cultural Organization (UNESCO), to support the conservation of the endangered Scalloped Hammerhead. These examples show how telemetry can provide helpful information for future management and conservation purposes beyond addressing purely ecological and biological questions.

Additionally, in many cases, tracking trajectories are shared on public websites or through other media, enhancing the dissemination of information and its impact by facilitating effective scientific communication (Cooke et al. 2017). There are only a few examples of data analysis to inform management decisions, and even fewer using telemetry-derived data (Liang et al. 2023). For example, radio tracking studies in the United Kingdom revealed that the Common Pipistrelle Bat (*Pipistrellus pipistrellus*), a protected species that cannot be easily studied based solely on observations, exploits specific habitats and thus requires tailored conservation measures (Davidson-Watts and Jones 2006). Moreover, biotelemetry research on anadromous salmon (*Salmo* spp. and *Oncorhynchus* spp.) has led to an improved understanding of mortality events from catch-and-release fishing interactions and physiological factors that influence spawning failure, which in turn justify the restrictions placed on fished populations (Nielsen et al. 2009, Drenner et al. 2012).

While telemetry technology has been increasingly used worldwide for marine species management and policy, its application, particularly in Latin America, remains limited, with few studies effectively bridging research and conservation actions for elasmobranchs. Although some reviews have focused on different taxa and have discussed the potential for using telemetry technology for marine species management (e.g., Cooke et al. 2008 [salmon]; Jeffers and Godley 2016 [sea turtles]) and policy (Barton et al. 2015), they have underemphasized the importance of defining clear links between research and management actions.

Only Mascarenhas-Junior (2023) of the Federal University of Pernambuco, Brazil, has truly addressed the need to ground the information from a Latin American perspective in his review of telemetry studies on the spatial use and movements of crocodilians. However, there is currently no work that similarly addresses elasmobranchs. Santana-Morales et al. (2021) were the only authors to provide conservation and management applications for an elasmobranch (i.e., the White Shark) based on active acoustic telemetry in Latin America. While there will always be a need for basic ecological research and discovery, the current biodiversity and conservation crisis (Ceballos 2020, Dulvy 2021, WWF 2024, Wang 2025), combined with the limited number of telemetry studies with direct applications for the conservation and management of elasmobranchs, highlights a critical gap in the need for these data.

Given the global investment in telemetry devices for threatened species, we have an ethical and practical obligation to maximize research investments that benefit conservation. We need new tools and frameworks to effectively link the growing catalogue of animal telemetry-derived data to conservation and management actions to improve the return on investment of these efforts. Approaches that explicitly evaluate how scientific data can reduce uncertainty in decision-making, such as the value of information analysis, should play an increasingly important role in guiding research priorities. For example, fusing telemetry data with other environmental and threat-based databases can help identify high-risk areas of management concern and inform bycatch reduction efforts for critically endangered species. This type of data analysis and approach could also be applied to other populations and species with available telemetry and point-source data (Liang 2023).

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3541/420421215.

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Data Availability

The data for this study are available from the corresponding author upon reasonable request.

Conflict of Interest

The authors declare that they have no conflict of interest.

Author Contributions

Conceptualization: CIVA, LMC; Data curation: CIVA; Formal analysis: CIVA; Investigation: CIVA, LMC; Methodology: CIVA, LMC; Supervision: LMC, OSM; Validation: LMC, OSM; Visualization: CIVA, LFAS; Writing–original draft: CIVA, LMC; Writing–review & editing: CIVA, LMC, OSM, LFAS.

Use of AI Tools

The first author of this work used AI tools to translate technical terms while drafting the English version of the manuscript.

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Cephalopod paralarvae (Cephalopoda: Mollusca) in the neritic environment of the northern Colombian Pacific

Manuela Davila-Arce[1], Arminda Mejía-Rebollo[2], Alan Giraldo[1]*

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CORRESPONDING AUTHOR
* E-mail: alan.giraldo@correounivalle.edu.co

[1] Grupo de Investigación en Ecología Animal, Departamento de Biología, Universidad del Valle, 760042 Valle del Cauca, Colombia.
[2] Laboratorio de Invertebrados Marinos, Centro de Investigaciones Biológicas del Noroeste, 23096 La Paz, Baja California Sur, Mexico.

ABSTRACT. Knowledge of the ecological aspects of cephalopod paralarvae is essential to understand the composition and dynamics of their populations, as well as to identify spawning seasons and areas. In the northern Colombian Pacific (NCP), studies on this early life stage are scarce. The purpose of this study was to establish the taxonomic composition of paralarvae in the neritic environment of the NCP, quantify their abundance, and describe their spatio-temporal variation. A total of 315 zooplankton samples were collected through surface tows between January and November 2022 in 3 sectors. One hundred and two paralarvae were found in 16.5% of the samples and were classified into 4 families: Loliginidae, Octopodidae, Ommastrephidae, and Ancistrocheiridae. The presence of loliginid squid paralarvae and the Chango Octopus (*Octopus* cf. *mimus*) is reported for the first time in this region. The highest abundance values were recorded in March (>6 Pl·1,000 m^{-3}) and coincided with the upwelling period, which suggests synchrony between reproductive events and the increase in biological productivity that favored paralarval survival. The distribution of the most representative groups was influenced by the ecological behavior of each family and the geomorphological characteristics of each sector. Octopodidae predominated in the northern and central NCP, where rocky bottoms and a narrow continental shelf are present, whereas Loliginidae were found in the southern sector, where the shelf is wider and sandy beaches predominate. The presence of early stages of commercially important groups suggests the importance of the NCP as a reproductive area for these cephalopods and highlights the need to deepen research on their reproductive biology and ecology. These findings provide the basis for understanding patterns of temporal variation in paralarval abundance in neritic environments of the Eastern Tropical Pacific.

Key words: squids, octopuses, morphological identification, paralarvae, Eastern Tropical Pacific, zooplankton.

INTRODUCTION

Cephalopods are key species in marine ecosystems and an essential fishery resource worldwide (Boyle and Rodhouse 2005, FAO 2024). Although they exhibit direct development and a consistent body plan throughout their life cycle, most species undergo a planktonic phase after hatching. This stage, known as the paralarva, differs from the adult mainly in its ecology, since as part of the zooplankton it occupies a habitat different from that of its neritic, pelagic, or benthic adult congeners. In contrast, some species hatch as juveniles and develop in the same habitat as the adults (Vidal and Shea 2023).

Knowledge of the ecological aspects of paralarvae allows us to understand the composition and dynamics of cephalopod populations, as well as the factors that affect their abundance and distribution, and the establishment of spawning seasons and areas. This is essential to determine recruitment and fishery stock of commercially important species (Vidal et al. 2010, Zaragoza et al. 2015). In addition, paralarvae can serve as indicators of species richness in a given area, since they are often easier and more accessible to sample than adults (Aceves-Medina et al. 2017, De Silva-Dávila et al. 2018).

Despite their importance, paralarvae have been little studied compared with other zooplankton groups (Boletzky 2003). Sweeney et al. (1992) mentioned that there is a high

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degree of taxonomic uncertainty, which persists to the present due to morphological similarity among species and the lack of detailed descriptions for most of them (Zaragoza et al. 2015).

In the eastern Pacific, most research on this taxonomic group has been conducted in the Mexican Pacific, where the most representative families are Ommastrephidae, Pyroteuthidae, Argonautidae, Enoploteuthidae, and Loliginidae (De Silva-Dávila et al. 2018). The relationship of paralarval communities with oceanographic conditions has also been explored, as well as the effects of mesoscale phenomena and the El Niño–Southern Oscillation on their abundance and spatio-temporal variation (Granados-Amores et al. 2010; Aceves-Medina et al. 2017; García-Guillén et al. 2018; Ruvalcaba-Aroche et al. 2018, 2020). However, in the southern sector of the eastern Pacific, studies are scarce. In Peru, Yatsu et al. (1999) described for the first time the paralarvae of the Jumbo Squid (*Dosidicus gigas*) through artificial fertilization, providing relevant information on hatching time, as well as on the size and morphological characteristics of the early stage of the species. More recently, the families Ommastrephidae and Octopodidae, the genus *Argonauta*, and the species *Abraliopsis* sp. were identified as the most abundant groups in that region (Orosco and Ayón 2022), while in southern Chile, the genera with the highest incidence were *Octopus* and *Gonatus* (Vega et al. 2000). In the Colombian Pacific, knowledge of paralarvae is restricted to the work of Vargas and López (2020), in which 8 families were identified, among which Ommastrephidae was dominant. In addition, Vargas and López (2020) reported that the high temperatures of the area favor early hatching of paralarvae and highlighted the importance of the neritic zone as a spawning ground.

The northern Colombian Pacific (NCP), located in the northwestern region of Colombia, is situated in the low atmospheric pressure zone of the Eastern Tropical Pacific (ETP), where the migration of the Intertropical Convergence Zone (ITCZ) modulates seasonal changes in climate, hydrography, and circulation. Between January and April, the season of lower precipitation occurs, during which the northerly trade winds intensify, causing the displacement of the ITCZ to its southernmost position. This leads to the strengthening of upwelling processes in the Panama Bight, causing the influx of colder and saltier waters into the surface layer, which results in the development of a shallow thermocline (around 15 m). Conversely, during the rainy season (May–November), the influence of the southerly trade winds intensifies, causing the displacement of the ITCZ to its northernmost position. This generates an increase in precipitation and, with it, a reduction in surface salinity and the dominance of warm surface waters (26–28 °C), which leads to the interruption of the upwelling process and deepening of the thermocline (around 90 m) (Valencia and Giraldo 2009; Jerez-Guerrero et al. 2017; Velandia et al. 2019; Valencia et al. 2019, 2024).

Along the NCP coastline, the continental shelf is narrow (1–6 km; >80 m depth) and dominated by cliffs, bays, and enclosed beaches along the shoreline (Díaz et al. 2016). In contrast, in the southern zone, the continental shelf is wider and shallower (16–20 km; <50 m depth), with extensive sandy beaches and intertidal flats with mangrove areas inland, as well as large river mouths (Velandia et al. 2019). This heterogeneity of the zone allows for a diversity of biological groups, including paralarvae.

This study aimed to describe the taxonomic composition of cephalopod paralarvae in the neritic environment of the NCP and to evaluate spatial and temporal changes in their abundance. Considering the temporal variation in oceanographic conditions and the effect of processes that enhance local productivity in the study area, such as upwelling, the central hypothesis of this work was that the highest abundance of paralarvae would occur during the dry season, when the presence of upwelling waters in the Panama Bight increases productivity and food availability in the neritic environment. Additionally, it was hypothesized that, taking into account the geomorphological characteristics of the NCP, a higher abundance of taxonomic groups with coastal habitats, particularly octopuses and loliginid squids, would be recorded.

MATERIALS AND METHODS

Study Area

Three sampling sectors were established in the NCP: the first between Cabo Marzo and the Gulf of Cupica (6.2–6.8°N; 18 stations), the second in the Gulf of Tribugá (5.5–5.9°N; 18 stations), and the third to the south, encompassing the coastal zone of Bajo Baudó (4.7–5.2°N; 17 stations) (Fig. 1). The study region has a warm climate throughout the year (between 27 and 30 °C) and is characterized as one of the rainiest in the world, with high precipitation ranging from 5,030 to 7,700 $\text{mm}\cdot\text{y}^{-1}$ (Velandia and Díaz 2016).

Sampling and environmental data

Six bimonthly oceanographic campaigns were conducted between January and November 2022, following a sampling grid of 53 stations systematically located across the 3 study sectors (Fig. 1). At each station, surface zooplankton tows were performed and environmental variables were recorded at 1 m depth from a small boat with an outboard motor, such as sea surface temperature (SST [°C]), salinity (PSU), dissolved oxygen (DO [$\text{mg}\cdot\text{L}^{-1}$]), and chlorophyll-*a* concentration ($\mu\text{g}\cdot\text{L}^{-1}$), which was calculated according to the protocol of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) (CalCOFI 2011). Due to adverse weather conditions, sampling was not completed at all established stations during September (52 stations) and November (51 stations).

Zooplankton samples were collected with 2 conical nets (diameter: 71 cm; mesh opening: 200 µm and 500 µm) equipped with flowmeters (model 438 110, Hydro-Bios, Altenholz, Germany) to quantify the volume of filtered water.

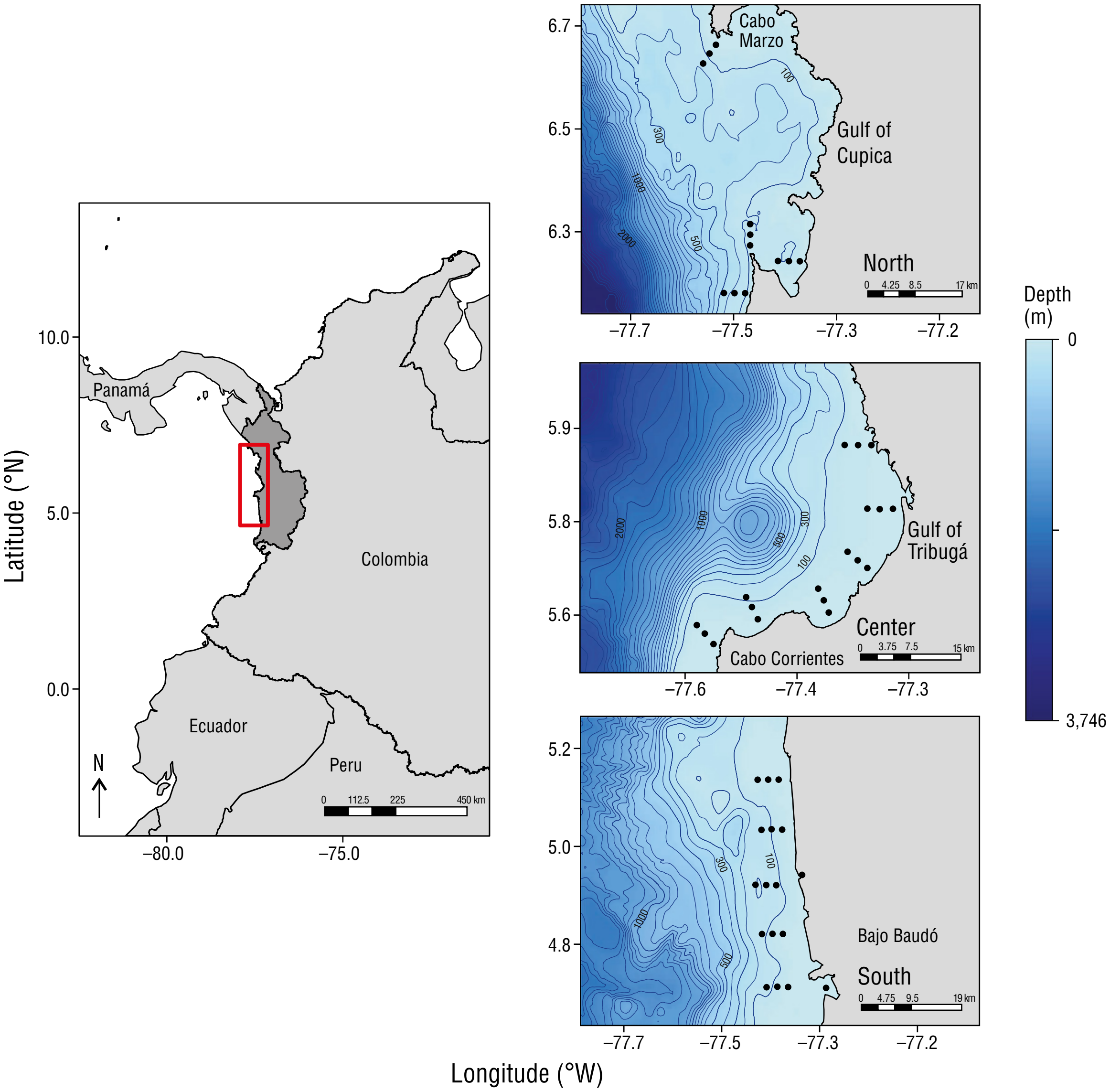

Figure 1. Geographic location of the northern Colombian Pacific (NCP) and sampling grid used for obtaining samples in each sector. Each station is located at a distance of 2 km..

The average tow duration was 4 min and 25 s. Samples were fixed onboard with 4% formalin neutralized with sodium borate. In the laboratory, all samples were examined to separate paralarvae using a stereomicroscope SMZ745T (Nikon, Tokyo, Japan), which were then preserved in 70% ethanol. Zooplankton biomass (mg·m^{-3}) was estimated as ash-free dry weight following the protocol of Giraldo et al. (2022) and considered as an indicator of biological productivity.

Taxonomic identification

The paralarvae found were classified to the most precise taxonomic level possible with the identification guides of Sweeney et al. (1992), Vecchione et al. (2001), Diekmann et al. (2002), Haimovici et al. (2002), and Zaragoza et al. (2015), and the criteria used by Granados-Amores (2008) and De Silva-Dávila (2013). Each specimen was measured for dorsal mantle length (ML, mm) using a stereomicroscope STEMI 2000-C (Carl Zeiss, Oberkochen, Germany) with a precision scale of 0.01 mm, coupled to an AxioCam ERc 5s camera (Carl Zeiss) and Zen Blue 3.7 software (Carl Zeiss). It should be noted that all characteristics were related to the size of each organism. The taxonomic identification characteristics reviewed included mantle shape (e.g., globose, oval, or bell-shaped), arm formula (Sweeney et al. 1992), eye type (pedunculated or fixed), number and arrangement of suckers on arms and tentacles, tentacular club differentiated or not differentiated, proboscis present or absent, photophores present or absent, shape of the cartilaginous funnel locking apparatus, chromatophore pattern, and siphon size. The chromatophore pattern and siphon size were determinant characteristics for identification and are described in detail in Table S1 (Supplementary Material).

In particular, for specimens of the family Octopodidae, a dissection was performed in the anterior region of the dorsal mantle surface in order to expose the surface of the digestive gland and describe the arrangement of chromatophores, referred to in this study as the chromatophore pattern of the digestive gland (DGCP). Taxonomic classification was carried out considering recent systematic revisions and the Integrated Taxonomic Information System (ITIS 2024). Individuals that were in poor condition or lacked sufficient morphological characteristics for identification were classified as "unidentified."

Data analysis

For the calculation of abundance, individuals recorded in both mouths of the bongo net (200 µm and 500 µm) were integrated so that each station was represented by a single sample. Subsequently, the samples were regrouped into units corresponding to all stations sampled within the same sector and month. Paralarval abundance in each unit was standardized to 1,000 m³ considering the total volume of filtered water, obtaining comparable values among sectors and study periods.

Relative abundance of each taxonomic group identified and its frequency of occurrence (*FO*) were calculated in the sampling units grouped by sector and month. The *FO* was calculated as the percentage of stations with presence of a taxonomic group relative to the total number of stations sampled in each unit.

Additionally, a species accumulation curve was constructed as a function of the samples examined to estimate sampling effort, considering species richness as the number of taxonomic groups found and the ecological richness indicators Jackknife1, Chao2, and Bootstrap in the program EstimateS v. 9.1.0.

To evaluate significant differences in paralarval abundance among sectors and sampling months, data were transformed to natural logarithm [$\log(x + 1)$] in order to reduce variability and correct distribution bias of the dataset. Although the Shapiro–Wilk normality test indicated non-compliance with the assumption of normality of the transformed data ($W = 0.84$; $P = 0.007$), Levene's test detected homogeneity of variances in the abundance among months ($F = 0.6192$; $P = 0.6881$) and sectors ($F = 0.3369$; $P = 0.7193$). Since the analysis of variance (ANOVA) is robust to deviations from normality (Meier 2022) and considering the homoscedasticity of the data, a two-factor ANOVA without interaction was applied. In this model, residuals showed a normal distribution ($W = 0.95119$; $P = 0.444$), so a Tukey post hoc test was performed for multiple comparisons ($\alpha = 0.05$). These analyses were carried out in RStudio v. 4.5.1.

RESULTS

Environmental conditions in the study area

During the study period, SST remained warm across the 3 sectors of the NCP without a defined spatial variation pattern, with mean values ranging from 26.33 ± 0.22 °C in the southern sector (November) to 28.63 ± 0.33 °C in the northern sector (March) (Fig. 2a, Table S2). Salinity showed the highest values in the northern and central sectors, ranging between 24.10 ± 0.46 PSU and 31.06 ± 0.28 PSU.

In contrast, the southern sector exhibited greater variability and the lowest values, fluctuating between 17.27 ± 3.10 PSU (September) and 25.11 ± 6.04 PSU (January) (Fig. 2b, Table S2). DO varied between 2.82 ± 0.62 $\mu g \cdot L^{-1}$ and 4.78 ± 0.40 $\mu g \cdot L^{-1}$, with the lowest concentrations recorded in the southern sector during September and November (Fig. 2c, Table S2). Meanwhile, chlorophyll-*a* concentration was higher in the southern sector, ranging from 1.27 ± 0.75 $\mu g \cdot L^{-1}$ (May and July) to 2.90 ± 1.05 $\mu g \cdot L^{-1}$ (November), whereas lower concentrations were recorded in the central and northern sectors, ranging from 0.24 ± 0.08 $\mu g \cdot L^{-1}$ to 0.94 ± 0.33 $\mu g \cdot L^{-1}$, with minimum values in July and maximum in March (Fig. 2d, Table S2). Finally, zooplankton biomass ranged from 2.16 ± 1.22 $mg \cdot m^{-3}$ to 42.79 ± 22.82 $mg \cdot m^{-3}$, reaching the highest values in March across all 3 sectors (Fig. 2e, Table S2).

Taxonomic composition

A total of 102 cephalopod paralarvae were found in 52 of the 315 zooplankton samples examined (16.5%), with the sampling effort carried out being representative of the taxonomic groups recorded (Fig. S1). The paralarvae were classified into 2 orders, Teuthida and Octopoda, comprising 4 families (Table 1). In the family Loliginidae, 3 distinct morphotypes were identified; in Ommastrephidae, a species complex composed of *Sthenoteuthis oualaniensis* and *D. gigas* (S–D complex) was recognized; and in the families Ancistrocheiridae and Octopodidae, *Ancistrocheirus* cf. *lesueurii* and *Octopus* cf. *mimus* were identified, respectively. Thirteen percent of the paralarvae corresponded to unidentified individuals. Table S3 shows the detailed description of each taxonomic group.

Individuals of the family Loliginidae Lesueur, 1821 (Fig. 3) exhibited an ocular membrane or cornea covering both eyes (Fig. 3a–b) and a straight cartilaginous funnel locking apparatus. Important differences were distinguished in the morphology of the tentacular club (arrangement and number of suckers), clearly differentiating 3 morphotypes (I, II, and III; Fig. 3c–h). Morphotype I ($n = 18$; $ML = 1.2$–2.0 mm) was characterized by an undifferentiated tentacular club, equal in width to the stalk, with 2 rows of suckers (Fig. 3c–d). Morphotype II ($n = 8$; $ML = 1.9$–2.9 mm) was characterized by a differentiated tentacular club wider than the stalk; stalk without suckers; a proximal region with 2 rows of suckers, and a medial and distal region with suckers arranged in 3 to 4 rows (Fig. 3e–f). Morphotype III (*n* = 4; *ML* = 1.8–2.8 mm) exhibited a differentiated tentacular club, stalk without suckers, and club suckers arranged in 4 rows (Fig. 3g–h).

Individuals of the family Ancistrocheiridae Pfeffer, 1912 (*n* = 6; *ML* = 0.8–1.1 mm) (Fig. 4) were characterized by a bell-shaped mantle, straight cartilaginous funnel locking apparatus, presence of gelatinous tissue covering the head, eyes, and proximal portion of the arm crown (Fig. 4a–b), and pedunculated tentacular suckers arranged in 2 rows (Fig. 4c–d). No photophores were observed on the mantle, head, arms, or tentacles at the sizes examined. Considering that the family Ancistrocheiridae is monotypic, individuals that met these characteristics were identified as a form

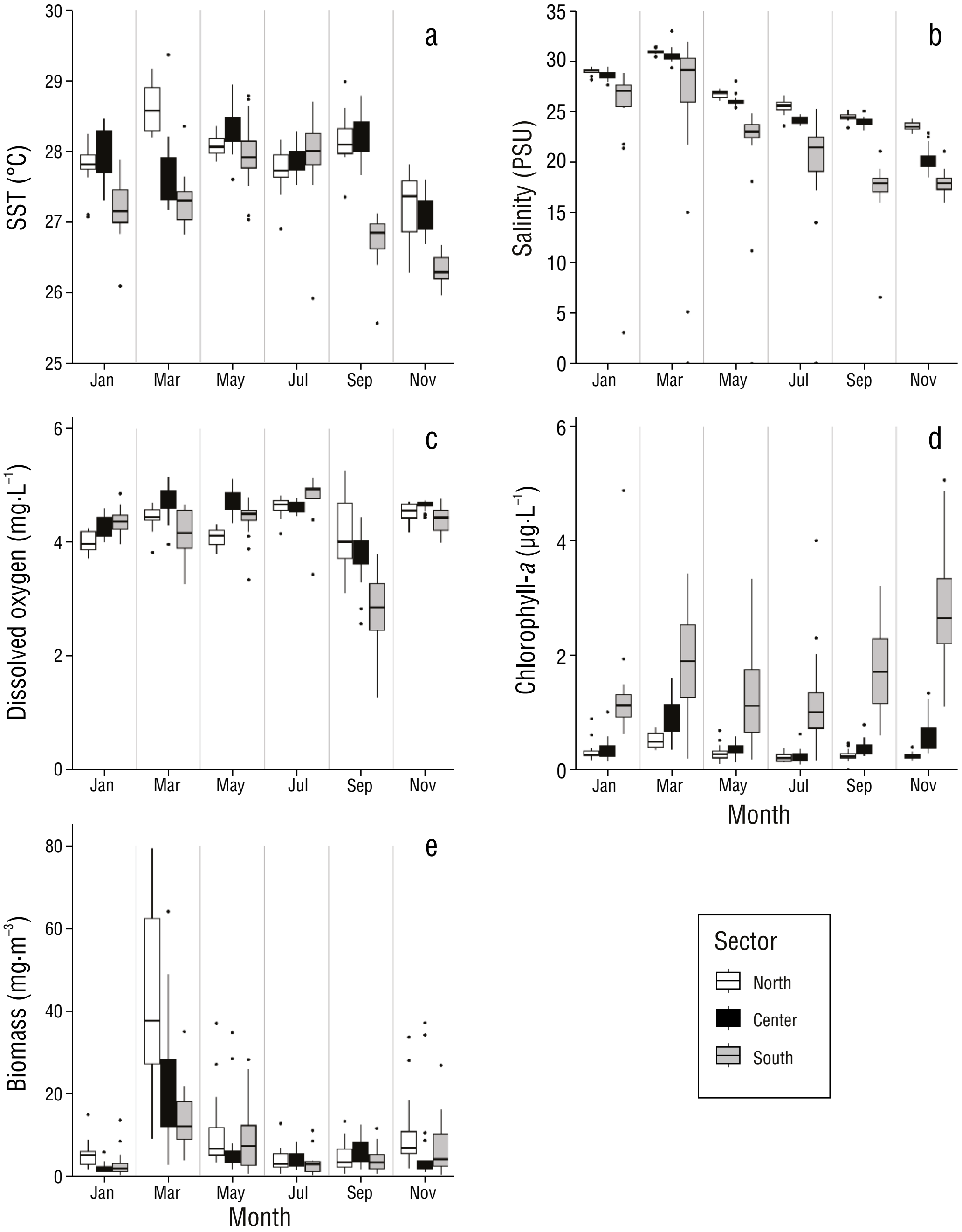

Figure 2. Spatio-temporal variation of environmental conditions in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022. Sea surface temperature (SST) (**a**), salinity (**b**), dissolved oxygen (**c**), chlorophyll-*a* (**d**), and zooplankton biomass (**e**).

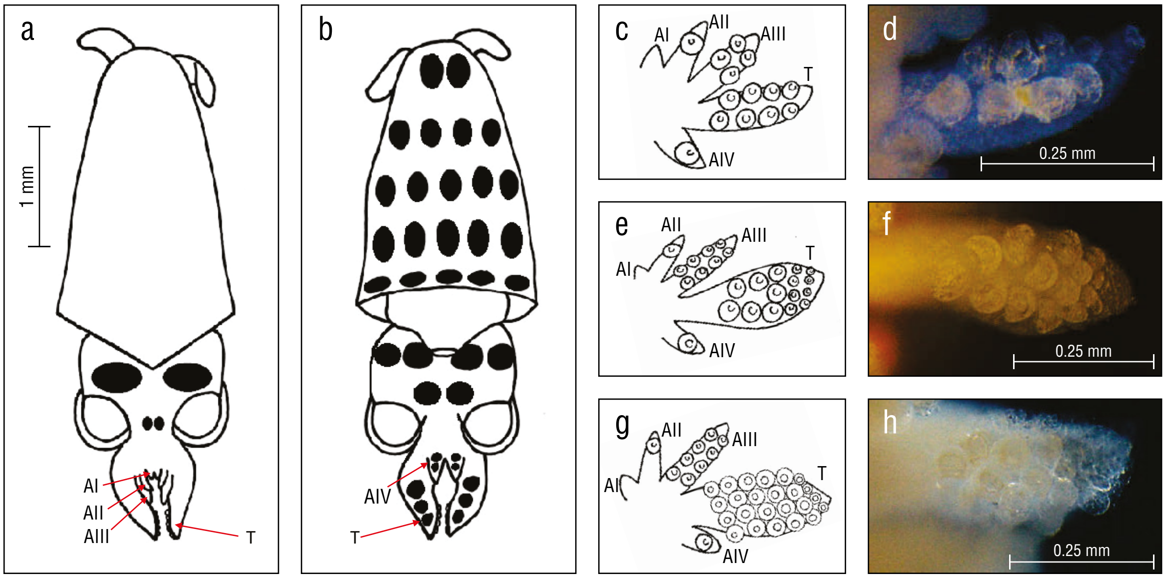

Figure 3. Generalized scheme of a paralarva of the family Loliginidae found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (*ML* = 2.8 mm). Dorsal view (**a**); ventral view (**b**); arm crown in oral view of Morphotypes I (**c**), II (**e**), and III (**g**); and details of the tentacular club of Morphotypes I (**d**), II (**f**), and III (**h**) (AI: arm I; AII: arm II; AIII: arm III; AIV: arm IV; T: tentacle).

of the species *Ancistrocheirus lesueurii* D'Orbigny, 1842 (*Ancistrocheirus* cf. *lesueurii*).

Individuals of the family Ommastrephidae Steenstrup, 1857 ($n = 28$; *ML* = 0.8–1.93 mm) (Fig. 5) were characterized by a pair of posterior paddle-shaped fins (Fig. 5a–b), a funnel locking apparatus shaped like an inverted "T," and a proboscis with 8 equal-sized distal suckers (Fig. 5c–d), without intestinal or ocular photophores. Individuals presenting these characteristics were identified as the species complex *S. oualaniensis* and *D. gigas* (S–D complex).

Paralarvae of the family Octopodidae D'Orbigny, 1842 ($n = 25$; *ML* = 0.73–1.45 mm) (Fig. 6) were characterized by a muscular, oval mantle without fins (Fig. 6a–b) and subequal arms with suckers arranged in a single row (Fig. 6c–d), characteristic of the genus *Octopus* Cuvier, 1797 (Sweeney et al. 1992, De Silva-Dávila 2013). The number and arrangement of suckers, as well as the DGCP (6 to 8 chromatophores, Fig. 6e–f), coincided with the observations of Castro-Fuentes et al. (2002) for the species *O. mimus* Gould, 1852 (Table 2); therefore, the individuals were identified as a form of the species (*Octopus* cf. *mimus*).

Abundance, distribution, and temporal variation

Paralarval abundance in the neritic environment of the NCP between January and November 2022 ranged from 0.6 to 9.2 Pl·1,000 m^{-3}, with a median of 0.7 Pl·1,000 m^{-3}. In most sampling events, low abundance values were obtained (<2.45 Pl·1,000 m^{-3}), although punctual peaks were observed in certain months and sectors (Fig. 7a). The highest abundance values were observed in March across the 3 sectors of the study area (north: 8.5 Pl·1,000 m^{-3}; center: 6.1 Pl·1,000 m^{-3}; south: 9.2 Pl·1,000 m^{-3}), mainly due to the contribution of the family Loliginidae in the south (7.9 Pl·1,000 m^{-3}) and center (3.0 Pl·1,000 m^{-3}) and of Octopodidae in the north (4.0 Pl·1,000 m^{-3}). In contrast, January, September, and November showed considerably lower abundances in the 3 sectors (<1.5 Pl·1,000 m^{-3}) (Fig. 7, Table 3). The analysis of variance detected significant differences in abundance among sampling months ($F = 10.097$; $P = 0.001$), but not among sectors ($F = 1.549$; $P = 0.259$), with March being the source of variation in abundance, showing significantly higher values than the others (Tukey post hoc, $P < 0.05$) (Table S4).

The composition of paralarval families identified showed variations among sampling months and sectors in the NCP (Fig. 7b, Table 3). In January, Ommastrephidae dominated in the northern sector, while Loliginidae and Octopodidae predominated in the center. In March, all families were recorded, with greater representativeness of Octopodidae in the north and Loliginidae in the central and southern sectors. In May, Ommastrephidae was dominant in the north, while Octopodidae and Ancistrocheiridae were evenly distributed in the center. In July, Ommastrephidae showed the highest representativeness in both the north and south, while Octopodidae and Loliginidae dominated in the center. In September, only

Table 1. Systematic list of cephalopod paralarval taxa identified in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022.

Phylum Mollusca Linaeus, 1758
Class Cephalopoda Cuvier, 1797
Subclass Coleoidea Bather, 1888

Superorder Decabrachia Boettger, 1952
Order Teuthida Naef, 1916
Suborder Myopsina D'Orbigny, 1841
Family Loliginidae Lesueur, 1821
Morphotype I
Morphotype II
Morphotype III
Suborder Oegopsina D'Orbigny, 1845
Family Ancistrocheiridae Pfeffer, 1912
Ancistrocheirus cf. *lesueurii* D'Orbigny, 1842
Family Ommastrephidae Steenstrup, 1857
S-D complex (*Sthenoteuthis oualaniensis–Dosidicus gigas*)

Superorder Octobrachia Fioroni, 1981
Order Octopoda Leach, 1818
Suborder Incirrina Grimpe, 1916
Family Octopodidae D'Orbigny, 1842
Octopus cf. *mimus* Gould, 1852

Octopodidae was recorded in the north, and in November Ommastrephidae was recorded in the south.

Complementarily, the frequency of occurrence of families showed marked spatial and temporal variations (Fig. 8, Table 3). Loliginidae exhibited the highest frequencies in the central and southern sectors, particularly in March (Fig. 8a), while Octopodidae showed high occurrence in both the north and center, especially during March and July (Fig. 8b). Ommastrephidae also showed marked occurrence in the north, reaching the highest frequencies in May and July (Fig. 8c). For its part, Ancistrocheiridae was the least frequent family in all sectors and sampling months (Fig. 8d).

DISCUSSION

The surface oceanographic conditions of the neritic environment of the NCP showed spatial and temporal variability, probably associated both with the dynamics of local precipitation and with the oceanographic processes characteristic of Panama Bight. According to Velásquez-Restrepo and Poveda (2019) and Valencia et al. (2024), the frequency of sunny days increases and precipitation levels decrease (350 to 400 mm·month^{-1}) in the NCP during the months of January and April, and therefore river discharges also decrease, which causes an increase in temperature and low variability in sea surface salinity. In contrast, maximum precipitation (650 to 750 mm·month^{-1}) occurs between June and November, increasing continental input and leading to the decrease of both variables. It is worth highlighting the spatial variability observed among sectors; the southern sector showed the greatest variability in salinity, along with the highest concentrations of chlorophyll-*a*. This behavior could be associated with the constant input of nutrients of continental origin from the discharge of the Baudó River, the third largest river in the region, with an estimated mean annual flow of 1,021.5 m^3·s^{-1} (Velásquez-Restrepo and Poveda 2019). In addition, this sector receives the highest annual precipitation, with 6,544 mm·year^{-1}, compared to the central and northern sectors, which receive 5,086 mm·year^{-1} (Lobo-Guerrero 1993, Restrepo 2006, Valencia et al. 2024), which intensifies river runoff during the rainy season and would explain the higher chlorophyll-*a* values recorded in November for this sector.

Among the families identified, Ommastrephidae, Ancistrocheiridae, and Octopodidae had already been previously reported in the Colombian Pacific (Vargas and López 2020). This study expands the knowledge of cephalopod paralarvae in the region by recording, for the first time, groups typical of coastal waters, such as *Octopus* cf. *mimus* (Octopodidae) and the family Loliginidae (morphotypes I, II, and III).

Regarding the family Loliginidae, records exist in the area of adults of the species *Lolliguncula argus*, *L. diomedeae*, and *L. panamensis*, which are considered of fishery and ecological importance (Gómez et al. 2003, Jereb and Roper 2010, Díaz et

Table 2. Chromatophore patterns in paralarvae of *Octopus mimus* (Octopodidae). Mean and standard deviation of mantle length of individuals (ML), chromatophore pattern of the mantle on the dorsal surface (DMCP), chromatophore pattern of the mantle on the ventral surface (VMCP), chromatophore pattern of the head on the dorsal surface (DHCP), chromatophore pattern of the digestive gland (DGCP), and chromatophore pattern of the siphon (SCP).

	Octopus mimus Castro-Fuentes et al. (2002)	*Octopus* cf. *mimus* (This study)
ML	1.53 ± 0.08	1.14 ± 0.21
DMCP	3 to 7	7 to 10
VMCP	24 to 31	20 to 33
DHCP	10 (2 + 4 + 4)	10 (2 + 4 + 4)
DGCP	6 to 8	6 to 8
SCP	6 (4 + 2)	5 (3 + 2) and 6 (4 + 2)

al. 2014). Nevertheless, no official fishery records exist (De la Hoz et al. 2017). Of these 3 species, only the paralarvae of *L. diomedeae* (1.20–1.39 mm ML) have been described, which present 2 rows of suckers on the tentacles and arm III and a single sucker on arms II and IV (Fernández-Álvarez et al. 2017). This arrangement of suckers is compatible with Morphotype I described in this study (arm III and tentacle with 2 rows of suckers and a single sucker on arms II and IV), so it could presumably correspond to the same species. It should be clarified that to confirm or discard such a situation, the corresponding molecular analyses are necessary, which, due to the fixation of the samples in formalin, could not be carried out in the present study. On the other hand, due to the absence of morphological descriptions of the paralarvae of *L. argus* and *L. panamensis*, it was not possible to associate them with morphotypes (II or III) described. The detailed description of the tentacular club of Morphotypes I, II, and III described in this family (Loliginidae) provides valuable morphological information that will facilitate future comparisons and taxonomic studies, thus contributing to the advancement of knowledge of the paralarvae of this family in the region.

In the family Ancistrocheiridae, the presence of photophores on the mantle, head, arms, and tentacles is a diagnostic character from 5–7 mm ML, as well as hooks on the arms and tentacles from 9 mm ML (Sweeney et al. 1992, Granados-Amores 2008). Given the size of the paralarvae examined belonging to this family (<2 mm ML), it was not possible to observe these characteristics. De Silva-Dávila (2013) described paralarvae of this family at sizes similar to those observed in the present study (2 mm LM), and we confirmed the correspondence in the peduculated arm crown covered with gelatinous tissue, as well as in the formula of the arms at 1.1 mm LM (Table S3), which suggests its identification as *Ancistrocheirus* cf. *lesueurii*. Currently, this family is considered monospecific; however, the variation in the arrangement of photophores in paralarvae from different oceans and the lack of critical comparisons with adult specimens suggest the possible existence of more than one species (Sweeney et al. 1992, Arnold et al. 2025). To contribute to this point, it would be valuable to have larger specimens from different regions to carry out morphological and genetic comparisons and, thus, provide more solid taxonomic conclusions.

Regarding the family Ommastrephidae, in the Colombian Pacific, *D. gigas* and *S. oualaniensis* coexist spatially and their paralarvae are morphologically similar at sizes <4 mm ML, showing proboscis suckers of equal size; in both cases, the intestinal or ocular photophores that allow for species differentiation are not yet present, so they are grouped as a species complex (S-D Complex) (Ramos-Castillejos et al. 2010, De Silva-Dávila et al. 2015, Sánchez-Velasco et al. 2016). The paralarvae examined from this family measured between 0.8 and 1.93 mm ML and had these characteristics, which confirms their identification as S-D Complex. It is worth noting that the chromatophore pattern of the mantle and head in dorsal view in the S-D Complex paralarvae identified in this study is similar to that reported by Ramos-Castillejos et al. (2010) for *D. gigas* at 3.2 mm ML (Table S3). However, in their description, Ramos-Castillejos et al. (2010) include a morphometric analysis corroborated molecularly. In the present work, such analyses were not contemplated, which prevents making a

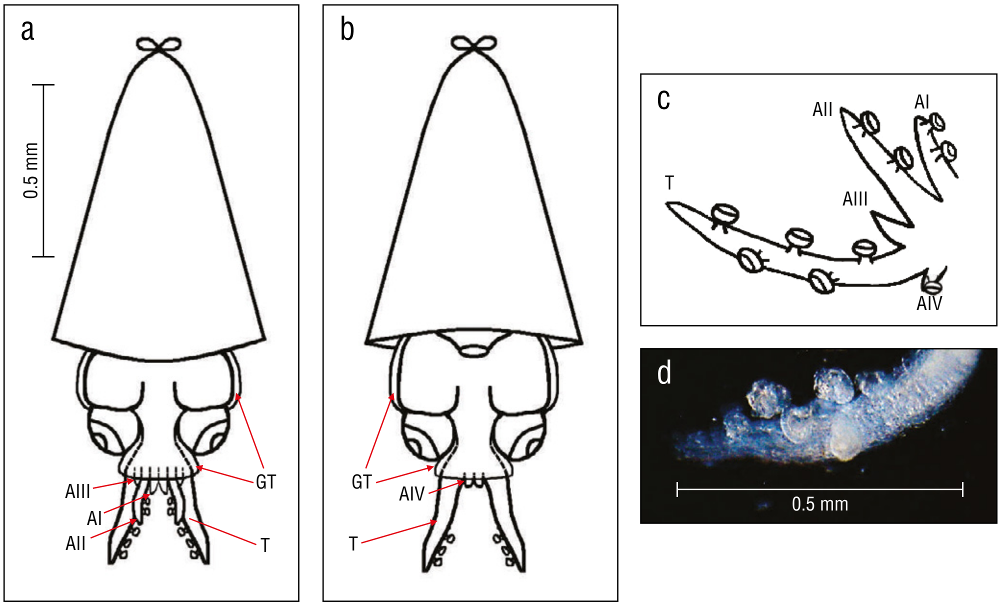

Figure 4. Scheme of a paralarva of the family Ancistrocheiridae: *Ancistrocheirus* cf. *lesueurii* found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (*ML* = 1 mm). Dorsal view (**a**), ventral view (**b**), arm crown in oral view (**c**), and detail of the tentacular club (**d**) (AI: arm I; AII: arm II; AIII: arm III; AIV: arm IV; T: tentacle; GT: gelatinous tissue).

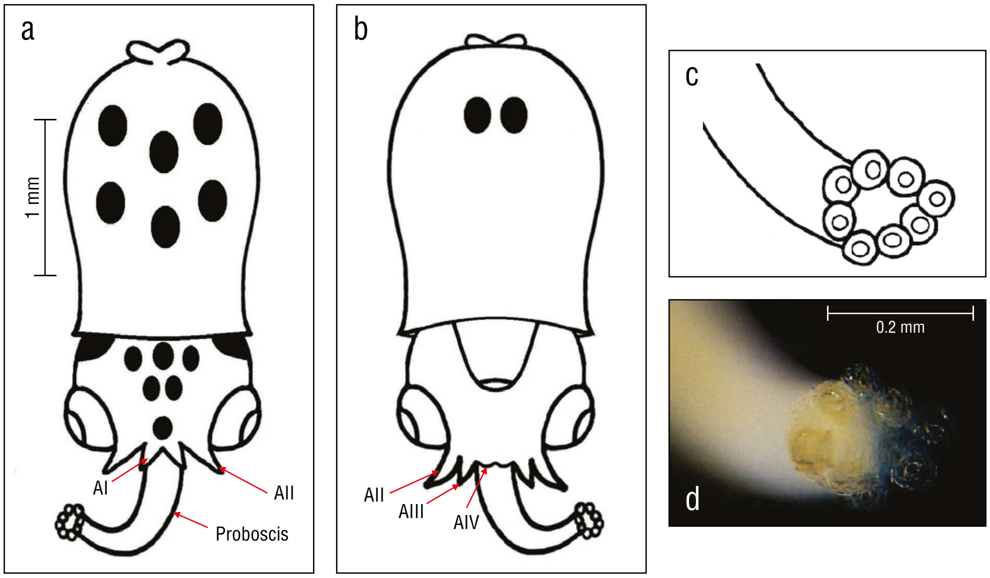

Figure 5. Scheme of a paralarva of the family Ommastrephidae (S–D complex: *Sthenoteuthis oualaniensis–Dosidicus gigas*) found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (ML = 1.69 mm). Dorsal view (**a**), ventral view (**b**), and detail of the proboscis (**c** and **d**).

direct comparison between both studies. The molecular and morphometric approach could be a future line of research that contributes more specifically to the separation of the S–D complex and supports morphological observations, providing greater certainty in taxonomic identification.

