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Review

Research trends on marine zooplankton in the southern Gulf of Mexico: A short review

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ABSTRACT. The Gulf of Mexico (GoM) is a large interior sea located on the North American continent, which shares its waters with Cuba, the USA, and Mexico. Owing to its complex circulation pattern, high biological productivity levels, and bathymetry, the GoM is one of the 21 Large Marine Ecosystems in the American continent. Besides, along their coasts, numerous lagoons host a high species richness and serve as refuges, growth, and feeding areas for numerous species of high ecological and commercial value. The high biological productivity of the GoM and its adjacent areas is directly linked to the organisms positioned at the lowest levels of the trophic web, specifically the zooplankton. Studies of zooplankton communities in the northern GoM began in the early 20th century. In the Mexican portion, thanks to the Russian-Cuban expeditions in the 1960s, substantial progress was made in understanding the composition and distribution patterns of some zooplankton groups, which has increased considerably over the last two decades. This paper presents a short synthesis and review of the research trends on marine zooplankton in the southern GoM. Due to their significant numerical contribution and importance in commercial fishing, copepods and fish larvae are two of the most studied zooplankton groups to date. Decapods, rotifers, and doliolids have been largely neglected. Other groups have recently attracted attention due to the threats they face. For example, due to the acidification scenarios documented in the GoM, holoplanktonic mollusks, such as pteropods and heteropods, represent key groups. This review also discusses the threats to which zooplanktonic populations in the GoM are subject. Indeed, warming, acidification, and deoxygenation events, as well as plastic pollution, are aspects that should be considered in future research.

Keywords: zooplankton; species richness; biomass; distribution patterns; southern Gulf of Mexico

INTRODUCTION

The Gulf of Mexico (GoM) is an interior sea recognized as one of the 64 Large Marine Ecosystems (LME) in the world and one of the 21 LMEs within the American continent, which is highlighted for their high dynamism, high biological productivity levels and for being the habitat of numerous emblematic species (Sherman & Hempel 2009) (Fig. 1a). With an area of more than 1.5 million km^2 and a complex bathymetry (up to more than 3,500 m depth) (Goff et al. 2016), the GoM shares its waters with three countries: Mexico, Cuba, and the USA.

In hydrographic terms, the GoM is a highly dynamic ecosystem due to the confluence of different oceanographic processes that occur at different spatiotemporal scales (Morey et al. 2024). One of the main physical features that characterize the circulation of the GoM is

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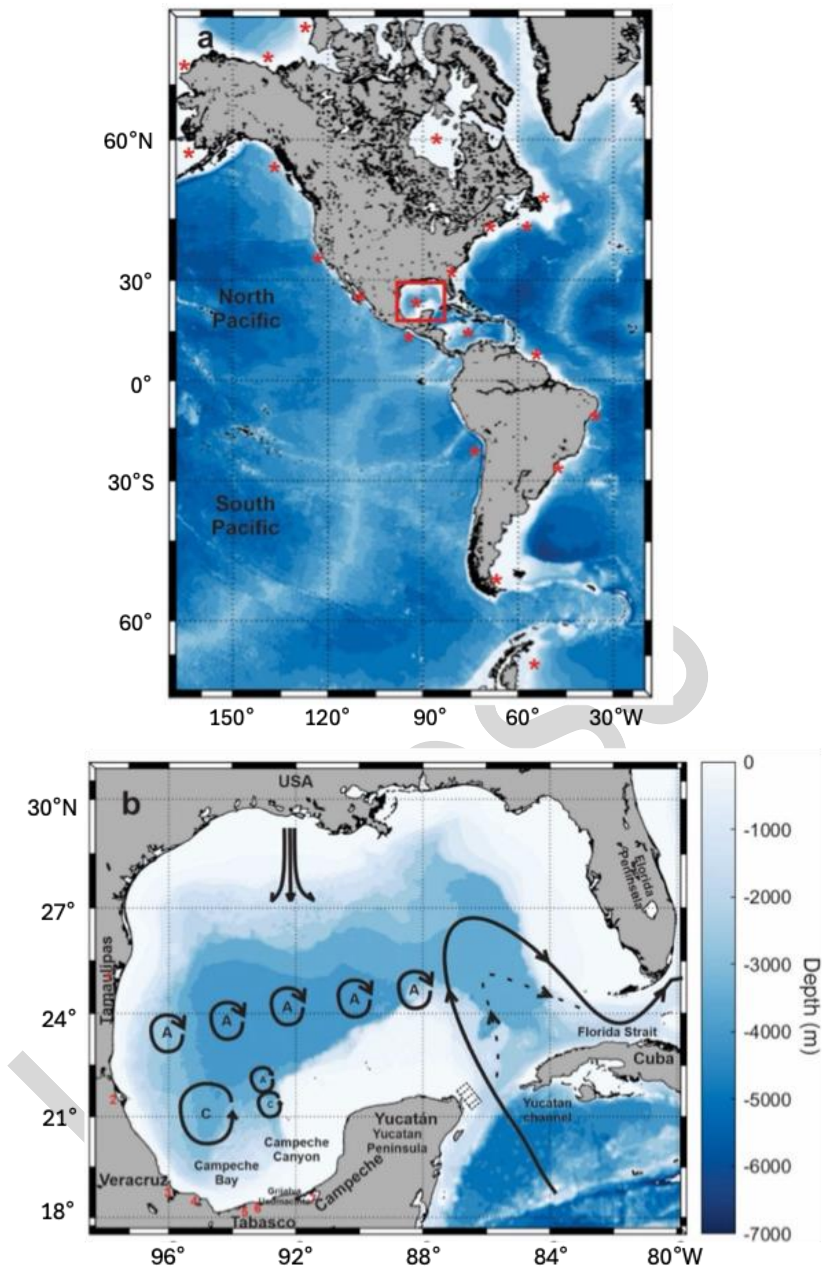

