



The holoplanktonic mollusks (Pteropoda and Pterotracheoidea) in surface waters of the Campeche Canyon (southern Gulf of Mexico) during a winter storm (“Nortes”) season

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Abstract. The holoplanktonic mollusks (Mollusca, Pteropoda and Pterotracheoidea) are independent and key groups of organisms in any marine ecosystem due to the role they play in the carbon and energy transfer along the marine trophic webs. We document the species of holoplanktonic mollusks collected in the surface waters (10 m depth) during an oceanographic expedition in the Campeche Canyon, southern Gulf of Mexico, during the February 2011 winter storm (“Nortes”) season. Organisms were collected using a close/open/close net system. Eighteen species belonging to 12 genera and nine families of pteropods were identified. Three species of Pterotracheoidea were identified. *Limacina trochiformis* (d’Orbigny, 1835), *Heliconoides inflatus* (d’Orbigny, 1835), and *Creseis conica* (Eschscholtz, 1829) were the species with highest density values (600.3, 678.5, and 746.8 ind · 100 m⁻³, respectively). The results presented here contribute to the knowledge of this group of organisms in oceanic waters of the southern Gulf of Mexico, especially during a time of year where observations are scarce.

Keywords. Gulf of Mexico, Nortes season, marine zooplankton, species diversity, planktonic gastropods

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Introduction

Zooplankton includes a heterogeneous and diverse heterotrophic group of organisms distributed along the water column in worldwide oceans and these organisms play a pivotal role in the sequestration, capture, and sinking of carbon towards the interior and bottom of the oceans (Brierley 2017).

As part of the marine zooplankton communities, the holoplanktonic mollusks Pteropoda and Pterotracheoidea (commonly named as heteropods or sea elephants)

are two independent and key groups in all marine ecosystems due to the role they play in the carbon and energy transfer along marine trophic webs (Lalli and Gilmer 1989; Burridge et al. 2017). These organisms constitute a direct link between the primary consumers and the organisms located at the lowest trophic levels mainly because they have diverse feeding habits (herbivores, omnivores, or carnivores) (Vaske et al. 2012; Wall-Palmer et al. 2016). Also, due to their size (0.5–5 mm), they are attractive prey for organisms of higher trophic levels, such as fishes, marine turtles, and even whales

(Lalli and Gilmer 1989; Moreno-Alcántara et al. 2017). These complex interactions allow these organisms to contribute significantly to the carbon flux throughout the water column, which also helps to the correct functioning of the biological/carbon pump (Le Quéré et al. 2005). Besides, they are important due to their contribution to the carbon cycle through developing shells rich in aragonite, which is useful as an indicator of water masses and in studies of marine sediments (Wall-Palmer et al. 2016; Peijnenburg et al. 2020). Pteropoda and Pterotrachoidea are protandrous hermaphrodites, with a reproductive system where individuals mature as males, but later may reproduce as females. This makes the identification of sex complex, and additionally the reproductive organs are located inside their aragonite shells (Lalli and Gilmer 1989).

In the last decade, studies on the holoplanktonic mollusks of the southern Gulf of Mexico have shown that these organisms are keystone species in the pelagic ecosystem, where they occur in high densities and high species richness. For example, Sanvicente-Añorve et al. (2013) analyzed the vertical distribution of five genera of holoplanktonic mollusks (*Cavolinia*, *Diacavolinia*, *Diacria*, *Oxygyrus*, and *Clio*) based on zooplankton samples collected in neritic waters of the southern gulf during May and November. They reported that juveniles of *Cavolinia*, *Diacavolinia*, and *Oxygyrus* inhabit the surface layer between the surface and depths of 18 m, while *Diacria* and *Clio* were more abundant at 45–105 m deep. Lemus-Santana et al. (2014a, 2014b) identified 14 species of heteropods and 27 species of pteropods in samples collected in the neritic epipelagic layer of the southern Gulf of Mexico during May and November. More recently, López-Arellanes et al. (2018) recorded more than 30 species of pteropods in 136 oblique hauls with Bongo nets done in the shelf waters of the southern Gulf of Mexico during 2006 and 2010 springs, which showed a high abundance in the neritic zone influenced by river discharges. These studies so far made possible to advance in the knowledge of these organisms. However, most studies have focused on the neritic zone (<200 m in depth) and mainly during the warmest months of the year, from May to August. Therefore, there are gaps in the knowledge of the community structure of these organisms in the deep waters of the Gulf of Mexico as well as during the coldest months of the year.