The DGCP observed in the specimens of the family Octopodidae in this study corresponds to that described for *O. mimus* (Castro-Fuentes et al. 2002) and *O. hubbsorum* (Montero-Ruíz et al. 2023), which suggests a case of synonymy, as affirmed by Pliego-Cárdenas et al. (2014) based on mitochondrial molecular data. To take a position in this regard with the paralarvae of the Colombian Pacific, further studies are required that include morphological and molecular identification, as well as the description of habitat and distribution of both adults and paralarvae.

During the study period, the highest abundance of paralarvae coincided with the dry season of the NCP, in which the upwelling of subsurface waters from the Panama Bight promotes an increase in productivity and zooplankton biomass in the region (Valencia et al. 2019). In this period, high abundance values have already been reported for other zooplankton organisms in neritic environments of the Colombian Pacific due to the increase in food availability (Valencia and Giraldo 2009; Giraldo et al. 2014; Jerez-Guerrero et al. 2017; Valencia et al. 2019, 2024). This trend of temporal variation in paralarval abundance associated with upwelling episodes has already been documented in several regions of the eastern Pacific (Vega et al. 2000, De Silva-Dávila et al. 2015, Aceves-Medina et al. 2017, García-Guillén et al. 2018, Ruvalcaba-Aroche et al. 2018) and the Atlantic Ocean (González et al. 2005, Moreno et al. 2009, Vidal et al. 2010, Otero et al. 2016), and has been related to increased survival, growth, and recruitment of cephalopod populations (Araujo and Gasalla 2018).

In this study, the family Loliginidae was the most abundant and frequent in the central and southern sectors of the NCP, where the continental shelf is wider and shallower and presents an important freshwater influx. Loliginids are characterized by inhabiting shallow coastal zones of low salinity and by preferring soft or sandy bottoms for spawning (Rodrigues and Gasalla 2008, Zeidberg et al. 2012, Fernández-Álvarez et al. 2018). Therefore, their presence in these sectors reflects the ecological habits of the group. On the other hand, the absence of paralarvae of this family in the northern sector may be related to the geomorphological characteristics of this area, which presents a narrow and relatively deep continental shelf with rocky bottoms. In this regard, Martínez-Soler et al. (2021) justified the absence of this family in zones that do not offer a suitable habitat for the benthic reproduction characteristic of the group.

In addition to the above, members of this family are known to migrate for feeding or reproductive purposes, which appears to be part of their life strategy to ensure the development and growth of their paralarvae. This has been reported for several species in different regions; for example, *L. panamensis* migrates to areas with greater enrichment and food availability (Arizmendi-Rodríguez et al. 2012), and *L. diomedeae* and *L. argus* exhibit opportunistic reproductive migrations in response to variations in environmental conditions (León-Guzmán et al. 2020, Olvera et al. 2023). This trend could explain the greater abundance of Loliginidae paralarvae in March, a period that corresponds to the dry season and the highest zooplankton biomass values in the study area. This suggests a synchronicity between the reproductive events of this family and periods of high secondary productivity associated with upwelling conditions, which increase food availability and favor paralarvae survival. On the other hand, although the highest chlorophyll-*a* concentrations were recorded in the southern sector during the rainy season, indicating high primary productivity, the characteristic increase in precipitation and river inflow of this season generates low salinity and greater turbidity in the water (Valencia et al. 2024). This could reduce secondary productivity and, therefore, the availability of food for paralarvae, which would explain the absence of the Loliginidae family in September and November.

On their part, the family Octopodidae is characterized by having different lifestyles. Most species are benthic and inhabit rocky and shallow areas. Within this group, some exhibit a planktonic free-swimming phase after hatching, such as paralarvae, while others hatch as more developed benthic juveniles (Jereb et al. 2016). These ecological preferences coincide with the geomorphological characteristics of the northern and central sectors of the study area, which present a narrow continental shelf with coral and rocky ecosystems dominating the subtidal and coastal landscape (Díaz et al. 2016). In this investigation, paralarvae of this family were present in almost all sampling months, except November, which coincides with the reproductive biology of the group. It has been documented that populations of *O. mimus* and *Octopus hubbsorum* spawn throughout the year, with defined peaks that vary among regions. For example, in the Gulf of California, these peaks occur in September and December (Pliego-Cárdenas et al. 2011); in the central Mexican Pacific, in June (López-Uriarte and Ríos-Jara 2009); and in the southern Mexican Pacific, between March–June and October–November (Alejo-Plata et al. 2009, Alejo-Plata and Gómez 2015). In addition, it has been documented that variation in the reproductive biology of *O. hubbsorum* depends on the environmental conditions of each region, with temperature being the most important factor (Alejo-Plata and Gómez 2015, Montero-Ruíz et al. 2023). Therefore, the high occurrence of this family could be related to the warm waters characteristic of the NCP and the low variability of SST throughout the study period (26–28 °C). In this sense, the higher abundance observed in March could be associated with the increase in food availability characteristic of this period, which would favor optimal conditions for paralarval development.

Paralarvae of the family Ommastrephidae (S–D complex) are considered the most abundant in surface-type tows (Staaf et al. 2013). Nevertheless, in this study their abundance and frequency of occurrence were lower than those recorded for Loliginidae and Octopodidae in most sectors and months of sampling. This finding contrasts with what has been previously reported in the Colombian Pacific (Vargas and López 2020) and the Mexican Pacific (Granados-Amores et al. 2010, García-Guillén et al. 2018), where this family has been the most representative group. This difference could be attributed to the presence of taxa with greater affinity to coastal environments, such as loliginid squids and octopuses, which were mainly highlighted in the southern and northern sectors, respectively. Ommastrephidae may have a lower probability of being captured in coastal waters due to their pelagic behavior. The recurrent presence of paralarvae of the S–D

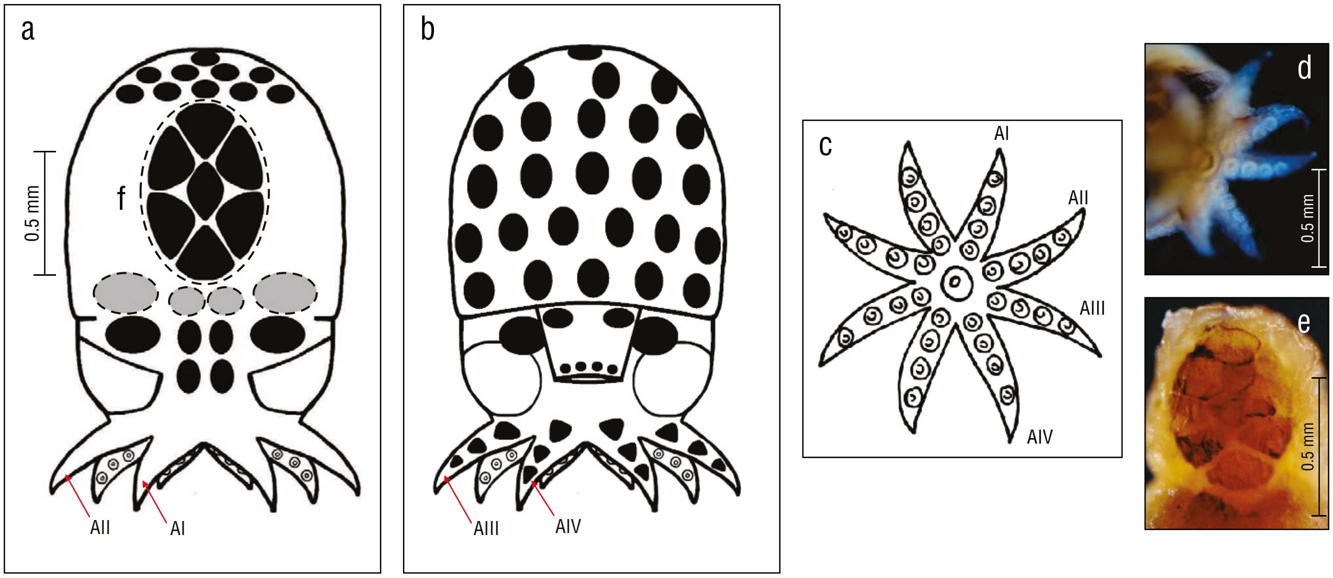

Figure 6. Scheme of a paralarva of the family Octopodidae (*Octopus* cf. *mimus*) found in the neritic environment of the northern Colombian Pacific (NCP) between January and November 2022 (*ML* = 1.3 mm). Dorsal view (**a**), ventral view (**b**), arm crown in oral view (**c** and **d**), and digestive gland with chromatophore pattern (**e** and **f**).

Table 3. Abundance and frequency of occurrence (*FO*) of cephalopod paralarval families (Pl) identified between January and November 2022 in the neritic environment of the northern Colombian Pacific (NCP) (N: north; C: center; S: south).

		Abundance (Pl·1,000 m^{-3}) | *FO* (%)			
Month	Sector	Loliginidae	Ommastrephidae	Ancistrocheiridae	Octopodidae
January	N	0.0	0.5 | 5.6	0.0	0.0
	C	0.5 | 11.1	0.3 | 5.6	0.0	0.5 | 11.1
	S	0.0	0.0	0.0	0.0
March	N	0.4 | 5.6	1.8 | 5.6	0.4 | 5.6	4.0 | 22.2
	C	3.0 | 27.8	0.0	0.4 | 5.6	1.1 | 16.7
	S	7.9 | 41.2	0.0	1.3 | 11.8	0.0
May	N	0.0	1.4 | 16.7	0.0	0.7 | 11.1
	C	0.0	0.0	0.3 | 5.6	0.3 | 5.6
	S	0.0	0.0	0.0	0.0
July	N	0.0	3.1 | 22.2	0.0	1.1 | 22.2
	C	0.4 | 5.6	0.0	0.0	0.4 | 5.6
	S	0.0	1.1 | 11.8	0.0	0.0
September	N	0.6 | 5.6	0.0	0.0	0.0
	C	0.0	0.0	0.0	0.0
	S	0.0	0.0	0.0	0.0
November	N	0.0	0.0	0.0	0.0
	C	0.0	0.0	0.0	0.0
	S	0.0	0.5 | 6.7	0.0	0.0

complex in most sampling months coincides with what has been reported for adults of *D. gigas* in the Colombian Pacific, which exhibit continuous reproductive activity throughout the year (Córdoba-Rojas et al. 2024). Furthermore, the increase in paralarval abundance observed in March could be related to the period of greater gonadal maturity recorded in the first months of the year by the same authors. Although in this study the direct effect of environmental variables was not evaluated nor mesoscale structures analyzed in relation to their abundance or distribution, previous studies have shown that paralarvae of the S–D complex are associated with the presence of anticyclonic eddies and convergence zones (Sánchez-Velasco et al. 2016, Ruvalcaba-Aroche et al. 2020). These structures appear to influence the distribution and aggregation of paralarvae, as they provide a favorable habitat for their retention, survival, and initial development (Ruvalcaba-Aroche et al. 2020). Considering that *D. gigas* is the main squid species captured globally (FAO 2024) and that in the Colombian Pacific it has gained relevance as a potential fishery resource for artisanal fishing (Díaz et al. 2014, Villanueva and Flores-Nava 2019, Córdoba et al. 2024), it is fundamental to continue studies that allow monitoring spatial and temporal variation of paralarvae in the study area in order to deepen knowledge of the ecology and reproductive biology of adults. Considering its greater abundance in surface tows, this sampling method could represent a low-cost and high-efficiency tool for monitoring its early stages in the Colombian Pacific, as suggested by García-Guillén et al. (2018) in their study of the Mexican Pacific.

The low representativeness and frequency of the family Ancistrocheiridae (*Ancistrocheirus* cf. *lesueurii*) could be related to its oceanic habitat, which reduces the probability of finding it in neritic environments. This coincides with what has been reported in the Colombian Pacific (Vargas and López 2020) and the Mexican Pacific (De Silva-Dávila et al. 2015), where Ancistrocheiridae represented less than 1% of the total taxa. Being a group of low abundance worldwide, its biology and ecology are poorly known, highlighting the importance of its paralarvae as a way to increase knowledge of its reproductive biology in the study regions.

Most paralarvae in this study had sizes smaller than 2 mm ML, which indicates recent spawning (Sweeney et al. 1992). These sizes coincide with what was found by Vargas and López (2020) in the Colombian Pacific, who mention that spawning and hatching are more frequent in the neritic zone. These sizes could also be due to the type of tow used for zooplankton collection, since as paralarvae grow they may occupy adult habitats. Therefore, an alternative for future research could be to complement surface tows with oblique tows, since the latter are usually more effective in providing a more complete view

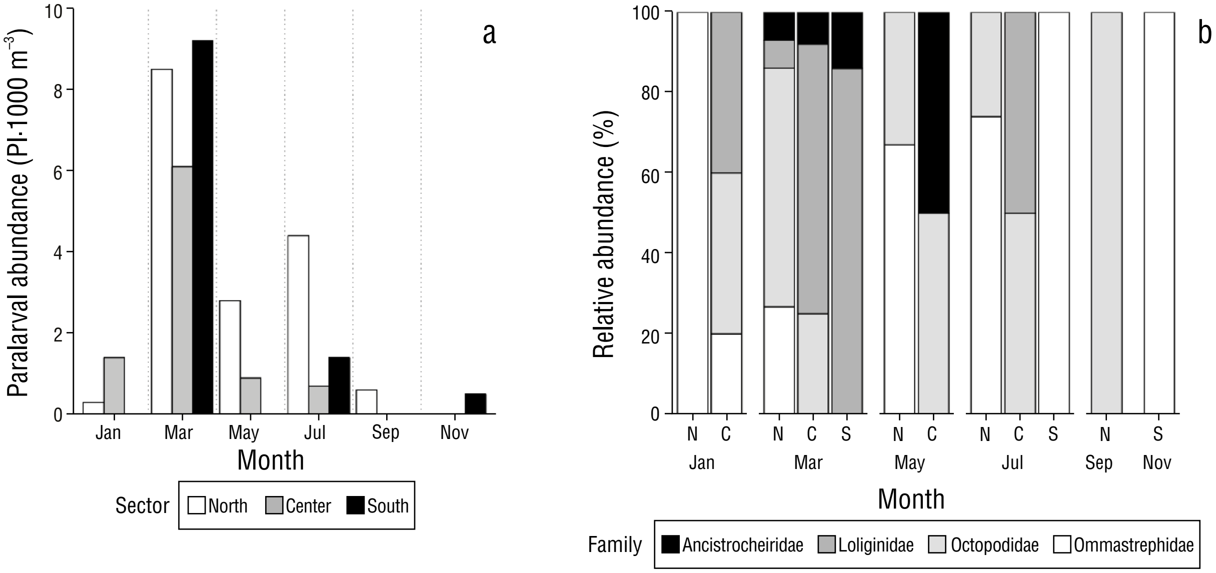

Figure 7. Spatio-temporal variation of cephalopod paralarval abundance found between January and November 2022 in the neritic environment of the northern Colombian Pacific (NCP). Paralarval abundance (Pl·1,000 m^{-3}); dotted lines represent separation of sampling months (**a**). Relative abundance of families recorded (N: north; C: center; S: south) (**b**).

of the paralarval community, as they capture more developed individuals, as well as greater diversity and species richness (De Silva-Dávila et al. 2015, García-Guillén et al. 2018). On the other hand, it is important to mention that the small sizes of the individuals found made paralarval identification difficult, since key taxonomic structures are not developed until larger sizes in many taxa (Camarillo-Coop 2006, Zaragoza et al. 2015). In addition, the lack of information on the reproductive biology and ecology of cephalopods in the Colombian Pacific, the high plasticity of the group, and the lack of morphological descriptions of paralarvae aggravate this situation, as they increase uncertainty in identification (Guarneros-Narváez et al. 2022). Therefore, to complement biological information on this important taxonomic group, it is necessary to implement molecular and genetic tools to better understand community structure, as has been done in the Gulf of Mexico (Guarneros-Narváez et al. 2022).

Conclusions

The taxonomic composition and the spatio-temporal variation patterns of paralarvae in the neritic environment of the NCP during 2022 were consistent with expectations based on adults reported in the region and in other areas of the Eastern Pacific. In this study, paralarval species richness in the NCP increased with the first record of the family Loliginidae, represented by 3 clearly differentiated morphotypes (Morphotype I, Morphotype II, and Morphotype III), and the first record of *Octopus* cf. *mimus*. It was demonstrated that the ecological behavior of each group, the hydrology, and the geomorphological characteristics of the study area influenced the taxonomic composition and distribution of the groups. In addition, it was confirmed that the highest abundance of paralarvae occurred during the upwelling season, evidencing synchrony between adult reproductive events and the conditions that favor paralarval development. It was also shown that the presence of Octopodidae and Loliginidae may be related to the availability of suitable habitats for their reproduction and the development of early stages. Therefore, the variety of ecosystems in the NCP constitutes a crucial and relevant factor for the conservation of these groups, for which biological and ecological knowledge is still limited.

The presence of paralarvae from groups considered of commercial interest, such as Loliginidae, Ommastrephidae, and Octopodidae, suggests the existence of active populations in the NCP that could become relevant for artisanal fishing activities. These findings highlight the importance of increasing knowledge of their reproductive biology and ecology in order to have the technical information necessary to propose conservation strategies and appropriate management of these resources. The limitations in the morphological identification of paralarvae reflect the need to complement it with genetic studies to achieve greater certainty in taxonomic identification. This work lays the foundation for understanding patterns of variation in paralarval abundance both in the neritic environment of the NCP and in the ETP and serves as a tool for future research aimed at increasing knowledge of cephalopods in the region.

English translation by the authors.

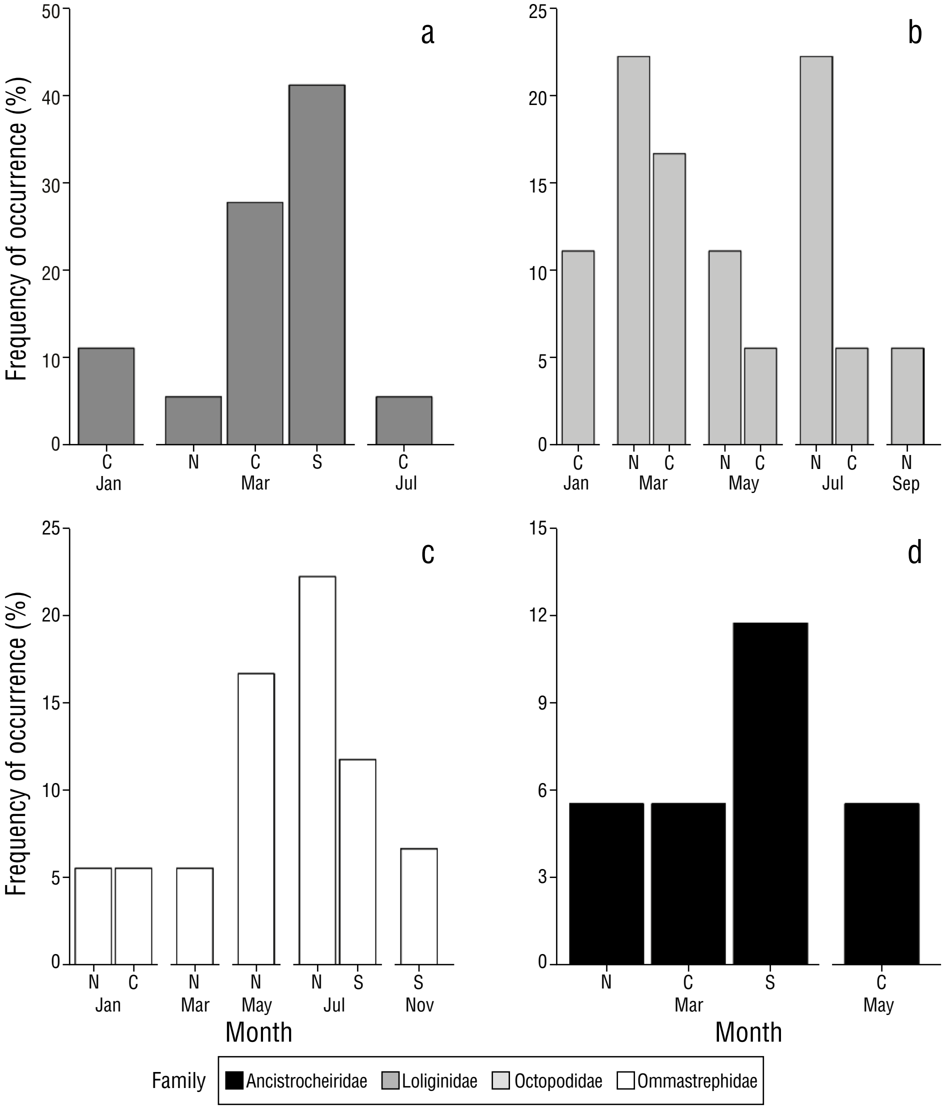

Figure 8. Spatio-temporal variation of frequency of occurrence (*FO*) of cephalopod paralarval families found between January and November 2022 in the neritic environment of the northern Colombian Pacific (NCP) (N: north; C: center; S: south). Loliginidae (**a**), Octopodidae (**b**), Ommastrephidae (**c**), and Ancistrocheiridae (**d**).

Declarations

Supplementary Material

Supplementary material for this study can be downloaded from: https://cienciasmarinas.com.mx/index.php/cmarinas/article/view/3538/420421262.

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Conflict of interest

The authors of this manuscript declare that we have no conflicts of interest.

Author contributions

Conceptualization: MD, AG; Data curation: MD; Formal analysis: MD; Funding acquisition: AG; Investigation: MD, AG; Methodology: MD, AG, AMR; Resources: AG, MD; Supervision: AMR, AG; Validation: AMR, AG; Visualization: MD; Writing—original draft: MD; Writing—review & editing: MD, AMR, AG.

Data availability

The data for this study are available from the corresponding author upon prior request.

Ethical approvals and permits for studies involving animals

The collection of zooplankton samples conducted for this work falls within the permit granted for the Biology academic program of Universidad del Valle, described in Resolution 1070 of August 28, 2015, issued by the National Authority of Environmental Licenses, which authorizes the collection and mobilization of specimens of wild biodiversity species within national territory, exclusively for the execution of non-commercial scientific research projects.

Use of AI tools

The authors did not use any AI tools in this work.

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Ciencias Marinas (2025), 51:e3564 **Research Article**

Spatiotemporal dynamics of the microbial community in the water column of Ojo de Liebre Lagoon, Baja California Sur, Mexico

Aileen Pimentel-Cabrera[1], Natalie Millán-Aguiñaga[1], Jorge López-Calderón[1], Marlene N Cardoza-Contreras[1], Monica Torres-Beltrán[1]*

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CORRESPONDING AUTHOR
* E-mail: monica.torres.beltran@uabc.edu.mx

[1] Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, 22860 Ensenada, Baja California, Mexico.

ABSTRACT. Microbial communities in hypersaline environments play a key role in biogeochemical cycles and ecological productivity. This is the first study to characterize the composition, structure, and metabolic potential of the prokaryotic community in the water column of Ojo de Liebre Lagoon (Baja California Sur, Mexico), a hypersaline ecosystem of ecological and socioeconomic importance. From the information obtained from 4 sampling campaigns (2021–2022) conducted at 18 stations, we analyzed physicochemical variables (salinity, temperature, and density) and sequenced the V4–V5 region of the 16S rRNA gene. Data were processed using QIIME2, and metabolic potential was inferred via PICRUSt2. The community was dominated by Actinobacteriota, Bacteroidota, Cyanobacteriota, Pseudomonadota, and Verrucomicrobiota, with spatiotemporal differences linked to temperature (r^2 = 0.77, P = 0.001) and salinity (r^2 = 0.39, P = 0.014) gradients. Rare taxa (<1% abundance), such as Thermoanaerobaculales and Desulfobacterota, contributed to diversity, particularly in November. Metabolic inference revealed significant pathways ($P < 0.05$), including vitamin B6 biosynthesis, chitin degradation, and nitrate reduction, suggesting roles in biogeochemical cycles and adaptation to extreme conditions. The prokaryotic community structure in the lagoon responded to physical and chemical variations, with a stable taxonomic core and rare taxa enhancing diversity under specific conditions. The inferred metabolic potential highlights their participation in biogeochemical processes and their capacity to degrade complex organic compounds. These results establish a baseline for understanding microbial dynamics in hypersaline systems and their impact on ecosystem function.

Key words: hypersaline environments, prokaryotic diversity, 16S rRNA sequencing, metabolic inference, biogeochemical cycles, spatiotemporal variation, Ojo de Liebre Lagoon.

INTRODUCTION

Microbial communities are made up of microorganisms that interact and perform a variety of functions in a space defined by physicochemical factors, where they find the necessary conditions for their survival (Díaz and Wacher 2003, Begon et al. 2006, Callieri et al. 2018). Microbial communities are key to ecological dynamics in the biosphere due to the close relationship between their composition, structure, and metabolism and the biogeochemical cycles of the planet. For example, due to their phylogenetic and genomic diversity, microbial communities carry out metabolic functions that are a crucial component in the continuous production and recycling of organic matter and nutrients; these functions promote energy flows between different trophic levels and, in addition, regulate a variety of biogeochemical transformations (Rousk and Bengtson 2014, Kost et al. 2023). Thus, evaluating the variations in the composition and structure of microbial communities that result from physicochemical factors allows us to predict the metabolisms that contribute to the energy flow in an ecosystem from the base of the food chain and, therefore, to understand the capacity of an ecosystem to sustain life.

The metabolic versatility of prokaryotic microorganisms has allowed them to adapt to virtually any ecosystem, including marine environments with physical and chemical conditions

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that exceed average salinity, temperature, and pressure and are therefore considered extreme environments (Oliart-Ros et al. 2016). Hypersaline water bodies are aquatic environments characterized by a salt concentration significantly higher than that of average seawater (35 PSU) (Karleskint et al. 2010). From an environmental and ecological perspective, hypersaline water bodies harbor a specialized biodiversity of microorganisms that are adapted to these high-salinity conditions, which enables them to survive and maintain ecosystem functionality (Oren 2002, 2010). Prokaryotic microbial communities in hypersaline environments show particular composition and structure characteristics; above all, these communities exhibit diverse adaptations (Kimbrel et al. 2018) that allow them to maintain essential metabolic activities, such as protein synthesis and DNA replication, under these conditions. Furthermore, these microorganisms exhibit specialized metabolic strategies, such as osmoregulation through the accumulation of compatible solutes and the production of exopolysaccharides, to maintain their osmotic balance (Oren 2002, 2008).

However, due to their sensitivity to environmental disturbances, hypersaline water bodies and the microorganisms that inhabit them can serve as indicators of environmental, climatic, and anthropogenic alterations, by reflecting these in changes in their composition and structure with effects on their metabolism that transcends as impacts on the function of the ecosystem (Ventosa et al. 1998). For example, many hypersaline bodies, such as coastal salt flats, are used for salt production, providing employment and important economic resources to local communities. At the same time, due to their unique enzymes and compounds, which could be applied in industries such as pharmaceuticals, cosmetics, and biotechnology, the microorganisms in these environments are of biotechnological interest (Ghosh et al. 2019). Therefore, culturally and historically, hypersaline ecosystems represent unique natural heritages that require conservation and protection to maintain their biodiversity and the ecosystem services they provide (Ventosa et al. 1998, Arahal et al. 2007). Thus, to better understand their ecological functions and maximize their benefits to society, it is essential to conserve and study these water bodies.

Ojo de Liebre Lagoon, located in the municipality of Mulegé, Baja California Sur, Mexico, is a shallow coastal lagoon (5–12 m) characterized by its hypersalinity (Villa-Guerrero 2019), which is mainly explained by the combination of high temperatures and winds that accelerate the evaporation process. In addition, the scarcity of rainfall for most of the year in the region results in a lack of freshwater input. Together, these factors create a salinity gradient, with values increasing towards the head of the lagoon, where salinity levels of up to 47 PSU have been recorded (Contreras 1985). This hypersaline lagoon is part of the El Vizcaíno Biosphere Reserve (REBIVI, for its acronym in Spanish) and is recognized as a World Heritage Site by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) due to its importance in terms of ecological interactions and socioeconomic activities. For example, it serves as a refuge for various bird species and the Gray Whale (*Eschrichtius robustus*) during its migration, and it provides habitat for endangered species, such as the Green Turtle (*Chelonia mydas*) (Bocanegra-Castillo 1998).

In addition to its ecological value, Ojo de Liebre Lagoon sustains a number of economic activities for local communities. An important economic activity in the region is the sustainable fishing of species, such as finfishes, the Maura Pen Shell (*Atrina maura*), and the Chocolata Clam (*Megapitaria squalida*) (Crespo-Guerrero and Jiménez-Pelcastre 2016). Tourism also boosts the local economy; specifically, the annual migration of the Gray Whale facilitates social interactions that attract visitors from around the world (Ponce-López 2002, Bermúdez-Almada 2003). Another crucial source of income is the presence of the largest solar saltworks in the world, with 303.51 km² of salt ponds; however, there is concern about brine spills and their potential to alter the physicochemical composition of the water (Ponce-López 2002).

Due to the above, prokaryotic microbial communities in the water column play a fundamental role in the functioning and health of ecosystems such as Ojo de Liebre Lagoon. These communities regulate energy flows, biogeochemical cycles, and organic matter remineralization, which enable diverse ecological and socioeconomic interactions. Nonetheless, the composition and structure of the prokaryotic microbial community in the water column of this ecosystem are still unknown. Therefore, the main objective of this study was to provide novel information on the composition, structure, and spatiotemporal changes of the prokaryotic microbial community to create baseline knowledge that facilitates assessment of the biogeochemical aspects of Ojo de Liebre Lagoon from the trophic base, which support its characteristic ecological and socioeconomic interactions.

Materials and methods

Sample collection

Four samplings were conducted in Ojo de Liebre Lagoon, during the months of August and November 2021 and March and June 2022. At each sampling event, water samples (4 L) were collected at 18 stations distributed along the lagoon (Fig. 1a), and data of physicochemical variables, such as salinity, temperature, density, and depth, were recorded using a CastAway YSI CTD (Yellow Springs Instruments, Yellow Springs, USA). Water samples were taken using a 5-L Niskin bottle at a maximum depth of 2 m from the surface. The water was then transferred to 5-L Nalgene dark bottles using a funnel covered with a 200-µm nylon mesh. The bottles were stored on ice until the water was filtered and processed to obtain biomass concentrations. To obtain the final biomass concentration, up to 2 L of water were filtered using 0.2-µm Track-end membrane filters (Nucleopore, Pleasanton, USA). The filters were stored at –20 °C until the subsequent DNA extraction in the laboratory.

Molecular analysis

To extract DNA, we used the DNeasy PowerWater® kit (Qiagen, Venlo, The Netherlands) and its Quick-Start protocol, which was modified with an additional incubation step at 65 °C for 60 min after the lysis buffer was added and prior to the mechanical lysis step. Subsequently, the total extracted DNA was quantified using a NanoDrop (Thermo Fisher Scientific, Waltham, USA). The total DNA was sent to the Integrated Microbiome Resource (IMR) center at Dalhousie University, Halifax, Canada, for library generation and 16S rRNA gene amplicon sequencing on the Illumina MiSeq platform (2 × 250 PE). According to the quality control protocols of IMR, samples with concentrations greater than or equal to 1 $\text{ng}\cdot\mu\text{L}^{-1}$ and a minimum value of 260/280 equal to 1.8 were considered. The libraries were generated using the V4–V5 region, with the universal primers 515FB (GTGYCAGCMGCCGCG-GTAA) and 926R (CCGYCAATTYMTTTRAGTTT) of the 16S rRNA gene (Parada et al. 2015, Walters 2015). According to IMR protocols, amplicon fragments were amplified by duplicate PCR from template DNA, using independent dilutions and the high-fidelity polymerase Phusion Plus (Sigma Aldrich, St. Louis, USA). A single round of PCR was performed using fusion primers containing Illumina adapters (San Diego, USA), indexes (identification codes), and V4–V5 universal primers, which enabled simultaneous amplification and library preparation for sequencing. PCR products were visually verified by electrophoresis on a high-throughput Nimbus Select workstation (Hamilton Company, Reno, USA) using Coastal Genomics analytical gels (Burnaby, Canada).

Bioinformatic analysis

An amplicon analysis of the 16S rRNA gene was performed using the QIIME2 platform to evaluate the composition and

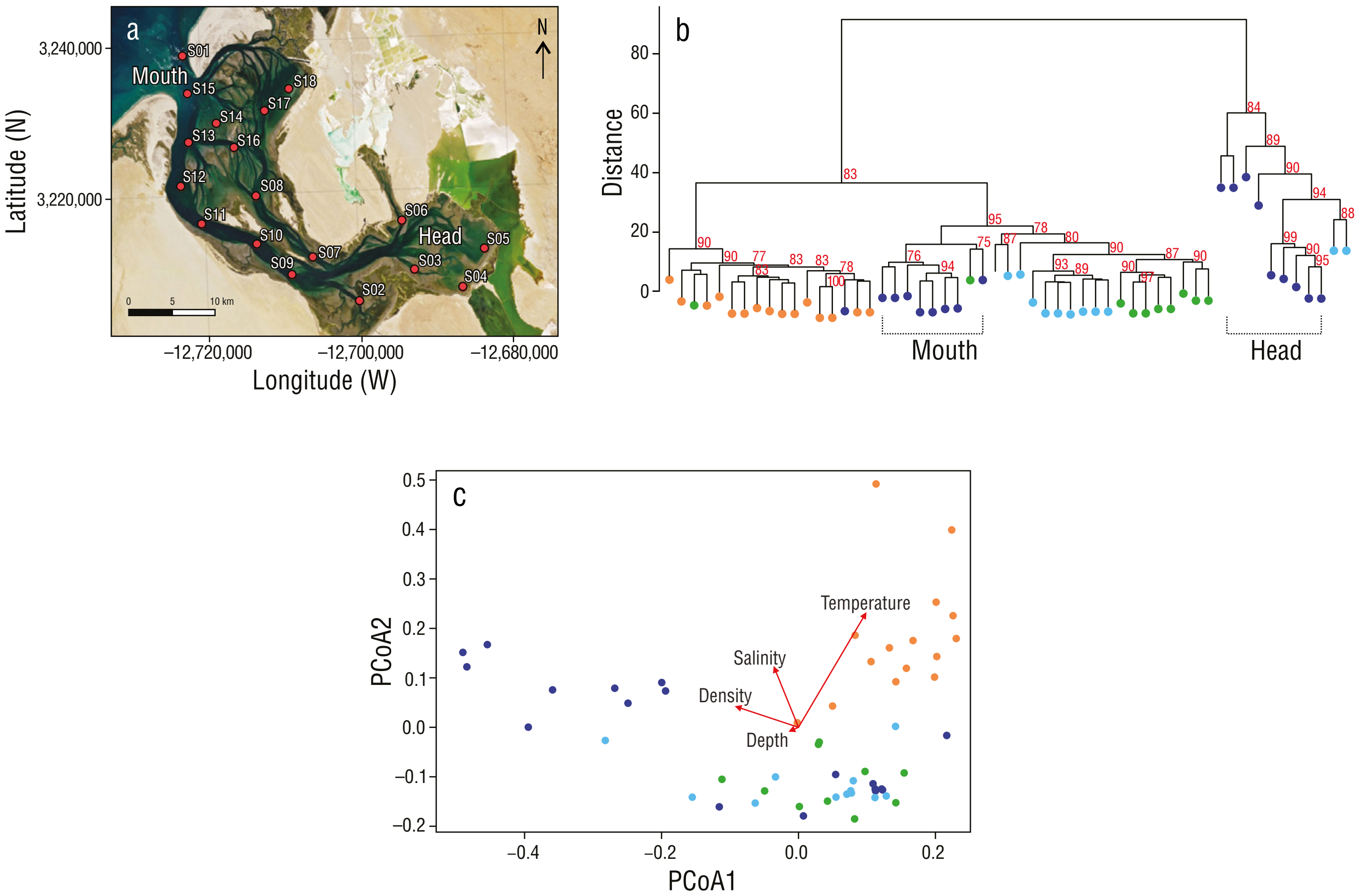

Figure 1. Analysis of the structure of the prokaryotic community in the water column of Ojo de Liebre Lagoon. Map of the location of sampling stations (S1–S18) (**a**). Hierarchical clustering dendrogram based on Manhattan distance, showing the similarity between samples from the 4 months of the study: August 2021 (orange), November 2021 (dark blue), March 2022 (green), and June 2022 (light blue). Values at the nodes indicate bootstrap support (>70%, based on 1,000 iterations) for significant clusterings ($P < 0.05$) (**b**). Principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarity. Vectors (red arrows) represent the direction and strength of the correlation between environmental variables (depth, temperature, salinity, and density) and community composition (**c**).

structure of the prokaryotic microbial community (Bolyen et al. 2019). As a result, a table was created with the taxonomic assignment of the amplicon sequence variants (ASVs) obtained using the Silva138 database (Yarza et al. 2014). After taxonomic assignment, ASVs that were likely contaminants or noise due to their low frequency (<0.5%) and their taxonomic label (i.e., mitochondria, chloroplasts, or unassigned) were removed. Based on this, a frequency table of the final ASVs was created using the 'feature-table filter-features' and 'taxa filter-table' commands in the QIIME2 environment. With this last ASV frequency table, the Shannon index was calculated as a metric of alpha diversity following the command 'diversity core-metrics-phylogenetic' in the QIIME2 environment. The relative abundance of ASVs was calculated using the 'dplyr' library in RStudio (RStudio Team 2020) by taking the absolute frequency of each ASV in a sample and dividing it by the total number of ASVs in the same.This process was performed independently for each sample, resulting in a proportional representation of each ASV.

The evaluation of differences in taxonomic composition and community structure in relation to physicochemical parameters was performed using the final ASV frequency table generated by the 'pvclust' library (Suzuki and Shimodaira 2006) and visualized with 'ggplot2' (Wickham 2016) in RStudio (RStudio Team 2020). The Manhattan distance with 1,000 replicates was used for the hierarchical clustering analysis, and the principal coordinate analysis (PCoA) was performed using a Bray–Curtis dissimilarity matrix with 1,000 replicates, including vectors corresponding to the correlation and significance of salinity, temperature, and density variables. The statistical analyses and visualization of this comparison were performed using the 'vegan' (Oksanen et al. 2019) and 'ggplot2' (Wickham 2016) libraries in the RStudio environment (RStudio Team 2020).

The PICRUSt2 tool was used as a module of QIIME2 to infer the microbial metabolism (Langille et al. 2013). A matrix of inferred metabolic pathways was obtained based on the presence and frequencies of representative taxonomic groups of different metabolic classes according to the databases of orthologous gene groups from the Kyoto Encyclopedia of Genes and Genomes (KEGG) and MetaCyc (Caspi et al. 2014). Finally, a temporal comparison of the genes and the resulting metabolic pathways was performed according to a differential abundance analysis with the package 'ggpicrust' (Chen et al. 2023), and the visualization of this comparison was performed with the library 'ggplot2' (Wickham 2016) in the RStudio environment (RStudio Team 2020).

Results

Physicochemical parameters

At the 18 sampling stations, temperature, salinity, and density variables were measured to assess the effect of environmental physicochemical factors on the microbial community, (Fig. 1a; Supplementary Material Table S1). In general, an upward gradient of salinity, temperature, and density was observed from the mouth to the head of the lagoon. Specifically, the maximum monthly average temperature was observed in August (25.66 ± 0.48 °C), whereas the minimum monthly average was recorded in March (16.75 ± 0.34 °C). For the salinity, the maximum monthly average was observed in August with a value of 35.00 ± 4.5, whereas the minimum monthly average was observed in March with a value of 33.50 ± 4.1. Density values ranged from 1,023 to 1,030 $kg \cdot m^{-3}$), whereas August had the lowest (∼1,023–1,024 $kg \cdot m^{-3}$) throughout the lagoon. March had the highest density range (∼1,024–1,029 $kg \cdot m^{-3}$), whereas August had the lowest (∼1,023–1,024 $kg \cdot m^{-3}$).

Structure of the prokaryotic community and its relationship with environmental variables

Two approaches were considered to define the community structure and highlight its spatiotemporal distribution. First, a hierarchical clustering analysis was performed to identify temporal patterns based on the dissimilarity of the community composition along the lagoon and during the 4 months of sampling. The results showed that the samples were mainly grouped in relation to the sampling season (Fig. 1b). For example, a group that corresponded mainly to the August sampling stations was observed; this group was characterized by having the highest values of temperature (25–27 °C) and salinity (∼34–45 PSU). A second group corresponded to the stations sampled in November, and an intermediate group corresponded to the stations sampled in March and June, with wider temperature ranges (16–24 °C) and lower salinities (∼34–41 PSU). Regarding spatial patterns, the distinction between the stations at the head and mouth of the lagoon was particularly evident in November, showing a greater distance from those located at the head (Fig. 1b).

In addition, a PCoA was performed using correlation vectors with physicochemical variables to identify the relationship between the environmental variables of temperature, salinity, and density and the community structure (Fig. 1c). Alike in the hierarchical cluster analysis, 3 main groups were identified in the PCoA: the first corresponding to August, the second composed mainly of March and June, and the third corresponding to November in the region of the head of the lagoon. In general, temperature ($r^2 = 0.77$, $P = 0.001$) and salinity ($r^2 = 0.39$, $P < 0.05$) significantly explained the prokaryotic community structure (Table 1). Specifically, temperature showed a direct association with the community in August, and salinity had an inverse association with the groups of March and June. Density did not show a significant correlation ($r^2 = 0.31$, $P = 0.088$), but its vector in the PCoA space suggested an association with the prokaryotic community in the head region in November (Fig. 1c).

Taxonomic composition of the prokaryotic community

To determine the composition and taxonomic structure of the prokaryotic community in the water column, we

Table 1. Correlation values (r^2) and significance (P-value) of the physicochemical factors with the principal coordinates (PCoA).

	X1	X2	r^2	P
Depth	–0.86	–0.52	0.05	0.05
Temperature	0.39	0.92	0.77	0.77
Salinity	–0.28	0.96	0.39	0.39
Density	–0.91	0.42	0.31	0.31

performed an analysis of the 16S rRNA gene sequences. We analyzed a total of 58 samples and generated a total of 3,528,490 sequences; after processing these, we identified a total of 1,700 ASVs. The taxonomic assignment of the ASVs allowed us to identify 2 domains, 207 phyla, 198 classes, and 181 orders. As a first approach to evaluate the composition of the prokaryotic community and identify general and robust patterns in the community structure along an environmental gradient, we identified the taxa considered "core" based on a relative abundance value of ≥1% (Custer et al. 2023) for a maximum taxonomic level of order, considering that they were present in all sampling stations and months. The cutoff value of 1% relative abundance, applied up to the taxonomic level of order, allowed us to distinguish between the dominant or "core" groups and the subdominant or "rare" groups (<1%; Custer et al. 2023) in the context of our taxonomic resolution and independently of the stations along the lagoon where their presence was found (Fig. 2).

In the core composition of the community, the dominant phyla within the Bacteria domain were Actinobacteriota, Bacteroidota, Cyanobacteriota, Pseudomonadota, Planctomycetota, and Verrucomicrobiota (Fig. 2a). Regarding the spatial characterization of the core of the prokaryotic community, the taxonomic composition was observed with greater resolution, and we identified different orders such as Flavobacteriales, Synechococcales, Pirellulales, Rhodobacterales, SAR11, Burkholderiales, and Verrucomicrobiales (Fig. 2b); in addition, we identified Thermoplasmata, which belongs to Marine Group II, as the only dominant class within the Archaea domain (Fig. 2a). Furthermore, temporal differences were observed between the classes of the different phyla, including the classes Bacteroidia (37.07%) and Alpha-proteobacteria (30.96%), which showed greater abundance compared to the class Gamma-proteobacteria (9.68%) during the 4 months of sampling (Fig. 2a). In particular, temporally, the phylum Actinobacteriota was observed as the dominant group, with the most representative classes being Acidimicrobia (1.49%) and Actinobacteria (1.32%). The relative abundance of the phylum Cyanobacteria was also observed; this was higher in March (16.62%) than in August (15.67%) and June (8.24%) and decreased in November (5.65%) (Fig. 2a). In addition, the phylum Thermoplasmata showed a greater abundance in November (4.70%) (Fig. 2a).