Figure 1. a) Map showing the 21 Large Marine Ecosystems of the American Continent (*red symbols), including the Gulf of Mexico, and b) the Gulf of Mexico showing the mean hydrodynamic features inside the gulf: the Loop Current, the anticyclonic eddies (A), the quasi-permanent cyclonic circulation (C) over the Campeche Bay, the dipole eddies (anticyclone-cyclone) over the Campeche Canyon and the upwelling on the Yucatan Peninsula (squared area). The black solid line represents the Loop Current in its expanded form, while the dotted black line represents the Loop Current in its retracted form. The numbers represent the main coastal lagoons in the southern gulf: 1. Laguna Madre, 2. Tamiahua Lagoon, 3. Alvarado Lagoon, 4. Sontecomapan Lagoon, 5. Carmen-Pajonal-Machona Lagoon, 6. Mecoacan Lagoon, and 7. Terminos Lagoon.

the Loop Current, a flow of warm water that enters the gulf from the Caribbean Sea through the Yucatan Strait and exits towards the Atlantic Ocean through the Strait of Florida (Athié et al. 2020) (Fig. 1b). This current presents two main forms of intrusion: 1) an extended form that occurs in summer, characterized by a maximum penetration of the current into the Gulf exceeding 26ºN, and 2) a retracted current that occurs in winter and is characterized by a minimal incursion into the gulf (Alvera-Azcárate et al. 2009, Delgado et al. 2019) (Fig. 1b). During its incursion into the GoM, a series of subsidiary eddies, mainly anticyclonic, are released from the Loop Current, which are transported westwards until they collide with the coasts of Veracruz and Tamaulipas, where they dissipate. The diameter of these eddies can exceed 100 km, and they can persist for more than 15 months (Leben 2005). During their journey, these eddies not only transport heat and energy but also transport water masses and planktonic organisms (Linacre et al. 2019).

While in the Campeche Bay, the circulation pattern is characterized by the presence of a quasi-permanent cyclonic circulation (Salas-de-León et al. 1998) benefiting zooplankton communities (Färber-Lorda et al. 2019), in the Campeche Canyon, the presence of dipole eddies (cyclone-anticyclone) has been reported with a strong impact on both phytoplankton and zooplankton communities (Salas-de-León et al. 2004, Durán-Campos et al. 2017). Another process that stimulates biological productivity within the gulf is the upwelling on the Yucatan shelf, which occurs due to the interaction between the Yucatan Current and the eastern Yucatan slope, inducing the resuspension of organic matter and nutrients that fertilize the euphotic layer, benefiting the plankton communities (Merino 1997, Reyes-Jiménez et al. 2023).

In climatic terms, the GoM is distinguished by three main seasons: the dry season that occurs between February and May; the rainy season that takes place between June and October; and the "Nortes" season that occurs between November and January, during which extreme (>80 km h^{-1}) and persistent northerly winds flow in the gulf, generating changes in the hydrographic properties of the water column and a deepening of the mixing layer below 70 m depth (Gómez-Ponce et al. 2021).

As a notable feature, the GoM hosts more than 20 lagoon systems, which are distinguished by their high species richness and serve as refuges, growth habitats, and feeding grounds for numerous species of high ecological and commercial value. These environments are characterized by their great environmental heterogeneity, which promotes species richness and high levels of secondary production (De la Lanza-Espino & Lozano 1999).

The high biological diversity supported by the GoM is directly linked to the effects that the hydrodynamic processes described above have on organisms positioned at the lower trophic levels of the food chain.

Zooplankton, a highly diverse group of organisms that includes virtually all phyla in the marine environment, serve as key consumers in the transfer and sequestration of carbon towards the interior and bottom of the oceans. This function, combined with their role in transferring energy along food webs, underscores the importance of zooplankton in marine ecosystems. Furthermore, zooplankton support fisheries of numerous species, many of which are of high commercial value (Steinberg & Landry 2017, Lomartire et al. 2021, Nowicki et al. 2022).

The study of zooplankton in the GoM has a rich history that spans over a century. Research in the northern gulf began in the early 20th century with the study of crustaceans off the coast of Louisiana (Foster 1904). In the Mexican portion of the gulf, formal research began in the 1960s, thanks to Russian-Cuban oceanographic expeditions (Okoldkov 2003). The 1970s witnessed significant progress, with expeditions led by the Mexican Navy contributing to a deeper understanding of various zooplankton groups (Almazán et al. 2022). However, it was not until the 1980s that regular monitoring programs were established, thanks to the acquisition of the research vessel "Justo Sierra" by the National Autonomous University of Mexico (UNAM, by its Spanish acronym), which marked a turning point in oceanographic research in Mexico, leading to numerous scientific cruises and the acquisition of numerous zooplankton samples, which significantly advanced our understanding of zooplankton dynamics.