We present the composition of holoplanktonic mollusks (Pteropoda and Pterotrachoidea), both shelled and unshelled, in waters of the Campeche Canyon, southern Gulf of Mexico, during February in the Nortes season. To the best of our knowledge, these results represent the first observational report of these organisms in the Campeche Canyon in a season when winds and waves are extreme and which make sampling activities challenging. Our objective is to add to the knowledge on the diversity of these groups of organisms; this can help advance our understanding of the Gulf of Mexico, which is recognized as a “large marine ecosystem” (a

region of the world’s oceans characterized by distinct bathymetry, hydrography, and high productivity levels following Sherman and Hempel 2009) and contribute to actions for better management strategies of the Gulf. This is certainly relevant nowadays when there is an increasing deterioration trend of marine ecosystems as a result of anthropogenic pressures. Among them, deoxygenation and acidification scenarios in the Gulf of Mexico (Lunden et al. 2014) represent a potential risk for these groups of organisms mainly affecting the calcification of their fragile aragonite shells (Mekkes et al. 2021; Wall-Palmer et al. 2021). Therefore, studies that document the holoplanktonic mollusks communities are necessary. The list presented here also represents a valuable dataset addition to the holoplanktonic mollusks of southern Gulf of Mexico, in particular for the oceanic waters.

Study Area

The Gulf of Mexico is a marginal sea located in the North American Continent between 18–30°N and 84–100°W (Fig. 1, top panel). It is an ecosystem recognized for its high biological diversity, which supports a wide variety of species of high ecological and commercial value. This is one of the reasons why it has been included in the list of the large marine ecosystems of the world (Sherman and Hempel 2009).

The Campeche Canyon in the southern Gulf of Mexico is a distinctive geomorphic feature of tectonic origin with depths greater than 2500 m (Goff et al. 2016) (Fig. 1, bottom panel). The region is highly dynamic, where the confluence of different oceanographic processes at different scales (e.g., internal waves, eddies, fronts, among others) exerts a significant influence on the mixing/stratification conditions of the water column and therefore on the supply of nutrients to the euphotic layer benefiting phytoplankton and subsequently zooplankton communities (Santiago-Arce and Salas de León 2012; Durán-Campos et al. 2017).

In climatic terms, three seasons characterize the southern Gulf of Mexico, the dry season from March to May, the rainy season from June to October, and the winter storms season, locally called “Nortes” season, from November to February. In this period, extreme and persistent northerly winds occur (>80 km/h), which exert an important influence on the hydrographic conditions of the water column (Ojeda et al. 2017). During the summer, the surface temperature in the Campeche Canyon is ~30 °C, and the thermocline is located at approximately 40 m deep (Durán-Campos et al. 2017), while in winter, the surface temperature is ~24 °C and the thermocline deepens to ~100 m (Arriola-Pizano et al. 2022).

Methods

Sampling. An oceanographic expedition (CAÑON-IV) was carried during the Nortes season of 2011 (February 22–27) on board the R/V Justo Sierra owned by the National Autonomous University of Mexico (UNAM,