Regarding rare taxa, they were observed in 4.92–35.32% of the total ASVs identified. However, temporal differences in their frequency were observed, with a direct effect on the total diversity of the sampling month. For example, November had the highest presence of rare taxa (35.32%), whereas August had the lowest (4.92%) (Fig. 2a). In addition, differences in community diversity were analyzed for the sampling months based on the Shannon diversity index (Fig. 2c). In particular, the distribution of the median, first quartile, and lower minimum limit varied temporally, with August and November marking the extremes of diversity. All communities temporally exhibited high diversity (values between 4.7 and 6.6), which is typical of environments considered complex; nonetheless, August showed the lowest value (4.7), whereas November showed the highest (6.6). Furthermore, it was possible to identify, within the sampling stations, those that showed a diversity value above or below the lower or upper limit (outliers) in a given season. For example, at station S3 (6.0), located at the head, the maximum value in August was an outlier; similarly, in June, stations S15 (6.6) and S5 (5.5), located at the mouth and head, respectively, also showed outliers (Fig. 2c).

Spatiotemporal variation in community composition

To assess specific changes in community composition related to spatiotemporal variation, we compared 6 stations distributed along the mouth (S12 and S13), middle part (S9 and S10), and head (S4 and S5) of the lagoon (Fig. 1a) during November and August. The stations and seasons were selected based on hierarchical clustering (Fig. 1b) and diversity (Fig. 2c) analyses. Differences in community composition were observed in relation to the regions of the lagoon, including the mouth region (S12 and S13). These differences were particularly evident during November, when an increase in Thermoplasmata from Marine Group II and an increase in Puniceispirillales were observed, along with the presence of Flavobacteriales and Synechococcales among the abundant orders. In the region of the islands (S9 and S10), a clear change was observed in the proportion of Thermoplasmata from Marine Group II and Verrucomicrobiales. Specifically, at station S10, there was a significant increase in the proportion of Pirellulales and Sphingomonadales in November, whereas Flavobateriales and Rhodobacteriales predominated in August. For the head region (S4 and S5), the proportion of SAR11 was significantly higher in November, whereas the proportion of Synechococcales was higher in August. Finally, at station S5, an increase in the Gammaproteobacteria class was observed in November, whereas Flavobacteriales and Rhodobacteriales had the highest abundances (Fig. 2b).

Furthermore, considering the contribution of rare groups to community diversity, we evaluated differences in their occurrence at the same selected stations (Supplementary Material:

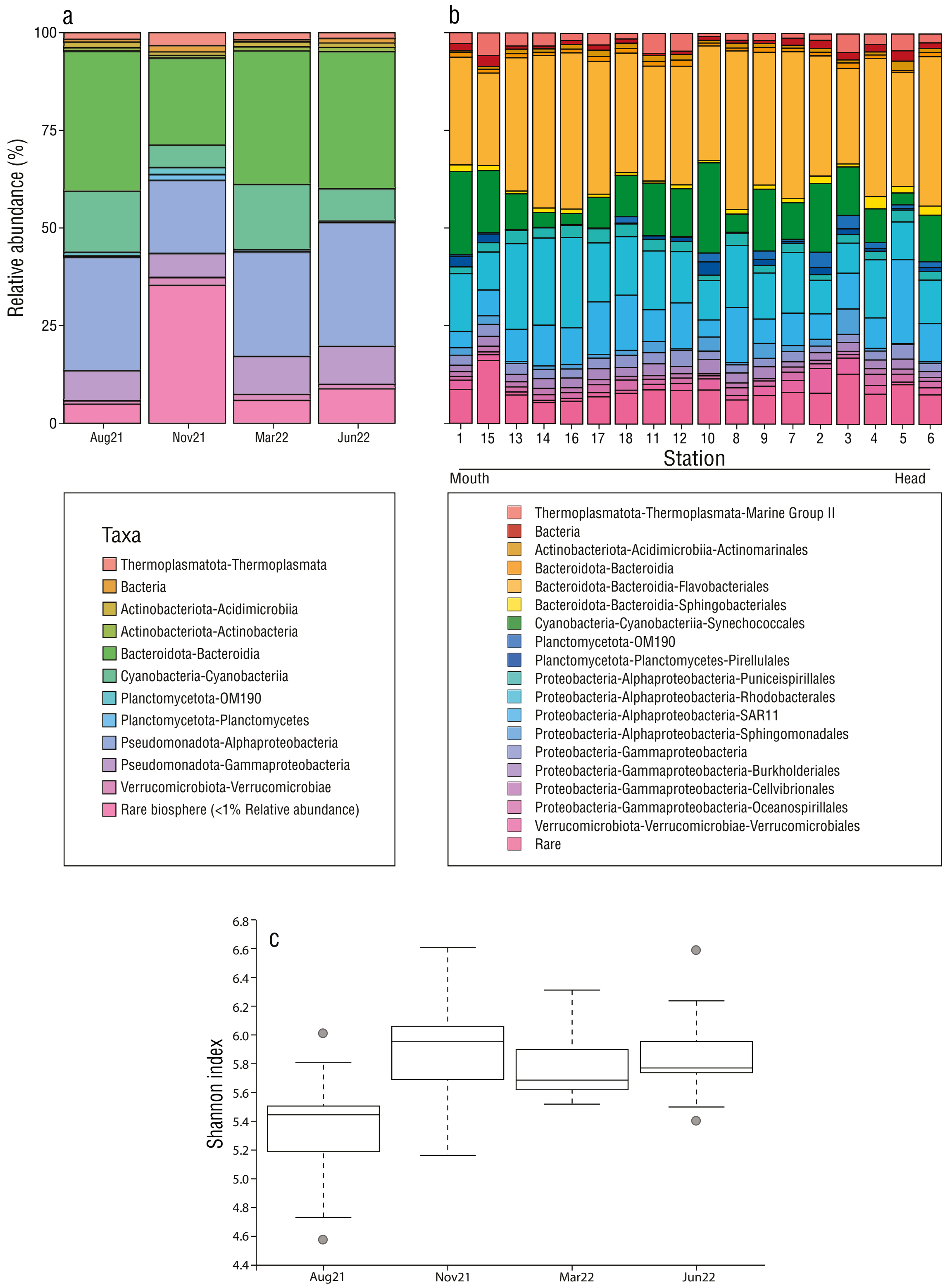

Figure 2. Composition and diversity of the prokaryotic community in the water column. Relative abundance (%) of the most representative taxonomic classes (>1% abundance) in the 4 sampling campaigns (August and November 2021; March and June 2022). Taxonomic assignment is indicated by the color code shown in the legend (**a**). Relative abundance (%) of the most representative taxonomic orders (>1% abundance) at the sampling stations in the lagoon (**b**). Alpha diversity of the community estimated using the Shannon index for each sampling season. The box represents the range between quartiles (lower = 25; upper = 75), the inner line represents the median, and the whiskers represent the range of the data. Individual points represent outliers (**c**).

Table S2 and Fig. S1). Primarily, previously unobserved taxa were identified, including the orders Thermoanaerobaculales, Microtrichales, Desulfobacterales, and Desulfobulbales. In addition, previously mentioned orders such as Corynebacteriales, PeM15, and Propionibacteriales of Actinobacteria, Chitinophagales of Bacteridia, and Vibrionales and Xanthomonadales of Gammaproteobacteria were observed. Distribution patterns were also identified in the different regions of the lagoon (Supplementary Material: Table S2 and Fig. S1). In the mouth region, at station S13, the order Vibrionales was observed. In the region of the islands, at station S9, Microtrichales and PeM15 were observed in August, whereas Chitinophagales was observed in November. At station S10, Corynebacteriales, Propionibacteriales, and Xanthomonadales were observed only in November. In the head region, station S4 only presented the order PeM15 in August; in November, no taxon was recorded. Finally, station S5 presented the archaeon Thermoanaerobaculia and the orders Desulfobacterales and Desulfobulbales, although only in November (Supplementary Material: Table S2 and Fig. S1).

Metabolism inference

To infer the metabolic potential in the water column, the sequences and taxonomic assignments of the ASVs that defined the taxonomic composition of the prokaryotic community were used. The differential analysis was performed using 2 main approaches, considering the seasonal difference in the community resolved with hierarchical clustering and diversity analyses: (1) gene inference and (2) metabolic pathway inference. Therefore, the inferences of genes and metabolic pathways present in August and November were analyzed and compared. The analysis of the seasonal differential abundance showed a total of 4,529 genes, of which 2,214 contributed significantly ($P < 0.05$) to this seasonal difference (Fig. 3a). Among the metabolic categories related to the inferred genes, the most prominent were the cofactor and vitamin metabolism (9%), xenobiotic degradation (2%), terpenoid and polyketide metabolism (2.7%), and secondary metabolite biosynthesis (0.5%), in addition to categories within the central metabolism such as carbohydrate (20%), lipid (4%), and amino acid (11%) metabolism, and energy generation (16%). In particular, genes within the categories of cofactor and vitamin metabolism, xenobiotic degradation, terpenoid and polyketide metabolism, and secondary metabolite biosynthesis were selected. The genes that stood out were those related to the metabolic pathways of vitamin B6, riboflavin (B2), and biotin (B7) (cofactor and vitamin metabolism); the biosynthesis of flavonoids and streptomycin (secondary metabolite biosynthesis); the biosynthesis of siderophores, carotenoids, and terpenoids (terpenoid and polyketide metabolism); and the degradation of ethylbenzene, styrene, nitrotoluene, benzoate, and chloroalkane (xenobiotic degradation) (Fig. 3a).

Regarding the inference of metabolic pathways, a total of 420 metabolic pathways were identified, of which 377 could be assigned to a category. Of the total assigned pathways, 86.47% were related to the biosynthesis of molecules, including amino acids; 11.93% were directly related to biogeochemical cycles, such as the carbon, nitrogen, and sulfur cycles; and 1.56% were related to hydrocarbon degradation. Furthermore, 130 metabolic pathways were found to contribute significantly ($P < 0.05$) to the seasonal differentiation of the inferred metabolism for the community (Fig. 3b). The nitrate reduction pathway, vitamin B6 biosynthesis, chitin degradation, and toluene 4-sulfonate degradation stood out among the significant categories observed.

DISCUSSION

In this study, we analyzed the spatiotemporal variation in the composition and structure of the prokaryotic microbial community in the water column of Ojo de Liebre Lagoon. The analysis of the 16S rRNA gene sequences revealed a prokaryotic community dominated by phyla commonly found in aquatic systems where salinity gradients occur. Specifically, the community structure was found to be significantly influenced by physicochemical variables, such as temperature and salinity, primarily dividing the community into 3 groups according to the sampling month; spatially, the communities at the mouth and head of the lagoon were well differentiated. Moreover, primary metabolic pathways related to the biosynthesis of molecules, such as amino acids, and heterotrophic metabolism were inferred, in addition to pathways related to the biogeochemical cycles of carbon, nitrogen, and sulfur, and hydrocarbon degradation. This suggests that Ojo de Liebre Lagoon is a diverse system with respect to the microbial community in the water column, which has the potential to directly contribute to the biogeochemistry of the ecosystem.

Seasonality of physicochemical factors

A temperature and salinity gradient was observed in Laguna Ojo de Liebre with a significant relationship to the structure of the prokaryotic community, which is spatially and temporally divided into groups (Fig. 1a), similar to what has been reported for other hypersaline environments (Thompson and Lee 2020). The greatest difference in community composition occurred between August and November, months associated with a physicochemical gradient influenced by neap tide periods during the sampling days. These periods favor seasonal differentiation, unlike spring tides, which promote a strong exchange of water with Vizcaíno Bay, modifying the temperature, salinity, and density of the lagoon (Álvarez-Borrego and Granados-Guzmán 1992). Temperature showed the most significant correlation ($r^2 = 0.77$, $P = 0.001$) with community composition, which explained the clustering of samples from August, the warmest month; this coincides with previous reports on the direct effect of temperature on marine microbial communities (Zhou et al. 1996). Furthermore, according to the ordination analysis, the relationship between density and the clustering of the November samples and their separation between the mouth and the inner lagoon is consistent with the dynamics reported for other hypersaline coastal lagoons influenced by tides, evaporation, circulation, and morphology (Clementino et al. 2008, Carvalho et al. 2024).

The spatial differentiation between the mouth and the head of the lagoon can be attributed to the effect of the tide on water residence time, which influences the turnover and persistence of taxa (Álvarez-Borrego and Granados-Guzmán 1992). For example, the longest residence time (124 days)

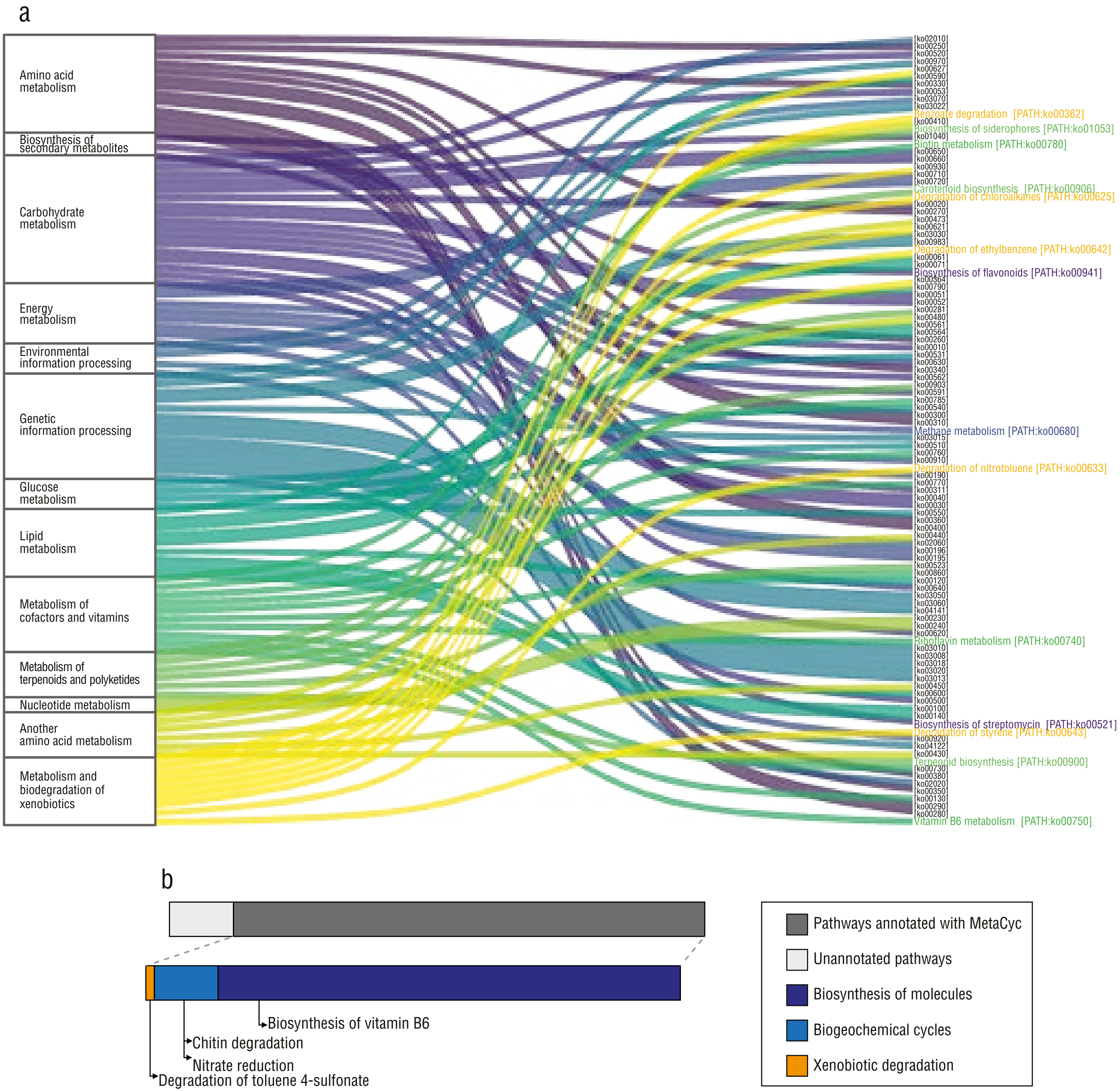

Figure 3. Inferred metabolic potential of the prokaryotic community using PICRUSt2. Abundance of genes associated with key metabolic pathways. Each horizontal bar represents a metabolic pathway (identified by its Kyoto Encyclopedia of Genes and Genomes Orthology [KO] ortholog), grouped by functional categories. Pathways involved in vitamin metabolism, xenobiotic degradation, and biosynthesis of secondary metabolites and terpenoids are highlighted (**a**). General functional profile of the community, showing the proportion of inferred metabolic pathways classified into MetaCyc categories. Relevant examples of biosynthesis (vitamin B6), biogeochemical cycles (chitin degradation and nitrate reduction), and biodegradation (toluene-4-sulfonate degradation) are highlighted (**b**).

recorded corresponds to the month of November (Soto-López 2024). Furthermore, during spring tides, the exchange of water masses is considerable in the mouth region, whereas residence time is longer in the head, depending on the circulation in Vizcaíno Bay and wind patterns (Soto-López 2024).

Composition and structure of the prokaryotic community

For the objectives of this study, which aimed to identify general patterns in the prokaryotic structure along an environmental gradient, the analysis at the order level proved pertinent and informative. It has been suggested that the definition of the microbial "core," including the taxonomic level and abundance cutoff, should be established according to the research questions and the ecological scale of the study (Custer et al. 2023). In this case, by working at the order level with a cutoff of >1% relative abundance, we sought to identify the main taxonomic groups that persistently formed the structural base of the community. This approach allowed us to discern the key taxa that responded to the environmental conditions of the time frame considered in this study. Although the time frame of this study only considered 1 annual cycle, the results obtained provide unprecedented information for Ojo de Liebre Lagoon regarding the influence of variations in physicochemical factors and dynamics in the water column on the composition of the microbial community. Thus, it was possible to differentiate a "core" formed by recurrent and abundant taxa, such as the phyla Pseudomonadota, Bacteroidota, Actinobacteriota, Cyanobacteria, and Verrucomicrobiota, which is similar to what has been reported in other hypersaline systems with comparable salinity and temperature ranges, such as Araruama Lagoon (salinity: 36–50; Clementino et al. 2008) and Thau Lagoon (salinity: 25–40; temperature: ~10–20 °C; Trombetta et al. 2022). This supports the consistency of our observations and establishes a baseline of knowledge for future interannual comparisons that will allow us to elucidate the influence of mesoscale climatic phenomena on the composition and structure of microbial communities in the lagoon.

Seasonal dynamics influenced the distribution and abundance of this core group (Fig. 2a). Cyanobacteria were most abundant in March and gradually decreased, whereas Planctomycetota and Verrucomicrobiota increased in November. These latter 2, typically classified as mesophiles (preferring ~20–35 °C) and associated with sediments rich in organic matter, often co-occur and participate in the degradation of complex compounds, including hydrocarbons (Schlesner and Stackebrandt 1987, Hedlund and Staley 2006, Lee et al. 2009). On the other hand, Actinobacteriota, with the class Acidimicrobia, has shown hypersalinity adaptations, with solute accumulation, spore formation, and metabolic versatility (Ventura et al. 2007). Furthermore, unlike in other hypersaline environments where Euryarchaeota, Thaumarchaeota, and Halobacteriota are common (Clementino et al. 2008, Trombetta et al. 2022), only the phylum Thermoplasmata (Marine Group II) was detected, which was reported previously in the microbial mats of Vizcaíno Bay (Robertson 2009, García-Maldonado et al. 2023). This group participates in the renewal of organic matter derived from phytoplankton (Hugoni et al. 2013), which is consistent with the high productivity of the lagoon.

Rare taxa (<1% relative abundance) also contributed to seasonal diversity (Supplementary Material Fig. S1), and these can influence biological interactions, food webs (Lyons et al. 2005), and the degradation of pollutants (Pester et al. 2010, Delgado-Baquerizo et al. 2016). The identification of rare groups such as Crenarchaeota, Acidobacteriota, Bdellovibrionota, Chloroflexota, Gemmatimonadota, Latescibacterota, Marinimicrobia, and Myxococcota suggests that the possible resuspension of sediments by environmental disturbances changes the composition of the sediment community, as has been observed in benthic microbial communities (Garsteki et al. 2002, Pusceddu et al. 2005). This is relevant in Ojo de Liebre Lagoon because the activity of boats and presence of the Gray Whale could favor mixing and sediment resuspension.

Diversity showed a spatiotemporal pattern in which November had the highest diversity and abundance of rare taxa, whereas August had the lowest values. In the head of the lagoon (S5), with a long residence time, Thermoanaerobaculia (Thermoanaerobaculales) and Desulfobacterota (Desulfobacterales and Desulfobulbales) were frequent. In the middle zone (S9 and S10), with greater water exchange, Actinobacteriota (e.g., Microtrichales and Corynebacteriales) predominated, which coincided with greater diversity. The variability in residence times, associated with the circulation in Vizcaíno Bay, affects water renewal and could explain the temporary presence of these rare groups in unique microhabitats during periods of low circulation (Mehrabi et al. 2014, Wu et al. 2024).

Inference of microbial metabolism

Metabolic inferences based on 16S rRNA data using PICRUSt2 provided a functional view of the metabolic potential of the prokaryotic community in the water column of the lagoon. However, it is crucial to consider the uncertainties inherent in this methodological approach. Agrawal et al. (2019) reported that PICRUSt can exhibit variations in the accuracy of its predictions compared to direct methods, such as shotgun metagenomics or real-time gene quantification (qPCR) (Agrawal et al. 2019). Therefore, we have interpreted the results obtained as a robust and qualitative indication of the potential presence of metabolic pathways in the ecosystem. In particular, the consistency in detecting enzymes related to the same pathway (i.e., associated with the nitrogen cycle or chitin degradation) strengthens the reliability of our inferences about the functional capabilities of the community, despite acknowledging the margin of error described for the tool.

The potential for vitamin B biosynthesis was identified. Among the key taxa were the orders Rhizobiales, Rhodobacterales, and Sphingomonadales, and the clade SAR11 (Pseudomonadota), as well as Flavobacteriales and Sphingomonadales (Bacteroidota), the latter potentially involved in biotin (B7) production (Sañudo-Wilhelmy et al. 2006). For example, vitamin B6 (such as PLP) facilitates the synthesis of osmoprotectants in microorganisms, such as SAR11 and cyanobacteria, in response to salinity fluctuations (Sañudo-Wilhelmy et al. 2012). Vitamin metabolism (B2, B6, and B7) is crucial for microbial survival in hypersaline environments. These vitamins, synthesized primarily by marine microorganisms, act as cofactors in essential processes, such as amino acid metabolism (B6), oxidation-reduction reactions (B2), and fatty acid synthesis (B7), directly affecting ecosystem productivity (Oren 2011, Sañudo-Wilhelmy et al. 2012, Sañudo-Wilhelmy et al. 2014, Wang et al. 2023). Their availability influences biogeochemical cycles and the activity of phytoplankton and bacterioplankton, as has been documented in coastal areas (Averianova et al. 2020).

Furthermore, metabolic inference suggests the production of secondary metabolites. The potential to synthesize antibiotics, such as streptomycin, was detected; this was supported by the previous isolation of the genus *Streptomyces* (phylum Actinobacteriota) in the lagoon (Zamora-Quintero et al. 2022). In addition, the biosynthesis of siderophores (i.e., deferrioxamine E, carotenoids, and terpenoids) was inferred; this is a key adaptive strategy in the face of oxidative stress, high UV radiation, and nutrient limitations, such as the generally reported absence of iron in the sediments (Gunde-Cimerman et al. 2018, Valdivieso-Ojeda et al. 2021, Zamora-Quintero et al. 2022). The environmental conditions during the study (salinity: 34–45; temperature: 19–27 °C; UV radiation: $<134.4\ \text{kW}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ in August) support the argument that these metabolisms are determinants in the structure of the microbial community (Alonso-Reyes et al. 2021, NASA POWER 2022) and regulate interactions by exclusion or dominance of taxa (Vraspir and Butler 2009, Oren 2014). An example of this environment-metabolism relationship is the seasonal fluctuation of the order Synechococcales. Its greater abundance at the head of the lagoon (station S4) in August, a period of higher salinity, temperature, and UV radiation, suggested a potential association with the production of flavonoids, a metabolic process that contributed significantly to the seasonal variation ($P < 0.05$). This is consistent with previous reports, which indicate that cyanobacteria, such as *Synechococcus*, synthesize these compounds for protection (Gunde-Cimerman et al. 2018).

Regarding the potential biodegradation of hydrocarbons, although halophilic archaea are known to degrade hydrocarbons in hypersaline environments (Oren 2014), their low diversity in this study (mainly Thermoplasmatota) suggests that the degradation of compounds such as toluene in the water column is limited. Potential sources of hydrocarbons in the lagoon include fuel spills associated with tourist boat activities, fishing, and salt transport. Despite the fact that the current regulatory actions of the lagoon management program promote that vessels entering the reserve avoid the dispersion of hydrocarbons in the water bodies (CONANP and SEMARNAT 2016), we suggest that subsequent studies quantify and characterize these compounds, which could be concentrated in the sediments and could be resuspended into the water column by the dynamics of the lagoon, and evaluate the activity of the hydrocarbonoclastic microbial community (Widdel and Rabus 2001).

Finally, the potential for chitin degradation, which is crucial for carbon and nitrogen recycling, is highlighted. Although the specialized orders Chitinophagales and Vibrionales were found in low abundance in November, their presence, along with the zooplankton activity reported in the lagoon (Sánchez-Cobarrubias et al. 2021), suggests that this process could be relevant after peaks in zooplankton abundance, connecting substrate availability with microbial metabolism and productivity (Keyhani and Roseman 1999, Souza et al. 2011).

CONCLUSIONS

This study is the first characterization of the prokaryotic community in the water column of Ojo de Liebre Lagoon. The results show that the prokaryotic community is primarily temperature-driven and composed of a microbial core that is characteristic of hypersaline environments. In addition, we identified potential ecological functions that the community could maintain, primarily the biogeochemical cycles fundamental to the ecosystem, which adds to the importance of our study. Furthermore, a fraction of rare taxa, which proliferate under conditions of low water renewal, have the potential to contribute specialized metabolic capabilities to ecosystem resilience. Thus, the combined results of this study suggest that the interaction between the stable core and the dynamic rare community is fundamental to sustaining the productivity and health of this vital coastal ecosystem.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

Supplementary material

The supplementary material for this work can be downloaded from: https://cienciasmarinas.com.mx/index.php/cmarinas/article/view/3564/420421270.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: APC, MTB, NMA; Data curation: APC, MTB; Formal analysis: APC, MTB; Funding acquisition: APC, JLC; Research: MTB, NMA, JLC, MNCC; Methodology: MTB, NMA; Project management: JLC; Resources: MTB, JLC; Software: APC, MTB; Supervision: MTB, NMA, JLC, MNCC; Validation: MTB, NMA, JLC, MNCC; Visualization: APC, MTB; Writing—original draft: APC; Writing—review and editing: MTB, NMA, JLC, MNCC.

Data availability

The sequencing data for this study are available from the National Center for Biotechnology Information (NCBI) (BioProject: PRJNA1274005). This study was conducted in accordance with current regulations and in compliance with the requirements of the El Vizcaíno Biosphere Reserve.

Use of AI tools

The authors did not employ any AI tools in this work.

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Geomorphological complexity and its association with submerged aquatic vegetation on the Yucatán coast

María de los A Liceaga-Correa[1], Edgar J González[2], Luis A Rincón-Sandoval[1], Héctor Hernández-Núñez[1], E Betzabeth Palafox-Juárez[1,3,4], Eduardo Cuevas[1,5]*

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CORRESPONDING AUTHOR
* E-mail: eduardo.cuevas@uabc.edu.mx

[1] Laboratorio de Percepción Remota y SIG, Departamento de Recursos del Mar, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, 97310 Mérida, Yucatán, Mexico.
[2] Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, 04510 Ciudad de México, Mexico.
[3] Departamento de Observación y Estudio de la Tierra, la Atmósfera y el Océano, El Colegio de la Frontera Sur, 77014 Chetumal, Quintana Roo, Mexico.
[4] Programa de Investigadoras e Investigadores por México, Secretaría de Ciencia, Humanidades, Tecnología e Innovación, Ciudad de México, Mexico.
[5] Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, 22860 Ensenada, Baja California, Mexico.

ABSTRACT. Shallow marine ecosystems with extensive communities of submerged aquatic vegetation, including seagrasses and macroalgae, are found along the northern coast of the Yucatán Peninsula. This study describes the geomorphological complexity of the nearshore seafloor in Yucatán, Mexico, and its association with submerged aquatic vegetation communities, constituting the first effort of its kind in this region. This work is relevant because ecological interactions between the seafloor and its inhabitants define the spatial structure of ecosystems, as well as ecological processes, many of which provide benefits to human society. The objectives of this study were to: (1) spatially delineate discrete geomorphological units (structures and zones) based on their depth, slope, and aspect; (2) describe the relative abundance of major groups of submerged aquatic vegetation (seagrasses, green algae, red algae, brown algae, and algal turf); and (3) assess the association between geomorphology and the presence of the vegetation groups under study. This information establishes a baseline for biological, ecological, and oceanographic analyses of the coastal marine ecosystems in southeastern Mexico. In addition, the results of this study are crucial for decision-making related to coastal development, adaptive management, and environmental conservation monitoring, and provide a foundation for functional ecosystem assessment studies.

Key words: digital elevation model, bathymetric position index, Bayesian multinomial logistic models, base line, historic data.

INTRODUCTION

Ecological interactions shape the distribution of marine communities, which in turn influences the ecosystem functions they perform, including the provision of ecosystem services to human communities (hurricane protection, carbon sequestration, provision of attractive landscapes, and support of fishing activities), and the resilience of marine landscapes. Therefore, it is strategic to understand associations between the physical and biological characteristics of these landscapes (Gladstone-Gallagher et al. 2019, Armoskaite et al. 2020, Borland et al. 2021, Lavialle et al. 2023).

In particular, the geomorphology (Öhman and Rajasuriya 1998), relief, and substrate type (Khalaf and Kochzius 2002) are recognized as determining influences for the distribution of benthic communities of corals (Mayorga-Martínez et al.

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2021), macroinvertebrates in the intertidal zone (Damveld et al. 2018), and seagrasses and macroalgae (Hemminga and Duarte 2000), to the extent that some authors propose the evaluation of the topography and complexity of the seafloor as a substitute indicator of benthic biodiversity for a rapid sampling strategy (Cooper et al. 2019; Schenone et al. 2023, 2025). In this context, it is relevant to emphasize the relevance of evaluating the relationship between benthic communities and the seafloor at multiple scales, including both the individual components of complexity and the geomorphological classes themselves (Gratwicke and Speight 2005, Pygas et al. 2020).

The shallow marine ecosystems of the northern Yucatán Peninsula, southeastern Mexico, are characterized by the presence of consolidated and unconsolidated calcareous sediments, where submerged aquatic vegetation (SAV) communities, such as seagrasses and macroalgae, develop. These communities provide key benefits, both tangible and intangible, associated with the blue carbon cycle (Cota-Lucero and Herrera-Silveira 2021), facilitate the establishment of coastal sediments (Short et al. 2006), contribute to the stabilization of sediments associated with nearby sandy beaches (Christianen et al. 2013, James et al. 2019), and constitute critical habitats for fauna species of high commercial and ecological interest (Boström et al. 2006, Sandoval-Gío et al. 2020, Chen et al. 2021). In addition, these communities serve as the basis for important livelihood activities for various coastal communities in Yucatán (Rebours et al. 2014, Coronado et al. 2020, Arcos-Aguilar et al. 2021, Quiñones-Peraza et al. 2023).

Seagrass and macroalgal communities have been described in this region, but not for the entire northern coast of the peninsula; in addition, the geomorphological complexity of the seafloor has not been evaluated, nor has the association between these ecosystem components been assessed (Bello-Pineda and Hernández-Stefanoni 2007, Cota-Lucero and Herrera-Silveira 2021, Lópes de Olmos Reyes et al. 2023, Ortegón-Aznar et al. 2024). Thus, the present study has a pertinent and relevant impact by providing spatially explicit products that contribute to the management of this maritime territory, as well as historical data that are made public and constitute a baseline for assessing landscape changes. Furthermore, it joins the philosophy of open ocean data promoted by the Ocean Decade, among others (Martin et al. 2025).

In this context, this study presents a geomorphological characterization of the shallow nearshore seafloor of Yucatán, Mexico, at a landscape scale (tens of kilometers) and from the perspective of the physical variables of the seafloor. The objectives of this study were: (1) to spatially delimit discrete geomorphological units (structures and zones) based on their components of depth, slope, and aspect; (2) to describe the relative abundances of major groups of SAV (seagrasses, green algae, red algae, brown algae, and algal turf); and (3) to evaluate the association between geomorphology and the presence of SAV groups in the same period as the geomorphological classification.

Materials and methods

Study area

Yucatán is located in southeastern Mexico, north of the Yucatán Peninsula, which is of karst origin and has a submarine continental shelf of sedimentary rocks on a Paleozoic crystalline basement (Lugo-Hubp et al. 1992).

The region lacks surface rivers, but underground laminar flows are recognized through the karst structures (Solleiro-Rebolledo et al. 2011). Its coast is a plain characterized by a narrow strip of recent marine deposits of biogenic carbonate origin and an accumulation shoreline (Lugo-Hubp et al. 1992). The marine area has low-energy waves, with dominant surface currents and a potential sediment transport from east to west, as a result of the waves (Martínez-López and Parés-Sierra 1998, Enríquez et al. 2010, Appendini et al. 2012). Regarding its geomorphology, bathymetric survey information is available only for specific areas and from nautical charts (SEMAR 2019).

The region is home to diverse and productive ecosystems (coral reefs, soft coral colonies, rocky reefs, seagrass meadows, and macroalgal forests) of ecological (e.g., refuge and feeding sites for a wide variety of benthic and pelagic species) and commercial interest for the region (Zarco-Perelló et al. 2013, Palafox-Juárez and Liceaga-Correa 2017, Cota-Lucero and Herrera-Silveira 2021).

The study area comprised a 356-km long polygon delimited by the –12 m isobath in the open sea, which gave it a variable width. Our study area covered a total of 4,968 km^2 (Fig. 1). The methodological approach was conducted at a regional landscape scale (Gladstone-Gallagher et al. 2019, Schenone et al. 2023), based on techniques from geomatics and ecological disciplines to link physical data, derived from echo sounders, with biological data at the level of communities and large taxonomic groups; this addresses the current challenge in marine sciences of associating data at different scales, ensuring an efficient relationship between spatial resolution, coverage, and costs (Lark et al. 2015, Cooper et al. 2019, Brunier et al. 2020, Hao et al. 2023).

Bathymetric data collection

To collect bathymetric data, we used acoustic equipment. With the data, we generated a digital elevation model (DEM), which was used to spatially delineate discrete geomorphological units. For this, 170 equidistant transects (2 km apart) were defined, from north to south, perpendicular to the coastline, covering depths between the –0.5 m and –12.0 m isobaths (Fig. 1). These data were acquired from a small vessel (27 ft in length) with an outboard motor, at an average speed of 12 km·h^{-1}, during the period from April 2012 to June 2013. The depth was measured with a Lowrance (Tulsa, USA) single-beam echosounder model LMS-37C (frequency: 200 MHz; beamwidth: 35°) coupled with an Ashteck (Gates

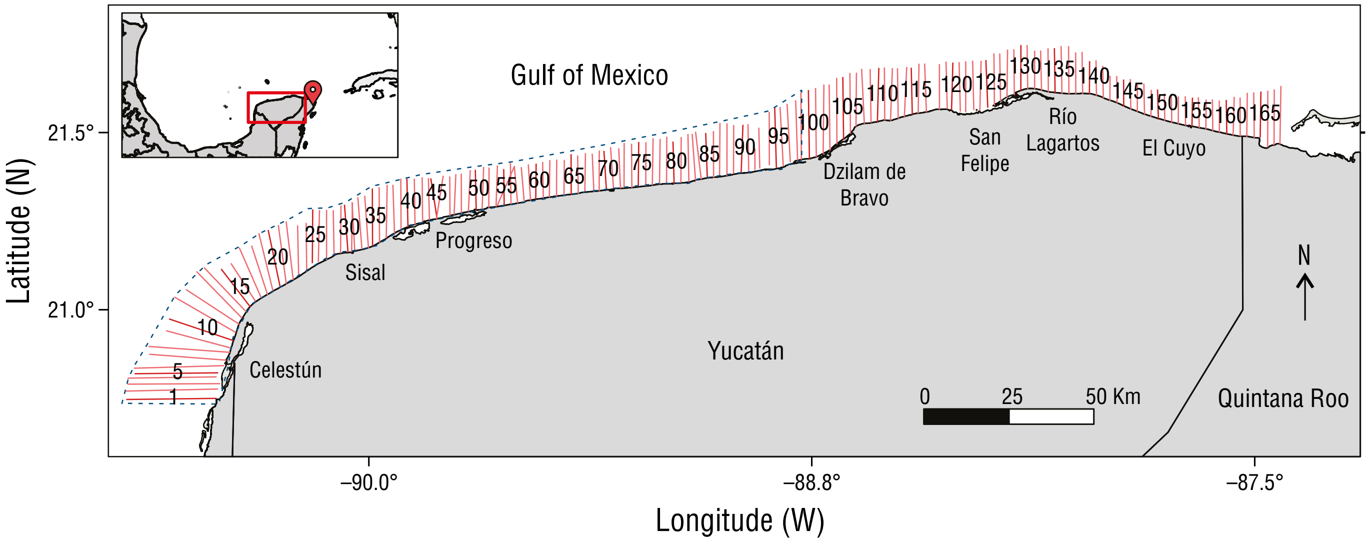

Figure 1. Study area on the northern shallow coast of the Yucatán Peninsula. The 170 transects (red lines perpendicular to the coast) used to collect bathymetric data are shown. The gray dotted line delimits the area for vegetation cover analysis. The main reference ports are indicated along the coast. In the macrolocation box, the red marker indicates the city of Cancún, as a reference location.

Mills, USA) differential global positioning system model Promark 500. The geographic coordinate data were orthometrically corrected in post-processing and, together with this article, the filtered data are made publicly available (https://goo.su/1RvqsCE). The boundary representing the coastline for the bathymetric model was defined by digitizing it in Landsat satellite images from the ETM+ sensor (spatial resolution: 30 m) obtained in April 2010 (Path/Row scenes: 19/045, 20/045, and 21/045).

Geomorphological classification of the seafloor

The distance between depth records on each transect was significantly smaller than the distance between 2 adjacent transects, which caused bias in the geostatistical model. To address this imbalance, a subset of bathymetric records (1,618 records) was selected from the centroids of a 2 × 2 km grid in the study area, thus standardizing the spatial resolution in both directions.

This data subset was assessed for spatial autocorrelation (semivariance) using the program Geostatistics for the Environmental Sciences (GS+) v. 9.0. We used the best-fitting nugget, range, and plateau parameterizations of the theoretical model in the semivariogram to construct a DEM by ordinary Kriging interpolation in ArcMap v. 10.2.2. Model accuracy was assessed by cross-validation analysis (predicted versus measured depth values) and by prediction efficiency (Villatoro et al. 2008), using a subset of the original bathymetric records (195,226 records; 20% of the total original data).

From the DEM, 2 of the main components of seafloor geomorphological complexity were calculated for multiscale categorization: slope and aspect (Wilson et al. 2007). These 2 components of marine relief, together with depth, play a preponderant role in configuring the geomorphological structures of the seafloor (Jerosch et al. 2015, Pygas et al. 2020). In this study, slope was defined as the maximum change in seafloor elevation within a given neighborhood, which is relevant to the sediment stability required for SAV to establish. Likewise, the orientation or aspect has a direct influence on the position of benthic communities with respect to the flow of currents and transportation of nutrients and was considered as the direction of the maximum inclination within the same neighborhood (Jerosch et al. 2015, Pygas et al. 2020). Both variables were generated in raster format using the Topographic Properties tool of the TNTmips program (Microimages, Raymond, USA) using the DEM.

For the geomorphological classification of the seafloor, the Benthic Terrain Modeler (BTM) v. 3.0 (ArcGIS v. 10.2.2) program was used with the bathymetric position index (BPI), which analyzes the values of each DEM pixel with respect to a set of pixels in a user-defined radial search neighborhood. Subsequently, based on a multivariate codification of the evaluated components (depth, slope, and aspect) and the BPI, the BTM program assigned a geomorphological classification to each DEM pixel (Wilson et al. 2007, Jerosch et al. 2015, Pygas et al. 2020).

In its calculation, the model included the analysis of the BPI index at 2 geographic scales for the radial search range. In this study, the fine (r) and broad (R) scale values were defined empirically and based on bibliographic references (Lundblad et al. 2006) with scales of 1:80,000 and 1:160,000. These values represented radial neighborhoods of 50 and 100 pixels for each pixel of the DEM, and both were standardized using a standard deviation as a reference and considering the autocorrelation of the bathymetric data (Verfaillie et al. 2007).

With these parameters defined, the calculations at the broad (BPI_{Bro}) and fine (BPI_{Fin}) scales of the geomorphological complexity model were done with equation (1):

$$BPI_x = Z_{Comp} - Z_{Comp\_Adjust\_x}, \qquad (1)$$

where x is the scale (broad or fine), Z_{Comp} is the value of the complexity components (depth, slope, and aspect) of cell Z, and $Z_{Comp\_Adjust\_x}$ is the average value of the complexity components of the neighborhood cells within radius x (broad or fine) (Wilson et al. 2007).

Based on the BPI values obtained in the broad and fine scale models, each pixel of the DEM was classified into a zone or structure defined in a catalog with threshold values (Jerosch et al. 2015) (Table 1).

Cover of submerged aquatic vegetation (SAV)

The geospatial distribution patterns of SAV were analyzed in the western and central regions of the Yucatán coast (from Celestún to Dzilam de Bravo) (Fig. 1). The eastern region was not included in this analysis due to a red tide event (COFEPRIS 2011) that severely modified benthic communities, an impact documented in other regions (Lee et al. 2007), which made conditions incomparable with those of the rest of the study area.

The methodological approach for this study was regional in scale and employed standard techniques demonstrated to be effective for mapping benthic habitats and seascapes (Swanborn et al. 2022, Schenone et al. 2023). We used a stratified random sampling design, which has been reported to be optimal to map SAV, to define the sites to quantify SAV cover (Hirzel and Guisan 2002, Wilson et al. 2019). We used an unsupervised classification of 2 Landsat 7 ETM+ images (paths: 20 and 21; row: 45) from April 2010 as a basis and applied the K-means algorithm (15 distinct unsupervised classes). A total of 219 sampling sites were randomly distributed within each unsupervised class (Mastrantonis et al. 2024), considering a minimum separation distance of 90 m between sites (same design as Palafox-Juárez and Liceaga-Correa 2017). Following a modified method by Aronson and Swanson (1997), we obtained a 5-min underwater video transect at each site, with an orientation perpendicular to the bottom and at a distance of 80 cm, covering an approximate area of 50 m^2 (1 m wide × 50 m long).

Video analysis followed standard procedures for benthic community mapping and was performed at the functional group level (e.g., algae and seagrass), which has been recommended as an effective and efficient approach at the seascape scale (Roelfsema and Phinn 2010, Herkül et al. 2013, Leiper et al. 2014, Greenfield et al. 2016, Pygas et al. 2020). The Coral Point Count with Excel extensions (CPCe) application (Kohler and Gill 2006) was used, overlaying 20 random sampling points per frame, and 28 frames per video were analyzed, representing approximately one photograph every 1.78 m along the recorded transect (Díaz-Aguilar 2012, Palafox-Juárez and Liceaga-Correa 2017). For each of the 20 random points in each frame, the taxonomic group of the SAV present was identified: seagrass, green algae, red algae, brown algae or algal turf.

Influence of geomorphology on submerged aquatic vegetation (SAV)

A Bayesian multinomial logistic model (BMLM) with a nonlinear structure was generated to recognize the complex relationship between geomorphological variables (depth, slope, and aspect) and the presence of different taxonomic groups of SAV. Splines were used to model this relationship (cyclic splines were considered for the aspect, given its circular nature). From this model, we estimated the probabilities of presence for each SAV taxonomic group based on each of the geomorphological characteristics of the seafloor.

Table 1. Characteristics used in the morphological classification of the seafloor of Yucatán. Summary of the morphological characteristics and their values at the broad and fine scales (a bathymetric position index [BPI] value of 100 corresponds to one standard deviation) that define the morphological classification.