This review is dedicated to summarizing the research trends on marine zooplankton in the Mexican southern GoM. To do this, a deep search was carried out (until August 2024) in several databases (e.g. Web of Science, Scopus, ScienceDirect, Google Scholar, and PubMed) using the keyword combinations (both in English and Spanish) "zooplankton", "zooplankton biomass", "copepods", "ichthyoplankton", "fish larvae", "holoplanktonic mollusks", "cnidarians", "ctenophores", "appendicularians", "siphonophores", "salps", "chaetognaths", "crustaceans", "amphipods", "euphausiids", "decapods", "ostracods", "crabs", "shrimps", "foraminifera", "rotifers", "Southern Gulf of Mexico", "Gulf of Mexico".

More than 250 works, including research articles, short communications, book chapters, technical reports, and conference papers, were recovered as a result of the search. These were individually analyzed, with repeated materials being discarded. The review primarily focused on scientific articles published in indexed journals with impact factors. However, this review also considered relevant works from "gray literature" (e.g. graduate and undergraduate theses, articles, and chapter books with local distribution, as well as Mexican workshop booklets) due to their potential to provide valuable insights that may not be found in traditional sources. These materials were retrieved from local repositories, including the UNAM, the National Commission for the Knowledge and Use of Biodiversity (CONABIO, by its Spanish acronym), the Metropolitan Autonomous University (UAM, by its Spanish acronym), and the National Polytechnic Institute (IPN, by its Spanish acronym), among others.

This review contributes to the understanding of zooplankton dynamics in the southern GoM. It highlights the need to continue multidisciplinary research on these key organisms in any ecosystem that is threatened by numerous circumstances. Currently, the Earth's climate system, including the GoM, is experiencing very severe changes that have negatively impacted biological diversity. To date, there is compelling scientific evidence that the GoM is under serious threat, including warming trends (Wang et al. 2023), deoxygenation scenarios in the northern gulf (Rabalais & Turner 2019), and fluctuations in pH levels that have led to acidification (Lunden et al. 2014). They have a significant impact on the life cycles of numerous zooplankton species. For example, while jellyfish are organisms sensitive to increasing temperatures (Enrique-Navarro et al. 2021), pteropods are extremely sensitive to changes in seawater pH (Wall-Palmer et al. 2021). In this context, multidisciplinary research becomes necessary.

Research trends on marine zooplankton in the southern GoM

The literature search for this review underscored the importance of focusing on underrepresented groups of zooplankton. While certain groups, such as copepods and fish larvae, have received significant attention, other groups, like decapods and doliolids, have been largely neglected (Fig. 2).

In the following sections, we provide a brief review of research published on specific zooplankton groups.

Copepods

Copepods are the most conspicuous zooplankton organisms and probably the most abundant crustaceans on Earth (Mauchline et al. 1998). Due to their notable contribution to the export of carbon and organic matter to the ocean interior, they have attracted the attention of numerous researchers worldwide.

The literature on the GoM is rich with early studies dating back to the 1950s and primarily focused on the northern region. Pioneering works by Davis (1950) and Fleminger (1956) were among the first to highlight the numerical importance of copepods in this area. Subsequent studies by Park (1970), Bjonrberg (1971), and Park (1975) furthered our understanding of copepod populations.

In the Mexican waters of the GoM, the study of Aguayo-Saviñon (1966) was a pivotal moment for copepod research. Her report on 22 species of calanoid copepods in the coastal waters off Veracruz not only recognized the numerical and ecological importance of these organisms but also laid the foundation for future research in oceanic waters.

Due to the Cuban-Russian expeditions in the 1960s, several samples were collected in the oceanic waters of the southern GoM. These samples were used to identify different zooplankton groups, including copepods. Six genera and 43 species were documented initially (De la Cruz 1971).

In the late 1970s and early 1980s, the Mexican Navy conducted a series of research cruises in Mexican waters of the GoM. These cruises covered more than 400 sampling sites in 11 expeditions, including the Yucatan shelf and the central and southern portions of the gulf, which were conducted in different climatic seasons. These cruises revealed that copepods comprise more than 50% of the total zooplankton density (Almazán et al. 2022).

In the 1980s, the field of copepods witnessed a significant evolution. Campos (1980) compiled one of the first faunistic lists, identifying 108 species and highlighting the distinctions between the populations in the gulf and those in the Caribbean Sea. By the end of this decade, the faunistic lists were rapidly expanding thanks to the work of Suárez-Morales & Gasca (1989), who identified 82 species from the Yucatan region. Suárez-Morales (1989) also contributed to this growth with his illustrations of these groups.

The taxonomic list of copepods increased at the beginning of the 1990s. In the Campeche Bank region, 113 species were reported, a significant number of which were found to be closely related to upwelling zones (Suárez-Morales 1990). In the western part of the gulf, 101 species were reported, whose horizontal distribution was found to be strongly related to changes in depth between the platform and oceanic waters (Suárez-Morales et al. 1990). Some years later, Suárez-Morales (1992a) compiled a list of 107 species of calanoid copepods from samples collected at 114 sites across different regions of the gulf. These sites encom-