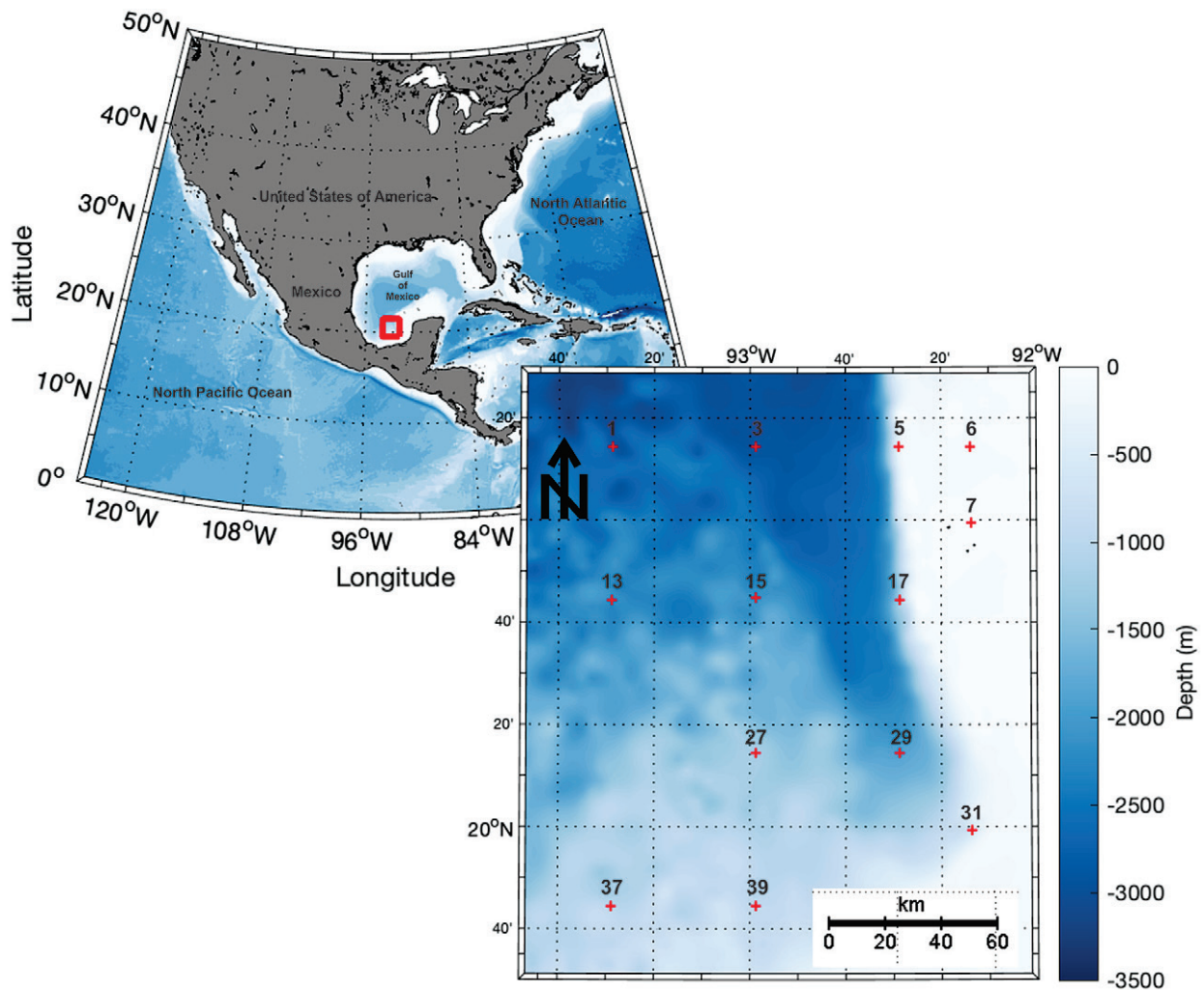


Figure 1. The Gulf of Mexico (top panel), the red rectangle shows the sampling site. The Campeche Canyon (bottom panel), + symbols represent the sampling localities (stations). The bathymetry is shown in meters.

Spanish acronym). During this period, zooplankton organisms were collected in a grid of 13 localities (stations) in the Campeche Canyon (Fig. 1, red “+” symbols in the bottom panel). Zooplankton hauls were made (day and night) using a close-open-close net system (General Oceanics) with a conical net (opening diameter 60 cm, 505 μm mesh size) and equipped with a flowmeter (General Oceanics 2030R, calibrated both pre- and post-cruise) located at the mouth. The sampling was done at surface waters, that we considered at 10 m depth, which was determined by calculating the cosine of the wire angle following standard specifications. Once 10 m depth was reached, the net was opened/closed with manual brass messengers at the start and finish of the haul. Each haul lasted 15 min. Once on board, the net was carefully inspected and rinsed with seawater, and the sample collected was fixed with a 4% formaldehyde solution adding sodium borate as a buffer. Afterwards the sample was transferred to glass bottles with a 70% ethanol solution for final preservation in dark conditions.

Laboratory analyses. In the laboratory, the holoplanktonic mollusks (Pteropoda and Pterotracheoidea), both

shelled and unshelled, were picked in a Petri glass dish and observed with a Carl Zeiss Stemi 508 stereomicroscope equipped with a Zeiss Axiocam ERc. The organisms were identified to species, following the keys of Richter and Seapy (1999), Van der Spoel and Dadon (1999), Gasca and Janssen (2014), and Wall-Palmer et al. (2018), compared and confirmed with online open-access databases (e.g. the World Register of Marine Species, the Biodiversity Heritage Library, the Tree of Life web project, and local repositories such as the National Commission for the Knowledge and Use of Biodiversity [CONABIO, Spanish acronym]). The abundance of each species was standardized to density units ($\text{ind} \cdot 100 \text{ m}^{-3}$) following Harris et al. (2000). Finally, the specimens were photographed in different planes and later processed with the Helicon Focus software. Photographs were finally edited with Adobe Photoshop software.

Results

Eighteen species belonging to 12 genus and nine families of pteropods were identified (Table 1). *Limacina trochiformis* (d’Orbigny, 1835), *Heliconoides inflatus* (d’Orbigny, 1835), and *Creseis conica* (Eschscholtz,

Table 1. Density values (ind. · 100 m⁻³) of the holoplanktonic mollusks (Pteropoda and Pterotracheoidea) of the Campeche Canyon (southern Gulf of Mexico) during a winter storm ("Nortes") season in each sampling station (see Fig. 1). Some general information of each site is also included: total depth (m) of each station, latitude, longitude; volume of filtered water (FW; m³) (see details in Methods). Local time (GMT-6).