Geomorphological classification	Clase	BPI Broad scale		BPI Fine scale		Slope	
Zone		Lower	Upper	Lower	Upper	Lower	Upper
	Elevation	100					
	Plaine	–100	100				0.042
	Gentle slope	–100	100			0.042	
Structure							
	Land depression	–100	100		–100		0.042
	Submarine hills	–100	100	100		0.042	

For the zones defined in the broad-scale BPI model, we created a second BMLM that used the geomorphological zoning as the predictor variable; from this, we obtained estimates of the probability of presence for each SAV group for each zone.

To achieve probabilities that summed to 100%, in the 2 previous BMLM models, we considered the additional group "Other," which included the remaining non-plant elements (i.e., flagstone, rock, sand, and other organisms) at each random point in each frame. This analysis was not performed for structures due to their small area, which did not include a sufficient number of sampling sites for such an analysis. The BMLMs were constructed using the 'brms' package (Bürkner 2017, 2018) in R (R Core Team 2020).

RESULTS

Bathymetric data collection

The 170 transects surveyed totaled 2,314 linear km sampled with the single-beam echosounder, which produced a total of 977,747 depth records after error correction. The longest transect (26.83 km) was recorded to the west, off the port of Celestún, and the shortest (7.42 km) was recorded to the east, off the port of El Cuyo (Fig. 1).

Geomorphological classification of the seafloor

Given the semivariance of the depth data, these were fitted to an isotropic Gaussian model (nugget = 0.01; plateau = 9.016; range = 12,903.78 m; $R^2 = 0.967$; $RSS = 1.86$), and a DEM spatial resolution of 40 m per pixel was defined, with a high cross-validation correlation ($R^2 = 0.946$) and a model prediction efficiency of 99.3%. This parameterization was essential for the repeatability and accuracy of the analyses presented here.

Depth (Fig. 2a) and slope (Fig. 2b) varied parallel to the coastline. The aspect showed the greatest variability in a direction perpendicular to the coast (Fig. 2c). Bathymetry was uniform longitudinally (E–W) and showed a consistent pattern latitudinally (N–S). A discrete slope with values less than one degree (<1°) predominated; this created a homogeneous plain with a predominant north–northwest aspect. Together, these features defined the geomorphological landscape of the shallow coastline studied (Fig. 2).

With the results of the BPI model and the definition of the geomorphological characteristics of the seafloor (Table 1), the study area was classified into 3 distinct zones (broad scale: elevation, plain, and gentle slope) and 2 types of structures (fine scale: submarine hills and depressions) (Fig. 3).

The section of the study area farthest from the coast, near the –12 m isobath, showed 3 depressions at both the broad and fine scales. These were classified as structures, together with 3 submarine hills or isolated elevations (Fig. 3), of which the one located in Celestún had unique morphological characteristics.

Effect of geomorphology on submerged aquatic vegetation (SAV)

The most abundant SAV species on the western coast of Yucatán were (in descending order) seagrasses (mainly *Thalassia testudinum*, although *Syringodium filiforme* and *Halodule wrightii* were also recorded), green algae (Chlorophyta), red algae (Rhodophyta), brown algae (Phaeophyta), and algal turf (a mixture of juvenile macroalgae, fast-growing filamentous species, brown algae, green algae, and cyanobacteria) (Fig. S1).

Geomorphological components (depth, slope, and aspect) had varying degrees of influence on the probability of presence of SAV taxonomic groups (Fig. 4). Based on the first BMLM (Table S1), depth was identified as the most important variable in determining the presence of SAV taxonomic groups on the western coast of Yucatán.

Seagrasses were distributed in areas with depths less than –5 m (Fig. 4a) and their presence markedly changed with increasing depth. The distribution area of seagrasses (Fig. S1) showed few variations with the slope and aspect variables; therefore, the influence of these variables was minimal (Fig. 4b, c).

Green algae were primarily distributed in areas with depths between 5 and 7 m (Fig. 4d) and on steeper slopes (Fig. 4e), and aspect was not an important factor in explaining their presence (Fig. 4f). On the other hand, red algae showed association patterns with the 3 geomorphological variables and were mainly distributed in the deeper areas, with steeper slopes (Fig. 4h) and a northerly aspect (Fig. 4i). Finally, brown algae had a lower presence than red algae but a similar distribution (Fig. 4j–l). Algal turf was mainly distributed in areas with depths greater than 2.5 m (Fig. 4m), low slopes (Fig. 4n), and a northerly aspect of the seafloor (Fig. 4o).

With the second BMLM, whose explanatory variable was geomorphological zoning, we identified that the elevation zone had the highest seagrass cover (39.7%), followed by green algae (19%), algal turf (14.5%), red algae (10.3%), and brown algae (2.6%). This zone had the highest diversity and presence of SAV taxonomic groups (seagrass, green algae, algal turf, red algae, and brown algae); for the zones identified as plains and gentle slopes, the presence of algal turf dominated, although seagrass, green algae, and red algae were also present (Table 2).

DISCUSSION

Mapping the seascape

Several conceptual approaches and recent studies have promoted the use of varied methodologies and technologies, with different spatial and grain size extensions, to study biodiversity across marine assemblages at the landscape scale, where benthic biodiversity is assessed at the functional group level (Gladstone-Gallagher et al. 2019). This scale allows addressing the heterogeneity of systems

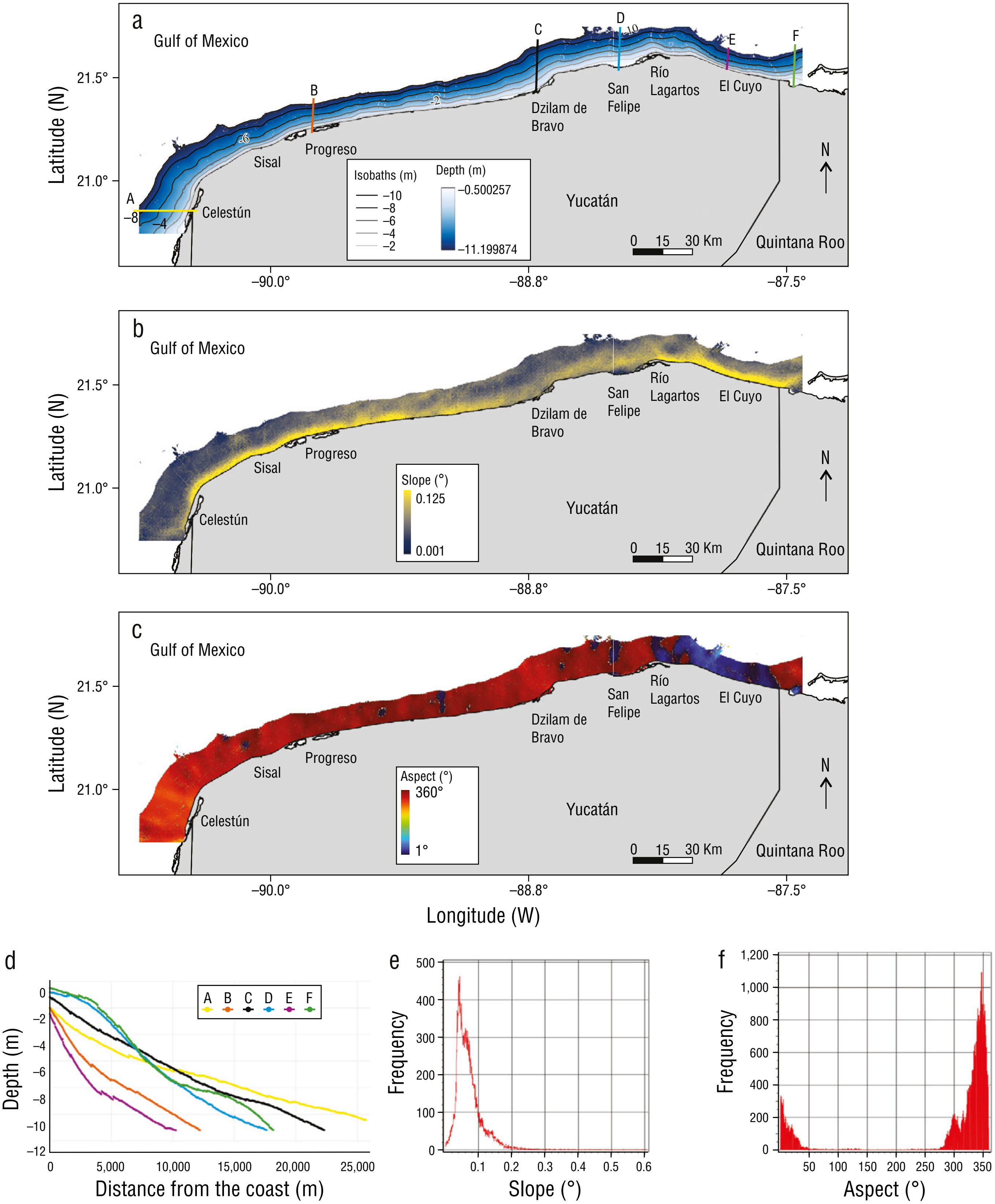

Figure 2. Representation of component variables of the geomorphology of the shallow coastline of the northern Yucatán Peninsula. From the digital elevation model (DEM) (**a**), seafloor slope (**b**) and aspect (**c**) were calculated. Depth profiles (**d**) indicated in (**a**) are shown, along with the frequencies of slope (**e**) and aspect (**f**) values.

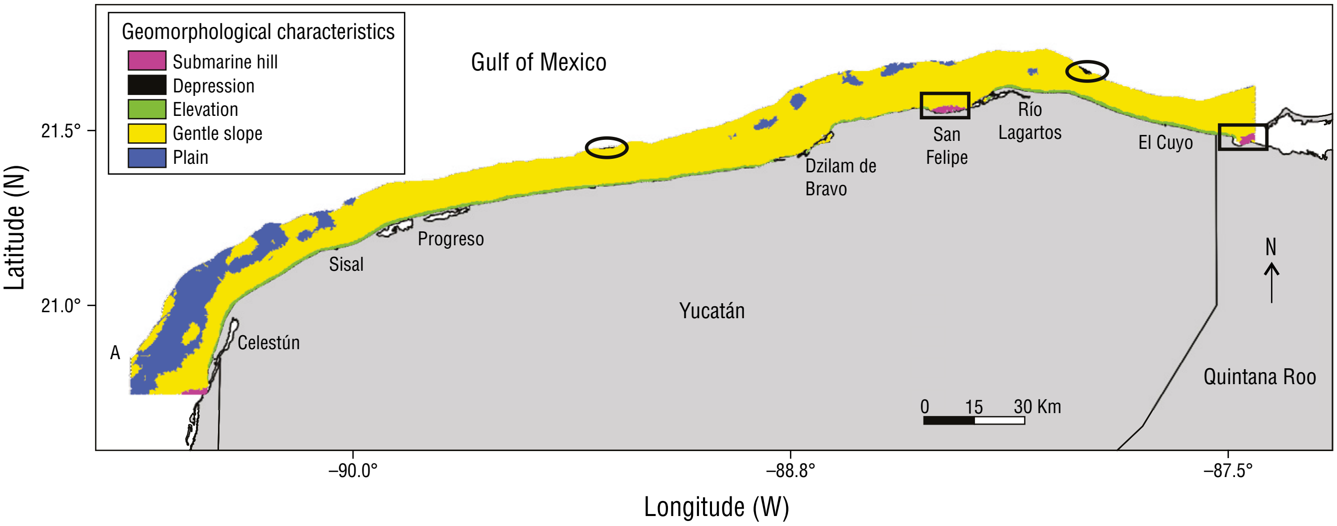

Figure 3. Geomorphological features of the surface of the nearshore seafloor of Yucatán; submarine hills, within squares, and depressions, within ellipses, are notable.

within a landscape, including groups with different biotic and abiotic requirements, functional redundancy, and varied responses to stressors, which is essential to understand ecological resilience and identify potential indicator groups of ecosystem processes (Kaskela et al. 2017, Brunier et al. 2020, Pygas et al. 2020, Swanborn et al. 2022).

In this context, the exponential growth of geographic information technologies (GIT), the development of geomatic analysis techniques, and the integration of multiscale observation platforms have enabled notable advances in the physical characterization of the seafloor and associated benthic communities (Schenone et al. 2023). Spatial products derived from these assemblages have fostered interdisciplinary methodologies and contributed to the establishment of comparable baselines in landscape analyses, even at interdecadal scales. Operational monitoring initiatives in the Baltic Sea, the Pacific Ocean, and other regions in Europe have implemented similar approaches with multiscale data (Kaskela et al. 2017, Hao et al. 2023).

The geomorphology of the seafloor, particularly in shallow regions such as the northern coast of Yucatán, tends not to experience abrupt changes, even after severe hydrometeorological events. For example, Cuevas et al. (2013a) documented submarine dune movements in some of the areas analyzed in this study and reported variations of only 3 to 10 m over more than 25 years. Therefore, the geomorphological information presented is considered to retain its temporal validity.

Two of the identified structures, Actam Chuleb and Punta Caracol, had been previously described (Cuevas et al. 2013b). The present study reports for the first time a third submarine hill in Celestún and 3 depressions around the –12 m isobath, which represents an original contribution to the understanding of the submarine relief of the region. These structures are particularly relevant because they are associated with submarine dune complexes that shift and shape the landscape with their associated seagrass communities and macroalgal forests (Cuevas et al. 2013a).

General ecological patterns of submerged aquatic vegetation (SAV)

Current spatial patterns of the SAV could differ from those observed at the time of the study due to ecological dynamics of the landscape; nonetheless, the ecological relationships described are assumed to remain representative. This is because the geomorphological complexity of the seafloor operates at broader temporal scales, which provides a relatively stable framework for the analysis of biotic associations.

The shallow coast of Yucatán is characterized by low topographic complexity, where zones of plains and gentle slopes, characteristic of the Campeche Bank, are clearly distinguishable. These are easily identifiable with the thresholds defined for each differentiating element in the BPI (Wright et al. 2012). Appendini et al. (2012) identified a critical strip for sediment transport between the 0 and –3 m isobaths, which coincides with the elevated zone identified in this study and is associated with a shallow strip close to the coastline, where unconsolidated sediment accumulates due to dynamics associated with those of the coastline.

The link between geomorphological features and biological communities is key to understanding the structure and functioning of ecosystems (Ordines et al. 2011). In the present study, depth was the variable most strongly associated with the presence of SAV, which is expected from

Table 2. Probability of presence for each group of submerged aquatic vegetation (SAV) in each of the identified geomorphological zones. Probability values estimated from the Bayesian multinomial logistic model (BMLM) with these zones as the explanatory variable. "Others" includes non-plant elements that do not correspond to a main taxonomic group of the SAV (e.g., flagstone, rock, sand, and other organisms); "Other" is included to show that the probabilities of presence add up to 100% in each geomorphological zone.

Zone	SAV Group	Probability of presence (%)	Credibility interval of 95%	
Elevation	Seagrass	39.7	38.2	41.1
	Green algae	19	17.9	20.2
	Red algae	10.3	9.4	11.2
	Brown algae	2.6	2.2	3.1
	Algal turf	14.5	13.5	15.6
	Other	13.9	12.9	14.9
	Seagrass	8.2	7.4	9.2
Plain	Green algae	7.7	6.9	8.6
	Red algae	4.1	3.5	4.8
	Brown algae	6.5	5.7	7.3
	Algal turf	13.8	12.7	14.9
	Other	59.7	58.1	61.3
Gentle slope	Seagrasses	3.9	3.6	4.4
	Green algae	10.2	9.7	10.8
	Red algae	11.1	10.5	11.7
	Brown algae	4.9	4.4	5.2
	Algal turf	27.1	26.3	27.9
	Other	42.8	41.9	43.7

an ecological perspective. However, we also documented the estimated distribution of SAV using geomorphological categories, as well as certain assemblage patterns, constituting a unique contribution for the southeastern Gulf of Mexico.

In their review of more than 50 studies on the influence of bottom morphology on benthic communities, Pygas et al. (2020) noted that the relationship between geomorphological complexity and the distribution of macroalgae has been scarcely studied. In this sense, both Pygas et al. (2020) and Kaskela et al. (2017) agreed on the relevance of the BPI to evaluate associations of morphological complexity with the distribution of benthic communities, demonstrating its effectiveness to identify suitable habitats for invertebrate organisms. Likewise, Kaskela et al. (2017) suggested that applied logistic models are robust tools to evaluate interactions between geomorphological variables and functional groups, and highlighted the influence of roughness, substrate variability and slope as key characteristics in the distribution of benthic communities.

Documenting and validating local patterns of association between SAV and seafloor features strengthens tools for assessing landscape changes following extreme events (e.g., hurricanes or red tides), or simply for multitemporal comparisons. Numerical functions derived from these associations allow geomorphological features to be used as surrogate variables for ecological inferences (Kaskela et al. 2017), as has been done for microtopography (Schenone et al. 2024) and sediment geomorphology (Brunier et al. 2020).

Despite progress, Kaskela et al. (2017) noted the need for additional studies to clarify the relationships between geomorphology and benthic communities, as ambiguities still prevail. In line with this, this study highlights the urgency of conducting analyses at higher ecological resolution, including in situ measurements of key physicochemical variables such as salinity, temperature, and transparency, which, together with geomorphology, govern the spatiotemporal distribution of SAV.

Implications for the management of the seascape in Yucatán

This work represents the first systematic categorization of the geomorphological complexity of the seafloor off the northern coast of the Yucatán Peninsula, establishing a

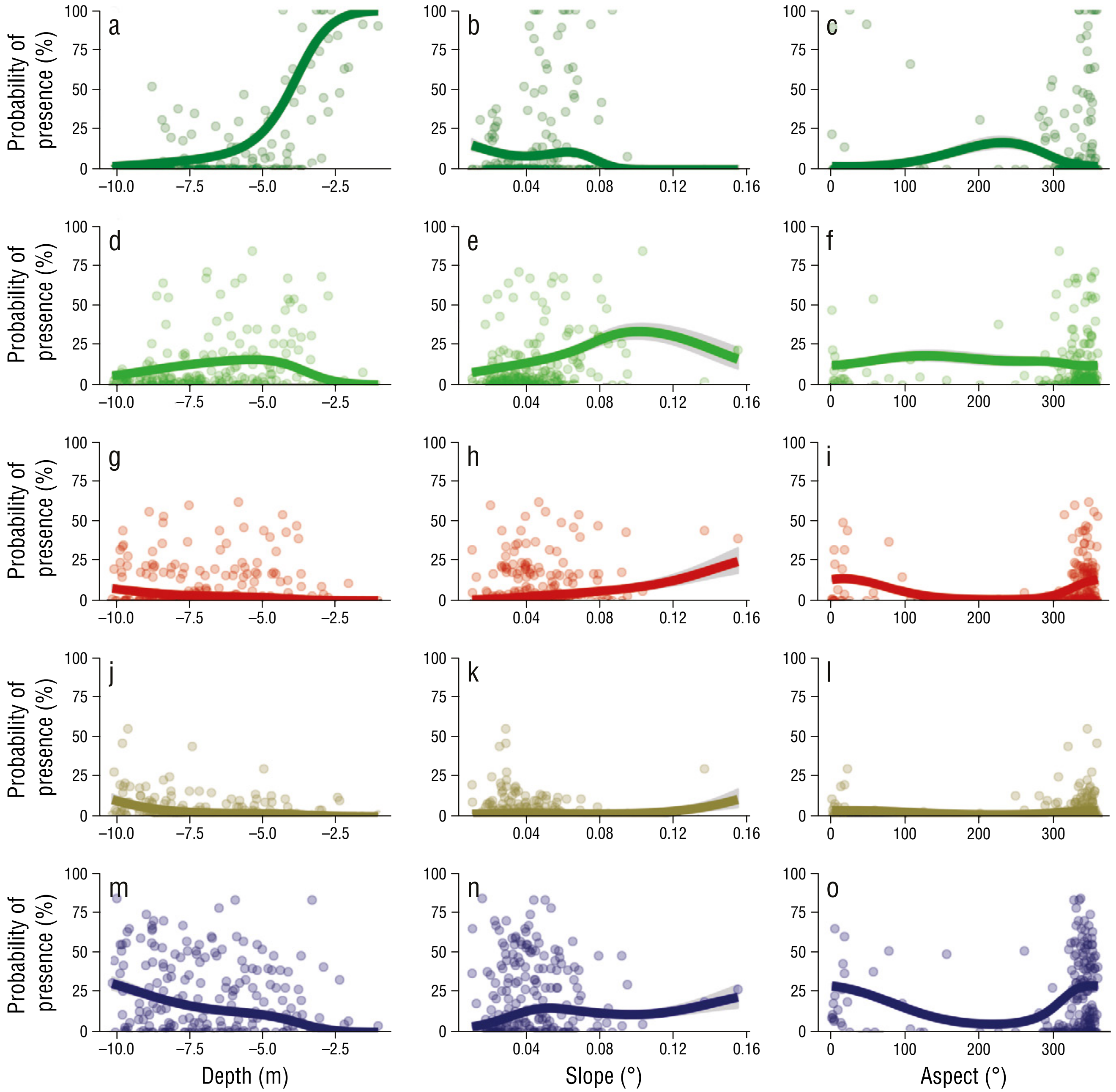

Figure 4. Estimated nonlinear relationships (curves) between geomorphological variables (*x*-axis) and the probability of presence (*y*-axis) of the 5 most abundant taxonomic groups of submerged aquatic vegetation on the west coast of the Yucatán Peninsula. The gray bands correspond to the confidence bands associated with the estimates of the adjusted multinomial logistic additive Bayesian model. Geomorphological variables: depth (left), slope (center), and aspect (right). Taxonomic groups: seagrasses (dark green), green algae (green), red algae (red), brown algae (brown), and algal turf (dark blue). The points correspond to field observations.

baseline for oceanographic, biological, and ecological studies in southeastern Mexico. Furthermore, it expands the knowledge of the Yucatán shallow coast and contributes to the understanding of processes such as hydrodynamics (Qian et al. 2020), sediment transport (Appendini et al. 2012), and ecological functioning (Wedding et al. 2008, Palafox-Juárez and Liceaga-Correa 2017), which are fundamental for decision-making regarding coastal development, adaptive management, and environmental conservation.

In addition, this study retrieves and makes publicly available a bathymetric database that includes SAV distribution data from over 14 years ago. This collection constitutes a critical reference for studies of landscape change, particularly in the face of pressures such as oil spills, infrastructure construction, harmful algal blooms, or the effects of climate change (Lotze and Worm 2009, Wilkinson et al. 2011, Hawkins et al. 2013, Thurstan et al. 2015, Bledsoe et al. 2022). Its availability and analysis promote evidence-based management and strengthen the ecological and social resilience of the Yucatecan coast.

Conclusions

The statistical and spatially explicit results in this study confirmed the ecological process documented at other latitudes regarding the influence of geomorphological complexity on the distribution of benthic communities, especially SAV. The geographic and ecological scope and scales addressed in this study provide opportunities for comparative analysis at the community and seascape levels, contributing strategic elements for the territorial management of the study area.

The complex landscape of the Yucatán Shelf is unique due to its size and low change rate in its slope, which create a vast marine territory where diverse interests and vocations associated with the benthic marine landscape coexist. This reinforces the need to implement management strategies based on scientific information and provide full legal certainty to ensure the provision of services from these ecosystems to oceans in general and, in particular, to the population of Yucatán.

English translation by Claudia Michel-Villalobos.

Declarations

Supplementary material

The supplementary material for this work can be downloaded from: https://www.cienciasmarinas.com.mx/index.php/cmarinas/article/view/3458/420421220.

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: MAL-C, EC; Data curation: LAR-S, HH-N, EBP-J, EC; Formal analysis: MAL-C, EJG, LAR-S, HH-N, EBP-J; Funding acquisition: MAL-C, EC; Research: MAL-C, EJG, LAR-S, EBP-J, EC; Methodology: MAL-EC, LAR-S, EBP-J, EC; Resources: MAL-C, EC; Software: EJG, HH-N, LAR-S; Supervision: MAL-C; Validation: EC, EJG; Visualization: EC; Writing—original draft: MAL-C, EJG, EBP-J, EC; Writing—review and editing: LAR-S, HH-N.

Data availability

The data for this study are available from the corresponding author by reasonable request.

Use of AI tools

The authors did not employ any AI tools in this work.

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Reproductive biology of the Polla Drum *Umbrina xanti* (Perciformes: Sciaenidae) in the central Mexican Pacific

Salvador Ruiz-Ramírez[1], Valeria E Reséndiz-Cruz[1], Gabriela Lucano-Ramírez[1]*, Rosa E Carretero-Montes[1], Raúl E Lara-Mendoza[2]

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CORRESPONDING AUTHOR
* E-mail: gabriela.lucano@academicos.udg.mx

[1] Laboratorio de Ecología de Peces e Histología, Departamento de Estudios para el Desarrollo Sustentable de Zonas Costeras, Universidad de Guadalajara, 48980 San Patricio-Melaque, Jalisco, Mexico.
[2] Instituto Nacional de Pesca y Acuacultura, Departamento de Evaluación de Recursos Pesqueros en el Atlántico, Dirección de Investigación Pesquera en el Atlántico, 4100 Mexico City, Mexico.

ABSTRACT. The Polla Drum *Umbrina xanti* is a commercially important species off the coast of Jalisco. However, as is the case with most of the fisheries in the country, information on the life history of this species is very limited. Thus, this work aimed to analyze the length at sexual maturity, reproductive season, and microscopic description of the gonads, among other aspects. Organisms were collected from 1998 to 2008 with gill nets by artisanal fisheries operating in the central Mexican Pacific. The gonadosomatic index (*GSI*), sexual maturity stages, oocyte diameter, condition factor, and sexual ratio were analyzed per month. Histology of the gonads was performed, and the average length of maturation was estimated. In total, 1,202 organisms between 17.9 and 42.3 cm *TL* were captured. The number of females was greater than that of males (1:0.88). The highest percentages of mature individuals occurred in February and in April–May. The *GSI* had maximum values from January to May. The largest oocyte diameters occurred from March to June. Oocyte development was asynchronous, and the testis showed unrestricted lobular-type development. The average maturation length for females was 27.37 and 28.78 cm for males. Because these average lengths at maturity were less than the average length, we can indicate that more than 50% of the organisms caught by commercial fishing had had a reproductive event.

Key words: reproduction, gonadosomatic index, length at maturity, Polla Drum, asynchronous development, lobular organization, oocyte diameter.

INTRODUCTION

Reproduction is a significant event in the life cycle of living beings and, along with growth and feeding, can ensure the persistence of organisms in the environments they inhabit (Nikolsky 1963). Studies describing fish reproduction in species involved in commercial fisheries are important. These studies provide basic information on the biology and population characteristics of fish, particularly concerning their reproduction. Therefore, these studies are essential inputs to evaluate and manage actions for fishery management (West 1990, Cailliet et al. 1996, Froese 2004).

The species of the Sciaenidae family are found in temperate and tropical regions worldwide, including the Indo-Pacific region, the Caribbean Sea, Amazon waters, the Mediterranean Sea, and the Atlantic and Pacific oceans. This is one of the most abundant families, with 69 genera and 289 species (Parenti 2020). In Mexico, it is distributed along the entire coast of the Pacific Ocean, including the Gulf of California (Robertson and Allen 2015), and is also observed on the Atlantic side, in the Gulf of Mexico (Nakamura 1981).

Sciaenids are known as croakers or drums due to the sounds they make. These sounds are used to locate aggregations; nevertheless, they can be heard more frequently during the reproductive period, especially while males attract females (Lagardère and Mariani 2006, Robertson and Allen 2015). Most species in this group are carnivorous and consume benthic macroinvertebrates, a variety of small fish, crustaceans, burrowing worms, and occasionally organic matter (FAO 1995, Robertson and Allen 2015). They are common in

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local markets because they are caught by fishers in the region (Robertson and Allen 2015).

Umbrina xanti is a species of the Sciaenidae family distributed from Mexico (Baja California) to northern Peru. It is a demersal fish that inhabits shallow coastal areas with sandy bottoms and can enter coastal lagoons and estuaries (Robertson and Allen 2015). It is a commercially important species in artisanal fisheries in the Mexican Pacific (Sandoval-Ramírez et al. 2020); in particular, its capture is frequent in the central Pacific (Espino-Barr et al. 2003, 2004; Gómez-Vanega et al. 2021), including in the region of the present study (Rojo-Vázquez et al. 2001, 2008). Despite this, and its particular ecological importance, little is known about certain aspects of its life history that would clarify population dynamics for fishery management.

With the reproduction of fish, the first life stage of an entire generation begins, and this introduction of new organisms is one of the main factors that influence the dynamics of fish populations (Csirke 1989). Because there is no information on the reproductive aspects of the Polla Drum *U. xanti*, the aim of this study was to estimate reproductive variables such as the gonadosomatic index, sex ratio, length at sexual maturity, and microscopic description of the gonads. The results of this study will expand the existing biological information on the species, which can be used by authorities to develop and design a fisheries management plan on the southern coast of Jalisco, Mexico.

Materials and methods

Fish were collected monthly for 5 consecutive days from January 1998 to December 2008. The organisms analyzed came from the commercial catch of artisanal fisheries operating in Bahía de Navidad (19°10′27″ to 19°13′18″ N, 104°41′54″ to 104°49′07″ W) located in the south of Jalisco, Mexico (Fig. 1). The fishers used nylon monofilament gillnets with different mesh sizes (7.20, 8.89, 10.16, and 11.43 cm) operating at the bottom for approximately 12 effective fishing hours at night. The total length ($TL \pm 1$ mm) and total weight ($TW \pm 0.1$ g) were obtained for each *U. xanti* individual. Sex and maturity were determined by direct observation of the gonads (Palazón-Fernández 2007), and their weight was recorded ($GW \pm 0.01$ g). The gonads were fixed in 10% neutral formalin (buffered with dibasic and monobasic sodium phosphate) for subsequent histological analysis.

A 0.5-cm transverse section was taken from the middle portion of the gonads to describe the internal structure. Histological sections of ovaries and testes were taken for each stage of development. For the histological process, samples were dehydrated in a series of ethyl alcohol solutions in increasing concentrations, from 50% up to the absolute concentration, embedded in paraplast, cutting sections of 3–5 µm, and stained with hematoxylin-eosin dyes (Lucano-Ramírez et al. 2001a). Gonads were observed and analyzed using a microscope (Primo Star HD, Carl Zeiss, Oberkochen, Germany) equipped with an integrated camera (Axiocam MRC5, Carl Zeiss), using AxioVision v. 4.8.2 software (Carl Zeiss). The different stages of oocyte development were classified according to Yamamoto and Yamazaki (1961), Lucano-Ramírez et al. (2001a), and Brown-Peterson et al. (2011). The structure of the internal cells of the testis was described according to the methods of Lucano-Ramírez et al. (2001b) and Uribe et al. (2018).

To identify the reproductive season, we used 3 complementary methods; the first was based on the monthly calculation of the gonadosomatic index (*GSI*) (Sánchez-Cárdenas et al. 2007):

$$GSI = \left[\frac{GW}{(TW - GW)}\right] \times 100 \ . \tag{1}$$

For the second, we applied the morpho-chromatic scale of 4 stages of gonadal development (immature, maturing, mature, and spawned or regressing) monthly, according to the criteria of Palazón-Fernández (2007). For the third method, we analyzed monthly variations in the average oocyte diameter, assuming that a larger average diameter corresponds to a greater degree of ovarian development; for this, we measured 30 oocytes from each stage of maturation from each ovary (largest diameter and smallest diameter of the oocytes that presented a nucleus) (West 1990, Lucano-Ramírez et al. 2014).

The weight-length relationship was calculated using the potential model equation proposed by Ricker (1975):

$$TW = aTL^{b} \quad , \tag{2}$$

where *TW* is the total weight, *TL* is the total length, and *a* and *b* are parameters of the fitted curve. The value of *b* of the weight-length relationship was used to calculate the relative condition factor (*CF*) for each organism (Froese 2006):

$$CF = \left(\frac{TW}{TL^{b}}\right) \times 100 \, , \tag{3}$$

where *TW* is total weight, *TL* is the total length and *b* is the parameter of the fitted curve. The sex ratio was obtained as the ratio of the number of males to the number of females and was calculated for the total sample, for each month, and by length class. The chi-square (χ^2) test with Yates' correction was used to assess whether the sex ratio differed from the expected value of 1:1 (Zar 2010).

The mean length at sexual maturity (L_{50}) was considered the length at which 50% of the sampled individuals had reached sexual maturity. To obtain this, the logistic model was fitted to the frequency of mature fish (in 2-cm intervals of *TL*). The L_{50} value for each sex was obtained with the estimated parameters in each case. The percentage of mature individuals at a given length (P_{TL}) was estimated:

$$P_{TL} = \frac{1}{[1 + e^{(bTL + a)}]} \times 100 \quad , \tag{4}$$

where *a* and *b* are the parameters of the logistic model. The L_{50} was estimated from the result of *a* divided by *b* (Echeverría 1987). This model was fitted for each sex with a nonlinear method based on the Levenberg-Maquard algorithm using STATISTICA v. 7.1 (Statsoft 2006). To evaluate possible differences in maturation ogives between sexes, a residuals or coincident curves analysis was performed (Chen et al. 1992).

The existence of significant differences between mean monthly values of *GSI*, *CF*, and oocyte diameter was verified using an analysis of variance (ANOVA), and the combined monthly variation between different variables was verified using the nonparametric Spearman's rank correlation test (r_s). For all tests, STATISTICA v. 7.1 (Statsoft 2006) was used, with a significance level of 0.05.

RESULTS

A total of 1,202 *U. xanti* organisms were collected, with *TL* values ranging from 17.9 to 42.3 cm. Of these, 80% were between 28 and 32 cm *TL*, and the remaining percentage had *TL* values <28 cm and >32 cm. The *TL* values of females ranged from 17.9 to 42.3 cm (mean: 29.73 ± 0.11 cm) and their *TW* values ranged from 67.0 to 837.7 g (mean: 293.54 ± 3.36 g). In males, *TL* values ranged from 23.6 to 42.1 cm (mean: 29.70 ± 0.09 cm) and their *TW* values ranged from 143.0 to 807.0 g (mean: 289.29 ± 3.11 g) (Fig. 2).

Sex ratio

The sex of 1,197 organisms was identified, of which 637 were females (53%) and 560 were males (47%); the sex ratio for the organisms analyzed was 1:0.88 (F:M). This differed significantly ($\chi^2 = 4.95$, $P = 0.03$) from the expected 1:1 ratio. In turn, the analysis of the number of females and males per length class showed no significant differences were observed with respect to the expected 1:1 ratio in any class (Fig. 1).

In the analysis of the monthly sex ratio, there were significant differences in March ($\chi^2 = 4.49$, $P = 0.03$), April ($\chi^2 = 7.91$, $P = 0.01$), and October ($\chi^2 = 7.26$, $P = 0.01$); in these 3 months the number of females exceeded that of males.

Reproductive season

The monthly distribution of gonadal maturity percentages indicated that the immature stage exhibited relatively low percentages in females (January, April, and September–December) and in males (January–June and November–December). The maturing stage and the spawning or regressing stage occurred in all months in both sexes, with percentages above 30% in several of them. The mature stage in females occurred from January to June, with high percentages of 51% in February and 55% in May. In males, this stage showed a similar trend to that of females; the highest percentages occurred from January to April, with 34% in January and 51% in March (Fig. 3).

The *GSI* of females showed significant variations throughout the year ($F_{11,\,625} = 11.98$, $P < 0.01$), with the highest values in March (4.75 ± 0.27) and April (4.62 ± 0.36). Conversely, the lowest value was obtained in August (0.98 ± 0.04). The average value of the *GSI* in females for the entire study was 2.8. In addition, the variation in the *GSI* in males was significant throughout the year ($F_{11,\,548} = 16.92$, $P < 0.01$), with the maximum value found in April (1.63 ± 0.14) and the minimum values in June (0.34 ± 0.04) and August (0.25 ± 0.03). The overall mean value of the *GSI* in males was 0.8. The SNK multiple contrast test identified groups with high values in March and April in both sexes (C and 3–4), and low values from June to December (A–B and 1–2), also in both sexes. The Spearman's correlation coefficient indicated a high correlation between the monthly averages of the *GSI* of males and females ($r_s = 0.867$, $P < 0.01$, $n = 12$); this suggests that the values in both sexes showed a similar seasonal trend (Fig. 4).

The monthly variation in *U. xanti* oocyte diameter was significant ($F_{11,\,7510} = 46.86$, $P < 0.01$), with the largest diameters occurring from March to June (groups 4 and 5). The smallest diameters (groups 1 and 2) were recorded from July to October and from December to January. A correlation was determined between oocyte diameter and the *GSI* of females ($r_s = 0.853$, $P < 0.01$, $n = 12$) (Fig. 5). The monthly variations in the percentages of gonadal maturity, the *GSI*, and oocyte diameter suggest that the species reproduces from January to May.

Relative condition factor

The relative condition factor (*CF*) varied significantly throughout the year for females ($F_{11,\,625} = 4.56$, $P < 0.01$) and males ($F_{11,\,548} = 4.48$, $P < 0.01$). In females, the lowest values occurred in July, August, and September; in males, they occurred in January, August, and September. The SNK test identified 2 groups for both sexes (A and B, 1 and 2), with overlaps occurring in several months. A similar seasonal trend was observed in both sexes, as the Spearman's correlation coefficient indicated a correlation between the monthly averages of the *CF* of females and males ($r_s = 0.60$, $P < 0.04$, $n = 12$) (Fig. 6).

The correlation analysis between the variables *GSI* and *CF* indicated no significance in females ($r_s = 0.524$, $P = 0.80$, $n = 12$). However, months with high *CF* values also showed high *GSI* values, which could indicate that there is no high cost or energy investment in females at the time of reproduction. In males, the correlation was also not significant ($r_s = -0.287$, $P = 0.37$, $n = 12$). However, in March, April, and May, the *CF* showed low values and, in the same months, the *GSI* showed the highest values. Therefore, we can infer that, in males, gonadal maturity could affect the physiological state of the organisms.

Microscopic description of the gonads

The ovaries are covered by the ovarian tunic, which is made of muscular tissue. Inside the ovary, we observed groups of oocytes at different stages of development, delimited by lamellae (Fig. 7). We identified 7 stages of oocyte development: 1) oocytes in primary growth, with an average diameter of 65.00 ± 2.10 µm, characterized by having little cytoplasm and a large nucleus with nucleoli. 2) Oocytes with vitelline vesicles or cortical alveoli with an average diameter of 135.15 ± 5.48 µm. Oil droplets are distinguished in the cytoplasm, and with these, the formation of the yolk begins. 3) Oocytes in primary vitellogenesis with an average diameter of 202.88 ± 7.51 µm. Yolk globules are observed in the cytoplasm. 4) Oocytes in secondary vitellogenesis with an average diameter of 307.38 ± 8.25 µm. A large number of yolk globules were present throughout the cytoplasm. 5) Oocytes in tertiary vitellogenesis with an average diameter of 319.58 ± 12.23 µm. The yolk globules began to fuse, and the nucleus was found migrating toward the animal pole. 6) Mature oocytes with a diameter of 335.64 ± 9.27 µm. The yolk was completely fused, and the nucleus was not observed. 7) Hydrated oocytes with an average diameter of

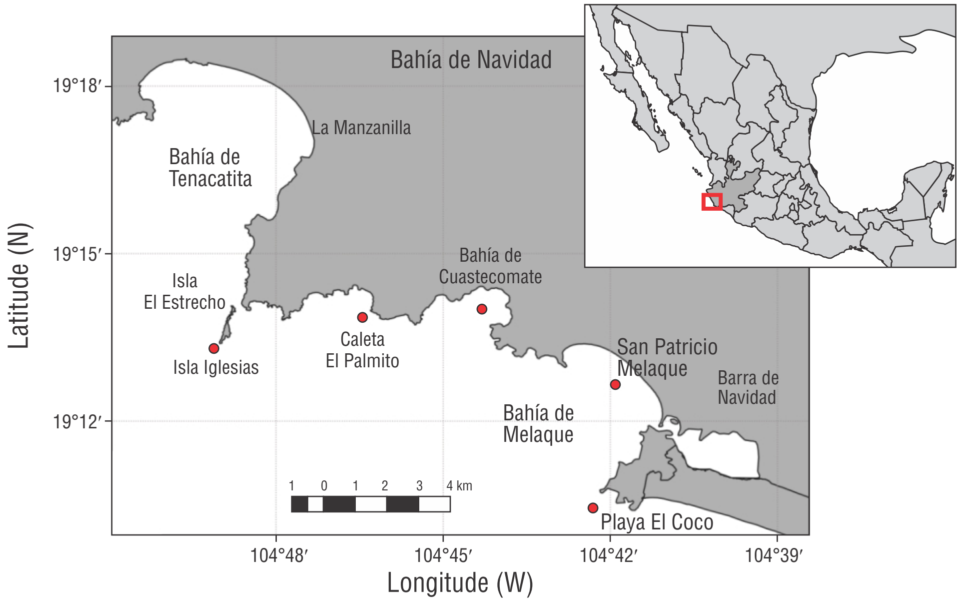

Figure 1. Study area: Bahía de Navidad, Jalisco, Mexico. The dots represent the sites where monthly sampling was conducted.

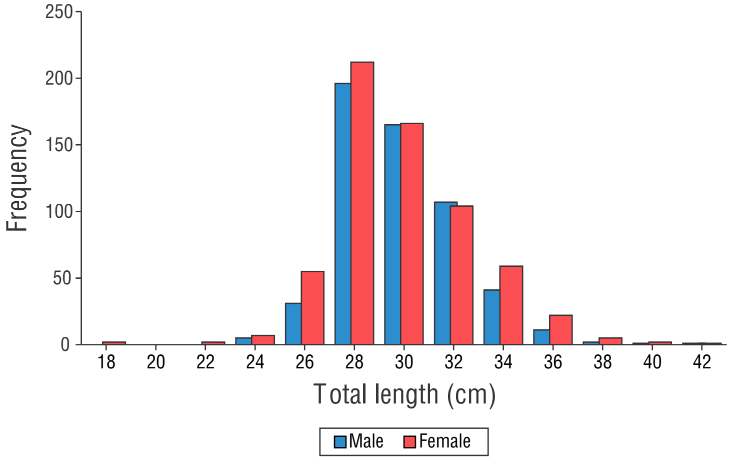

Figure 2. Frequency distribution of the total length of females and males of *Umbrina xanti* captured in the central Mexican Pacific.

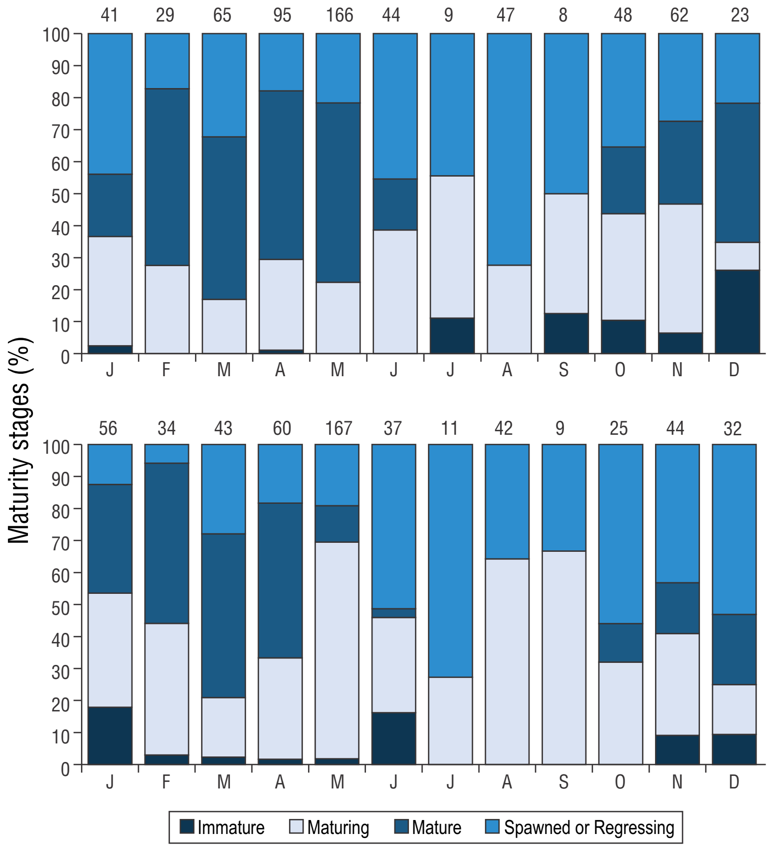

Figure 3. Monthly percentages of gonadal maturity stages of female (top) and male (bottom) *Umbrina xanti* in the central Mexican Pacific. Numbers at the top indicate sample size.