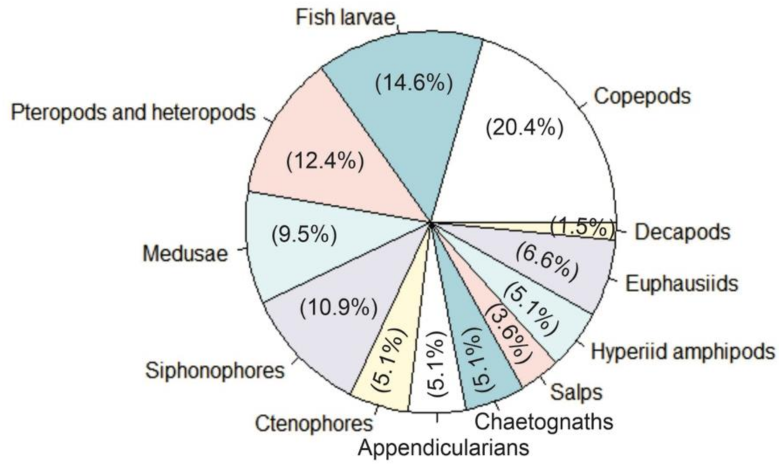

Figure 2. Research trends on marine zooplankton in the southern Gulf of Mexico (until August 2024). The figure highlights the need to focus research efforts on some zooplankton groups. The contribution of the studies for each group is indicated in percentage.

passed coastal areas, continental shelf regions, and deep waters. Due to the extensive spatial coverage, the study examined biogeographical affinities, revealing that 82% of species have a tropical affinity. It was in this decade that the first identification keys for species from the GoM appeared, marking a significant advance in copepod research (e.g. Campos & Suárez-Morales 1993, 1995), and the number of publications that included illustrated descriptions increased, further enhancing the understanding of this group (e.g. Suárez-Morales 1991a,b).

Subsequently, based on the analysis of a large number of samples (170 samples) collected in three oceanographic cruises, Suarez-Morales (1992b) provided a taxonomic list that increased the knowledge of copepods by identifying 150 species belonging to 27 families and 43 genera of the three main orders of copepods: Calanoida, Cyclopoida, and Harpacticoida.

In the late 1990s and early 2000s, a new wave of research emerged in the scientific literature, introducing a novel perspective that linked the surface and subsurface circulation patterns of the GoM to zooplankton organisms, a departure from the previously documented circulation pattern of the GoM by numerous authors (e.g. Biggs 1992, Monreal-Gómez et al. 1992, Salas de León et al. 1992, Vidal et al. 1992, among others). One of the pioneering works was that of Biggs et al. (1997), who identified that the presence of a cold-core cyclonic eddy determined the distribution, composition, and abundance of microcrustaceans, including euphausiids. In the western part of the GoM, López-Salgado et al. (2000) studied the pelagic copepod community and its connection to the circulation pattern. They identified 106 copepod species whose density was concentrated in the center of a mesoscale cyclonic eddy.

Over the past decade, the knowledge of copepods in the southern GoM has greatly improved, including the discovery of new genera (Suárez-Morales & Almeyda-Artigas 2015), studies conducted in previously overlooked areas such as reefs (Cházaro-Olvera et al. 2019), and an increase in multidisciplinary research. Indeed, the study by Almazán et al. (2022) used historical data to identify the role of mesoscale processes, particularly eddies, in the distribution and composition of zooplankton, including copepods; these eddies contribute to fertilizing the euphotic zone, benefiting phytoplankton and leading to an increase in the abundance of herbivorous and filter-feeding zooplankton, such as some copepods. More recently, Gaona-Hernández et al. (2024) have conducted a comprehensive analysis of the role of hydrography and the circulation pattern of the southern GoM in shaping calanoid copepod communities. The study documented a total of 117 species, each with a unique and dynamic horizontal distribution pattern influenced by physical factors. Notably, the Bay of Campeche, due to its unique physical dynamics, has emerged as a region of paramount importance, exhibiting the highest biomass and abundance values, with over 140,000 ind per 1,000 m^3. These findings not only enhance our understanding of copepod communities in the gulf but also pave the way for future research, inspiring new investigations.

Fish larvae

Due to the signing of international agreements to carry out larval censuses of species of marine and fishery resources (e.g. the Cooperative Investigations of the Caribbean and Adjacent Regions (CICAR) and the MEXUS-GULF), much of the existing research in the GoM has focused on fish larvae or ichthyoplankton (Fagetti 1975, Richards 1987). Understanding ichthyoplankton, which includes eggs and fish larvae found in near-surface waters (upper 200 m) (Moser 1996), is a crucial aspect in the gulf, not only because represents the most critical stage of development in the life cycle of fish, but its study is crucial for the management and conservation of fisheries, many of them of high commercial value, which represent a source of food for human populations (Syahailatua et al. 2024).

Research on fish larvae in the GoM dates back to the 1970s-1980s and has been crucial in understanding several aspects, such as composition, abundance, and distribution patterns. Initially focused on coastal lagoons such as Tamiahua, Alvarado, and Terminos, along with their adjacent areas (e.g. Álvarez-Cadena 1978, Flores-Coto et al. 1983, Flores-Coto 1987, Sánchez-Velasco et al. 1996), the studies later expanded to include oceanic waters, marking a significant advancement in ichthyoplankton research.

In the oceanic waters of the GoM, early studies conducted onboard ships of the Mexican Navy reported a remarkable diversity. Of the 65 families identified, Gobiidae, Clupeidae, Scombridae, Engraulidae, and Myctophidae stood out for their abundance, showcasing the richness of this group (Ayala-Duval 1980).

As mentioned above, the arrival of the R/V Justo Sierra in Mexico enabled the expansion of ichthyoplankton studies to blue waters, leading to the implementation of more regular monitoring programs. These programs have resulted in taxonomic lists that include 306 species, distributed across 283 genera and 120 families (Flores-Coto et al. 2009).