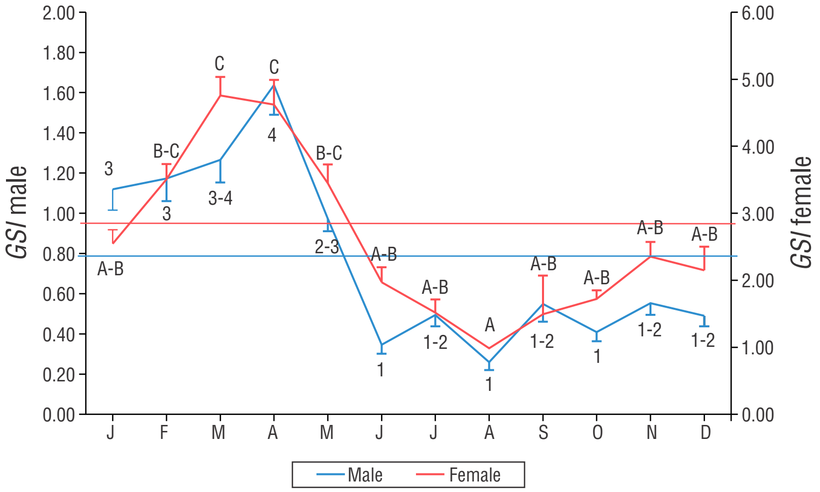

Figure 4. Monthly variation in the gonadosomatic index (*GSI*) of female and male *Umbrina xanti* captured in the central Mexican Pacific. Bars indicate the standard error. Transverse lines represent the mean. Numbers (males) and letters (females) indicate significant differences.

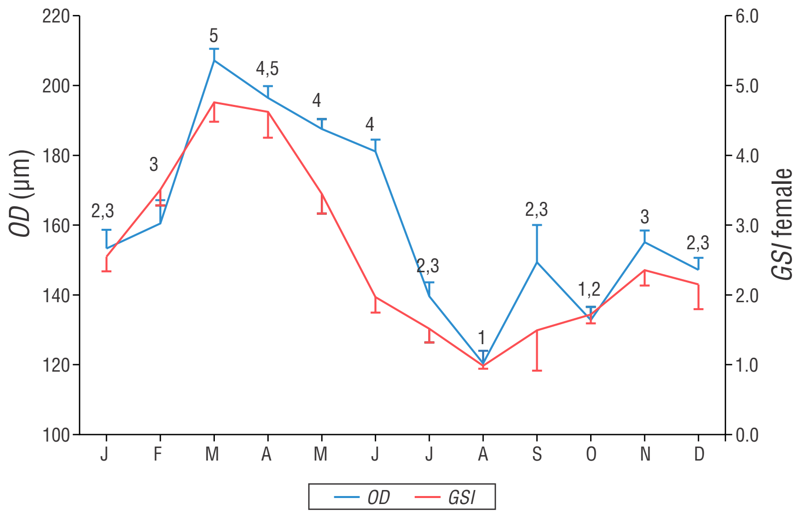

Figure 5. Monthly variation in the gonadosomatic index (*GSI*) and oocyte diameter (*OD*) of female *Umbrina xanti* captured in the central Mexican Pacific. Bars indicate the standard error. Numbers (*OD*) represent the multiple contrast test.

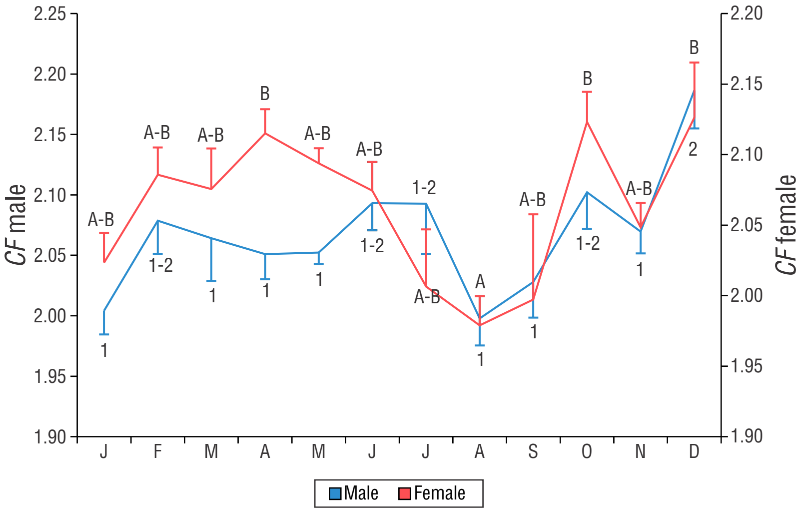

Figure 6. Monthly variation in the relative condition factor (*CF*) of female and male *Umbrina xanti* captured in the central Mexican Pacific. Bars indicate the standard error. Numbers (males) and letters (females) indicate significant differences.

367.03 ± 19.62 µm. The simultaneous presence of oocytes in different development stages in the mature ovary indicates that *U. xanti* has an asynchronous-type development (Fig. 6).

The germ cells within the testis were found organized into lobules and, within these, clusters of cells were observed forming cysts; this is where the entire process of spermatogenesis took place. Once the sperm were formed, they concentrated in the lumen of the lobules and subsequently accumulated in the receptor duct to be expelled. This type of sex cell arrangement suggests an unrestricted lobular type development (Fig. 8).

Average length at sexual maturity (L_{50})

The smallest female with mature gonads had a *TL* value of 22.6 cm, and the smallest male with the same characteristic had a *TL* value of 24.5 cm. According to the results obtained with the calculation of the average length at maturity, 50% of females reached sexual maturity at 27.37 cm *TL* and males at 28.78 cm *TL*. The overall average length for the females analyzed was 29.48 cm, which corresponds to 68% of the females having characteristics of gonadal maturity. For males, the overall average length was 29.27 cm, which corresponds to 66% of the males sampled having mature gonads. Thus, we can deduce that more than 50% of the organisms obtained from commercial captures would have had at least one reproductive event. For each of the 4 nets used in this study, the average length was greater than that of sexual maturity; it is worth mentioning that the 7.20-cm net caught only 28% of the organisms below the sexual maturity length. The residuals or coincident curves analysis indicated that the maturation curves between sexes showed no significant difference ($F = 2.054$, $P = 0.14$); therefore, the average length at maturity for combined sexes was 27.98 cm *TL* with a slope value of 0.31 (Fig. 9).

DISCUSSION

The study of reproductive aspects in commercially important species, and even in those without this status, contributes useful basic elements to manage commercial fishing appropriately. This information can be used to estimate the potential impacts of environmental and anthropogenic effects on the population dynamics of *U. xanti*.

Total length distribution

The average length and the intervals with the highest frequency of *U. xanti* organisms collected in the present study were similar to those found by Espino-Barr et al. (2003) in Colima (30.16 cm) and Espino-Barr et al. (2004) in Jalisco (29.62 cm), where the highest *TL* values of the organisms captured were between 25.35 and 32.25 cm and 27.16 and 31.46 cm, respectively. The similarity between values obtained in previous studies and those obtained in this study could be due to the fish coming from commercial fisheries, which use gillnets with similar characteristics, and the study areas being close together.

Sex ratio

The ratio of females to males is an important element that allows us to understand reproductive dynamics in a population. Most species that reproduce sexually have a sex ratio close to 1:1; this maximizes reproductive success and genetic diversity and tends to increase resilience to changes and disturbances. However, when there are greater numbers of either sex, these tend to balance out over time through natural selection (Fisher 1930, Nikolsky 1963). In the present study, females were more abundant than males; this result is similar to those found in other studies conducted with sciaenids, such as *Sciaena umbra* in Spain, where Grau et al. (2009) also found that females dominated over males with a ratio of 1.3:1.0 (F:M). The same was observed for *Bairdiella ronchus* in the Colombian Caribbean, with a notable abundance of females (1.7:1.0; F:M) (Torres-Castro et al. 1999). In addition, Fennessy (2000) described this same pattern in sciaenids off the coast of South Africa. This difference between sexes, according to Sadovy and Shapiro (1987), occurs in gonochoric species due to differences in growth and longevity, spatial segregation, sexual survival rate, and spawning migration. Furthermore, Silberschneider and Gray (2008) noted that in some species a higher survival rate has been recorded in females.

Reproductive season

One of the simplest, most widely used, and fastest methods to assess the level of gonadal development is the use of macroscopic scales (West 1990, Brown-Peterson et al. 2011). The scale proposed by Palazón-Fernández (2007) to characterize ovarian and testicular development consists of 4 maturation stages, which were identified by specific characteristics such as coloration, size, and the presence or absence of fluids and oocytes. This scale was used in the present study and, conjointly with the *GSI*, allowed us to identify the reproductive period of *U. xanti*. However, other authors have used different maturation scales that adapt more closely to the characteristics they observed in a particular species; for example, Prista et al. (2014) used a 5-stage scale to characterize female and male maturation in the croaker *Argyrosomus regius*.

Microscopic studies help confirm the degree of gonad maturity and define the type of oocyte development and arrangement of sperm cells in the testicle. At the microscopic level, the stage of testicle maturation can be distinguished based on structures and characteristics, such as the thickening of the tunica albuginea, the presence or absence of sperm, the amount of interstitial tissue, and the differentiation of the receptor duct; these vary depending on the degree of maturity (Grier et al. 2009). The testes of *U. xanti* males were heavier when mature because they are ready to release sperm. This development stage shows well-defined branches of the lobes, revealing the interstitial tissue, which is arranged radially and extends to the tunica albuginea (Grier 1981). Sperm accumulate in the ducts toward the receptor duct and cluster in it; these characteristics are specific to lobular testicular development. The species of sciaenids that exhibit these characteristics and the same developmental pattern are *Micropogonias ondulatus* (Barbieri et al. 1994), *Roncador stearnsii* (Miller et al. 2009), *Umbrina roncador* (Miller et al. 2009), and *Larimichthys polyactis* (Kyu-Lim et al. 2010).

The mature ovary of *U. xanti* shows 7 stages of oocyte development simultaneously. The increase in oocyte size is very clear from the beginning of vitellogenesis; the oocyte grows gradually due to the accumulation of yolk in the cytoplasm. Grau et al. (2009) classified oocyte development in *S. umbra* into 7 stages based on the diameter shown in each of the oocyte stages. The fact that various stages of oocyte development occurred simultaneously in mature *U. xanti* ovaries could confirm that they develop asynchronously. Consequently, oocytes are expected to be released in multiple spawnings. Another study on *S. umbra* off the coast of Turkey recorded 12 stages of oocyte development in the ovary; the authors assumed that oocyte development was asynchronous

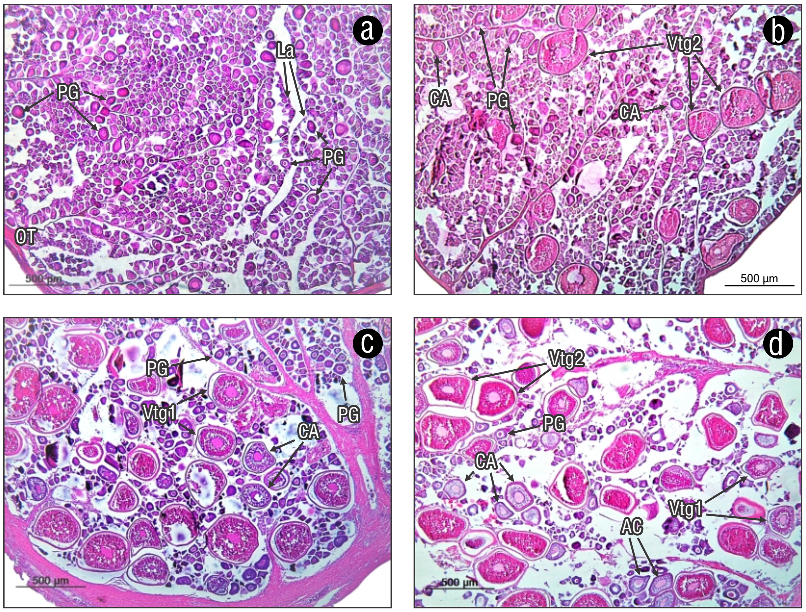

Figure 7. Cross sections of ovaries at different stages of maturity of *Umbrina xanti*: immature (**a**), maturing (**b**), mature (**c**), and spawned or regressing (**d**). Hematoxylin-eosin staining. Scale: 500 µm. OT = ovarian tunic; PG = primary growth oocyte; CA = oocyte in cortical alveolus; Vtg1 = oocyte in primary vitellogenesis; Vtg2 = oocyte in secondary vitellogenesis; La = lamella.

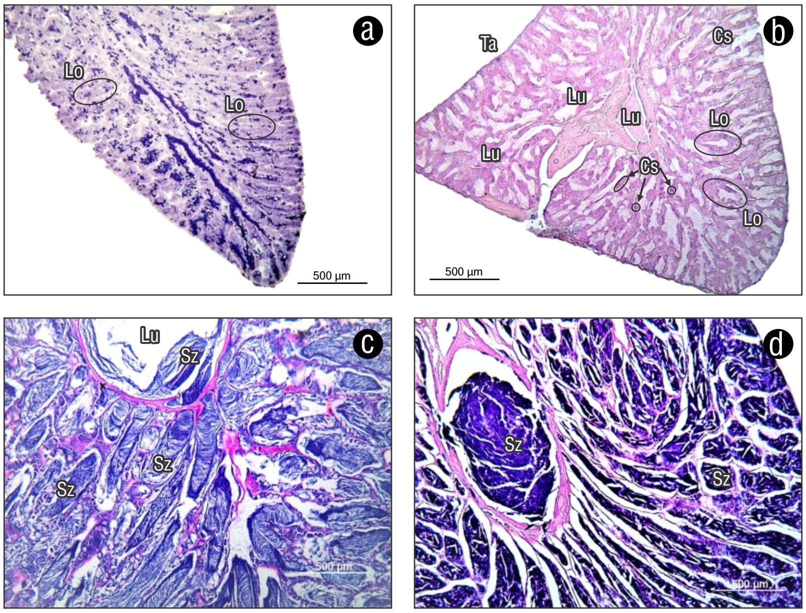

Figure 8. Cross-sections of testes at different stages of maturity of *Umbrina xanti*: immature (**a**), maturing (**b**), mature (**c**), and spawned or regressing (**d**). Hematoxylin-eosin staining. Scale: 500 µm. Ta = tunica albuginea; Lu = lumen; Lo = lobes; Cs = cyst; Ez = sperm.

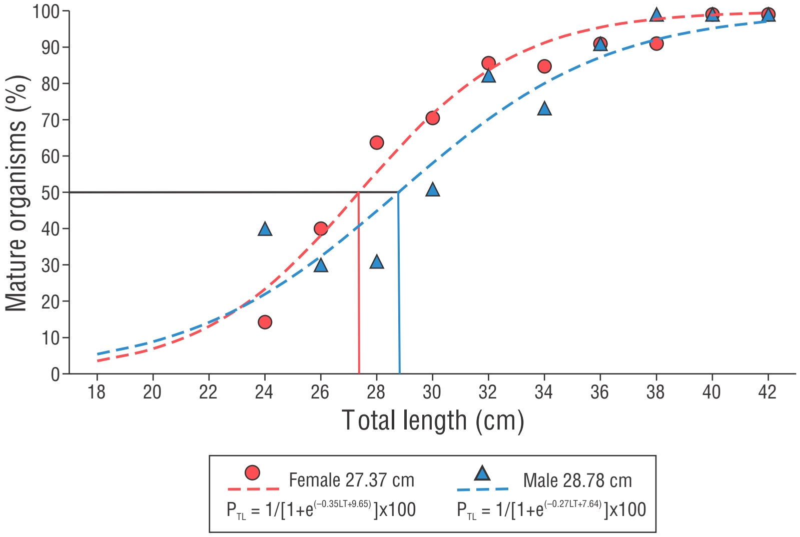

Figura 9. Percentage of mature female and male *Umbrina xanti* organisms captured in the central Mexican Pacific. The vertical lines indicate the L_{50} value for each sex; red line for females and blue line for males. P_{TL} = Percentage total length.

and considered this species to be iteroparous and gonochoric with multiple spawning events (Engin and Seyhan 2009). Different species of the Sciaenidae family, such as *M. ondulatus* (Baribieri et al. 1994), *Sciaenops ocellatus* (Wilson and Nieland 1994), *Micropogonias furnieri* (Vizziano et al. 2005), *R. stearnsii* (Miller et al. 2009), *L. polyactis* (Kyu-Lim et al. 2010), *Menticirrhus americanus* (Clardy et al. 2014), and *Macrodon ancylodon* (Dos Santos-Cardoso et al. 2018), show this same type of asynchronous development. Species that have oocytes with asynchronous development usually have partial spawning or multiple spawning, with a relatively broad reproductive season or with several reproductive events per year (González and Oyarzún 2002, Dos Santos-Cardoso et al. 2018).

The *GSI* is frequently used to identify reproductive periods (Brewer et al. 2007). In this study, both sexes of *U. xanti* showed maximum *GSI* values in spring. According to Mendo and Samame (1988), *GSI* values increase during the reproductive season and decrease after spawning. In the study region, coastal upwelling occurs from February to May (Ambriz-Arreola et al. 2012); this could support the increased reproductive activity of *U. xanti*, since during this period the larvae could benefit from increased primary productivity due to these coastal upwellings. In addition, Cárdenas (2012) mentions that this family reproduces mainly in warm temperatures, when conditions are more favorable for egg development and larval growth; therefore, several species of sciaenids have greater reproductive activity in spring and summer. This is also observed in *Argyrosomus japonicus*, which has a reproductive period between March and June in Taiwan (Ueng et al. 2007), and in *A. regius*, which reproduces between March and August off the coast of Spain (Jiménez et al. 2007). In turn, Vizziano et al. (2005) recorded the reproductive period from December to March for *M. furnieri* off the coast of Brazil. Meanwhile, for *Cynoscion nebulosus* in the Gulf of Mexico, spawning occurs from May to July (Brown-Peterson et al. 2002) and for *S. umbra* from March to June in the Mediterranean Sea (Chakroun-Marzouk and Ktari 2003).

Relative condition factor

The relative condition factor (*CF*) is a variable that reflects the body condition of fish and can be related to the quantity, quality, and availability of food in the environment where each species thrives (Froese 2006). High *CF* values indicate that organisms are in good or better physiological condition. In Bahía Navidad, Mexico, *U. xanti* females had peak *CF* values in April, October, and December, and males in February, June–July, October, and December. High *CF* values are usually associated with periods of increased or improved feeding.

In the study region, coastal upwellings were reported to increase productivity in these areas from February to May (Ambriz-Arreola et al. 2012), which could explain the increased *CF* during these months. The increased *CF* observed at the end of the year may be the effect of an intermediate climatic condition, since it is the final stretch of the rainy season and a transition period between tropical-subtropical and temperate conditions, where no single environmental condition clearly dominates (Ambriz-Arreola et al. 2012).

The highest *CF* values were observed at the beginning and end of the year (more pronounced in females), and increases in *GSI* were also recorded during this same period. The relationship between *GSI* and *CF* was not very clear in *U. xanti*. In females, reproduction does not appear to affect body condition; however, a negative trend was observed in males, although not significant. In some species, as reported by Wootton (1990), the energy investment of females results from the accumulation of yolk during oogenesis, though this is not the case in *U. xanti*. However, it has also been mentioned that energy expenditure for both sexes is due to the requirements of individuals, such as survival, growth, or reproduction, in relation to the environment in which they develop. In the case of reproduction, the investment could be associated with the increase in gonad size relative to the weight of the organism, which indicates that during this period the gonads are at their peak maturity. In some species, a decrease in *CF* values indicates a decrease in energy stored in the form of body lipids and proteins; these substances help meet energy requirements during reproduction (González and Oyarzún 2002).

Length at sexual maturity

In *U. xanti*, the average length of maturation did not differ between females and males. Similar to the findings in this study, on the Brazilian coast, Dos Santos-Cardoso et al. (2018) observed that both sexes of *M. ancylodon* mature at 21.3 cm, and for *M. furnieri*, maturation occurred at 11 cm (Vizziano et al. 2005); the authors suppose that this is possible if both sexes perform the same migrations and feed in similar locations; therefore, they reach sexual maturity at the same time. Other studies with sciaenids indicate that females reach sexual maturity at a greater length than males; in *S. umbra*, females matured at 23.4 cm and males at 22.1 cm (Chakroun-Marzouk and Ktari 2003). For the same species, Grau et al. (2009) reported that females reached sexual maturity at 29.9 cm and males at 25.4 cm. In turn, for *B. ronchus* in the Colombian Caribbean, females had an average length at sexual maturity of 15.8 cm and males of 15.4 cm (Torres-Castro et al. 1999). In most sciaenids, females reproduce at a greater length than males (Cárdenas 2012); this could be because females, in order to begin reproduction, need a greater amount of food to grow first and subsequently produce the number of eggs necessary to ensure an increase in the number of individuals in the population (Kunz 2004).

In *U. xanti*, the average capture length (29.7 cm) was slightly greater than the mean length at sexual maturity (28.1 cm). This suggests that slightly more than half of the captured organisms had already had at least one reproductive event. The average capture length was greater than the maturation length, which is a desirable situation in species subject to commercial exploitation according to Espino-Barr et al. (2008). In any case, future studies are needed to continue analyzing the population dynamics of species, mainly and especially those that are subject to continuous commercial capture.

CONCLUSIONS

The 3 methods used to identify the reproductive period of *U. xanti* indicated that both females and males had a prolonged reproductive period, which lasted from January to May. *Umbrina xanti* is a gonochoric species; microscopically, the germline cells of the testis display an unrestricted lobular organization, and oocyte development in the ovary is asynchronous. The average maturation length suggests that 62% of females and 61% of males had already had at least one reproductive event. The present study provides basic information on the reproduction of *U. xanti*, a species of commercial interest in the central Mexican Pacific. This information can be used to estimate the potential impacts of environmental and anthropogenic effects on the population dynamics of *U. xanti*.

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DECLARATIONS

Supplementary material

This work does not include supplementary material.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

Conceptualization: SRR, GLR, VERC; Formal analysis: SRR, GLR, VERC, RELM; Funding acquisition: GLR, SRR; Research: SRR, GLR, VERC, RELM; Methodology: GLR, SRR, VERC, RECM; Resources: GLR, SRR, RECM; Writing—original draft: GLR, SRR, VERC; Writing—review and editing: GLR, SRR, VERC, RECM, RELM.

Data availability

Partial use of the data from this study may be obtained upon reasonable request through the corresponding author.

Use of AI tools

The authors did not employ any AI tools in this work.

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Morphological and molecular characterization of the free-living *Symbiodinium natans*-clade A (Dinophyceae) from Bahía de La Paz, Gulf of California

Ana E Ramos-Santiago[1], Ignacio Leyva-Valencia[1,2], Yuri B Okolodkov[3], Christine J Band-Schmidt[1]*

CORRESPONDING AUTHOR
* E-mail: cbands@ipn.mx

[1] Departamento de Plancton y Ecología Marina, Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, 23079 La Paz, Baja California Sur, Mexico.
[2] Programa de Investigadoras e Investigadores por México, Secretaría de Ciencia, Humanidades, Tecnología e Innovación, Mexico City, Mexico.
[3] Laboratorio de Botánica Marina y Planctología, Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, 94294 Boca del Río, Veracruz, Mexico.

Abstract. The genus *Symbiodinium* is a group of mostly endosymbiotic dinoflagellates, commonly known as zooxanthellae, which live in association with marine invertebrates and protists. The objective of the present study was the morphological and molecular identification of 2 strains of Symbiodiniales (SNCETMAR-1 and SNCETMAR-2) isolated from the anemone *Actinostella* sp. from Bahía de La Paz, Gulf of California. Culture identification was conducted via photomicroscopy, including epifluorescence and scanning electron microscopy. A sequence of the SNCETMAR-2 strain was obtained from the 28S rDNA region. The combination of methods allowed the strains to be identified as *Symbiodinium natans*-clade A. This taxon is a group of endosymbiotic and free-living organisms, which facilitated the cultivation of the strains in the laboratory. The life cycle of this group presented 2 phases, a motile and a non-motile phase in the coccoid state, the last stage where both sexual and asexual division occur. This study extends the reports of clade A of the family Symbiodiniaceae in the Gulf of California and provides valuable information for its culture, identification, and phylogenetic analysis.

Key words: *Actinostella*, endosymbiont, Gulf of California, life stages, *Symbiodinium*, zooxanthellae.

Introduction

Symbiodinium Gert Hansen & Daugbjerg is a photosynthetic genus with opportunistic and free-living clades and subclades, which is distributed in tropical and subtropical areas (Takabayashi et al. 2012, Granados-Cifuentes et al. 2015, Hoppenrath et al. 2023). The genus name is considered neutral and means "living together" and "whirling" (LaJeunesse et al. 2018). These organisms have also been called *Zooxanthella* K. Brandt (Guiry and Andersen 2018). This refers to the mutualistic symbiosis shown by the alga, which in this case is the symbiosis of the dinoflagellate with invertebrates such as cnidarians, clams, copepods, flatworms, sponges, and some protozoans, such as foraminiferans, radiolarians, and ciliates (Baker 2003, Hirose et al. 2008, LaJeunesse et al. 2018). In addition, they are classified as cytobionts or intracellular symbionts (Taylor and Harrison 1983).

Species of the Symbiodiniaceae family (e.g., *Symbiodinium microadriaticum* LaJeunesse and *Symbiodinium pilosum* Trench & R.J. Blank ex La Jeunesse) show different photosynthetic responses under identical laboratory conditions. These photosynthetic differences explain the presence of this family in the diverse niches they can occupy (Iglesias-Prieto and Trench 1994). Host–symbiont specificity demonstrates the ability of a symbiont to be specialized for a certain host that inhabits a specific region; in addition, variations in said

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specificity are shown over wide geographic ranges. Physical (temperature and irradiance) and biological (host diversity and abundance and symbiont diversity and abundance) variables modulate symbiont–host specificity (Iglesias-Prieto et al. 1992, 2004; Iglesias-Prieto and Trench 1994, 1997). In addition to their role as symbionts, extracts of strains of the Symbiodiniaceae family isolated from the anemone *Stichodactyla haddoni* (Saville-Kent) have been reported to be cytotoxic to the crustacean *Artemia salina* (Linnaeus) (Bigham-Soostani et al. 2021).

The Symbiodiniaceae family is a diverse group comprising several generic and subgeneric clades, each consisting of an unknown number of subspecies or subclades (Iglesias-Prieto et al. 2004, LaJeunesse et al. 2018). Phylogenetic reconstructions with ribosomal (28S and 23S) and chloroplast (psbA) genes have revealed 9 clades (A to I) (Hirose et al. 2008, Hansen and Daugbjerg 2009, Pochon and Gates 2010, Yamashita and Koike 2013, LaJeunesse et al. 2018). New genera have been proposed with respect to phylogenetic groupings: *Symbiodinium* Gert Hansen & Daugbjerg (clade A), *Breviolum* J.E. Parkinson & LaJeunesse (clade B), *Cladocopium* (clade C), *Durusdinium* LaJeunesse (clade D), *Effrenium* LaJeunesse & H.J. Jeong (clade E), *Fugacium* LaJeunesse (clade F), and *Gerakladium* LaJeunesse (clade G) (LaJeunesse et al. 2018). Few clades show apparent morphological differences: clade B has cell sizes of 6 to 12 µm, and clade C has an apical groove called acrobase (LaJeunesse et al. 2018).

The strains analyzed in this study belong to clade A, corresponding to the oldest lineage of the Symbiodiniaceae family, which is made up of *S. microadriaticum*, *Symbiodinium necroappetens* LaJeunesse, S. Y. Lee, Knowlton & H. J. Jeong, *Symbiodinium tridacnidarum* S. Y. Lee, H. J. Jeong, N. S. Kang & LaJeunesse, *Symbiodinium natans* Gert Hansen & Daugbjerg, and *Symbiodinium linucheae* (Hansen and Daugbjerg 2009, LaJeunesse et al. 2018). Clade A includes free-living species, such as *S. pilosum* and *S. natans* (Yamashita and Koike 2013, LaJeunesse et al. 2015), in addition to groups with transient, opportunistic, free-living, and symbiotic forms that can be found associated with invertebrate hosts or protists (LaJeunesse et al. 2018). It can also inhabit different substrates, such as sand (Carlos et al. 1999, Hoppenrath et al. 2023), and form symbioses with soft corals (e.g., *Stereonephthya cundabiluensis* Verseveldt), stony corals, or hard corals, such as *Orbicella faveolata* (Ellis & Solander) (Hirose et al. 2008, Kemp et al. 2014).

MATERIALS AND METHODS

Isolation and growing conditions

Cells were isolated from the column of the solitary anemone *Actinostella* sp. (Hexacorallia: Actinaria: Actiniidae; Fig. 1) that was collected by Ana E Ramos-Santiago on August 9, 2018, at the CETMAR beach (4°08′39.2″ N, 110°20′41.0″ W; Fig. 2), Bahía de La Paz, in the southwestern Gulf of California, Mexico. Non-motile cells were isolated on an AXIO Vert.A1 inverted microscope (Carl Zeiss, Oberkochen, Germany), using capillaries with reduced tips. A progressive escalation was carried out until we obtained 25-mL cultures in flat 50-mL tubes. The SNCETMAR-1 and SNCETMAR-2 strains were kept in GSe medium with vermicompost extract (Bustillos-Guzmán et al. 2015) and K medium (Keller et al. 1987) modified with vermicompost extract at 34 salinity, 24 °C ± 1 °C temperature, continuous 150-µmol $E \cdot m^{-2} \cdot s^{-1}$ illumination, and a 12 h light:12 h dark cycle.

Morphological identification

Strain identification was done with the help of specialized literature (LaJeunesse et al. 2015, 2018; Hoppenrath et al. 2023). We evaluated morphometry and obtained micrographs of live cells on the Axio Vert.A1 inverted photonic microscope (Carl Zeiss) in bright field. In addition, we used the Axio Scope.A1 epifluorescence microscope (Carl Zeiss) with a 6-megapixel Axiocam 506 color digital camera to observe cells stained with the fluorescent marker DAPI (4',6-diamidino-2-phenylindole; Sigma) and visualize the position and size of the nucleus. To process samples for scanning electron microscopy (SEM), we followed the protocol used by Ramos-Santiago (2023) for naked dinoflagellates. Broadly, the methodology consisted of a prefixation process with 4% glutaraldehyde, postfixation with 2% osmium tetroxide (OsO_4), in-between washes to eliminate fixative residues, dehydration with an ethanol gradient (EtOH) at 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, and twice at 99%, and a drying process of the samples with hexamethyldisilazane (HMDS). The samples were sent to the Academic Service of Scanning Electron Microscopy (SAMEB) of the *Instituto de Ciencias del Mar y Limnología* (ICMyL), *Universidad Nacional Autónoma de México* (UNAM), Mexico City, Mexico.

Molecular identification

DNA extraction and amplification

DNA extraction from the SNCETMAR-1 and SNCETMAR-2 strains was performed using the Quick-DNA Miniprep Plus Universal kit (Zymo Research, USA). For amplification, a mixture of 6.25 µL of DreamTaq Green PCR 2X (Thermo Scientific, USA), 2 µL of milli-Q H_2O, 1 µL of each primer (F and R), and 1 µL of DNA was used. Primers for 28S rDNA were used (Hosoi-Tanabe et al. 2006). Amplification conditions consisted of a denaturation step at 95 °C for 5 min, followed by 35 cycles at 95 °C for 1 min, at an annealing temperature of 52 °C for 1 min, 72 °C for 2 min, and, finally, an extension at 72 °C for 7 min. The PCR samples were verified by 1.5% agarose gel electrophoresis with 1X TBE Buffer. The image was digitized under the Bio-Rad ChemiDoc XRS+ system. The PCR products were sent for purification and sequencing to the company Macrogen (Seoul, South Korea). It is important to note that DNA extraction was successful in both strains; however, amplification was only achieved with the SNCETMAR-2 strain.

Phylogenetic analysis

The sequence was edited with the Sequencher program v. 4.1.4. Sequences from the GenBank database were used to perform a BLAST analysis of the consensus sequence (Forward + Reverse). Sequences from the different clades of the Symbiodiniaceae family from the 28S rDNA region

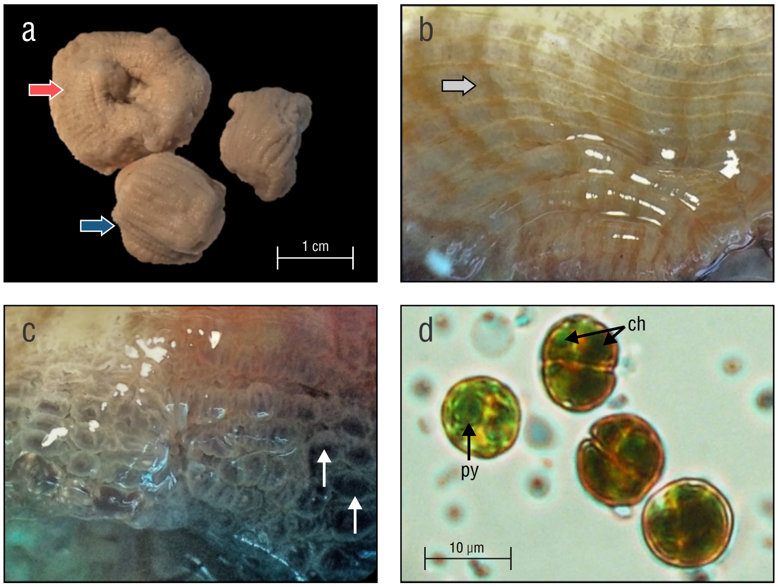

Figure 1. *Symbiodinium*-clade A and the host anemone *Actinostella* sp. Specimen of the anemone *Actinostella* sp. preserved in 4% formalin, the top view of the collar and oral disc with retracted tentacles is observed (red arrow); lateral view of the spine (blue arrow) (**a**). Details of live *Actinostella* sp., coloration is observed, lower detail of the collar with small aligned warts (gray arrow) (**b**). Lateral view of the spine with large and numerous warts (white arrows) (**c**). Freshly isolated cells of *Symbiodinium* sp. (SNCETMAR-2 strain), with green–yellow chloroplasts (ch) and pyrenoid (py) (black arrows) (**d**).

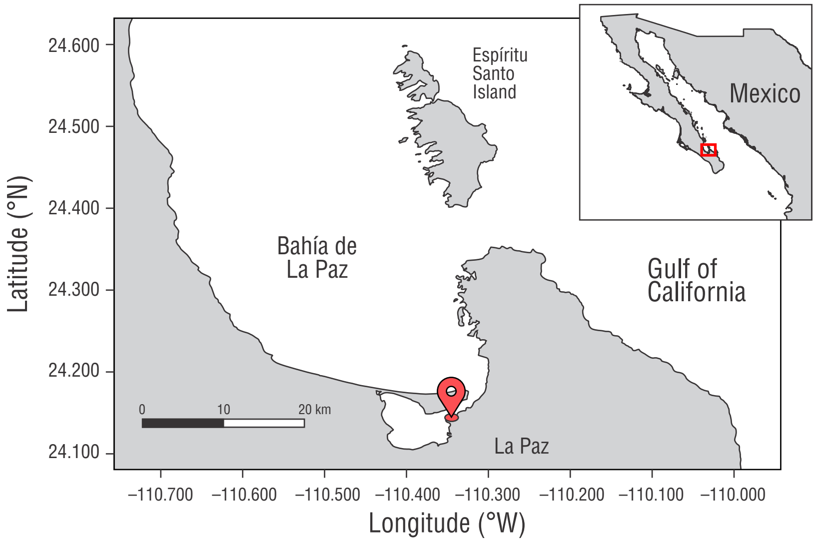

Figure 2. Location of Bahía de La Paz, Baja California Sur, Mexico. The red marker indicates the location of the CETMAR beach sampling site (24°08′39.2″ N, 110°20′41.0″ W).

were selected for the reconstruction of the phylogenetic trees. Sequence alignment was performed with the MEGA v. 10.0.5 program, with the MUSCLE alignment algorithm. The model that best described the nucleotide substitution rates of the sequences was selected with the JModel test v. 2.1.10, using the general time reversible (GTR) model for the phylogenetic analysis, which was done with the maximum likelihood (ML) and maximum parsimony (MP) algorithms in the MEGA v. 10.0.5 program and Bayesian inference (BI) with the MrBayes program v. 3.2.7a. Trees were constructed with a bootstrap of 1,000 replicates for ML and 3 × 106 generations for BI. The trees were edited with Photoshop CS6 v. 13.1.2.

Results

Symbiodinium-clade A morphology

Solitary cells, reddish in color, with rotating movement, which are distributed at the bottom and on the walls of the culture tube (Fig. 3a, b). Reticulated, brownish, and peripheral chloroplasts (Fig. 3c). The pyrenoid is located in the central area of the cell and has a diameter of 2.65 ± 0.52 µm (Fig. 3c–e). The mastigote (motile) cells are mushroom-shaped, laterally compressed, with the epicone slightly larger than the hypocone (Fig. 3c–i). Motile cells measure 10.93 ± 0.98 µm long and 7.79 ± 1.06 µm wide (mean ± SD; *n* = 30) in strain SNCETMAR-1 (Table S1), and 11.78 ± 1.05 µm long and 8.02 ± 1.38 µm wide (mean ± SD; *n* = 30) in the SNCETMAR-2 strain (Table S1). The nucleus is located in the anterior part of the cell (Fig. 3h, l). Another morphotype observed were coccoid non-motile cells, with a diameter of 12.01 ± 0.83 µm (mean ± SD; *n* = 30; Fig. 3j–l). The non-motile morphotype lacks morphological characteristics typical of motile cells.

We documented 2 life forms in both strains of *Symbiodinium*, motile cells and non-motile cells in the coccoid state, the latter being the dominant phase. Non-motile cells were observed in pre-division (Fig. 4a–c). Different phases of the division processes were documented: dyads with duplicated pyrenoids and the presence of one accumulation body and, on the other hand, cells with 2 accumulation bodies, which could indicate the fusion of 2 gametes (Fig. 4c–f). Cells forming clusters in triads and tetrads (Fig. 3g–j) and the presence of zygotes formed by fusion (syngamy) of gametes (Fig. 4k, l) were also observed. In coccoid cells in the process of reproduction, red-orange accumulation bodies were observed; these are probably lipids used as reserve substances or an eyespot (Fig. 5).

With SEM, the morphology of motile cells and the aforementioned reproductive stages were corroborated, as well as the cingulum, which is descending and displaced approximately one width of the cingulum (Fig. 6). We were unable to observe the arrangement of amphiesmal plates with this technique.

Molecular identification

We obtained a 514 bp sequence of the 28S rDNA region of strain SNCETMAR-2 (PP563703). In BLAST analyses performed in this study, the sequence showed 100% identity with the OQ449283 sequence, identified as *S. natans*. However, efforts were made to ensure that the selected sequences came from published studies or subsequent research in which their molecular identification has been corroborated. For the phylogenetic reconstruction of this taxonomic group, we included sequences from the 9 clades accepted for the Symbiodiniaceae family (Table 1). The sequence from this study clustered within clade A, with bootstrap support values of 91 and 97 for MP and ML, and posterior probability of 0.98 with BI (Fig. 7). The SNCETMAR-2 strain sequence formed a subclade with *S. natans* sequences with bootstrap support values between 70 and 89 (Fig. 7). We compared 2 *S. natans* sequences (AB704055 and AB704058) with the SNCETMAR-2 sequence; the AB704055 sequence showed a transition (C to T) at position 416, whereas in the AB704058 sequence there is a transition (A to G) at position 461. The analysis of the pairwise genetic divergences between the sequences identified as clade A revealed low values, ranging between 0.025 and 0.032. In contrast, divergences with sequences from other clades were greater than 0.141 (Table 2).

Discussion

The size of motile *S. natans*-clade A cells can range from 9.5 to 11.5 µm in length and 7.4 to 9 µm in width (Hansen and Daugbjerg 2009, LaJeunesse et al. 2015, Lee et al. 2015, Guiry and Guiry 2024), which agrees with what was reported in this study. The subclades *S. necroappetens* and *S. microadriaticum* show similar morphologies; nonetheless, these have cell sizes ranging from 9 to 12 µm (larger than *S. natans*) and from 7 to 10 µm (smaller than *S. natans*), respectively (LaJeunesse et al. 2015).

Currently, morphological and molecular identification within the Symbiodiniaceae family is complex. The number, shape, and position of the amphiesmal plates are used as descriptive morphological characteristics for the group; however, these are not sufficient for specific identification, as they may be similar or different within and between the groups that make up the clades (Lee et al. 2015, LaJeunesse et al. 2018). On the other hand, the morphological information of the amphiesmal plates in the motile stage (mastigote) of distantly related clades can yield different morphological information, as in clades A and E (Lee et al. 2015). The shape and size of the pyrenoid, chloroplasts, and nucleus have been used as morphological characters; however, in the Symbiodiniaceae family these characters are shared and cannot be used to differentiate clades or subclades (Lee et al. 2015). There is only

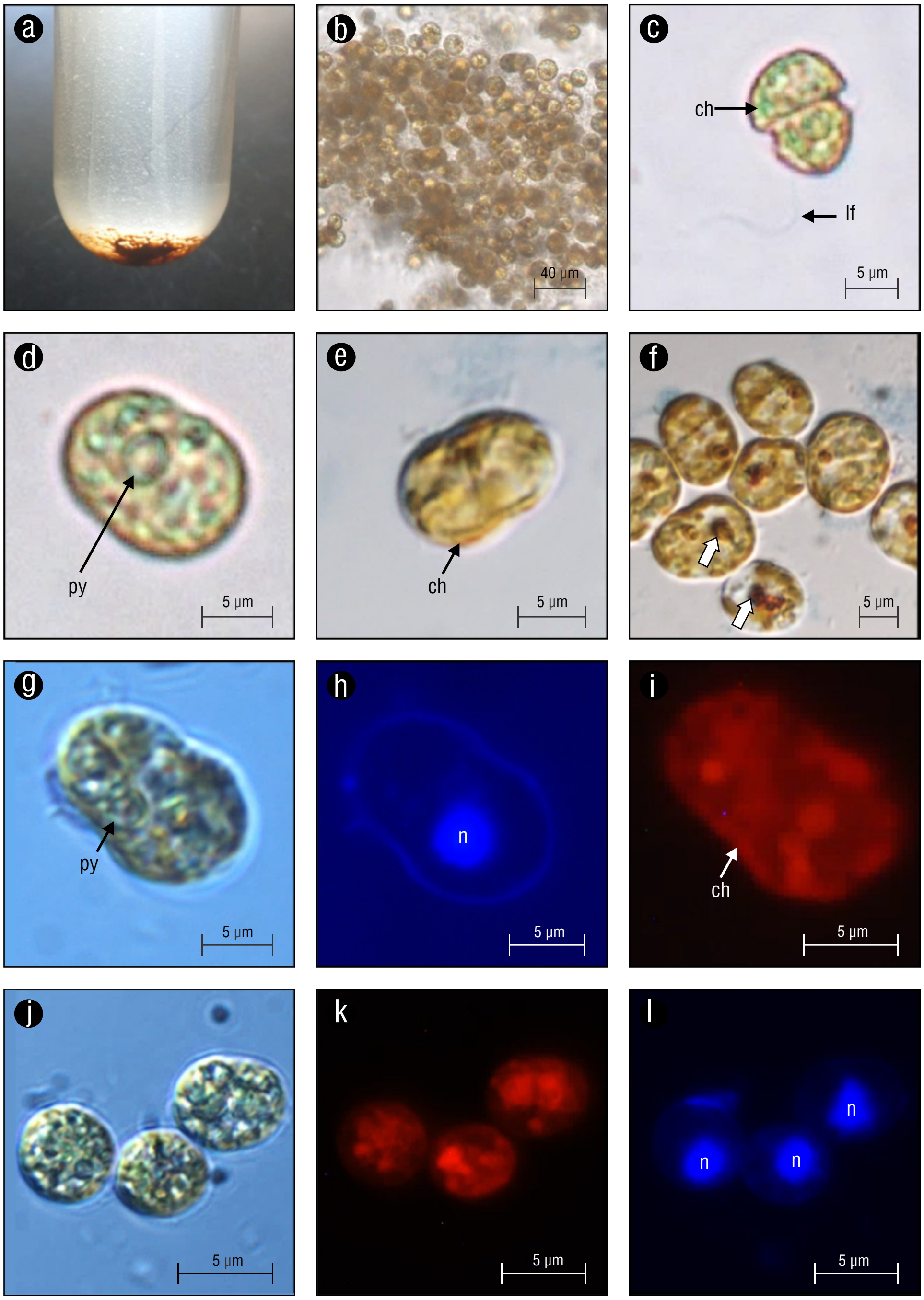

Figure 3. Subclade *Symbiodinium natans*-clade A from Bahía de La Paz. SNCETMAR-2 strain in GSe medium (**a**). SNCETMAR-1 strain (**c**–**f**). SNCETMAR-2 strain (**b**, **g**–**l**). Coccoid cells, non-motile, grouped together by mucilage (**b**). Ventral view of motile cells with the typical mushroom shape (**c**–**e**). Rounded and elongated reproductive cysts, they show reserve substances or an eye spot (white arrows) (**f**). Non-motile mushroom-shaped cells and coccoid state (**g**, **j**). DAPI staining shows the position and shape of the nucleus (n) in the 2 phases of the life cycle of *Symbiodinium* sp. (**h**, **l**). Epifluorescence images of chloroplasts (**i**, **k**). ch = chloroplasts, py = pyrenoid, lf = longitudinal flagellum.