Studies carried out in the southern GoM allowed the identification and definition of three main ichthyoplankton communities called (1) neritic-coastal, (2) neritic and (3) oceanic; (1) includes species with a life cycle linked to lagoon and estuarine systems, environments that are used as feeding and spawning sites, (2) is characterized by including species that do not enter coastal regions and adults generally spawn in neritic waters, and (3) includes species whose adults live in mesopelagic waters (Flores-Coto et al. 1988, 1991, 1993, Flores-Coto & Sánchez-Ramírez 1989, Sanvicente-Añorve et al. 1998).

Since the late 1990s, multidisciplinary works focused on understanding hydrographic variables and those physical processes that influence ichthyoplankton communities began to appear in the scientific literature, identifying that tides, wind-induced currents, salinity gradients derived from the contribution of fresh water to the coastal zone, the mixing processes and the presence of eddies are the processes that have the greatest influence on the composition, distribution, and abundance of these organisms (Salas-de-León et al. 1998, Sanvicente-Añorve et al. 2000).

Subsequently, the effect that freshwater discharges (particularly from the Grijalva-Usumacinta river system) have on ichthyoplankton communities was addressed by different authors. For example, Flores-Coto et al. (2000) documented that species from the Engraulidae and Gobiidae families tend to be more abundant near the river mouth, a phenomenon intricately linked to the complex interplay of salinity and density gradients. The authors also noted that throughout the year, there are differences in species abundances depending on the freshwater discharge to the GoM. Some years later, some authors confirmed the seasonal variability of ichthyoplankton based on the discharge of freshwater by the Grijalva-Usumacinta, which fluctuates throughout the year, affecting not only the species composition but also zooplankton biomass (Espinosa-Fuentes & Flores-Coto 2003, Espinosa-Fuentes et al. 2009).

In recent years, a growing body of multidisciplinary research has emerged in the scientific literature, focusing on the role of circulation patterns and the presence of eddies in fish larvae. It has been documented that the presence of cyclonic and anticyclonic eddies in the gulf is crucial for the advection of fish larvae from coastal to oceanic areas (Compaire et al. 2021). Additionally, it has been recently documented that in the Bay of Campeche, the larval fish assemblage is closely related to the cyclonic circulation of the region, which induces high larval abundance values of more than 1,500 ind per 1,000 m^3 (Echeverri-García et al. 2022). Furthermore, it has been documented that the density of some species is higher in regions with high concentrations of nutrients and chlorophyll-*a* (indicative of food availability), which in turn is directly related to the presence of cyclonic eddies (Daudén-Bengoa et al. 2023).

Holoplanktonic mollusks

Pteropods and Pterotrachoidea (heteropods)

Pteropods and Pterotrachoidea (commonly referred to as heteropods) are two distinct zooplankton groups that are highly relevant in any marine ecosystem due to their roles in carbon sequestration and energy transfer along trophic webs (López-Cabello et al. 2022). Currently, these organisms (particularly pteropods) are seriously threatened by anthropogenic pressure that alters marine ecosystems. For example, fluctuations in seawater pH levels resulting from increased CO_2 emissions pose a serious threat to their calcification rates (Mekkes et al. 2021).

The study of these groups in the southern GoM dates back to the 1960s with the work of Leal-Rodríguez (1965), who provided the first taxonomic lists of the pteropods of the coastal region of Veracruz. Due to the subsequent Cuban-Soviet expeditions in the southern GoM, the knowledge on these organisms increased considerably since the investigations considered hydrographic aspects (e.g. Jromov 1965, 1967, Bogdanov 1968).

In the 1970s, international cooperation projects, such as CICAR, led to research cruises being conducted on board Mexican Navy ships. These cruises significantly advanced the understanding of these groups. Indeed, in the Bay of Campeche, the initial taxonomic lists identified 20 species of pteropods, with the *Creseis* genus being the most abundant (Matsubara-Oda 1975).

Subsequent research on pteropods has documented up to 51 species (Suárez-Morales 1994), with significant seasonal variability. For instance, during the coldest months of the year (January), 15 species have been reported (Suárez & Gasca 1992), in August have been reported 18 species (Flores-Coto et al. 2013), 27 species in May and November (Lemus-Santana et al. 2014a), 29 species in June (López-Arellanes et al. 2018), and 18 species in February (López-Cabello et al. 2022), with new records recently reported in the Campeche Canyon region (López-Cabello et al. 2024). Besides, some studies have identified that the vertical distribution of these organisms is highly heterogeneous. At the same time, species of the genera *Cavolinia* and *Diacavolinia* inhabit the surface layer (between 0 and 18 m deep). In comparison, species of the genera *Diacria* and *Clio* tend to be more abundant at depths between 45 and 105 m (Sanvicente-Añorve et al. 2013).

Regarding heteropods, some studies have documented 14 species in May and November (Lemus-Santana et al. 2014b), 14 species in June (Espinosa-Balvanera 2017), 4 species in July (Castellanos & Suárez-Morales 2001), and 3 species in February ("Nortes" season) (López-Cabello et al. 2024). In all cases, *Oxygyrus*, *Atlanta*, and *Firoloida* have been reported as the most conspicuous genera.

Gelatinous zooplankton

A zooplanktonic organism is considered gelatinous when its water content is greater than 80% (Larson 1986). Then, numerous groups of organisms correspond to this category. In the GoM, this group of organisms has been the focus of numerous investigations that have addressed aspects of its composition, distribution, and abundance, as well as genetic aspects, more recently.

Medusae

As with research on copepods, research on medusae in the northern GoM is vast, but in Mexican waters, there is a smaller proportion.

Research on medusae in the southern GoM dates back to the study of Alvariño (1972), who documented some species not only from the region but also from adjacent seas such as the Caribbean.

The 1990s marked a significant increase in medusae research in the southern gulf. By this time, 43 species of Hydromedusae and 2 species of Scyphomedusae from the Yucatan shelf region had been documented, with species of the genera *Aglaura* and *Nausithoe* being the most representative (Segura-Puertas 1992). Later, 63 species of Hydromedusae belonging to 3 orders and 25 families were documented in the deep region of the GoM for the spring and summer seasons (Valenca-Correia 1992). Particularly in the Campeche Bank, 48 species of Hydromedusae and 7 species of Scyphomedusae were documented (Segura-Puertas & Ordoñez-López 1994). At this time, new records for Mexican waters of the GoM were included (Valenca-Correia & Segura-Puertas 1995).

In the early 2000s, the first checklist of medusae (Hydrozoa, Scyphozoa, and Cubozoa) for Mexican waters was published, listing a total of 75 species for the GoM (Segura-Puertas et al. 2003). In this decade, research on this group has advanced through a collaborative, multidisciplinary effort involving environmental aspects. For example, 12 species of jellyfish were documented across a cold-core eddy (Suárez-Morales et al. 2002), and 38 species were reported in the southern GoM, their distribution pattern influenced by the oceanic circulation pattern that occurs on the continental shelf (Loman-Ramos et al. 2007). Additionally, a comprehensive review of the group was published (Segura-Puertas et al. 2009). The latest update was subsequently presented, accounting for 167 species (Gasca & Loman-Ramos 2014).

In recent years, knowledge about this group has increased considerably, and it is now more common to find multidisciplinary studies in the literature. Martell-Hernández et al. (2014) reported 68 species of medusae, whose horizontal distribution presented different zonations based on hydrographic aspects, including the surface circulation pattern and the discharge of freshwater from the Grijalva-Usumacinta system. Additionally, during the dry season (May-June), 42 species of medusae (40 Hydrozoa and 2 Scyphozoa) have been documented, whose distribution is primarily influenced by temperature and the discharge of freshwater into the gulf (Puente-Tapia et al. 2022). Similar observations were presented more recently for the western region of the gulf (off Tuxpan, Veracruz), where the composition of medusae seems to be controlled by temperature (López-Torres et al. 2023).

Siphonophores

The faunal composition of the siphonophores of the southern GoM is relatively well-defined (Gasca & Suárez 1989a).

The work of Alvariño (1972) was a significant advance, as it highlighted the numerical importance of siphonophores and provided the first taxonomic list, enumerating a total of 25 species from both the gulf and the Caribbean Sea followed by a more specific taxonomic list for the southern gulf, which listed 22 species (Vasiliev 1974).

Later, works appeared on the Yucatan shelf that related the richness and abundance of siphonophores with the upwelling that occurs in this region, showing that the distribution of the species is closely related to this fertilization process (Gasca & Suárez-Morales 1989b, Gasca & Suárez 1991). A few years later, taxonomic lists were published that increased the number of species from 31 to 33 (Gasca 1990, 1993), with species of the genera *Diphyes*, *Abylopsis*, *Eudoxoides*, and *Chelophyes* being the most abundant. Also, new records of different species for the GoM region were presented (Suárez-Morales 1992c).

By the late 1990s and early 2000s, studies began to emerge that linked the environmental variability and oceanographic conditions of the GoM with the richness of siphonophores (e.g. Gasca 1998, Suárez-Morales et al. 2002). Among them, these multidisciplinary studies aimed to understand the role of mesoscale eddies in the composition, distribution, and abundance of this group, revealing that the abundance of some of the 31 recorded species was higher in the area influenced by the cyclonic eddy (Gasca 1999).

A few years later, comprehensive reviews of the group appeared, summarizing existing research in Mexican waters, including the GoM (Gasca 2002). Taxonomic lists also appeared, accounting for 82 species for the entire gulf (Pugh & Gasca 2009). Besides, similar to what occurs with other zooplankton groups, it has been identified that in the southern portion of the gulf, siphonophores are closely related to the discharge of freshwater from the Grijalva-Usumacinta system, which generates fluctuations of more than seven ups in salinity levels, which in turn generates changes in the distribution of species (Sanvicente-Añorve et al. 2007, 2009).

Ctenophores

Ctenophores are a group of exclusively marine organisms that are usually a very numerous component of zooplankton (Mianzan et al. 2009). Although there are numerous studies around the world on this group, very few works have been done in Mexican waters in general and in the GoM in particular.

Initially, studies on this group in GoM waters were restricted to coastal lagoons of Veracruz (e.g. Gómez-Aguirre 1977, Esquivel et al. 1980); despite this, these works identified its importance.

Subsequently, work began to appear in oceanic waters; however, these have been fragmented. For example, in the western part of the gulf (off Tamaulipas), the work of Biggs et al. (1984) documented some species of ctenophores, with the genus *Beroe* as the most abundant. In the coastal waters off Veracruz, some works documented species belonging to three genera (*Beroe*, *Pleurobrachia*, and *Mnemiopsis*) as the most abundant (Ruíz-Guerrero & López-Portillo 2006). Subsequently, a checklist for the entire gulf was presented, which includes a total of 18 species of ctenophores, comprising 14 species belonging to the class Tentaculata and 4 species of the class Nuda, distributed in a depth range from the surface to more than 700 m (Moss 2009). More recently, an updated checklist for the southern gulf was presented by Puente-Tapia et al. (2021), which accounts for 12 species, including the latest new records for the region reported by Ocaña-Luna et al. (2017).