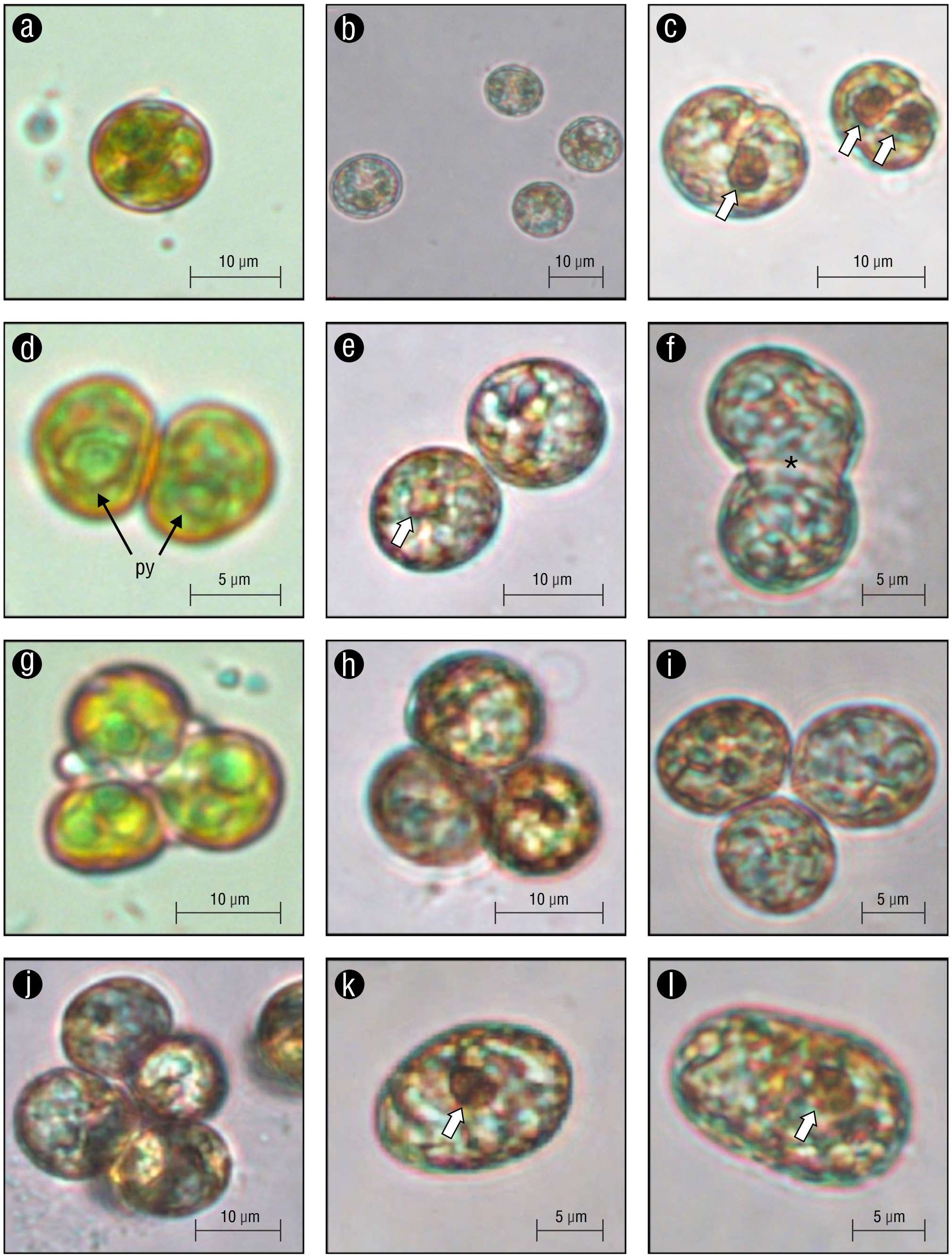

Figure 4. *Symbiodinium natans*-clade A cysts from Bahía de La Paz. SNCETMAR-1 strain (**e**, **h**, **j**–**l**). SNCETMAR-2 strain (**a**, **b**, **c**, **d**, **f**, **g**, **i**). Non-motile predivision cyst or coccoid stage (**a**–**c**). Bicellular division cyst (dyad phase) (**d**–**f**). Meiosis I, triad phase (**g**–**i**). Meiosis II, tetrad phase, where 4 haploid cells are formed (**j**). Zygote (diploid) (**k**, **l**). White arrow with margin = reserve substances (lipids) or an eyespot, asterisk (*) = binary fission process, py = pyrenoid.

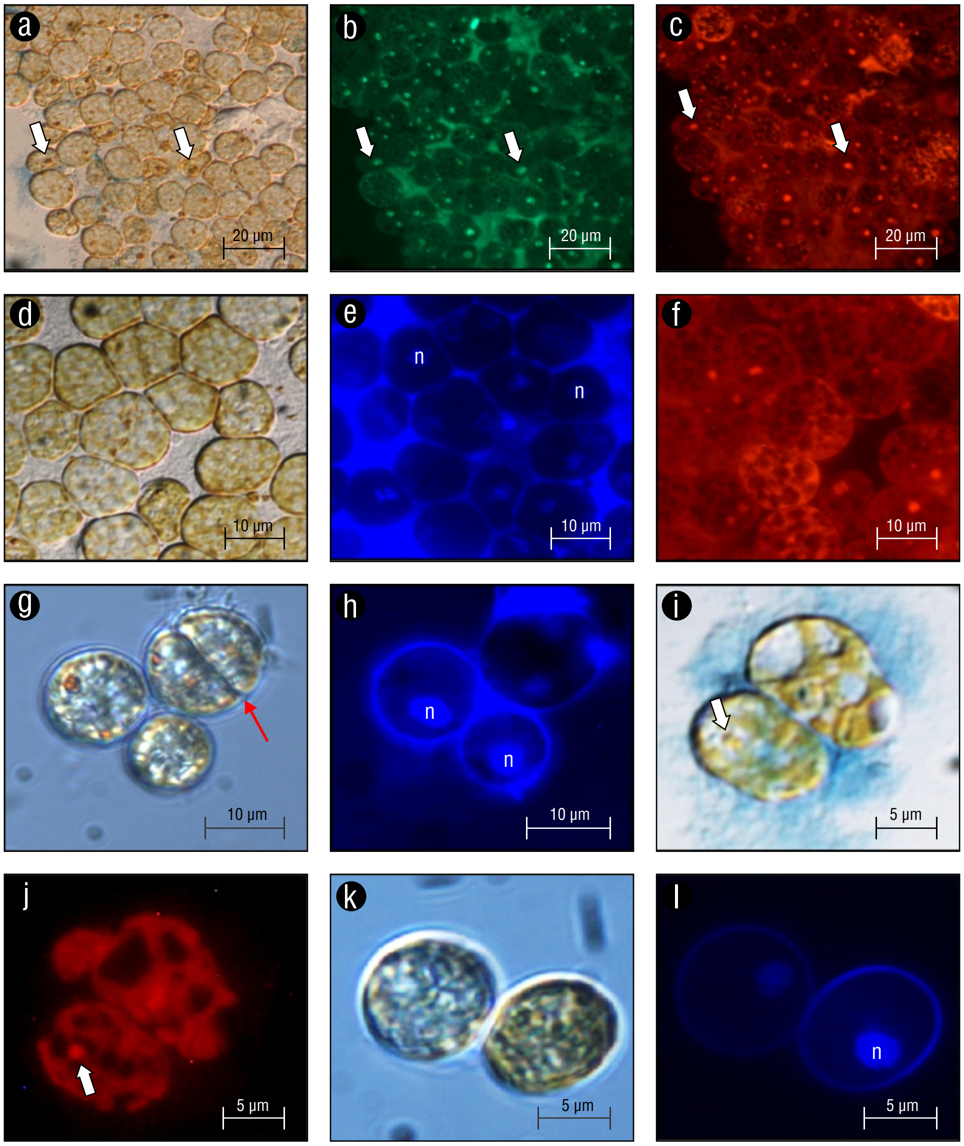

Figure 5. *Symbiodinium*-clade A cells (SNCETMAR-2 strain) in epifluorescence microscope. Optical micrographs of non-motile cysts (**a**, **d**, **g**, **i**, **k**). Chloroplast autofluorescence in ventral view (**b**, **c**, **f**, **j**). DAPI staining of the nucleus (n) (**e**, **h**, **l**). White arrow with margin = lipids as storage products or eyespot, red arrow = division plane.

one autapomorphy character, which is the reduction of a pronounced elongated apical vesicle (acrobase or apical groove), a characteristic observed in clade C (LaJeunesse et al. 2018). Nevertheless, members belonging to clade A lack this character, so this structure is not relevant in the strains analyzed in this study.

The morphology of the group can vary depending on the phase, with an observable coccoid phase, typical of asexual reproduction, and ellipsoidal to mushroom shapes (motile phase). Coccoid cells can measure 8–10 µm in diameter (LaJeunesse et al. 2018), whereas motile cells can average 6–12 µm in length (Hansen and Daugbjerg 2009, LaJeunesse et al. 2018). In culture, cells were observed forming groups in triads and tetrads, corresponding to meiosis I and late meiosis II of sexual reproduction, respectively. Figueroa et al. (2021) reported these reproductive phases in a *Symbiodinium* strain of clade C (*Cladocopium latusorum* Turnham, Sampayo & LaJeunesse) from Moorea in French Polynesia, South Pacific Ocean.

Phylogenetic reconstructions with ribosomal (28S and 23S) and chloroplast (psbA) genes reveal 9 evolutionarily divergent clades (A to I) (*see* Table 2, Pochon and Gates 2010, LaJeunesse et al. 2018). The high and low pairwise genetic divergence values in this study were very similar to those of Pochon and Gates (2010) because we included some long subunit sequences identified by these authors as clade E (AF060899), clade F3 (AJ830916, AJ291525), clade G (AJ291539), clade H (AJ291513), and clade I

(FN561562). The different clades of the Symbiodiniaceae family have different genetic, physiological, and ecological attributes; therefore, these clades can be subdivided into an unknown number of phylospecies (Hirose et al. 2008, De Palmas et al. 2015, LaJeunesse et al. 2018). The 9 clades accepted for the group were obtained with the analysis of the 28S region. The sequence from this study had greater genetic affinity with sequences from clade A; specifically, with sequences from the free-living species *S. natans* from Japan and Spain (Yamashita and Koike 2013, LaJeunesse et al. 2015). Although this clade shows high genetic diversity (around 15 subclades), the 28S marker helped us identify clade A and the presence of 4 subclades within it; however, a highly variable marker such as the ITS set has been observed to help identify specificities with respect to the environments where these microorganisms develop (pelagic and benthic) and their symbiotic associations to understand the divergence within the same clade or group (Mordret et al. 2016).

Clade A is widely distributed in the Atlantic, Pacific, and Indian oceans and in the Red Sea. Nevertheless, some subclades may be limited to certain ocean basins, for example, the Caribbean Sea, which has the highest number of reports (LaJeunesse et al. 2015). The clade has been reported in Callao Salvaje, Tenerife, in the Canary Islands (Hansen and Daugbjerg 2009, Guiry and Guiry 2024); Japan and Hawaii (Carlos et al. 1999, Hirose et al. 2008, Yamashita and Koike 2013); Florida Keys in the USA (Lee et al. 2015); and Puerto Morelos in the Mexican Caribbean (Kemp et al. 2014).

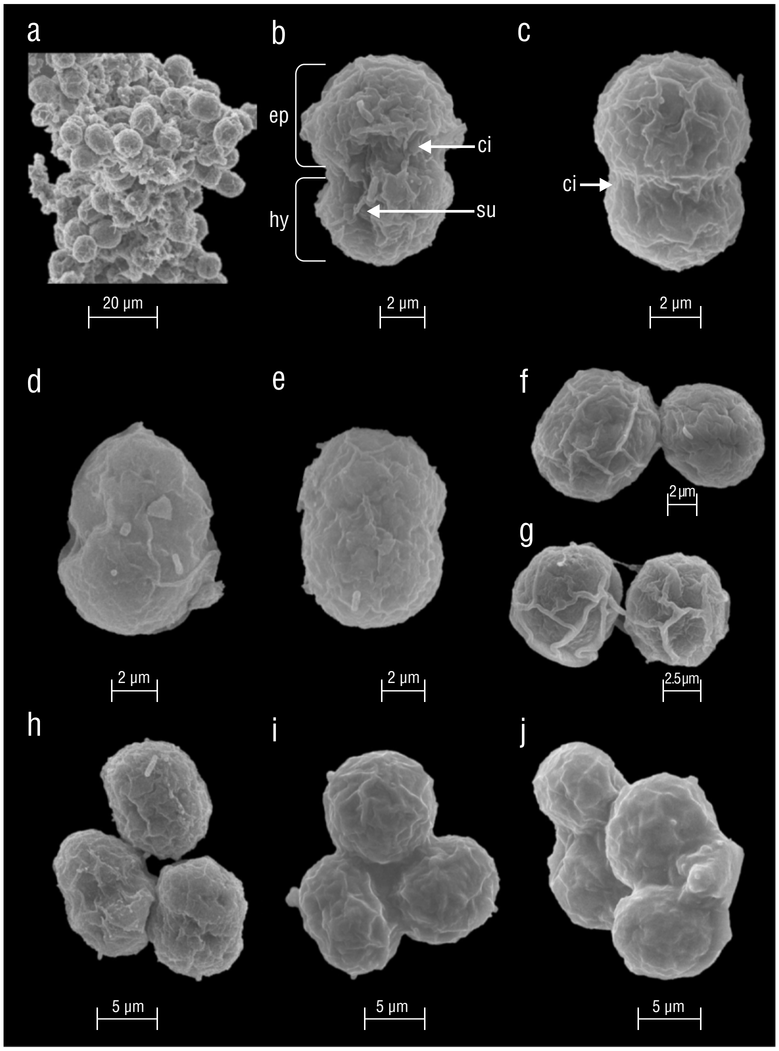

Figure 6. Vegetative cells of *Symbiodinium natans*-clade A observed under a scanning electron microscope. SNCETMAR-1 strain (**b**, **c**, **g**, **h**). SNCETMAR-2 strain (**a**, **d**, **e**, **f**, **i**, **j**). Vegetative cysts, the dominant phase of *Symbiodinium* sp. (**a**). Ventral view (**b**). Dorsal view (**c**, **e**). Zoosporangium with cingulum housing the transverse flagellum (**d**). Binary fission process (**f**, **g**). Meiosis I (**h**, **i**). Meiosis II (**j**). ci = cingulum, su = sulcus, ep = epicone, hy = hypocone.

Table 1. Sequences of the Symbiodiniaceae family included in the phylogenetic analysis of the 28S rDNA region and *Gymnodinium catenatum*, which was used as an outgroup.

GenBank ID	Taxon	Strain	Isolation origin	Site	Reference
PP563703	*Symbiodinium natans*	SNCETMAR-2	*Actinostella* sp.	Bahía de La Paz, Mexico	This study
AB704058	*Symbiodinium natans*	FGS-D6-Sy	Sand	Gahi Island, Okinawa, Japan	Yamashita and Koike (2013)
AB704055	*Symbiodinium natans*	GTP-A6-Sy	Tide pool	Gahi Island, Okinawa, Japan	Yamashita and Koike (2013)
EU315917	*Symbiodinium natans*	CAT2393	ND	Tenerife, Spain	Hansen and Daugbjerg (2009)
KT634312	*Symbiodinium* sp.	zs12xd	*Zoanthus* sp.	Tavernier, Florida Keys, USA	Graham et al. (2015)
LK934674	*Symbiodinium* sp.	CCMP2456	*Alveopora japonica* Eguchi, 1965	Jeju, South Korea	Not published
AB778578	*Symbiodinium* sp.	KMG004-a-02	*Pteraeolidia ianthina* (Angas, 1864)	Chiba, Japan	Yorifuji et al. (2015)
KF740671	*Symbiodinium pilosum*	rt-185	*Zoanthus sociatus* (Ellis, 1768)	Jamaica	Jeong et al. (2014)
ON263282	*Symbiodinium necroappetens*	A13	ND	ND	Not published
MK692538	*Symbiodinium linucheae*	SSA01	ND	ND	Not published
KM972549	*Symbiodinium microadriaticum*	rt-061	*Cassiopea xamachana* Bigelow, 1892	Florida, USA	Lee et al. (2015)
LK934669	*Symbiodinium microadriaticum*	CCMP2467	*Alveopora japonica*	Jeju, South Korea	Not published
KT149349	*Symbiodinium minutum*	Mf1.05b	ND	Caribbean	Parkinson et al. (2015)
LK934670	*Symbiodinium minutum*	CCMP830	*Alveopora japonica*	Jeju, South Korea	Not published
KT149351	*Symbiodinium psygmophilum*	PurPFlex	ND	Caribbean	Parkinson et al. (2015)
KF364606	*Symbiodinium* sp.	RCC 1521	Surface net trawl	Blanes, Mediterranean Sea	Jeong et al. (2014)
AF060899	*Gymnodinium varians*	CCMP 421	ND	ND	Wilcox (1998)
AJ291539	*Symbiodinium* sp.	1584	*Amphisorus* sp.	Guam	Pawlowski et al. (2001)

(*continued on next page*)

Table 1 (*continued*)

GenBank ID	Taxon	Strain	Isolation origin	Site	Reference
AJ291536	*Symbiodinium* sp.	1643	*Marginopora*	Luminao, Guam	Pawlowski et al. (2001)
KF740689	*Symbiodinium* sp.	MTB4	*Orbicella faveolata* (Ellis & Solander, 1786)	USA	Jeong et al. (2014)
KF740686	*Symbiodinium* sp.	Tha09-57	*Oulastrea crispata* (Lamarck, 1816)	Thailand	Jeong et al. (2014)
FN561562	*Symbiodinium* sp.	nr-i4	Foraminífera subfamily Soritinae Ehrenberg	Oahu, Hawaii, USA	Pochon and Gates (2010)
AJ291513	*Symbiodinium* sp.	751	*Sorites* sp.	Florida, USA	Pawlowski et al. (2001)
KF740682	*Symbiodinium* sp.	Zam03-3m-83	*Millepora* Linnaeus, 1758	Japan	Jeong et al. (2014)
FJ529530	*Symbiodinium* sp.	C3nt	*Seriatopora hystrix* Dana, 1846	Australia	Sampayo et al. (2009)
AJ830916	*Symbiodinium* sp.	MS26_5244x	*Amphisorus hemprichii* Ehrenberg, 1965	Guam Island	Not published
AJ291525	*Symbiodinium* sp.	1635	*Marginopora* sp.	Piti, Guam	Pawlowski et al. (2001)
KU359161	*Symbiodinium kawagutii*	symka	ND	ND	Not published
AF360577	*Symbiodinium kawagutii*	Clade C	*Montipora verrucosa* (Lamarck, 1816)	Hawaii, USA	Santos et al. (2001)
SD	*Gymnodinium catenatum*	BAPAZ 16	ND	Bahía de La Paz, BCS, Mexico	Not published

+ND: No data.

In the southern Gulf of California, studies report clade C (abundant and widely distributed) associated with *Pavona gigantea* (Verrill) and clade D (extremophiles, its distribution centered in the Indo-West Pacific) with *Pocillopora verrucosa* (Ellis & Solander) (Iglesias-Prieto et al. 2004, LaJeunesse et al. 2018, Méndez-Méndez 2020). This study expands the list of *Symbiodinium* clades in the Gulf of California and describes the presence of clade A associated with the anemone *Actinostella* sp.

Usually, *Symbiodinium* clade A is associated with shallow water corals in the Caribbean and tidal pools, which generated the hypothesis that this clade is adapted to shallow areas (less than 1 m) due to the presence of photoacclimation and photoprotection pathways that counteract the high irradiance and high temperatures that can occur in these environments (Iglesias-Prieto and Trench 1997, Hirose et al. 2008, Takahashi et al. 2009, Yamashita and Koike 2013, Kemp et al. 2014). The results of the present study agree with this hypothesis, since the dinoflagellate was isolated in Bahía de La Paz, at a depth of less than 1 m (benthic habitat), in an area with high irradiance and high temperatures, which can reach 27 to 32 °C in the summer (Sea temperature 2024).

Clade A has been shown to be one of the easiest to culture due to its physiological and ecological characteristics and can occur in non-symbiotic, free-living form. This study provides information on the laboratory culture of symbiotic dinoflagellates from clade A from Bahía de La Paz; these strains have been maintained since 2018 to the present and can be cultured in specialized media (e.g., ASP-8A) and conventional media used for planktonic and benthic dinoflagellates, such as IMK, L1, modified GSe, and modified K media (this study, Hirose et al. 2008, LaJeunesse et al. 2015, Lee et al. 2015).

CONCLUSIONS

The results of the morphometric analyses combined with the phylogenetic analysis are conclusive for the *Symbiodinium*-clade A taxon. The phylogenetic analysis of the 28S region showed 9 clades currently accepted for the Symbiodiniaceae family. Clade A was divided into different subclades of phylospecies, showing that the PP563703 sequence of strain SNCETMAR-2 has phylogenetic affinity with sequences from *S. natans* (currently accepted taxon). This study reported the first detailed description of *S. natans*-clade A for Bahía de La Paz, Gulf of California; this dinoflagellate alternates between 2 life phases, a free-living (planktonic) phase and a non-obligate symbiotic phase (benthic) that showed an association with the sea anemone *Actinostella* sp.

English translation by Claudia Michel-Villalobos.

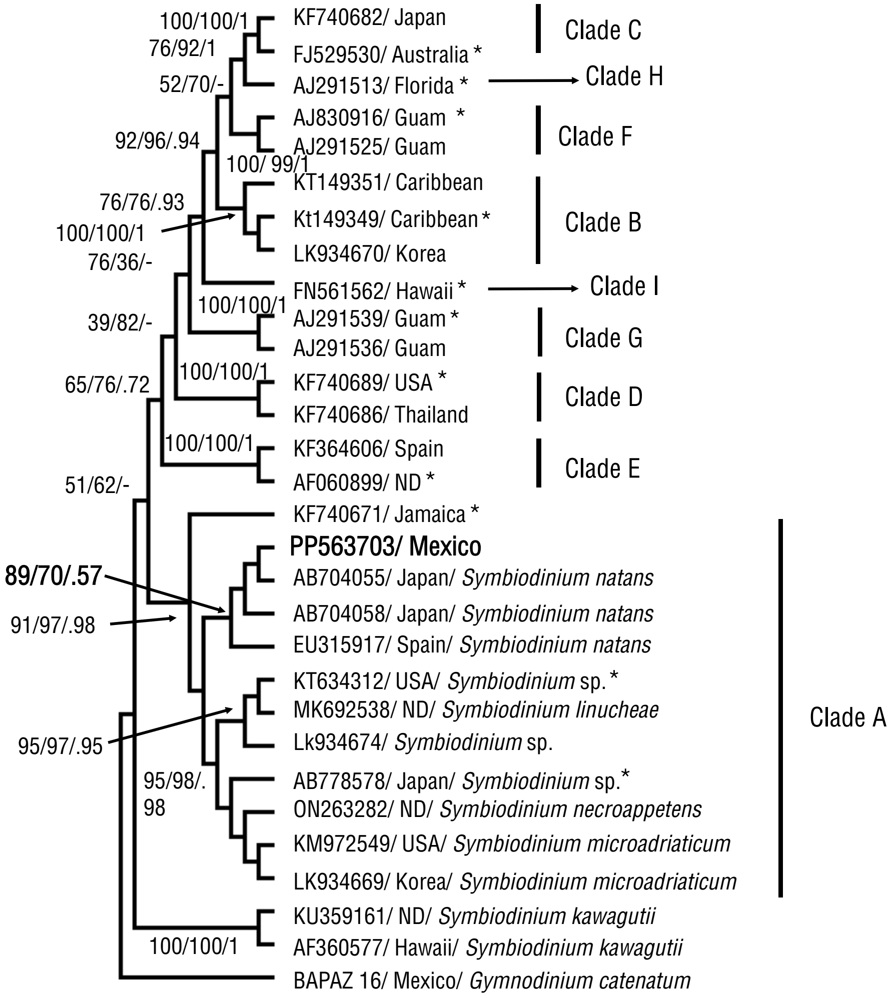

Figure 7. *Symbiodinium* phylogenetic tree of the 28S rDNA region. The sequence of the SNCETMAR-2 strain (PP563703) from this study is shown in bold. The analysis was deduced using the method of maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). The percentage of bootstrap support values and posterior probability of the clades and subclades are shown in the nodes. The analysis included 30 sequences and analyzed partial sequences of 558 bp. Sequences selected for genetic divergence analysis in Table 2 are indicated with asterisks. ND = no data.

Table 2. Pairwise genetic distances based on 13 Symbiodiniaceae family sequences selected from the 28S rDNA region. The genetic divergences observed between the sequence of this study (*) belonging to clade A and the other clades are shown in bold. The letters A–I indicate the clades of the family Symbiodiniaceae.

		A				B	C	D	E	F	G	H	I	*Symbiodinium kawagutii*
		KF740671	**PP563703***	KT634312	AB778578	KT149349	FJ529530	KF740689	AF060899	AJ830916	AJ291539	AJ291513	FN561562	AF360577
A	KF740671													
	PP563703*	0.025												
	KT634312	0.028	**0.014**											
	AB778578	0.032	**0.018**	0.004										
B	KT149349	0.237	**0.240**	0.240	0.244									
C	FJ529530	0.208	**0.208**	0.212	0.216	0.134								
D	KF740689	0.198	**0.219**	0.219	0.216	0.208	0.170							
E	AF060899	0.155	**0.141**	0.155	0.159	0.216	0.187	0.194						
F	AJ830916	0.212	**0.212**	0.216	0.219	0.120	0.092	0.198	0.201					
G	AJ291539	0.265	**0.265**	0.265	0.261	0.226	0.184	0.177	0.233	0.216				
H	AJ291513	0.187	**0.191**	0.194	0.198	0.124	0.049	0.159	0.180	0.085	0.184			
I	FN561562	0.205	**0.212**	0.219	0.219	0.159	0.134	0.177	0.205	0.141	0.201	0.127		
Symbiodinium kawagutii	AF360577	0.449	**0.452**	0.449	0.452	0.484	0.470	0.473	0.466	0.491	0.516	0.459	0.456	

DECLARATIONS

Supplementary Material

The supplementary material for this work can be downloaded from: https://cienciasmarinas.com.mx/index.php/cmarinas/article/view/3498/420421145

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: AER-S, IL-V, CJB-S; Data curation: AER-S; Formal analysis: AER-S, IL-V, YBO; Funding acquisition: CJB-S; Investigation: AER-S, IL-V, YBO, CJB-S; Methodology: AER-S, IL-V, YBO; Project administration: CJB-S; Resources: IIL-V, YBO, CJB-S; Software: IL-V, YBO; Supervision: IL-V, CJB-S, YBO; Validation: IL-V, CJB-S, YBO; Visualization: AER-S, IL-V, CJB-S, YBO; Writing–original draft: AER-S; Writing, review, and editing: AER-S, IL-V, YBO, CJB-S.

Data availability

The data for this study are available from the corresponding author by reasonable request.

Use of AI tools

The authors did not employ any AI tools in this work.

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First record of a population of *Caulerpa okamurae* (Bryopsidales) in the Mexican Pacific

Laura González-Ortíz[1,2], Alejandra Mazariegos-Villarreal[2], Ruth Noemí Aguila-Ramírez[3], Juan Manuel López-Vivas[4], Ilie S Racotta[2], Víctor Hugo Cruz-Escalona[3], Crisalejandra Rivera-Pérez[2], Sergio Scarry González-Peláez[2], Alejandra Piñon-Gimate[3], Arturo del Pino-Machado[3], Mauricio Muñoz-Ochoa[3], Karla León-Cisneros[4], Christine J Band-Schmidt[3], Tonatiuh Chávez-Sánchez[3], Elisa Serviere-Zaragoza[2]*

CORRESPONDING AUTHOR
* E-mail: serviere04@cibnor.mx

[1] Unión de Acuacultores del Complejo Lagunar de la Biosfera el Vizcaino S. de R.L. de C.V., 23940 Guerrero Negro, Baja California Sur, Mexico.
[2] Centro de Investigaciones Biológicas del Noroeste, S.C., 23096 La Paz, Baja California Sur, Mexico.
[3] Instituto Politécnico Nacional - Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN), 23096 La Paz, Baja California Sur, Mexico.
[4] Universidad Autónoma de Baja California Sur, 23080, La Paz Baja California Sur, Mexico.

ABSTRACT. On the western coast of the Baja California Peninsula, 5 *Caulerpa* species have been recorded as part of a regional floristic checklist. However, in late 2023, the presence of *Caulerpa okamurae* was detected in Ojo de Liebre Lagoon, on the Pacific coast of Baja California Sur, where its abundance increased notably during 2024–2025. This macroalga adheres to oyster cultivation systems, increases cleaning costs, and threatens seagrass meadows and other habitats, with potential effects on fishery resources. Distinguishing between cryptogenic, non-native, and invasive populations is crucial in research on species introductions, as a species is considered invasive when its presence threatens biodiversity, the economy, or health. In Mexico, guidelines and a national strategy exist to prevent, detect, and control these species. This work presents the first record of a *C. okamurae* population on the coasts of the Mexican Pacific, based on morphological evidence from specimens collected in Ojo de Liebre Lagoon, in the absence of previous records in Mexico. Confirmation of this finding adds to the 16 introduced macroalgae already documented in the Mexican Pacific, the majority of which originate in Japan and Korea and whose spread is associated with maritime traffic and aquaculture. Given the introduction and potential establishment of *C. okamurae* to Ojo de Liebre Lagoon, it is essential to implement continuous and rigorous monitoring programs to precisely determine its spatiotemporal distribution.

Key words: green algae, non-native species, invasive species, macroalgae, Mexico.

INTRODUCTION

Considerations for non-native and invasive species

To begin with, it is important to distinguish between a non-native or "exotic" species and an invasive species, since legislation often groups both concepts together. The *Ley General de Vida Silvestre* (General Wildlife Law of Mexico), in its section XVII, defines an invasive exotic species as: "any species or population that is not native, that is found outside its natural range, that is capable of surviving, reproducing and establishing itself in natural habitats and ecosystems, and that threatens native biological diversity, the economy or public health" (DOF 2010). On the other hand, the *Comisión Nacional para el Conocimiento y Uso de la Biodiversidad* (National Commission for the Knowledge and Use of Biodiversity; CONABIO, for its acronym in Spanish), the *Comisión Nacional de Áreas Protegidas* (National Commission of Protected Areas; CONANP, for its acronym in Spanish), and the *Secretaría de Medio Ambiente y Recursos Naturales* (Ministry of Environment and Natural Resources; SEMARNAT, for its acronym in Spanish) consider that invasive specimens or populations are all those individuals or populations of an exotic species, introduced accidentally or

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intentionally outside their current or past natural distribution area, including their gametes, seeds, propagules, or eggs, with the capacity to colonize, invade, and persist, and whose introduction, establishment and dispersal threaten biological diversity, or cause damage to the environment, the economy, and human health (Comité Asesor Nacional sobre Especies Invasoras 2010).

As part of the commitments made by Mexico under the Convention on Biological Diversity (CBD) and the National Biodiversity Strategy, and in response to the challenges of biological invasions, SEMARNAT identified the need to create the "*Estrategia nacional sobre especies invasoras en México*: *prevención*, *control* y *erradicación*" (national strategy on invasive species in Mexico: prevention, control, and eradication), coordinated by CONABIO with the support of a national advisory committee on invasive species. The central objective of this strategy is to "contribute to the conservation of natural capital and human well-being through decisions aimed at the prevention, control, and eradication of invasive species in Mexico through the coordinated, proactive, and responsible participation of all stakeholders" (Comité Asesor sobre Especies Invasoras 2010). By 2020, the country was expected to have systems in place for prevention, early detection, and early response, and a comprehensive legal framework to address the problem of invasive species.

For the purposes of this document, it is important to distinguish between an exotic species, which is defined as one that is not native, is found outside its natural range, and is capable of surviving, reproducing, and establishing itself in natural habitats and ecosystems, and an invasive species, which is defined as one that threatens native biodiversity, the economy, or public health. Based on these assertions, distinguishing between populations whose origin cannot be classified with certainty (cryptogenic), those that are non-native, and those that are invasive is key in species introduction studies. Identifications of species considered in the literature as non-native, but supported only by morphological observations without molecular evidence, were categorized as cryptogenic in the sense of Carlton (1996), given the uncertainty regarding their introduction routes or dispersal vehicles and the potential effects they could have on the surrounding ecosystems (Pedroche and Aguilar-Rosas 2025).

This study presents the first record of a population of *Caulerpa okamurae* on the Pacific coast of Mexico, based on morphological evidence from specimens collected in Ojo de Liebre Lagoon, Baja California Sur, in the absence of previous records in Mexico (Pedroche and Sentíes 2020).

Introduced macroalgae in the Mexican Pacific

In the Mexican Pacific, the presence of 16 introduced marine macroalgae has been documented, of which 2 are green, 7 brown, and 7 red (Aguilar-Rosas et al. 2014). Of these, 8 can be considered invasive species due to their high abundance in areas where they have been recorded. Among them, 4 species are brown algae (Ochrophyta): *Cladostephus spongiosus* (Hudson) C Agardh, *Sargassum horneri* (Turner) C Agardh, *Sargassum muticum* (Yendo) Fensholt, and *Undaria pinnatifida* (Harvey) Suringar; and 4 are red algae (Rhodophyta): *Chondracanthus squarrulosus* (Setchell and NL Gardner) Hughey, PC Silva and Hommersand, *Grateloupia turuturu* Yamada, *Gracilaria vermiculophylla* (Ohmi) Papenfuss, and *Acanthophora spicifera* (Vahl) Børgesen. No green algae with invasive characteristics have been recorded to date (Aguilar-Rosas et al. 2014).

Approximately, 80% of these species are native to Japan or Korea. In most cases, studies suggest that their introduction occurred through maritime traffic, and to a lesser extent, through activities related to aquaculture or fishing. In the latter case, the introduction of *Sargassum muticum* to the Canadian Pacific coast has been attributed to an accidental event associated with the transport of the Japanese Oyster *Magallana gigas* (Thunberg, 1793) (as *Crassostrea gigas* Thunberg, 1793), whose shells possibly had small plantlets attached to them (Scagel 1956). After this event, studies have suggested that ocean currents have facilitated their natural dispersal southward, even reaching the coast of Baja California Sur in Mexico (Aguilar-Rosas et al. 2014). However, the lack of reliable information on the introduction routes or specific vectors for each of the non-native macroalgae has been noted. Therefore, it is considered a priority to develop studies aimed at identifying the introduction mechanisms of each of the species, which will enable the establishment of effective prevention measures.

In addition, 2 macroalgae, *Dactylosiphon durvillei* (Bory) Santiañez, KM Lee, SM Boo and Kogame (as C*olpomenia phaeodactyla* MJ Wynne and JN Norris) and *Ishige sinicola* (Setchell and NL Gardner) Chihara, have been registered within the list of macroalgae considered as introduced and invasive or potential to enter the coasts of the Mexican Pacific, in a CONABIO project entitled "*Estado actual de las especies de macroalgas introducidas e invasoras en la costa Pacífico de México*" (Current status of introduced and invasive macroalgae species on the Pacific coast of Mexico; CONABIO 2025).

The genus *Caulerpa*

The genus *Caulerpa* comprises several species of green algae and is distributed worldwide in marine environments. In general, *Caulerpa* species are found in shallow tropical and subtropical waters, although some species can inhabit brackish lagoons. In each *Caulerpa* species, the thallus is composed of coenocytic filaments, which means that they are formed by a single cell with multiple nuclei that lack dividing cell walls. These filaments exhibit numerous trabeculae, which are branched, cylindrical outgrowths of the cell wall.

Caulerpa species exhibit 2 types of propagation, sexual and vegetative, which allow even small fragments to give rise to new individuals and confer a high growth rate. These characteristics, along with the frequent presence of toxigenic compounds that protect them from herbivores, especially in new environments, facilitate the rapid colonization of new areas (Gao et al. 2019). Furthermore, *Caulerpa* species possess adaptations that allow them to tolerate a wide range of environmental conditions, which further enhances their high potential for colonizing other locations (Park et al. 2022).

In Mexico, along the western coast of the Baja California Peninsula, 5 species of the genus *Caulerpa* have been recorded as part of the flora from various sites: *Caulerpa chemnitzia* (Esper) JV Lamouroux (as *Caulerpa peltata* JV Lamouroux), *Caulerpa cylindracea* Sonder (as *Caulerpa racemosa* [var. *laetevirens*] f. *cylindracea* [Sonder] Weber Bosse), *Caulerpa racemosa* (Forsskål) J Agardh var. *racemosa* (as *Caulerpa racemosa* var. *macrophysa* [Sonder ex Kützing] WR Taylor), *Caulerpa sertularioides* (SG Gmelin) M Howe, and *Caulerpa chemnitzia* var. *vanbosseae* (Setchell and NL Gardner) Fernández-García and Riosmena-Rodríguez (as *Caulerpa vanbosseae* Setchell and NL Gardner) (Francisco F Pedroche, pers. comm., November 2025). However, in late 2023, riverine fishers observed the presence of a green macroalga in Ojo de Liebre Lagoon, on the western coast of Baja California Sur, which had not been present previously. Subsequently, in late 2024, the presence and abundance of this macroalga was observed to have increased considerably (Fig. 1a). The specimens were identified as *C. okamurae* by researchers from the *Centro de Investigaciones Biológicas del Noroeste S.C.* (Northwest Biological Research Center; CIBNOR, for its acronym in Spanish) and the *Universidad Autónoma de Baja California Sur* (Autonomous University of Baja California Sur; UABCS, for its acronym in Spanish). The arrival of this macroalga, along with the increase in its biomass and subsequent sightings at various sites in Ojo de Liebre Lagoon, poses a threat to seagrass meadows (Fig. 1b) and other macroalgae distributed in the area, and to various resources that are key elements of the ecosystem, such as habitat and food, including those of commercial importance. The impact is evident in oyster farming systems, in particular, which receive influxes of this macroalga. The cleanup efforts carried out by members of fishing cooperatives are exhausting and largely ineffective, given the ability of the alga to recolonize the farming systems in just a few weeks (Fig. 1c, d).

MATERIALS AND METHODS

Examined material

Specimens were collected manually on March 10, 2025, in Ojo de Liebre Lagoon, Baja California Sur, Mexico (La Concha, 27°48′51″N, –114°13′53″W) (Figs. 2, 3). The specimens were growing on sandy substrate, on oyster sacs, and, in some cases, on the shells of bivalve mollusks. Reference specimens were deposited in the *Herbario Ficológico de Baja California Sur*, UABCS (Phycological Herbarium of Baja California Sur, UABCS; FBCS 20347).

RESULTS

Taxonomic classification of *Caulerpa okamurae* Weber Bosse

Empire: Eukaryota.

Kingdom: Plantae.

Subkingdom: Viridiplantae.

Phylum: Chlorophyta.

Subphylum: Chlorophytina.

Class: Ulvophyceae.

Order: Bryopsidales.

Family: Caulerpaceae.

Genus: *Caulerpa*.

Species: *Caulerpa okamurae* Weber Bosse.

Okamura, 1897: p. 5, pl. I; Figs. 13, 14 (‘*Okamurai*’). Weber-van Bosse, 1898: p. 385, pl. XXXIV; Fig. 9. Okamura, 1923: p. 11, pl. CIIV; Figs. 1-8.

Syntype locality: Japan; Suruga, Mikawa, Oki, Noto.

Heterotypic synonym: *Caulerpa okamura*e f. *minor* S Narita.

Morphological description of *Caulerpa okamurae* Weber Bosse

The fronds arise from a creeping axis that branches in several directions, forming a dense covering over the substrate. The rhizoids are arranged at irregular intervals (0.4 mm to 17.6 mm), generally in groups of 3 to 5. The fronds also arise at irregular intervals, from 5.7 mm to 43.4 mm, and occasionally in pairs. The fronds are cylindrical, single or with 1 to 4 irregular branches, and reach a maximum height of 14 cm (Fig. 2). The creeping axis has a diameter of 1.1 mm to 1.5 mm. The fronds have a similar diameter at their base (1.1 mm to 1.4 mm) and are slightly thinner at the apex (diameter: 1.1 mm to 1.2 mm). Throughout their extension, fronds are covered with branchlets arranged more or less densely imbricated. The color of the fronds varies; the exposed parts are bright green, whereas the unexposed parts are a dull straw color. The branchlets can be arranged distichously or oppositely, predominantly near the base of the frond, and gradually overlap or imbricate towards the apex. The axis is slightly constricted at the point of insertion of the branchlets, projecting laterally below the constriction, giving rise to a short pedicel from which the branchlet emerges. The junction between the branchlet and the pedicel is clearly constricted. In general, basal branchlets are shorter than upper ones and are obovate; upper branchlets are oblong or subclavate-cylindrical. The apical portion of the branchlets is slightly thicker than their basal portion (Fig. 3). At the base of the frond, the branchlets

Figure 1. Incidence of the macroalga *Caulerpa okamurae* in the oyster farming systems of the *Unión de Acuacultores del Complejo Lagunar de la Reserva de la Biosfera el Vizcaino* (Union of Aquaculture Producers of the Lagoon Complex of the El Vizcaino Biosphere Reserve). First observation at the end of 2024 in oyster farming in bags on beds (**a**). Coexistence and coverage of seagrass at the end of 2024 (**b**). Massive invasion in oyster farming lines in suspended bags (**c**). Cleaning efforts carried out by members of the Union of Aquaculture Producers of the Lagoon Complex of the El Vizcaino Biosphere Reserve in May 2025 (**d**). Photographs: Laura González-Ortiz, Sergio Scarry González-Peláez, and Ilie S Racotta.

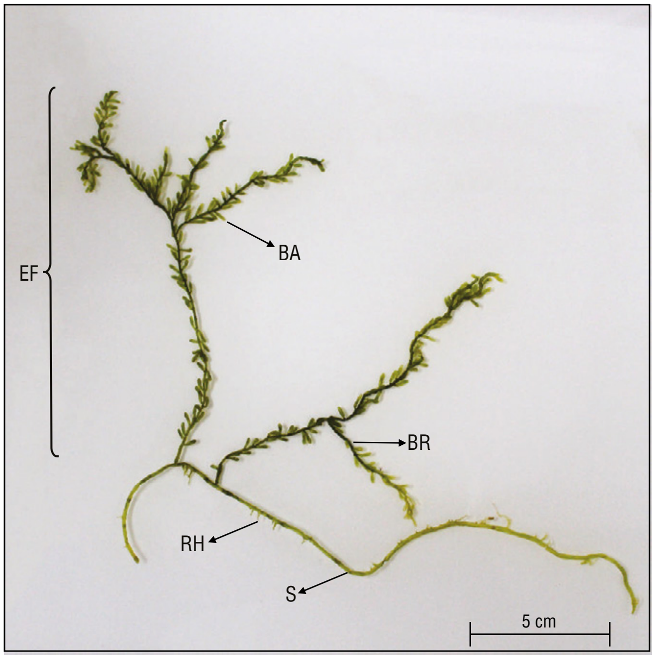

Figure 2. *Caulerpa okamurae* collected in Ojo de Liebre Lagoon, Baja California Sur, Mexico. Erect frond (EF), branchlet (BA), rhizoid (RH), branching (BR), and stolon (S). Photograph: Alejandra Mazariegos-Villarreal, *Laboratorio de Macroalgas*, *Centro de Investigaciones Biológicas del Noroeste S.C.* (CIBNOR).

measure 4.9–6.2 mm in length, with a basal diameter of 0.9–1.3 mm and an apical diameter of 1.2–1.7 mm. At the apical portion of the fronds, the branchlets are 4.7–6.8 mm long, with a basal diameter of 0.9–1.4 mm and an apical diameter of 1.1–1.5 mm.

The characteristics and dimensions of the specimens collected at Ojo de Liebre Lagoon correspond to the description of the species *C. okamurae* according to Okamura (1897). One form and an ecad of this species have been described; however, these were not observed in the specimens collected at Ojo de Liebre Lagoon. *Caulerpa okamurae* f. *oligophylla* Okamura has very elongated fronds, reaching or exceeding 15 cm in length, with irregular branching and a reduced number of pedicellate branchlets that are, occasionally, slightly imbricated (Okamura 1916). *Caulerpa okamurae* ecad *lamourouxii* is characterized by having a compressed axis (Prud'Homme Van Reine et al. 1996).