Appendicularians

Appendicularians, a crucial group within marine zooplankton, play a significant role as indicators of environmental change. Their sensitivity to these changes has led to their use as proxies of water masses and as indicators of waters with high nutrient concentrations (Esnal 1999).

Studies on this group in the southern GoM are scarce. One of the first works was that of Flores-Coto (1974), who reported 20 species in the coastal waters of the western GoM. After a gap of more than 20 years without a report on this group, Escamilla-Sanchez (1996) work documented three species of the genus *Oikopleura* from the Yucatan shelf. By the end of 1990, a key was presented for identifying this group, including species of the GoM (Castellanos & Gasca 1998). Subsequently, with samples collected at 24 sites near the Grijalva-Usumacinta River and in the Campeche Canyon region, 13 species belonging to the genera *Oikopleura*, *Stegosoma*, and *Fritillaria* were documented (Campos-Torres 2005). By the end of the 2000s, a checklist of this group was presented, accounting for 23 species restricted to epipelagic layers (0-200 m) (Castellanos & Suárez-Morales 2009).

Only a few studies have delved into the distribution and diversity of appendicularians in the waters of the southern GoM concerning environmental factors. These studies have documented 20 species, with a high abundance of organisms of the genus *Fritillaria*. The distribution of *Fritillaria* is notably influenced by changes in salinity levels resulting from continental water discharge, the temperature regime, and the presence of eddies (Flores-Coto et al. 2010a). Similarly, the highest densities of *Oikopleura* species have been linked to upwelling waters on the Yucatan shelf (Flores-Coto et al. 2010b).

Chaetognaths

The study of this group in the southern GoM dates back to the 1960s, with the work of Vega-Rodríguez (1965), who documented the chaetognaths community in the vicinity of the Veracruz reef system in different months (November, January, and March) and provided a taxonomic list of nine species.

Studies on the Campeche Bank and the Yucatan shelf have documented up to 12 species of chaetognaths, with *Flaccisagitta enflata* being the most abundant (Rivero-Beltrán 1975, Mille-Pagaza et al. 1997, Mille-Pagaza & Carrillo-Laguna 1999).

Comprehensive studies carried out in the southern GoM, off the mouth of the Grijalva-Usumacinta system, have documented a total of 11 species. These studies have revealed that the horizontal distribution of these species is related to the salinity gradient generated by the freshwater discharge (González-Flores 2005). On the Tamaulipas shelf, 13 species have been documented (Mille-Pagaza & Carillo-Laguna 2003), while 17 species have been reported on the coasts off Veracruz (Sierra-Zapata 2021). Once again, *F. enflata* was reported as the most abundant species.

Salps

The composition of salps along the southern GoM is a topic that still holds many mysteries, as this group remains among the less studied despite being conspicuous members of the gelatinous zooplankton (Hereu & Suárez-Morales 2012).

One of the first taxonomic lists of this group was presented by Esnal (1979), who reported 11 species forming dense aggregations over the Campeche Bank and the Yucatan shelf. It took many years for a new checklist to appear until Cole & Lambert (2009) reported only 5 species.

Some years later, it was noticed that salps usually generate blooms that considerably increase the zooplankton biomass in the southern GoM during the summer in association with the high precipitation that occurs during this time of year (Färber-Lorda et al. 2019). More recently, Hereu et al. (2020) reported a total of 10 species of salps from samples collected in the southern gulf, including its deepest portion. Notably, the study found that the species richness and abundance were low in regions influenced by anticyclonic eddies.

Other crustaceans

Hyperiid amphipods

Hyperiid amphipods are pelagic crustaceans distributed throughout the water column, ranging from bathypelagic depths (1,000-4,000 m) to the surface layers (Vinogradov 1999).

After copepods, this group has received relatively good attention in the southern GoM.

It is currently known that this community has a high richness of species whose numerical value changes depending on the time of year and is closely related to the circulation patterns that occur in the gulf. For example, in winter, the number of species documented ranges from 39 (Manzanilla-Domínguez 2006) to 56 (Gasca 2003a), whose horizontal distribution depends on the presence of cold-core eddies; these features induce a higher abundance of the species towards the center. In spring, 79 species have been reported (Gasca 2003b), while in summer, the number of documented species ranges from 56 (Hereu et al. 2020) to 57 (Gasca et al. 2009) and up to 71 (Gasca 2004). Likewise, the presence of cyclonic eddies strongly determines the abundance and distribution of species. To date, new records continue to be reported, and research on this group has expanded to regions where coverage was limited (Sanvicente-Añorve et al. 2023).

Euphausiids

Euphausiids are another group of crustaceans that have received relatively good attention from researchers. Pioneering works have shown the role that the hydrography of the southern gulf plays in the composition and distribution of this group (e.g. Herrera-Castillo & Martínez-López 1992). The above was confirmed some years later by the work of Biggs et al. (1997), who, following the trajectory of a mesoscale cyclonic eddy, documented changes in the composition and abundance of species between the center and the periphery of the eddy. During this time, taxonomic lists were reported that included 11 species (Castellanos & Gasca 1996), 21 species (Castellanos & Gasca 1999), and up to 31 species (Brinton 1996), with the genera *Stylocheiron* and *Euphausia* being the most conspicuous.

Some years later, the taxonomic lists of this group were documented from 17 species (Gasca et al. 2001) to 34 species (Castellanos & Suárez-Morales 2002a,b). More recently, studies conducted in the Campeche Canyon region reported 24 species whose horizontal and vertical distribution was strongly influenced by the presence of a thermohaline front induced by a dipole eddy (cyclone-anticyclone) (Arriola-Pizano et al. 2022).

Decapods

Although luciferid shrimp species (Decapoda: Luciferidae) play a significant role in the holoplanktonic community and often dominate the zooplankton in the epipelagic waters of the global ocean (Xu 2010), limited research exists on this group in the southern GoM.

A few studies have examined the ecological aspects of certain species in this group in the coastal regions of Veracruz, revealing that the highest biomass occurs at the end of winter and the beginning of spring (Cházaro-Olvera et al. 2017). More recently, ecological aspects of two species (*Belzebub faxoni* and *Lucifer typus*) off Tamaulipas indicated that the reproduction of both species occurs throughout the year, with a peak during summer, and noticed that while *B. faxoni* is restricted to shallow waters where food resources are abundant, *L. typus*, on the other hand, tends to be more abundant in oceanic waters with stable salinity levels (Sanvicente-Añorve et al. 2021).

Final remarks

As can be seen, research on zooplankton in the southern GoM is vast and diverse, with a history dating back to the 1960s. Research has increased over the last decade, and more robust works involving different disciplines are currently being presented, which has helped considerably not only to document species richness but also to interpret their distribution patterns. However, due to the changing conditions of the region and the threats that the GoM faces, numerous challenges arise in research.

Climate change, a consequence of human activities, has become a pressing global concern. The rapid increase in CO_2 emissions is causing significant changes in the physicochemical conditions of the water column, leading to fluctuations in acidity levels. As mentioned earlier, holoplanktonic mollusks (pteropods and heteropods) are highly sensitive to these pH changes due to their fragile aragonite shells. The documented pH level shifts in GoM waters over the past decade highlight the potential loss of these organisms, urging us to take responsibility for our actions. For example, scientific evidence indicates that the net calcification of some coral colonies in the GoM is significantly declining (Lunden et al. 2014). Unfortunately, to our knowledge, no studies have assessed the impact of acidification on zooplankton organisms in general, and holoplanktonic mollusks in particular.

Another environmental issue caused by human activities in the GoM is the fluctuation in dissolved oxygen levels. Recent research has shown that eutrophication has increased, and oxygen concentrations have declined over the past twenty years in the southern gulf (Machaín-Castillo et al. 2020). The effects of deoxygenation in GoM waters on zooplankton populations remain a mystery. However, in other parts of the world, such as the Pacific Ocean, there is strong evidence showing that as oxygen levels decline, the biomass of several zooplankton taxa, including copepods, euphausiids, and fish larvae, also decreases (Wishner et al. 2018, Färber-Lorda & Färber-Data 2023). Furthermore, particularly in copepod populations in the eastern tropical North Pacific, it has been documented that deoxygenation levels impact both the life cycle of these organisms and their nychthemeral vertical migration patterns (Fernández-Álamo & Färber-Lorda 2006, Wishner et al. 2020).

Another of the most pressing threats from the GoM is plastic pollution. When subjected to chemical and mechanical degradation, it forms microplastics (MP) ~5 mm in diameter. These tiny particles, due to their resemblance to natural food, are consumed by a wide variety of marine organisms, including zooplankton (Auta et al. 2017, Chassignet et al. 2021). The research on the ingestion of MP by marine zooplankton, especially copepods, is gaining momentum owing to its importance in healthy ecosystems. Numerous reports in the literature confirm the ingestion of MP by copepods in several regions, including the Atlantic Ocean (Cole et al. 2013), the Mediterranean Sea (Costa et al. 2020), and the Yellow Sea (Zheng et al. 2021). In all cases, serious effects have been reported, including alterations in their life cycle and impacts on their feeding and escape strategies.

Furthermore, the transfer of MP through the food chain poses a threat not only to marine life but also to human health. However, in the waters of the southern GoM, these types of studies are practically nonexistent and are limited to coastal water bodies. For example, it was recently documented that copepods in the Terminos Lagoon ingest a considerable amount of MP of different types, including fragments, microspheres, and fibers in a higher proportion of up to 85%; it was also reported that there are changes in ingestion depending on the time of year, being higher during the dry season due to the lower rivers discharge, so MP tend to accumulate and thus be more available for consumption by copepods (Montoya-Melgoza et al. 2024). This research underscores the need for further investigation into the impact of microplastic ingestion on copepods and the potential implications for the wider marine ecosystem.

The importance of the GoM as one of the most dynamic ecosystems in the world was noted many years ago. To date, the importance of a continuing monitoring program will yield important results. The long-term sampling will provide a comprehensive view of the system's dynamics, thereby increasing the value of the database each year as the data accumulate and refine the dynamic properties of the zooplankton communities. Then, by directing our research towards these underrepresented groups, we can gain a more holistic understanding of the GoM Large Marine Ecosystem.

Credit author contribution

E. Coria-Monter: conceptualization, methodology, formal analysis, writing-original draft, review and editing; E. Durán-Campos: conceptualization, methodology, formal analysis, writing-original draft, review and editing. Both authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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