DISCUSSION

Distribution

The genus *Caulerpa* includes 104 species distributed across a wide geographic range, from temperate to tropical regions (De Gaillande et al. 2017, Zubia et al. 2020, Guiry and Guiry 2025). Some of these species, such as *Caulerpa taxifolia* (M Vahl) C Agardh, *Caulerpa brachypus* Harvey, and *C. racemosa*, are well-known invasive species that exhibit a highly effective vegetative propagation mechanism (Boudouresque et al. 1995, Smith and Walters 1999).

The distribution of *C. okamurae*, native to the Asian Pacific, is restricted to Asia and some sites in Oceania and islands in the Pacific, with records from Asia (China, Japan, and Korea), Australia and New Zealand (Queensland), and Pacific Islands (Federated States of Micronesia and New Caledonia) (Guiry and Guiry 2025) (Fig. 4). In this study, *C. okamurae* is recorded for the first time in Mexico, specifically in Ojo de Liebre Lagoon, Baja California Sur (Fig. 4). In general, *C. okamurae* grows in shallow waters (to a depth of 5 m in the sublittoral zone). In Korea, the biomass of *C. okamurae* exhibits seasonal variations in natural habitats, with a maximum during the summer (Gao et al. 2019).

In the Mexican Pacific, *C. okamurae* is considered a non-native population, given the lack of bibliographic records and herbarium specimens confirming its prior presence in the region (Pedroche et al. 2005, Pedroche and Sentíes 2020).

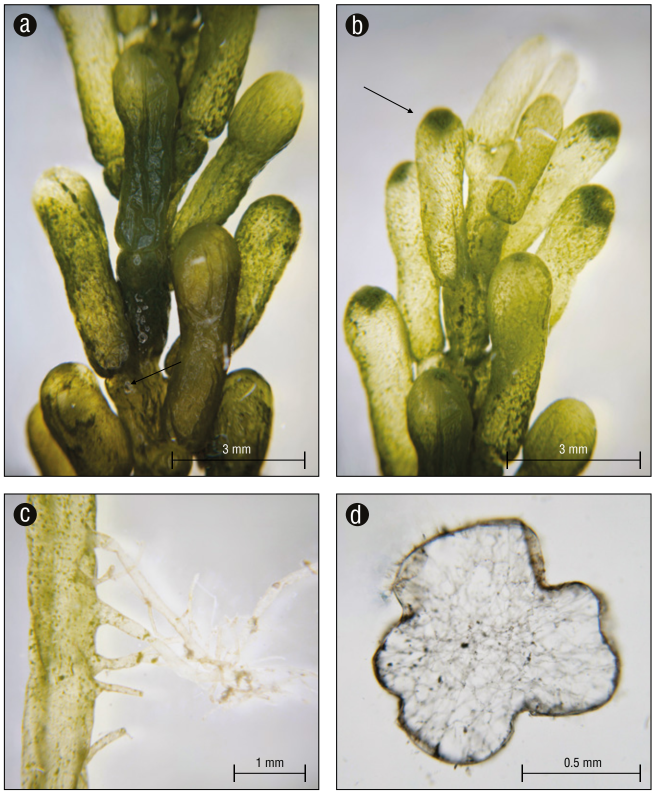

Figure 3. *Caulerpa okamurae*. Detail of the branching in the middle part of the frond; the short pedicel from which a branchlet and its constriction arise are indicated by an arrow (**a**). Detail of the branching at the apex of the frond; a branchlet is indicated by an arrow (**b**). Detail of the creeping axis showing a cluster of rhizoids (**c**). Cross-section of the creeping axis showing the trabeculae (**d**). Photographs: Alejandra Mazariegos-Villarreal, *Laboratorio de Macroalgas*, *Centro de Investigaciones Biológicas del Noroeste S.C.* (CIBNOR).

Draisma et al. (2025) suggest that *C. okamurae* may be restricted to the northwestern temperate Pacific. This absence of records, along with the morphological evidence, strongly suggests its non-native status. However, following the terminology of Carlton (1996), it could be considered cryptogenic until its taxonomic identity is definitively confirmed. Thus, ongoing molecular analyses are crucial to ratify its taxonomic identity and, if possible, its geographic origin.

Caulerpa okamurae has the capacity to rapidly increase its biomass and cover, giving it a high potential for expanding its geographic distribution. Its propagation occurs through 2 vegetative growth patterns: creeping stolon growth, which attaches via several groups of rhizoids (rhizophores), and vertical growth of highly dense assimilators arising from the stolon (Shin et al. 2021, Park et al. 2022). Both assimilators and fragmented stolons have shown a high capacity for regeneration under laboratory conditions (Gao et al. 2019, Shin et al. 2021, Park et al. 2022). This is a known capacity within the genus, as fragmented fronds of *Caulerpa* species can produce new thalli (Smith and Walters 1999). In wild populations, these fragments can result from wave action or herbivory and subsequently become buried in various types of sediments, such as silt or sand with different grain sizes. In fact, previous studies have shown that fragments of other *Caulerpa* species (e.g., *C. taxifolia*, *C. racemosa*, and *Caulerpa lentillifera* J. Agardh) can survive, readhere to various substrates, and even grow in mud (Horstmann 1983, Trono 1990, Ceccherelli and Piazzi 2001, Wright and Davis 2006, Mary et al. 2009). Likewise, in natural environments, the fronds of *C. okamurae* can adhere to various substrates such as silt, sand, rock, gravel, shells, and sponges. Finally, species of the genus *Caulerpa* exhibit resistance to herbivory by fish due to their high content of sesquiterpenes and other phytochemical compounds, which act as a chemical defense (Paul et al. 1987).

Invasions by the genus *Caulerpa* often cause serious ecological impacts, such as loss of biodiversity and alteration of native habitats (e.g., Santini-Bellan et al. 1996; Ceccherelli et al. 2000; Piazzi et al. 2001; Fernández-García and Cortés-Nuñez 2005, 2009; Smith et al. 2010), which lead to severe economic consequences (Francour et al. 1995, Baskin 1996). In the case of Ojo de Liebre Lagoon, invasions have already resulted in strong impacts on oyster farming, with an estimated 60% loss of production since the end of 2024, and competition for space with seagrasses. Given these evident ecological and economic impacts, taxonomic confirmation and determination of the possible geographic origin of this population through molecular analyses are priority steps. These data will not only help confirm the status of *C. okamurae* as a non-native species in Mexico but will

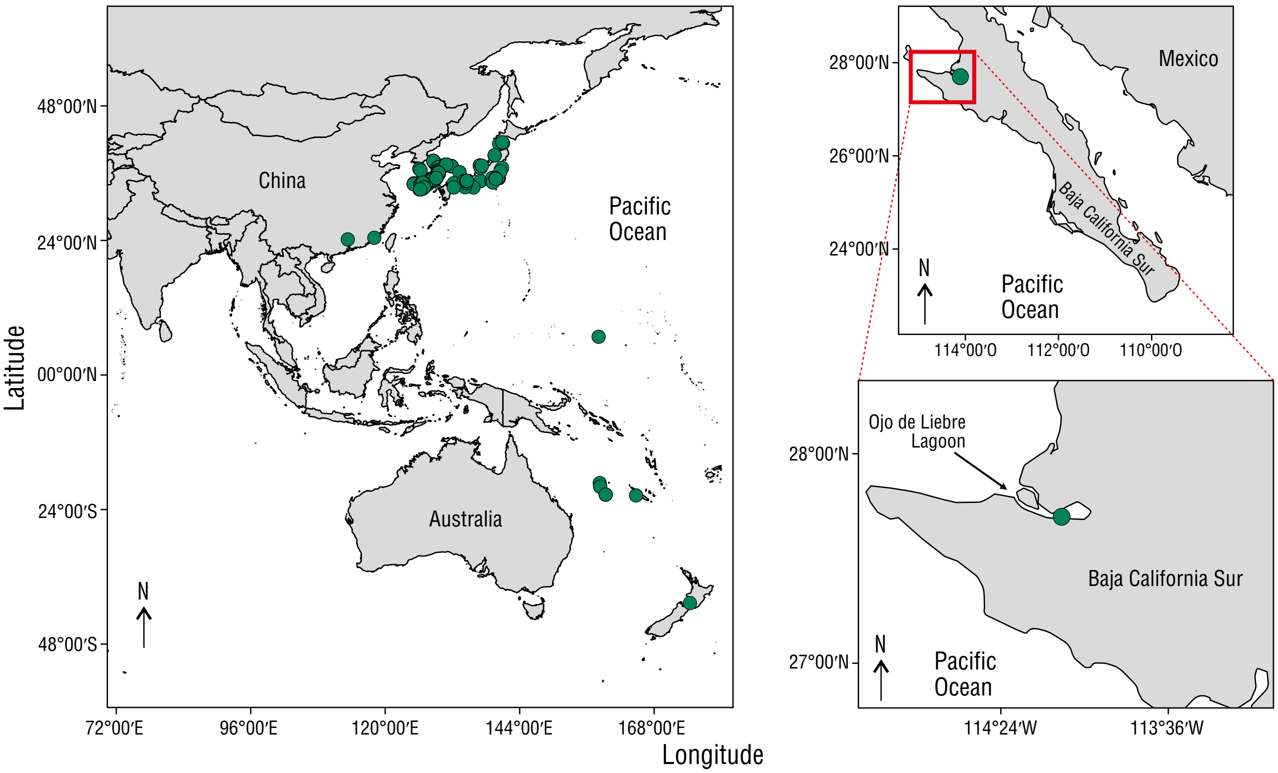

Figure 4. Distribution of *Caulerpa okamurae* (left) and location of Ojo de Liebre Lagoon, Baja California Sur, Mexico (right). Elaborated by: José Antonio González Rousseau, *Laboratorio Botánica Marina*, *Universidad Autónoma de Baja California Sur* (UABCS).

also be essential to assess the real risk of colonization in the northwest region of the country and will be the basis for designing and implementing management, control, and mitigation strategies.

CONCLUSIONS

Given its introduction and potential establishment, it is essential to implement continuous and rigorous monitoring programs to accurately determine the spatial and temporal distribution of *C. okamurae*. These efforts must go beyond mapping and include a thorough assessment of the existence of impacts on native biodiversity, ecosystem functions, and environmental services, as well as economic repercussions on fisheries and aquaculture, and potential implications for human health. This information will support evidence-based management decisions and guide public policies for the prevention, early detection, control, and mitigation of its effects. To this end, we propose the following goals.

Integral and early monitoring

It is necessary to evaluate the distribution and seasonality of *C. okamurae* and its potential impact on marine populations, combining data from transects or plots with information obtained using drones and eDNA to confirm its identity and areas of expansion.

Standardization and key metrics

It is necessary to evaluate the cover (%), biomass ($g \cdot m^{-2}$), recolonization rate (day^{-1}), cleaning effort ($person \cdot t^{-1}$), and meadow integrity.

Impact evaluation designs

It is necessary to quantify the effects on seagrass meadows, native macroalgae, and the productive performance (growth, survival, and biofouling) of oysters and other commercial sessile species.

Biosecurity and vectors

It is necessary to define protocols to standardize the disinfection and quarantine of equipment and vessels, improve the management of waste without viable fragmentation, implement controls at docks and transfer routes, and ensure the traceability of equipment between sites.

Control options

Pilot tests are required to evaluate the efficiency of targeted manual removal and physical barriers, with plans for safe disposal and subsequent follow-up to prevent regrowth.

Responsible exploitation

It is necessary to evaluate the potential uses (e.g., food, composting, biogas, and biomolecules), safety, and life cycle of *C. okamurae* to ensure that its exploitation does not facilitate its dispersal.

Taxonomic confirmation

Genetic analyses (e.g., COI and qPCR with specific primers) are required to confirm the identity of *C. okamurae*, avoid confusion with other *Caulerpa* species, and support its inclusion in official lists as a non-native or invasive species.

Governance and participation

It is necessary to promote interinstitutional coordination, between environmental authorities, academia, and fishing cooperatives, and the implementation of citizen science programs to ensure that the data they collect can be reliably integrated into reports.

Environmental scenarios

Climate variability (e.g., marine heat waves) and ecosystem eutrophication need to be incorporated into distribution and risk models to identify critical sites and prioritize them in conservation strategies.

Cost-benefit

It is necessary to estimate and compare the costs of inaction and those of management strategies, define action thresholds and establish measurable goals for 6–24 months.

English translation by Claudia Michel-Villalobos.

FINAL DECLARATIONS

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: ISR, VHCE, ESZ; Data curation: AMV, KLC, ESZ; Formal analysis: AMV, JMLV, ESZ; Investigation: LGO, ISR, ESZ; Methodology: AMV, JMLV, SSGP, ESZ; Resources: ISR, SSGP, ESZ; Software: AMV, JMLV, SSGP; Supervision: ISR, CRP, ESZ; Validation: RNAR, JMLV, ISR, VHCE, ESZ; Visualization: ISR, VHCE, ESZ; Writing—original draft: LGO, RNAR, ISR, VHCE, CRP, ESZ; Writing, review, and editing: LGO, AMV, RNAR, JMLV, ISR, VHCE, CRP, SSGP, APG, APM, MMO, KLC, CJBS, TChS, ESZ.

Data availability

The data for this study are available from the corresponding author upon reasonable request.

Ethical approvals and permissions for animal studies

The specimens were collected under the corresponding fishing permit No. PPF/DGOPA-073/25.

Use of AI tools

The authors did not employ any AI tools in this work.

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Ciencias Marinas (2025), 51:e3553 **Research Note**

Ciencias Marinas Journal/Revista

Presence of the invasive species Indo-Pacific Swimming Crab *Charybdis hellerii* A. Milne-Edwards, 1867 on the Mexican Pacific coast detected by molecular identification

Miguel A Del Río-Portilla[1]*, Carmen E Vargas-Peralta[1], Fabiola Lafarga-De la Cruz[1], Mauricio Salas-Maldonado[2], Alejandro J Gallardo-Valencia[3], Laura A Flores-Ramírez[2], Alberto Bartoleño Sánchez[2], Casandra López-Terán[2], Cathy L Valdez-Domínguez[4]

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CORRESPONDING AUTHOR
* E-mail: mdelrio@cicese.mx

[1] Departamento de Acuicultura, Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE), 22860 Ensenada, Baja California, Mexico.
[2] Centro Regional de Investigación Acuícola y Pesquera de Manzanillo, Instituto Mexicano de Investigación en Pesca y Acuacultura Sustentable, 28200 Manzanillo, Colima, Mexico.
[3] Departamento de Sanidad y Nutrición Acuícola, Instituto Mexicano de Investigación en Pesca y Acuacultura Sustentable, 04100 Ciudad de México, Mexico.
[4] Centro Regional de Investigación Acuícola y Pesquera de Ensenada, Instituto Mexicano de Investigación en Pesca y Acuacultura Sustentable, 22760 Ensenada, Baja California, Mexico.

ABSTRACT. Crabs of the species *Callinectes arcuatus* Ordway, 1863 were caught in Cuyutlán Lagoon, Colima, Mexico (19°0′38.48″N, 104°14′50.65″W). Among them, 1 specimen of *Charybdis hellerii* A. Milne-Edwards, 1867 was caught. This specimen was molecularly identified by the forensic information nucleotide sequencing (FINS) procedure using a fragment of the 16S rRNA gene (518 bp). The 16S rRNA sequence of *C. hellerii* (GenBank accession number PQ800082) showed 83% identity with the *C. arcuatus* sequences in the GenBank database and those obtained here (GenBank accession numbers PQ800080 and PQ800081). Reports by citizen scientists on iNaturalist have indicated the presence of *C. hellerii* in the waters of Colima since 2019. However, this is the first time that molecular markers confirm its presence on the Mexican Pacific coast. Further research is needed to understand the extent of *C. hellerii* propagation along the Mexican Pacific coast, as its presence since 2019 could indicate an established population in this area. The presence of this species is concerning, as it could affect the populations of other commercially important native crab species.

Key words: Indo-Pacific Swimming Crab, forensically informative nucleotide sequencing, FINS, molecular identification, 16S rRNA gene.

INTRODUCTION

In Mexico, the crab fishery is considered a traditional artisanal fishery with great socioeconomic value in the coastal zone of the Pacific Ocean, mainly in the states of Sonora and Sinaloa (DOF 2023). The target species are the Cortez or Warrior Swimming Crab (*Callinectes bellicosus* Simpson, 1859), the Arched Swimming Crab (*Callinectes arcuatus* Ordway, 1863), and the Black Crab (*Callinectes toxotes* Ordway, 1863).

In the state of Colima, Mexico, the artisanal *C. arcuatus* fishery has an official record of 24 small vessels (DOF 2023), with a production volume of 46 t in 2024 and an estimated value of $1,343,318 MXN according to the 2024 statistical production yearbook database (CONAPESCA 2024). Although the crab fishery in the central Mexican Pacific, specifically in Cuyutlán Lagoon, Colima, is small-scale, it shows great growth potential for the fishing communities in the state (Estrada-Valencia 1999), compared to the potential of

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the northern states, where production oscillates around 54% of the national production (27,173 t) in Sinaloa and where considerable fishing effort data are recorded (1,069 vessels) (DOF 2023).

During their daily work, some fishermen off the coast of Colima have found crabs that are morphologically distinct to the blue crab, which has raised the following question: to which species do these specimens belong? The presence of other species could influence the fishery of *C. arcuatus*, which is of great importance in Cuyutlán Lagoon, Colima (Estrada-Valencia 1999, Salas-Maldonado et al. 2021). Furthermore, the ecological and socioeconomic implications of the presence of invasive crab species in the coastal lagoon are unknown. In Mexico, the presence of the Spiny Hands Crab or Indo-Pacific Swimming Crab (*Charybdis hellerii* A. Milne-Edwards, 1867), the only invasive alien species of the Portunidae family on the Checklist of Invasive Alien Species of Mexico (DOF 2016), has been detected in Yucatan (Simoes et al. 2019). On the other hand, in the northeastern Pacific, the presence of 3 invasive crab species has been reported: the Common Sea Crab or European Green Crab (*Carcinus maenas* Linnaeus, 1758), the Harris Mud Crab (*Rhithropanopeus harrisii* Gould, 1841), and the Chinese Mitten Crab (*Eriocheir sinensis* H. Milne Edwards, 1853).

Traditionally, the taxonomic identification of most species is based on phenotypic characters, but in some cases morphological differences are not definitive, as for some fish species such as the Common Snook (*Centropomus undecimalis*) (Martínez-Brown et al. 2021). On the other hand, forensically informative nucleotide sequencing (FINS) is one of the procedures to identify biological specimens; this consists of the extraction of DNA, amplification of a specific segment by the polymerase chain reaction (PCR), sequencing of the amplified fragment, and phylogenetic analysis of the sequence, which is compared with databases to identify the species that is genetically closest (Bartlett and Davidson 1992). This procedure has served to elucidate snooks species and establish new morphological characteristics for each one (Martínez-Brown et al. 2021).

The objective of this work was to use the FINS technique to molecularly identify crabs caught in Cuyutlán Lagoon, Colima, Mexico, to evaluate the presence of invasive species previously reported in the northeastern Pacific or in Mexico (*C. maenas*, *R. harrisii*, *E. sinensis*, and *C. hellerii*).

MATERIALS AND METHODS

In Cuyutlán Lagoon, Colima, Mexico, 6 crabs were caught using artisanal fishing (Fig. 1). Of these, 1 specimen showed distinct morphological characteristics (Table 1). The specimens were transported to the *Centro Regional de Investigación Acuícola y Pesquera* of Manzanillo, Colima, where they were measured with a Vernier caliper (precision of 1 mm) and weighed with a granataria balance (precision of 1 g). Pleopod and muscle samples from all crabs were fixed in 96% ethanol. The fixed samples were transported to the facilities of the *Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California* (CICESE) and kept at –20 ºC until processing. DNA extraction was performed using the salt method (Sambrook and William 2001). DNA integrity was confirmed by 1% agarose gel electrophoresis and its concentration and purity by spectrophotometry (Nanodrop; Thermo Fisher Scientific, Waltham, USA), evaluating the absorbance ratios at 260/230 and 260/280 nm. Subsequently, of the 6 crab samples (called j1–j6; Fig. 1), 4 (j1, j4, j5, and j6) amplified adequately for the 16S rRNA gene fragment by PCR with the primers reported by Geller et al. (1993): 16SAR (5'-CGCCTGT-TTATCAAAAACAT-3') and 16SBR (5'-CCGGTCTGAACT-CAGATCACGT-3'). These have been used in molecular phylogenetic analyses of *Callinectes* using *C. hellerii* as an outgroup (Robles et al. 2007).

The PCR reaction mix consisted of 0.20 µM primers (final concentration) and the Kapa Biosystems PCR kit (Willmington, USA). A magnesium buffer A was used for a final reaction volume of 12 µL, with 0.2 mM dNTPs and 0.5 U of Taq polymerase (Kapa Biosystems) per reaction. Finally, the PCR product was sent to Eton Bioscience (San Diego, USA) for cleanup and bidirectional Sanger sequencing.

Once the sequencing files were obtained, low-quality regions were removed using CLC Genomics Workbench v. 10.1 (QIAGEN CLC Genomics, Aarhus, Denmark), and the 2 sequences were assembled to obtain a unique fragment per organism. A search for similar segments was performed using the BLAST tool of the National Center for Biotechnology Information (NCBI) using the blastn option (BLAST-NCBI 2024) to identify species by comparing the obtained sequences with the public database. Sequences were subsequently submitted to NCBI GenBank (NCBI 2024). Subsequently, Clustal Omega (Sievers et al. 2011, Sievers and Higgins 2018) was used to align fragments with some sequences found using BLAST results (Table 2) and using *C. maenas* (GenBank accession number: FM208763) as an outgroup. The best-fitting nucleotide substitution model was selected using default settings with the jModelTest2 tool (Guindon and Gascuel 2003, Darriba et al. 2012). The phylogenetic tree was then constructed with MrBayes v. 3.2 (Ronquist and Huelsenbeck 2003), using the best-fitting Hasegawa–Kishino–Yano model with gamma distribution and a gamma-distributed rate variation between sites (HKY+I+G). A Markov chain Monte Carlo simulation was performed with 50,000 generations, a sampling frequency of 100, and default settings. Finally, FigTree v. 1.4.4 (Rambaut 2018) was used to generate the phylogenetic tree image from the information generated by the MrBayes program, and the figure was edited with Python v. 3.08.

Once the BLAST results were obtained, we conducted a search for records of the presence of the identified species in the locality, surrounding areas of Colima, and the Mexican Pacific. Various databases and public reports were reviewed

Figure 1. Photographs of the 6 crabs caught for this study from Cuyutlán Lagoon, Colima, Mexico: Crab 1–Crab 5 (*Callinectes arcuatus*) and Crab 6 (*Charybdis hellerii*).

to corroborate the presence of the species detected through the FINS analysis, including iNaturalist (iNaturalist 2024), a platform with accurate information for species identification (Unger et al. 2021, Callaghan et al. 2022).

RESULTS

Morphological characteristics allowed us to differentiate the Arched Swimming Crab (j1–j5 [blue stripes on its body]) from the unknown crab (j6; Fig. 1 and Table 1). The average (± standard deviation) carapace width (Cw) of the Arched Swimming Crab samples was 100.0 (± 4.4) mm, whereas the average total length (TL) was 56.4 ± 3.8 mm and the average weight was 60.0 ± 7.2 g. The unknown crab was a smaller female (Cw: 67 mm; TL: 49 mm), with a weight of 30 g.

Good quality DNA was obtained to amplify a ~560 bp fragment in 4 of the 6 sampled crabs. The 3 *C. arcuatus* samples (j1 [male], j4 [female], and j5 [male]) with the highest quality amplifications were sent for sequencing (Table 1). After primer removal, 517 bp fragments were obtained for j1, j4, and j5; the fragment was 518 bp for j6. The amplified fragments from j1 and j4 were identical (GenBank accession number PQ800080), whereas the fragment from j5 differed by only 1 nucleotide (GenBank accession number PQ800081). BLAST analysis detected 100% identity of 2 samples (j1 and j4) with *C. arcuatus* sequences in the GenBank database, one from Nicaragua (GenBank accession number: MW264141) (Windsor et al. 2019, Marco-Herrero et al. 2021) and another from Oaxaca, Mexico (GenBank accession number: DQ407669) (Robles et al. 2007). The amplified fragment from sample j5 had 99.91% identity with these same *C. arcuatus* sequences, indicating a new sequence and 16S rRNA segment for this species. However, the corresponding 518 bp fragment from sample j6 (GenBank accession number: PQ800082) had 100% identity with *C. hellerii* when compared with the 7 sequences deposited in the database (GenBank accession

Table 1. Morphometric data of crabs collected in Cuyutlán Lagoon, Colima, Mexico.

Common name	Species	Organism	Geographic coordinates	Sex	Carapace width (mm)	Carapace length (mm)	Total weight (g)
Arched Swimming Crab	*Callinectes arcuatus*	j1	19°0′33.67″N, 104°12′27.94″W	Male	95.0	57.0	64.0
		j2	18°59′53.84″N, 104°11′41.92″W	Male	107.0	60.0	66.0
		j3	18°59′56.86″N, 104°11′0.26″W	Male	99.0	50.0	57.0
		j4	18°59′56.86″N, 104°11′0.26″W	Female	99.0	58.0	49.0
		j5	18°59′56.86″N, 104°11′0.26″W	Male	100.0	57.0	65.0
Average					100.0	56.4	60.20
Standard deviation					4.4	3.8	7.19
Crab	Unidentified at the time of capture	j6		Female	67.0	30.0	

numbers: KX060544, KX060532, KX060500, KX060489, KX060443, PP118357, and NC_060621; Table 2). The latter (NC_060621) belongs to the complete mitochondrial genome of *C. hellerii*. However, since information on the location and date of collection was unavailable, it was not included in subsequent analyses.

An attempt was made to identify the origin of the j6 crab by considering the distributions reported in the sequence metadata. However, because the sequence timeline and geographic information did not match, its possible origin could not be elucidated (Table 2). In other words, it was not possible to determine the origin of the crab found on Mexican coasts and whether it came from the Indian Ocean or the Atlantic Ocean.

BLAST and phylogenetic analyses of the sequences from 4 crabs (j1, j4, j5, and j6) showed a clear separation between the genera *Callinectes* and *Charybdis* (Fig. 2). *Charybdis* was found in the *Thalamita* clade, whereas *Callinectes* was found in the *Arenaeus* clade.

No record of the presence of *C. hellerii* was found on the Mexican Pacific coasts until December 2024. However, when consulting the photographs recorded in iNaturalist, the presence of the invasive species *C. hellerii* was detected on the coasts of Colima (Table 3) on 5 occasions (the first in 2019 and the others in 2024). In the case of the native species *C. arcuatus*, only one record was found in 2024.

DISCUSSION

The artisanal fishery of *C. arcuatus* in Cuyutlán Lagoon, Colima, is an activity of great socioeconomic importance for the region, so the presence of invasive species could impact the abundance of this fishing resource through ecological competition for habitat or food.

The FINS analysis of the ~560 bp fragment of the 16S rRNA gene was sufficient to identify the specimen that was morphologically distinct from *C. arcuatus* to be the invasive crab *C. hellerii*. A fragment of this gene has been used, together with a segment of the *COI* gene, to identify megalopa (late larval stage) of different crab species, including *C. arcuatus* and *C. hellerii* from different parts of the world, with good results for species differentiation (Negri et al. 2018, Marco-Herrero et al. 2021).

Charybdis hellerii is native to the Indo-Pacific and is considered an invasive species that has spread throughout the Mediterranean Sea, the Pacific Ocean, and the Atlantic Ocean (Brockerhoff and McLay 2011). Its presence has already been detected on the Yucatán Peninsula (Simoes et al. 2019). There are keys to its identification in the Mexican Caribbean and a rapid assessment method for its invasiveness (Gob Mx 2024a). Note that, of the 5 reports on iNaturalist (iNaturalist 2024), the first record dates back to 2019. Based on all the records made on this platform, the frequency of sightings may have increased in recent years in the same area, without having been detected elsewhere in the Mexican Pacific.

iNaturalist is an initiative of the California Academy of Sciences (San Francisco, USA) in conjunction with the National Geographic Society (Washington, D.C., USA) that began in 2017. It has an application that can be installed on smartphones to upload photographs and, through its algorithm, identify the species to which the organism in the photograph corresponds. This application has been used in

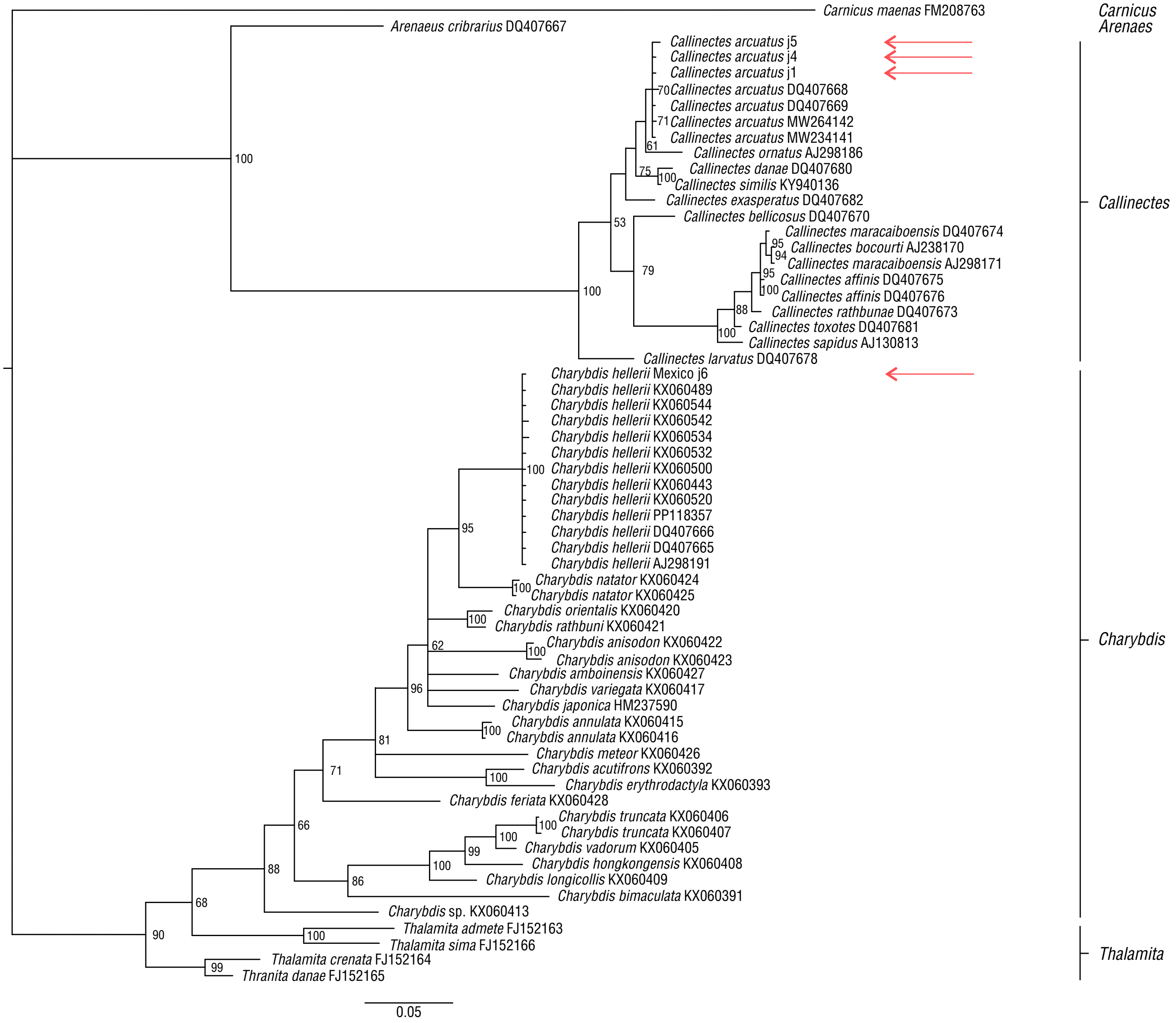

Figure 2. Phylogenetic tree obtained with the amplification of the 16S rRNA segment of 3 samples of the Arched Swimming Crab (*Callinectes arcuatus*) and 1 of the Indo-Pacific Swimming Crab (*Charybdis hellerii*) caught in the Cuyutlán Lagoon, Colima, Mexico (red arrows).

educational activities and is considered highly accurate in identifying known species (Unger et al. 2021, Callaghan et al. 2022). In addition, the results of the FINS analysis confirmed the identified species. Therefore, it is considered important to use citizen science reports in species identification, as they provide valuable information and continue to gain global relevance.

For now, the presence of *C. hellerii* could be considered restricted to the coasts of Colima, as there are no other sightings recorded in surrounding areas. However, other questions arise, such as: How did it reach these areas? What is its current distribution? And does it have an established population? Ballast water has been reported to spread *C. hellerii* in different parts of the world (Negri et al. 2018), and this is likely how it reached the coasts of Manzanillo, Colima. The Port of Manzanillo is of great national commercial importance in terms of container movement, accounting for 68% of the total movement in the Mexican Pacific and 46% of the total movement in the country. Large vessels from different parts of Mexico arrive at this port, as well as container ships from various countries such as Canada, the United States, Guatemala, Colombia, Ecuador, Chile, South Africa, Japan,

Table 2. Information on the sequences that had 100% identity with sample j6 from the Cuyutlán Lagoon, Colima, Mexico, which corresponded to the species *Charybdis hellerii.*

GenBank accession number	Location	Date	Reference
KX060544	Port Jackson, New South Wales, Australia	May 1974	Negri et al. (2018)
KX060532	Tolo Port, Hong Kong, China	September 1986	Negri et al. (2018)
KX060500	Baguala Bay, Maluku, Indonesia	December 1990	Negri et al. (2018)
KX060489	Apra Harbor, Sasa Bay, Mariana Island, Guam	January 2000	Negri et al. (2018)
KX060443	Angra dos Reis, Rio de Janeiro, Brazil	April 2011	Negri et al. (2018)
PP118357	Guinea-Bissau	2011	Muñoz et al. (2024)
NC_060621*	Not indicated		Gong et al. (Not published)

*Not included in further analysis because the location was not provided.

China, Taiwan, Korea, Indonesia, Malaysia, Singapore, and the Philippines, and from the European Union (Spain, Russia, and Germany) and Oceania (Australia and New Zealand) (Gob Mx 2024b). There is a possibility that this species may be transported from this area to other parts of Mexico or to the Pacific Ocean in the same way it arrived in Colima.

The use of the 16S rRNA fragment allowed the identification of the species *C. hellerii*, but the analysis of only a fragment was not sufficiently detailed to identify the possible biogeographic origin of the specimen found in the artisanal fishery of the Arched Swimming Crab in Cuyutlán Lagoon because this haplotype has been detected in various parts of the world (Table 2). Therefore, we recommend conducting further in-depth genetic research on this species in the locality and relating it to other studies of the distribution of *C. hellerii* worldwide (Negri et al. 2018). In addition, systematic monitoring is required in Colima and other locations to obtain a greater number of samples, produce more genomic data through (partial) genome sequencing of the species, and conduct a population genetic analysis to identify the geographic origin of the invasion.

On the other hand, given that the first record dates back 5 years (2019), it is highly likely that a local population of *C. hellerii* already exists. Therefore, the following questions arise: How could it affect native populations of the Arched Swimming Crab? And was there a single introduction or have there been multiple introductions? Knowing the answers to these questions is of utmost importance because reports, in some cases, indicate there could be a greater impact on populations of other crabs with low genetic diversity (Negri et al. 2018). Furthermore, *C. arcuatus* reaches carapace width sizes larger than the minimum legal size of 95 mm (DOF 2014, Ortega-Lizárraga et al. 2016), whereas *C. hellerii* reaches carapace width sizes of up to 65 mm on Brazilian coasts (Medina-Mantelatto and Biagi-Garcia 2001). This would imply that, if a specific management plan is not implemented, *C. hellerii* would be excluded from the fishery because it does not reach the minimum legal size for the Arched Swimming Crab.

Furthermore, the fact that there is only 1 record of *C. arcuatus* on the iNaturalist website is worth noting, given that it is a native species exploited in the region. Given that *C. arcuatus* is the native species and a fishery has existed for decades, a greater number of sightings of *C. arcuatus* than of *C. hellerii* would be expected. However, these records are not considered to be associated with the abundance of the species, as there are biases among those who observe and report on iNaturalist (Dimson and Gillespie 2023). Therefore, encouraging the population (primarily fishermen and divers) to record sightings of these crab species is recommended to support studies on their presence and dispersal.

CONCLUSIONS

The presence of the Indo-Pacific Swimming Crab *C. hellerii* was detected in Cuyutlán Lagoon, Colima, Mexico, using the FINS method. Species identification through citizen science projects can be very useful to detect invasive species in new areas. It is important to conduct studies on the current distribution of this species, given that reports from 2019 in the Manzanillo region of Colima,

Table 3. List of photographic sightings of the Indo-Pacific Swimming Crab (*Charybdis hellerii* A. Milne-Edwards, 1867) and the Arched Swimming Crab (*Callinectes arcuatus* Ordway, 1863) on the coasts of Colima, Mexico.

Species	Website	Observer	Geographic coordinates	Date
Indo-Pacific Swimming Crab (*Charybdis hellerii*)	https://mexico.inaturalist.org/observations/24484267	alboertoalcala	19°6′13.994″N, 104°23′56.767″W	3 May 2019
	https://mexico.inaturalist.org/observations/212167157	alboertoalcala	19°6′14.704″N, 104°23′56.511″W	29 April 2024
	https://mexico.inaturalist.org/observations/198085794	guillermomtz11	19°0′4.06″N, 104°16′17.537″W	31 January 2024
	https://mexico.inaturalist.org/observations/218041232	hectorjmz	19°6′15.012″N, 104°23′57.191″W	24 May 2025
	https://mexico.inaturalist.org/observations/218020269	fernando0c	19°6′15.001″N, 104°23′56.908″W	24 May 2024
Arched Swimming Crab (*Callinectes arcuatus*)	https://www.inaturalist.org/observations/226341793	hannia_aseret	19°6′19.731″N 104°23′58.477″W	30 June 2024

*The words *jaiba* and *cangrejo* (Spanish words for crab) are used interchangeably on the iNaturalist platform.

Mexico, suggest the existence of a population that may already be established on these coasts.

English translation by Claudia Michel-Villalobos.

DECLARATIONS

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Conflict of interest

The authors declare they have no conflict of interest.

Data availability

The sequences were submitted to GenBank and have the access numbers: PQ800080 and PQ800081 for *C. arcuatus* and PQ800082 for *C. hellerii*.

Author contributions

Conceptualization: MADRP, LAFR, CLVD; Data curation: MADRP, CEVP, MSM Formal analysis: MADRP; Funding acquisition: AJGV, MADRP; Research: MADRP, FLDC, CEVP, MSM; Methodology: MADRP, MSM; Project management: MADRP, AJGV; LAFR, CLVD; Resources: AJGV, FLDC; Software: MADRP; Supervision: CEVP; Validation: CEVP; Visualization: MADRP; Writing—original draft: MADRP; Writing—review and editing: MADRP, FLDC, CEVP, MSM, AJGV, LAFR, CLT, CLVD.

Use of AI tools

The authors did not employ any AI tools in this work.

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Measurement of lactate as an indicator of stress in *Rhizoprionodon longurio* and *Sphyrna lewini* during shark tagging

Abigail Prieto[1]*, Angelina Quintero[1], Jacinto A Pérez[2,3,4,5], Yehudi Rodríguez Arriatti[6]

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CORRESPONDING AUTHOR
* E-mail: abigailester24@gmail.com

[1] Facultad de Medicina Veterinaria, Universidad de Panamá, Panama City, Panama.
[2] Instituto Conmemorativo Gorgas de Estudios de la Salud, Panama City, Panama.
[3] Facultad de Ciencias Naturales, Ciencias Exactas y Tecnología, Departamento de Genética y Biología Molecular, Universidad de Panamá, Panama City, Panama.
[4] Facultad de Ciencias de la Salud, Escuela de Biotecnología, Universidad Latina de Panamá, Panama City, Panama.
[5] Facultad de Ciencias de la Salud, Universidad Americana, Panama City, Panama.
[6] Shark Defenders, Panama City, Panama.

ABSTRACT. Lactate is considered one of the main metabolic indicators of stress in sharks because it is closely related to the anaerobic metabolism that occurs during exhaustive exercise. The objective of this study was to evaluate the effect of the tagging process by measuring blood lactate levels in 2 species of sharks. Lactate levels were measured in 17 juvenile sharks, including *Rhizoprionodon longurio* ($n = 8$) and *Sphyrna lewini* ($n = 9$), captured as bycatch using small pelagic purse seine gear. The results showed that both handling time ($P = 0.0012$) and species ($P = 0.022$) significantly affected blood lactate levels, according to the generalized linear model. On the other hand, the differences between species were explained by the higher sensitivity of *R. longurio*, which showed a greater tendency to present higher lactate values compared to *S. lewini* ($P = 0.0088$). For both species, handling time should remain between 15 to 25 min, from capture during seine closure to release, to reduce the probability of mortality. This study has corroborated that the tagging technique in sharks causes high blood lactate levels as a function of handling time and species. However, it is recommended that future studies work with a larger sample in conjunction with post-capture monitoring in order to conclusively establish that lactate is an indicator of animal welfare in relation to handling time and species.

Key words: marine ecosystem, marine conservation, fishery management, shark, vulnerability, physiology, capture, tagging.

INTRODUCTION

Shark tagging, such as acoustic (Espinoza et al. 2015, Madrigal-Mora et al. 2024), satellite (Elliott et al. 2022), and conventional tagging (Bartes et al. 2021), has been a useful tool for conservation purposes in its different modalities. Fish tagging represents a physical stress caused by handling and capture, which provokes a physiological adaptive response of escape or confrontation that activates the hypothalamic-pituitary-interrenal axis (De los Santos 2017). First, the organism displays a primary response involving the release of cortisol, which leads to a secondary response with elevations in lactate due to the alteration of the metabolism. Generally, this secondary response may appear within minutes or up to an hour after exposure to stress. In the final phase, the secondary response may trigger a tertiary response associated with chronic stress. This occurs when the animal is not able to reach homeostasis, which can affect growth, reproduction, and the immune system, and can even result in death (Aguilar 2018). During an acute stress situation, oxygen consumption and anaerobic metabolism increase, resulting in plasma hyperlactatemia. This occurs because lactate is produced as a by-product of glycolysis (Murray et al. 2015, Aguilar 2018). The baseline lactate value reported by Brooks

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et al. (2012) and Gallagher et al. (2014) in unstressed sharks ranges between 0 and 1 mmol·L^{-1}.

Research on shark tagging is recent in Panama; satellite tags have been used for *Rhincodon typus* (Guzman et al. 2018, Guzman et al. 2022) and conventional spaghetti tags for juvenile sharks and rays (Rodríguez-Arriatti 2023). In Panama, there are few studies focused on the impact of fishing activities on shark populations, despite the fact that catches obtained with different fishing gears include mainly juveniles (Vega et al. 2008, Rodríguez-Arriatti et al. 2021). Tagging research on the Panamanian Pacific coasts has focused on determining shark movement patterns and residency time in different sites, laying the groundwork for conservation efforts. Specifically, this study aimed to provide information on sharks of great ecological importance and in critical conservation status caught in the Eastern Tropical Pacific (ETP) by purse seine nets, due to the lack of information available on this fishing gear and the species involved.

If the stress caused by handling during tagging is prolonged, and the organism has a low homeostatic capacity, a lethal event could be triggered in the elasmobranch (De los Santos 2017). Mortality of certain shark species can be influenced by the handling time and species-specific susceptibility. According to Gallagher et al. (2014), each species has a particular degree of response to stress, some being more vulnerable to the impact of handling. For example, the hammerhead shark (*Sphyrna mokarran*) is notably more sensitive to stress than the blacktip shark (*Carcharhinus limbatus*), or bull shark (*Carcharhinus leucas*), which makes recaptures difficult and further threatens these endangered species (Gallagher et al. 2014). Hoolihan et al. (2011) concluded that the blue shark (*Prionace glauca*) undergoes behavioral changes post-tagging due to the trauma of capture and handling, the tagging procedure, and the wearing of the tags. In a subsequent study, Hays et al. (2016) highlighted the need for the addition of ethical regulations for vulnerable megafauna species that may be sensitive to stress associated with capture, handling, and tagging. Therefore, it is imperative to investigate the welfare of sharks during the tagging procedure.

In their study with mako sharks (*Isurus oxyrinchus*), Marshall et al. (2012) found that lactate could be a potential indicator of mortality in 16–20% of cases compared to other blood markers (Na^+, Ca^{2+}, Cl^-, Mg^{2+}, and glucose). Mohan et al. (2020) pointed out that in immediate deaths observed in *C. limbatus*, there was a significant increase in lactate (median of 2.8 mmol·L^{-1} in survivors and 5.9 mmol·L^{-1} in individuals in which immediate mortality was observed). Therefore, through this biomarker, it is possible to evaluate the impact of events considered hostile, such as capture, and to identify possible stress factors (e.g., time or species), which can help us assess the probability of survival, resilience, or risk of death of the animal (Jerome et al. 2017, Aguilar 2018). In addition, it should be taken into consideration that all scientific studies should ensure the refinement of techniques to reduce the stress associated with handling and capture. In this context, the objectives of the study were to measure blood lactate levels after handling in 2 species of sharks (*Rhizoprionodon longurio* and *Sphyrna lewini*), and compare these lactate levels by handling time and species.

MATERIALS AND METHODS

Study area

Sampling was carried out at multiple locations along the ETP coast (Table 1) during October 2022. This is characterized by the rainy season with warm atmospheric temperatures around 27.5 °C (González and D'Croz 2007).

Data collection

Seventeen individuals of *R. longurio* (*n* = 8) and *S. lewini* (*n* = 9) were collected, including both females and males. These sharks were caught as bycatch in the purse seine fishery for small pelagics in which the target species are *Opisthonema libertate* and *Cetengraulis mysticetus*. These industrial vessels used purse seine nets of 627.9 m long by 54.6 m high, with a mesh opening of 2.54 cm. Each shark was tagged using spaghetti tags (T-Bar FD-68B FF, Floy FD-68B FF, Floy Tag & Mfg., Inc., Seattle, USA). A blood sample was taken from each shark with a caudal peduncle puncture using 1-mL syringes and 25-G needles. Lactate was measured with a portable Accutrend Plus meter (Roche Diagnostics, Basel, Switzerland). Handling time ranged from 10 to 35 min. This time started when the shark was sighted in the purse seine net and ended when the shark was released into the sea, including the time during which the shark was caught with a small net and brought aboard. While sharks were aboard, the following data were recorded: species, total length (TL), sex, maturity stage, and capture coordinates using a W84 GPS (Garmin, Ltd., Olathe, USA).

When the shark was on board, the conventional tag was attached, and the blood sample was collected. The average manipulation time was 4 min. On the other hand, the fighting time, which refers to the interval from first sighting to total seine closure, ranged from 5 to 30 min. It is important to emphasize that the percentage of encirclement was approximately 90% and, during this phase, the net (bag) became saturated with organisms, which confirmed successful capture. This definition of fighting time differs from that described by Brownscombe et al. (2016), who based their observations on fish caught with hook-and-line fishing gear and defined fighting time as the interval between a shark taking the hook and when it was physically immobilized. Lastly, the soaking time of the net was approximately 40 min to 120 min.

Statistical analysis

The normality and homoscedasticity of the variables handling time (minutes), body measurement (cm), and blood lactate concentration ($\text{mmol}\cdot\text{L}^{-1}$) were analyzed using Shapiro–Wilk and Levene's tests, respectively. The relationship between lactate concentration for each shark species as a function of its size and the handling time was determined using a univariate general linear model (GLM) (considering species, sex, size, and handling time by lactate concentration), and multivariate GLM with a logarithmic distribution (lactate concentration by species and handling time), together with the values of the McFadden's pseudo-R^2 (R^2_{MF}), which were calculated with the 'MASS' and 'Performance' packages and the GLM trend prediction profiler.

The Kaplan–Meier method was employed to determine the range of handling time that could cause a lethal increase in lactate in both species. According to IBM Corporation (2024), this method employs a calculation based on mortality tables to estimate the hazard or survival function at the times when events occur. This model is based on calculating the conditional probabilities associated with each instant and using the cumulative product of these probabilities to determine the survival rate at each point in time. Statistical differences between lactate concentration by species and handling time were determined with the Wilcoxon, Pearson's Chi-square, and Wald's Chi-square tests. Significant differences were evaluated with a value of $P < 0.05$. All analyses were performed in Jump Pro v. 14.0, R. v. 4.4.0. (R Core Team 2024), and RStudio v. 2024.09.1+394 (Posit Team 2024).

Results

A total of 17 peripheral blood samples were collected from juvenile sharks of *R. longurio* ($n = 8$) and *S. lewini* ($n = 9$). The study population had a median TL of 54 cm. The

Table 1. Information on fishing catches sampled during October 2022 in Puerto Caimito.

Fishing area	Latitude (N)	Longitude (W)	Species	Sex
Cerro Tigre	8°29′37.7406″	79°44′17.2788″	*Sphyrna lewini*	Female
Cerro Tigre	8°29′37.7406″	79°44′17.2788″	*Sphyrna lewini*	Female
Isla Chaman	8°45′0.5394″	79°36′16.9806″	*Rhizoprionodon longurio*	Female
Isla Verde	8°44′44.6994″	79°40′30.6012″	*Rhizoprionodon longurio*	Male
Isla Chaman	8°46′38.28″	79°36′22.2006″	*Rhizoprionodon longurio*	Male
Isla Chaman	8°46′38.28″	79°36′22.2006″	*Rhizoprionodon longurio*	Female
Isla Chaman	8°46′38.28″	79°36′22.2006″	*Rhizoprionodon longurio*	Male
Isla Chaman	8°46′38.28″	79°36′22.2006″	*Sphyrna lewini*	Female
Isla Chaman	8°46′38.28″	79°36′22.2006″	*Sphyrna lewini*	Female
Isla Chaman	8°46′ 38.28″	79°36′22.2006″	*Rhizoprionodon longurio*	Female
Isla Chaman	8°46′38.28″	79°36′22.2006″	*Rhizoprionodon longurio*	Female
Isla Chaman	8°46′38.28″	79°36′22.2006″	*Rhizoprionodon longurio*	Male
Isla Chaman	8°43′14.0412″	79°39′6.3612″	*Sphyrna lewini*	Female
Isla Chaman	8°43′14.0412″	79°39′6.3612″	*Sphyrna lewini*	Female
Isla Chaman	8°43′14.0412″	79°39′6.3612″	*Sphyrna lewini*	Male
Isla Chaman	8°43′14.0412″	79°39′6.3612″	*Sphyrna lewini*	Female
Chame	8°39'54.18″	79°38'13.8582″	*Sphyrna lewini*	Female

Table 2. General characteristics of the shark population under study. In parentheses is the percentage of n. $\bar{x}$: mean; Me: median; SD: standard deviation; $S\bar{x}$: standard error; IQR: interquartile range. All individuals captured were juveniles.

	Sphyrna lewini	*Rhizoprionodon longurio*	Total
General characteristics	n = 9 (%)	n = 8 (%)	N = 17 (%)
Sex			
Male	1 (11.11)	4 (50.00)	5 (29.41)
Female	8 (88.89)	4 (50.00)	12 (70.59)
Total length (TL) (cm)			
45–49	0 (0.00)	5 (62.50)	5 (29.41)
50–54	2 (22.22)	3 (37.50)	5 (29.41)
55–59	3 (33.33)	0 (0.00)	3 (17.65)
60–64	3 (33.33)	0 (0.00)	3 (17.65)
65–69	1 (11.12)	0 (0.00)	1 (5.88)
$\bar{x}$ (±SD)	58.39 (4.34)	49.62 (1.38)	54.26 (5.53)
$S\bar{x}$	1.44	0.49	1.34
Me (IQR)	56.00 (54.75–62.25)	49.00 (48.62–50.88)	54.00 (49.00–58.00)
Lactate concentration (mmol·L^{-1})			
1.0–2.9	4 (44.44)	2 (25.00)	6 (35.29)
3.0–4.9	5 (55.56)	2 (25.00)	7 (41.18)
5.0–6.9	0 (0.00)	1 (12.50)	1 (5.88)
7.0–8.9	0 (0.00)	2 (25.00)	2 (11.77)
>9.0	0 (0.00)	1 (12.50)	1 (5.88)
$\bar{x}$ (±SD)	2.88 (0.99)	5.11 (3.05)	3.93 (2.42)
$S\bar{x}$	0.33	1.08	0.59
Me (IQR)	3.10 (2.25–3.35)	4.85 (2.12–8.20)	3.10 (2.25–5.60)
Handling time (min)			
Low (≤10)	1 (11.11)	1 (12.50)	2 (11.76)
Medium (10.1–19.9)	2 (22.22)	2 (25.00)	4 (23.53)
High (≥20)	6 (66.67)	5 (62.50)	11 (64.71)
$\bar{x}$ (±SD)	21.33 (5.85)	21.12 (8.77)	21.23 (7.13)
$S\bar{x}$	1.95	3.10	1.73
Me (IQR)	21.00 (17.50–5.00)	20.00 (12.75–29.50)	21.00 (16.00–26.50)

median lactate concentration was 3.10 mmol·L^{-1} for *S. lewini* and 4.85 mmol·L^{-1} for *R. longurio*. Only one specimen of *S. lewini* reported a lactate value of 1 mmol·L^{-1}. Most sharks (65%) had high handling times, with a median of 21 min for both species (Table 2). The time values and body measurements showed normal distributions and homogeneous variances ($P > 0.05$) based on Shapiro–Wilk and Levene's tests, respectively. In contrast, lactate concentration values showed non-parametric behavior, with non-normal distribution ($P = 0.0097$). The correlation of lactate concentration with species, sex, body size, and handling time showed a R^2_{MF} value of 0.608 ($P = 0.0031$), indicating that 61% of the variability in blood lactate concentration was explained by the variables. The univariate GLM revealed significant dependence of lactate concentration with respect to shark species ($R^2_{\mathrm{MF}} = 0.272$, $P = 0.022$) and handling time ($R^2_{\mathrm{MF}} = 0.474$, $P = 0.0012$). The relationship with body size was marginally significant ($R^2_{\mathrm{MF}} = 0.216$, $P = 0.0497$) and no significant relationship was found with sex ($R^2_{\mathrm{MF}}= 0.081$, $P = 0.223$). The multivariate model showed that time is the variable that most contributes ($P = 0.0015$) to blood lactate concentration (Fig. 1).

The median handling time, when the increase in blood lactate levels was observed, was 21 min (range 15–25 min) for both species. This means, when the handling time threshold was exceeded, lactate levels increased, which increased the probability of mortality in the animal. According to the Kaplan–Meier analysis, there was no difference in the median handling time ($\chi^2 = 0.037$, $P = 0.84$) between the 2 shark species (Fig. 2). However, for the evaluation of blood lactate levels by species, it was observed that *R. longurio* tended to have higher lactate levels than those of *S. lewini* ($\chi^2 = 6.86$, $P = 0.0088$) at different handling times (Fig. 3).

DISCUSSION

This study confirmed that an increase in shark handling time during the tagging process led to elevated blood lactate level in sharks (Fig. 1). To avoid reducing the chances of survival for both species analyzed, handling time should be limited to between 15 min and 25 min, measured from the initial sighting of the animals in the net until their release. Prolonged handling time could trigger their death (Fig. 2) (Aguilar 2018). Murray et al. (2015) observed that dogfish sharks (*Scyliorhinus canicula*) exposed to 40 min of handling showed higher blood lactate concentrations compared to those handled for only 15 min. The results found by Fuller et al. (2020) for the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) indicate that, despite the use of hooks for capture, the results were consistent with those obtained in this study. In the investigation by Fuller et al. (2020), lactate concentrations were obtained by a commercial lactate measuring device, and it was found that levels increased significantly at handling times between 45 min and 60 min, reaching values between 4 mmol·L^{-1} and 8 mmol·L^{-1}. The results of the Kaplan–Meier analysis in this study, combined with the findings of Fuller et al. (2020), suggest that increased handling time is associated with a higher risk of shark mortality. This is due to the negative effects associated with elevated lactate levels, as previously documented (Dumetz et al. 2008, Marshall et al. 2012, Jerome et al. 2017).

In this study, *R. longurio* showed a greater increase in blood lactate concentration compared to *S. lewini* (Fig. 3). The average lactate concentrations for *S. lewini* (3.10 mmol·L^{-1}) and *R. longurio* (4.85 mmol·L^{-1}) suggest high levels compared to the indicator values reported by

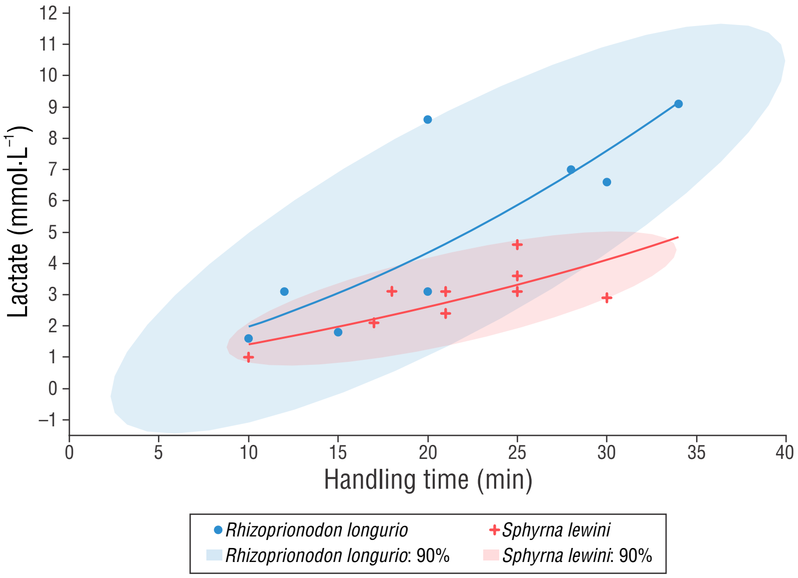

Figure 1. Multivariate analysis with Pseudo-R^2_{MF}, which shows the significant dependence of lactate measurements as a function of species and handling time ($R^2_{\mathrm{MF}}= 0.630$, $P = 0.0046$).

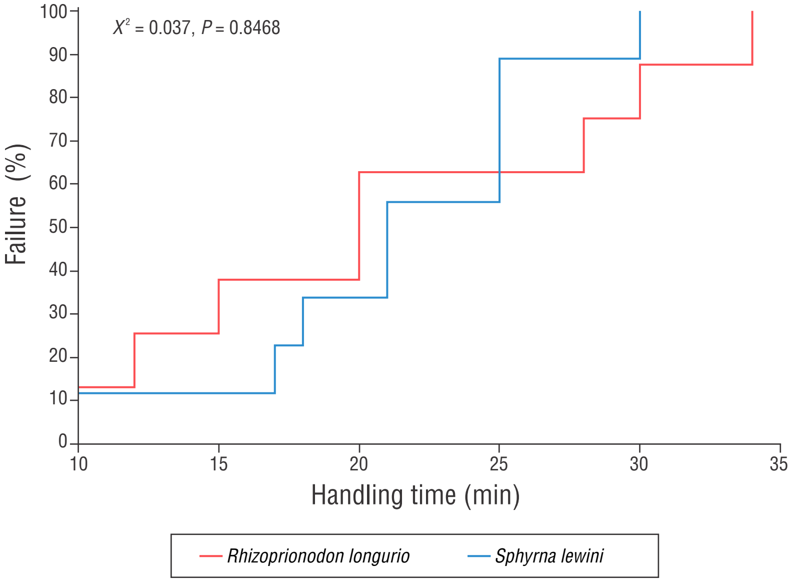

Figure 2. Kaplan–Meier analysis of lactate concentration by manipulation time for each individual, where the median manipulation time is 21 min.

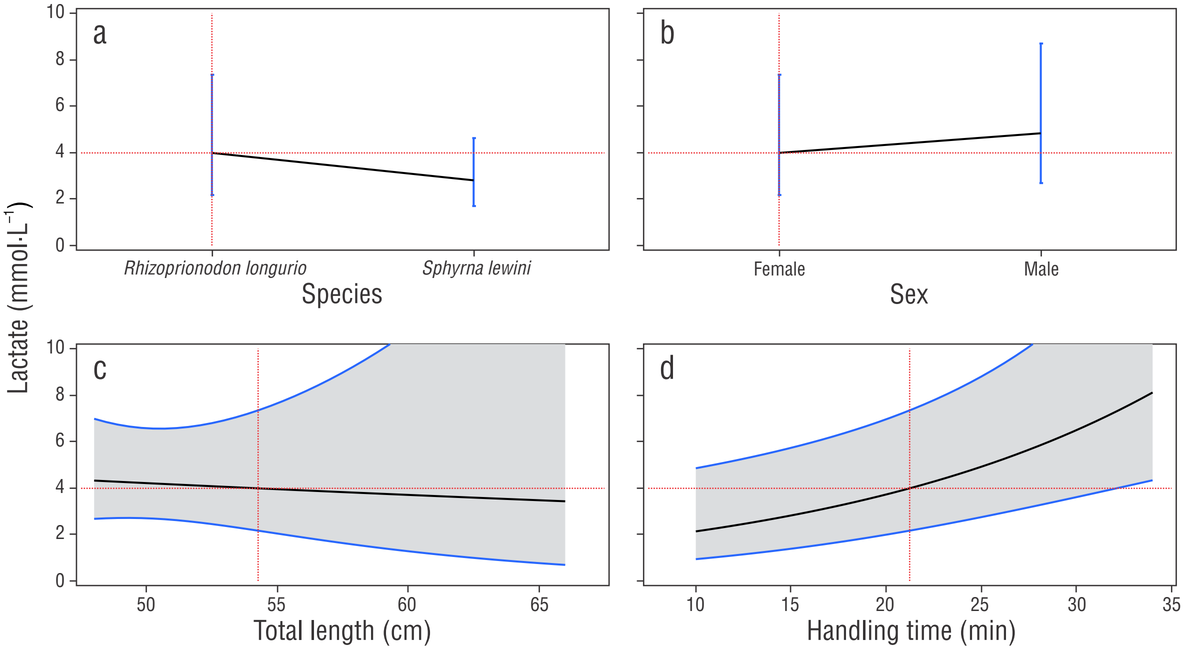

Figure 3. Trend prediction profiler of lactate (mmol·L^{-1}) per species.

Brooks et al. (2012) and Gallagher et al. (2014), who noted that the range of lactate concentrations in unstressed sharks ranged from 0 mmol·L^{-1} to 1 mmol·L^{-1}.

When comparing the values from this study with those reported by Fuller et al. (2020), which were described previously, the range of lactate in *R. terraenovae* was 2 mmol·L^{-1} to 6 mmol·L^{-1}. Ecologically and biologically, the species most similar to *S. lewini* is *C. limbatus*. Mohan et al. (2020) reported a mean of 2.8 mmol·L^{-1} for *C. limbatus* in surviving adult sharks and a value of 5.9 mmol·L^{-1} for those with immediate mortality. During the juvenile stage, *S. lewini* occupies a benthic habit (Klimley 1983, Torres-Rojas et al. 2010), so its lactate values may be more comparable with genera with benthic habitats such as shark species of the genus *Rhizoprionodon*. Giesy et al. (2025) determined that anthropogenic factors, such as intensive fishing, pollution, and the destruction of habitat and their interactions, may have a greater impact on benthic species, like nurse sharks

(*Ginglymostoma cirratum*), than capture and handling stress. In this sense, benthic species are more susceptible to physiological stress, which was reflected in elevated lactate levels (0.7 $\mathrm{mmol{\cdot}L^{-1}}$ to 22.1 $\mathrm{mmol{\cdot}L^{-1}}$) (Giesy et al. 2025) compared to their pelagic counterparts that inhabit areas farther away from human influence. Regardless of the causes, this indicates that *R. longurio* and *S. lewini* undergo changes in their metabolism when manipulated, either due to species-specific metabolic reactions (Jerome et al. 2017), to the methodology used, or to other variables not analyzed in this study.

CONCLUSIONS

This study demonstrates that the conventional shark tagging technique increases blood lactate levels, an indicator of stress, depending on handling time and species. The tested individuals of *R. longurio* had higher blood lactate concentrations compared to those of *S. lewini*. Based on the results, handling time should be less than 25 min. We hope this critical range serves as a practical guideline for future studies using this tagging technique on these species. The fact that the shark is out of its environment will affect its physiological functions. It is prudent to take into account that the team should capture the shark as quickly as possible, both to prevent the shark from getting exhaustive exercise in order to escape and to prevent it from getting injured by the net or the boat. It is also necessary to carry out the manipulation during the tagging in such a way that the animal does not exhaust its energies or increase its blood lactate to critical ranges and to release the organisms under post-capture surveillance to maximize the likelihood of survival. Monitoring should be carried out in the short, medium, and long term to assess the survival rate, especially for sharks with a critical conservation status, thus strengthening conservation efforts.

English translation by authors.

DECLARATIONS

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Conflict of interest

The authors declare they have no conflict of interest.

Author contributions

Conceptualization: AP; Data curation: JP; Formal analysis: JP; Funding acquisition: YA and AP; Investigation: AP; Methodology: AP and AQ; Project administration: AP; Resources: AP; Software: JP; Supervision: AQ; Validation: AP, AQ; Visualization: AP, JP; Writing–original draft: AP, AQ, YA, JP; Writing–review and editing: JP, YA, AP.

Data availability

The data for this study are available from the corresponding author by reasonable request.

Use of AI tools

The authors, who are responsible for the content of this publication, employed DeepL and ChatGpt to conduct spelling and grammar checks.

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Ciencias Marinas (2025), 51:e3528 **Research Note**

Ciencias Marinas Journal/Revista

First record of the Indo-Pacific species *Electroma vexillum* (Bivalvia: Pteriidae) in the Gulf of Mexico

Vicencio de la Cruz-Francisco[1]*

Abstract. *Electroma vexillum* is a bivalve native to the Indo-Pacific that was introduced to the Mediterranean Sea. This study provides records of its presence in the Gulf of Mexico. Organism sighting and collection was carried out between 2018 and 2019 and from November 2021 to July 2024 on 2 coasts of northern Veracruz, Mexico. The individuals identified as *E. vexillum* were small (<6 mm in length), had fragile and thin valves, and were found in the intertidal zone attached to red algae and green algae. The accidental introduction of this species could be related to international maritime transport, as Tuxpan seaport is located north of Veracruz. After 6 years of observations (2018–2024), *E. vexillum* can be considered an established exotic species in the southern Gulf of Mexico.

Key words: bivalves, epibionts, intertidal, exotic, Veracruz.

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Corresponding author
* E-mail: viccruz@uv.mx

[1] Facultad de Ciencias Biológicas y
Agropecuarias, Universidad Veracruzana,
92895 Tuxpan, Veracruz, Mexico.

Introduction

Electroma vexillum (Reeve, 1857) is a bivalve native to the Indo-Pacific, which is distributed in the Red Sea, the Persian Gulf, and southern India (Dekker and Orlin 2000, Zenetos 2010, Asha et al. 2016, Oliver et al. 2023, GBIF 2024). It differs from other bivalve species due to its distinctive morphological characteristics, such as small (<10 mm length), fragile and translucent valves, and the absence of hinge teeth (Çevik et al. 2008, Tëmkin 2010). Furthermore, *E. vexillum* inhabits shallow waters associated with macroalgae, seagrass beds, and artificial structures (Asha et al. 2016). This species has been reported as exotic in several locations in the Mediterranean Sea, such as Turkey (Çevik et al. 2008, Albayrak 2010, Çinar et al. 2021), and after almost 20 years of these records, its presence has been confirmed with a recent report in Israel (Albano et al. 2024). The presence of an introduced species identified as *Electroma* sp. has been reported in the western Atlantic, specifically in 1983 and 1995 on the coasts of Colombia and Venezuela (Borrero and Díaz 1998). However, this region lacks updated data, so the current status of this record is unknown (Álvarez-León et al. 2007).

In the Gulf of Mexico, which is the region closest to the southern Caribbean, the presence of *E. vexillum* as an introduced species has not been documented (Okolodkov et al. 2007, Mendoza-Alfaro et al. 2014, León-González et al. 2021, CONABIO 2024). Furthermore, *E. vexillum* does not appear in the taxonomic lists of marine and coastal ecosystems (Pérez-Rodríguez 1997, Hicks et al. 2001, García-Cubas and Reguero 2007, Tunnell et al. 2007, Turgeon et al. 2009, Correa-Sandoval and Rodríguez-Castro 2013, Suárez-Mozo et al. 2024), nor has it been reported in recent studies on the benthic macrofauna of the Veracruz coast (Vassallo et al. 2014, De la Cruz-Francisco et al. 2017, Rodríguez-Muñoz et al. 2023).

Northern Veracruz is characterized by a predominantly sandy coastline, although artificial protection structures, such as breakwaters and groins, are also present, as are rocky sandstone promontories to a lesser extent (López-Portillo et al. 2023, Rodríguez-Muñoz et al. 2023). These solid substrates provide habitats for macroalgae and marine macrofauna to establish; these have been previously documented in the region (De la Cruz-Francisco et al. 2017; Rodríguez-Muñoz et al. 2023; Mateo-Cid et al. 2024; De la Cruz-Francisco 2025a,

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b). However, studies have indicated that these artificial structures can also facilitate the establishment of introduced or exotic species (Vaselli et al. 2008, Mineur et al. 2012), a phenomenon that has been scarcely explored in this area.

Therefore, the aims of this study were to document the first records of the Indo-Pacific species *E. vexillum* in the Gulf of Mexico, describe the external morphological characteristics of specimens collected from 2 coastal areas in northern Veracruz, and contribute to the understanding of the distribution and habitat of this species in the region. The information provided by this study will serve as a basis for future studies evaluating the ecology of *E. vexillum*, its impact on local ecosystems, and its interaction with native species.

Materials and methods

Study sites: coastline of northern Veracruz

The coast of Tuxpan, located in the municipality of Tuxpan, is primarily sandy with a gentle slope. The Tuxpan River flows into the central part of the coastline, flanked by two ~1-km long breakwater structures, as well as 16 straight groins, each 60 m long, located perpendicular to the shoreline. Communities of benthic algae and marine invertebrates grow on the rocks of the Tuxpan coastline. This coastline is particularly active in national and international maritime traffic, due to the presence of an industrial and commercial seaport, with cargo moving overseas to the United States, Cuba, Russia, Canada, China, Latvia, and Ukraine (López-Portillo et al. 2023) (Fig. 1b; site A).

The coast of Cazones, located in the municipality of Cazones de Herrera and bordering the Tuxpan municipality to the north, is sandy and has rocky sandstone promontories and a ~950-m-long and 40-m-wide abrasive platform, known as Playa El Pulpo, which is is inhabited by algae, grasses, and marine invertebrates (De la Cruz-Francisco et al. 2017, Rodríguez-Muñoz et al. 2023) (Fig. 1b; site B).

These coastlines experience seasonal changes throughout the year. During autumn (September–December) and winter (December–March), the water is cold (22–23 °C) and surface currents flow from north to south; in spring (March–June) and summer (June–September), the water is warmer (27–28 °C) and currents flow from south to north (Zavala-Hidalgo et al. 2003, Mendelssohn et al. 2017).

Sampling

The indirect method was used for organism sighting and collection. This method consisted in searching for small bivalves attached to the benthic macroalgae on the artificial structures along the coastline of Tuxpan and the rocky coastline of Cazones. Samplings were conducted during the lowest tides, walking along artificial and rocky substrates. The first collections occurred in November 2018 on the rocky coastline of Cazones, during samplings aimed at studying the benthic community (Rodríguez-Muñoz et al. 2023). Collected organisms were preserved in 70% ethyl alcohol; however, due to the small size and fragility of the valves, it was not possible to identify them taxonomically during that period. Subsequently, in November 2019 and 2021, sightings of bivalves attached to algae continued in the same area, and more individuals with similar characteristics were collected in June 2022. Regarding the groins along the Tuxpan coast, during searches for sponges and sea slugs between May and June 2023 (De la Cruz-Francisco 2025a, b), more bivalves were sighted associated with macroalgae. These sightings continued in July 2024, and more individuals were collected for taxonomic identification (Fig. 1).

All bivalves collected and identified as *E. vexillum* were preserved in ethyl alcohol and deposited in the biological collection of the *Facultad de Ciencias Biológicas y Agropecuarias* of the *Universidad Veracruzana*. The taxonomic identification of the species was based on the size, coloration, and morphology of the valves; these characteristics were described in Borrero and Díaz (1998), Çevik et al. (2008), and Tëmkin (2010). The updated taxonomic classification for the species was verified in MolluscaBase (MolluscaBase 2025). A Nikon optical microscope (Tokyo, Japan) was used to observe the external characteristics of the valves. Length and height measurements of the collected bivalves were also recorded. From these data, the following descriptive parameters of the valves were calculated: minimum, mean ± standard deviation, and maximum.

Results

A total of 54 *E. vexillum* individuals were collected. In the rocky intertidal zone of Cazones, 7 individuals were collected in November 2018 on green algae, and 12 more individuals were collected in June 2022 (20°44′20.22″N, 97°11′36.36″W), associated with 2 species of green algae. Finally, 35 specimens were collected in July 2024 on the coastal groins of Tuxpan, Veracruz (20°59′34.38″N, 97°19′8.25″W), associated with several species of green and red algae. Regarding bivalve dimensions, the average length and height values were slightly higher in the few individuals collected along the Cazones coast in November 2018, compared to those of individuals collected in June 2022 and July 2024 (Table 1). The systematics, morphology, and habitat of *E. vexillum* are described below.

Systematics

Order Ostreida Férussac, 1822. Family Vulsellidae Gray, 1854. Genus Electroma Stoliczka, 1871. Species *Electroma vexillum* (Reeve, 1857). Synonyms: *Avicula vexillum* Reeve, 1857.

Morphology

Small, wedge-shaped bivalves, measuring 2.5 to 5.6 mm in length and 1.7 to 4.5 mm in height (Table 1). The valves

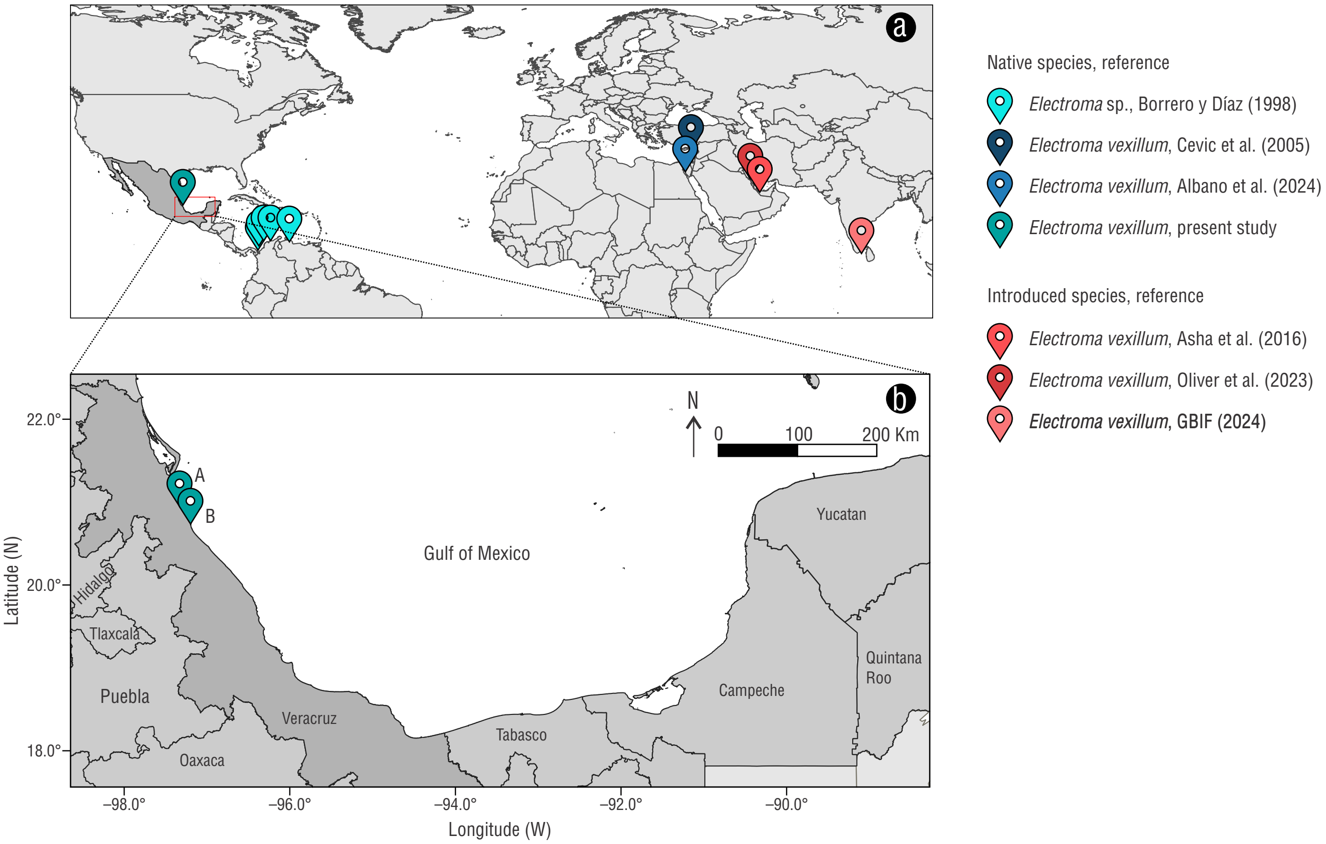

Figure 1. Distribution of *Electroma vexillum* as a native and introduced species (**a**). Coasts of Tuxpan (A) and Cazones (B) in the Gulf of Mexico (**b**).

are fragile, thin, and convex, and lacked auricles, scales, and radial ribs. Concentric lines can be seen in some individuals (Fig. 2a, b). The valves are unequal (inequivalve); the ventral valve is smaller and slightly convex, with a groove toward the posterior margin; the dorsal valve is larger and convex anteriorly, with an umbonal carina (Fig. 2c, d). The umbo is elevated and displaced forward (prosocline). The hinge is straight, but toothless. In most specimens, external coloration was amber with a dark brown zigzag stripe pattern. Some individuals had a brown band toward the posterior part of the umbonal carina (Fig. 2a). The specimens had fibrous filaments that attach them to benthic algae fronds (Fig. 2d, e).

Habitat

All bivalves were found associated with different species of green and red algae (Fig. 3). In the Tuxpan coastal groins, *E. vexillum* was observed as an epibiont on 4 species of green algae: *Ulva lactuca* Linnaeus, 1753 (Fig. 3a); *Bryopsis pennata* J.V. Lamouroux, 1809 (Fig. 3b); *Caulerpa sertulariodes* (S.G. Gmelin) M. Howe, 1905 (Fig. 3c); and *Caulerpa mexicana* Sonder ex Kützing, 1849 (Fig. 3d). In addition, it was observed as an epibiont on 7 species of red algae: *Acanthophora spicifera* (M. Vahl) Børgesen, 1910 (Fig. 3e); *Alsidium triquetrum* (S.G. Gmelin) Trevisan, 1845; *Hypnea musciformis* (Wulfen) J.V. Lamouroux, 1813; *Agardhiella subulata* (C. Agardh) Kraft & M.J. Wynne, 1979; *Gracilaria blodgettii* Harvey, 1853; *Gracilaria domingensis* Sonder ex Dickie, 1874 (Fig. 3f), and *Solieria filiformis* (Kützing) P.W. Gabrielson, 1985 (with high abundance) (Fig. 3g–h). Meanwhile, in the rocky intertidal zone of Cazones, aggregations of *E. vexillum* were recorded on 2 species of green algae: *U. lactuca* and *Caulerpa racemosa*. It is worth mentioning that other groups of invertebrates associated with benthic algae, such as hydras, polychaetes, pycnogonids, amphipods, isopods, tanaidaceans, decapods, gastropods, bryozoans, and ascidians, were also observed.

Discussion

Morphologically, *E. vexillum* is distinguished from species native to the Gulf of Mexico by the absence of hinge teeth, auricles, scales, and radial ribs, characteristics that are present in species of the genera *Isognomon*, *Pteria*, *Ischadium*, and *Modiolus*, which are larger in size (12–75 mm) and adhere mainly to rocks, mangrove roots, oysters, and octocorals

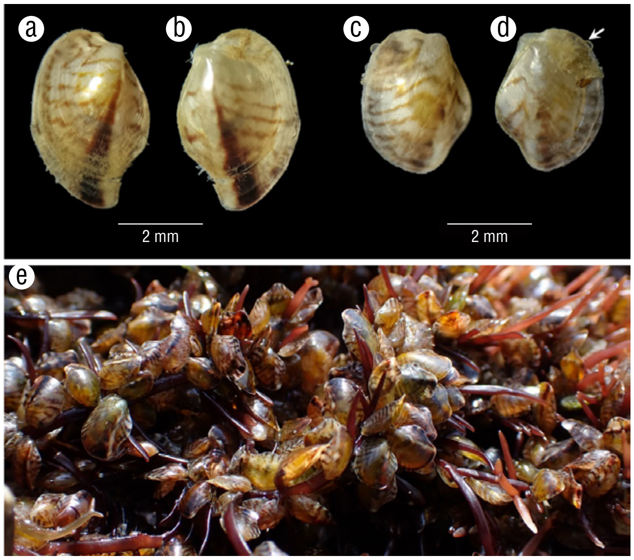

Figure 2. Two individuals of *Electroma vexillum* collected from benthic marine algae on the groins of Tuxpan, Veracruz. The first individual is 4 mm long: dorsal valve (**a**) and ventral valve (**b**). The second individual is 3 mm long: dorsal valve (**c**) and ventral valve (**d**). The byssus filaments are visible (white arrow). Aggregation of *E. vexillum* on red algae (**e**).

(García-Cubas and Reguero 2007). On the other hand, individuals of *E. vexillum* are small (<6 mm) and were found exclusively in benthic macroalgae. This type of association has also been reported in the southern Caribbean (Borrero and Díaz 1998), the Mediterranean Sea (Bakır et al. 2012), and in India, where *E. vexillum* has also been found associated with seagrasses (Asha et al. 2016). In addition, *E. vexillum* has been reported to colonize rocks and artificial substrates in Colombia and Turkey, the Mediterranean Sea (Borrero and Díaz 1998, Bakır et al. 2012), and soft bottoms in Israel (Albano et al. 2024).

Although *E. vexillum* abundance was not estimated in this work, it is important to note that dense aggregations were observed on red and green algae on the Tuxpan coast (July 2024), which could signal the invasive capacity of this exotic bivalve in the region. A similar case was reported for the species *Electroma* sp. in the southern Caribbean, where it was considered to hinder the collection of seeds from commercially important bivalves in the Colombian region (Borrero and Díaz 1998). The presence of *E. vexillum* could alter the habitat due to competition with the native benthic community, which is composed of diverse groups of invertebrates, such as hydras, polychaetes, pycnogonids, crustaceans, and gastropods, which are also associated with native benthic algae.

Electroma vexillum was found exclusively on intertidal benthic algae growing on artificial structures (groins) and natural rocky promontories (rocky intertidal zones). However, this does not rule out the possibility that the species also occurs in deeper coastal waters, as it has been reported at depths of 2–10 m in other locations (Borrero and Díaz 1998) and up to 20 m (Albano et al. 2024). Furthermore, its dispersion most likely expands in other ecosystems of the northern region of Veracruz, such as coral reefs located 12 km from the coast, where benthic algae are common and abundant (González-González et al. 2016, De la Cruz-Francisco et al. 2020).

Maritime transport has been suggested as the main route of introduction of *E. vexillum* into the Mediterranean Sea (Çevik et al. 2008, Albano et al. 2024) and of *Electroma* sp. into the southern Caribbean (Borrero and Díaz 1998). The accidental introduction of *E. vexillum* into the Gulf of Mexico is most likely linked to maritime transport, which is frequent along the Tuxpan coast due to its proximity to the seaport (6 km away), where national and international vessels dock. Maritime navigation has also been linked to the dispersal of other exotic species into the Gulf of Mexico, such as the encrusting coral *Oculina patagonica* Angelis D'Ossat, 1908 and the regal demoiselle fish *Neopomacentrus cyanomos* (Bleeker, 1856), which are established on the coasts of Tuxpan and Cazones and have spread along the coast of Veracruz (González-Gándara and De la Cruz-Francisco 2014; De la Cruz-Francisco et al. 2015, 2017; Colín-García et al. 2018; Rodríguez-Muñoz et al. 2023).

The preference of *E. vexillum* for inhabiting different species of benthic algae could be an indication of its invasive potential. This threat could extend throughout the Gulf of Mexico, given that benthic algae are widely distributed in this region (Mateo-Cid et al. 2024). However, the invasive capacity of *E. vexillum* and its effect on native species are still unknown; therefore, it is necessary to analyze its impact on the morphology, growth, photosynthesis, diversity, and abundance

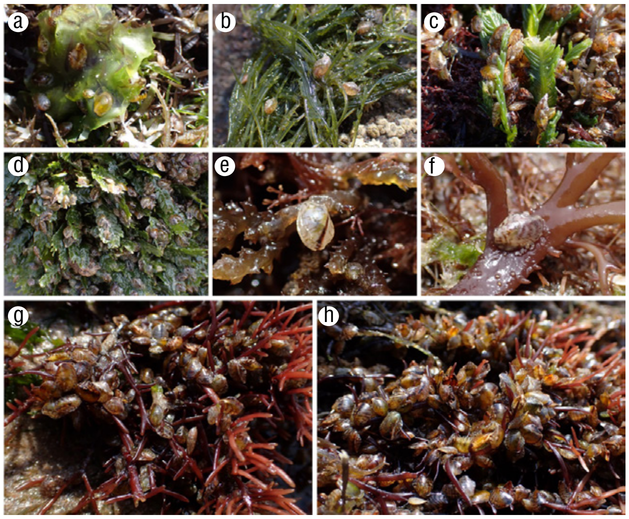

Figure 3. Aggregations of *Electroma vexillum* on benthic marine algae on the groins of the Tuxpan coast, Veracruz, Mexico, in July 2024. Benthic algae species: *Ulva lactuca* (**a**), *Bryopsis plumosa* (**b**), *Caulerpa sertularioides* (**c**), *Caulerpa mexicana* (**d**), *Acantophora specifiera* (**e**), *Gracilaria dominguensis* (**f**), and *Solieria filiformis* (**g**–**h**).

Table 1. Comparative data of the length and height of *Electroma vexillum* collected on the coasts of Tuxpan and Cazones, Veracruz, Mexico. Descriptive measures: minimum, mean ± standard deviation, maximum, and number of individuals (*n*).

	Cazones 2018 (*n* = 7)			Cazones 2022 (*n* = 12)			Tuxpan 2024 (*n* = 35)		
Dimensions	Minimum	Mean ± SD	Maximum	Minimum	Mean ± SD	Maximum	Minimum	Mean ± SD	Maximum
Length	4.2	4.7 ± 0.3	5.2	3.9	4.5 ± 0.4	5.3	2.7	4.2 ± 0.8	5.6
Height	2.8	3.7 ± 0.6	4.3	2.4	3.8 ± 0.6	4.5	1.7	3.1 ± 0.7	4.5

of basibiont algae. Furthermore, the community structure of the benthic fauna associated with these algae should be evaluated to determine possible changes driven by the presence of this exotic species. In addition, studies of the biology of *E. vexillum* directed toward topics related to its life cycle, reproductive period, population growth, dispersal mechanisms, and tolerance to environmental factors are essential.

Finally, it is important to recognize that the identification of this exotic species was based exclusively on the external morphology of the valves, using morphological characteristics that coincide with the taxonomic descriptions of *E. vexillum*. Therefore, it is essential to conduct molecular analyses, such as sequencing of the 18S rRNA and COI (cytochrome c oxidase subunit 1) genes. These techniques will allow us to more precisely validate the identity of *E. vexillum*, identify its geographic origin, and determine the routes of its introduction into the Gulf of Mexico.

CONCLUSIONS

After 6 years of observations and records in the coasts of Tuxpan and Cazones, Veracruz, *E. vexillum* is considered an established exotic species in the Gulf of Mexico. Thus, it is essential to conduct studies focusing on its ecology and distribution in the region because it inhabits intertidal benthic algae, which serve as habitat for many native marine invertebrates and epiphytic algae. Furthermore, molecular analyses are needed to validate the identification of this exotic species with greater precision and determine its geographic origin.

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Conflict of interest

The author declares no conflict of interest.

Author contributions

Conceptualization: VCF; Data curation: VCF; Formal analysis: VCF; Funding acquisition: VCF; Investigation: VCF; Methodology: VCF; Project administration: VCF; Resources: VCF; Supervision: VCF; Validation: VCF; Visualization: VCF; Writing—original draft: VCF; Writing—review and editing: VCF.

Data availability

The data for this study are available from the corresponding author by reasonable request.

Use of AI tools

The author did not employ any AI tools in this work.

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