Station Num	1	3	5	6	7	13	15	17	29	27	31	37	39	Total density (ind. · 100 m ⁻³)
Local Time	23:55	5:35	11:05	13:01	15:00	13:16	11:06	18:10	23:57	19:50	5:10	19:20	0:40	
Depth (m)	2837	2906	661	65	53	2315	2239	1909	1940	1123	77	1195	886	
Latitude °N	21.25	21.25	21.25	21.25	21	20.75	20.76	20.75	20.25	20.25	20	19.75	19.75	
Longitude °W	93.5	93	92.5	92.5	92.25	93.5	93	92.5	92.5	93	92.25	93.5	93.5	
FW (m ³)	224	175	240	72	162	184	196	33	180	148	142	138	148	
PTEROPODA														
<i>Heliconoides inflatus</i> (d'Orbigny, 1835)	9.4	5.1	0.0	0.0	2.5	40.7	0.0	0.0	210.0	4.1	7.7	225.2	173.7	678.6
<i>Limacina trochiformis</i> (d'Orbigny, 1835)	8.5	7.4	22.9	23.5	11.1	67.9	4.1	162.0	33.3	35.2	81.7	125.3	17.5	600.3
<i>Limacina bulimoides</i> (d'Orbigny, 1835)	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	4.1
<i>Limacina lesueurii</i> (d'Orbigny, 1836)	36.2	1.1	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.7	2.1	5.1	1.3	49.9
<i>Cavolinia inflexa inflexa</i> (Lesueur, 1813)	0.0	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.7	2.3
<i>Cavolinia inflexa</i> (Lesueur, 1813)	0.0	1.7	36.2	0.0	3.1	16.3	0.5	82.6	18.8	4.7	41.5	15.9	6.7	228.1
<i>Cavolinia uncinata</i> (d'Orbigny, 1835)	0.9	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	1.4	0.0	4.5
<i>Diavolinia constricta</i> (van der Spoel, Bleeker & Kobayasi, 1993)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	3.4
<i>Diatria danae</i> (van Leyen & van der Spoel, 1982)	3.1	7.4	0.0	0.0	0.0	6.5	0.0	0.0	8.9	1.4	13.4	18.8	3.4	62.9
<i>Creseis acicula</i> (Rang, 1828)	0.9	0.0	0.0	105.0	0.0	5.4	4.1	18.3	16.1	1.4	25.3	36.2	0.7	213.4
<i>Creseis conica</i> (Eschscholtz, 1829)	10.7	9.1	20.4	5.5	19.7	33.7	22.0	52.0	65.4	35.2	138.7	255.7	78.8	746.8
<i>Creseis virgula</i> (Rang, 1828)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	2.0
<i>Hyalocylis striata</i> (Rang, 1828)	1.8	21.7	0.0	0.0	0.0	2.7	0.0	0.0	0.6	4.7	12.0	28.2	0.0	71.7
<i>Styliola subula</i> (Quoy & Gaimard, 1827)	8.1	4.0	0.0	0.0	0.6	2.2	0.0	0.0	0.6	0.0	3.5	3.6	0.0	22.5
<i>Desmopteris papilio</i> (Chun, 1889)	0.4	0.6	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.7	0.0	6.5	0.0	11.0
<i>Peracle reticulata</i> (d'Orbigny, 1835)	2.7	1.1	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.4
<i>Paracione longicaudata</i> (Souleyet, 1852)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.1	1.1	0.0	0.0	0.0	0.0	4.2
<i>Pneumoderma violaceum</i> (d'Orbigny, 1835)	0.0	2.9	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	1.3	5.3
PTEROTRACHEOIDEA														
<i>Oxygyrus inflatus</i> (Benson, 1835)	1.3	0.6	1.2	0.0	0.0	0.5	0.0	3.1	0.6	3.4	2.8	2.9	0.0	16.4
<i>Firoida desmarestii</i> (Lesueur, 1817)	2.7	7.4	0.8	0.0	0.0	3.8	0.0	0.0	0.0	0.0	0.0	1.4	0.7	16.9
<i>Carinaria pseudorugosa</i> (Vayssi�re, 1904)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	2.2	0.0	2.9

1829) were the species with highest density values (600.3, 678.5, and 746.8 ind·100 m⁻³, respectively), while *Creseis virgula* (Rang, 1828) showed the lowest density value (only 2.0 ind·100 m⁻³) (Table 1). Photographs of these organisms are shown in Figure 2.

Pterotracheoidea included three families and three species. *Firoloidea desmarestia* (Lesueur, 1817) was the species with the highest density value (16.8 ind·100 m⁻³), while *Carinaria pseudorugosa* (Vayssière, 1904) was the species with the lowest value (2.8 ind·100 m⁻³) (Table 1). Photographs of these organisms are shown in Figure 3.

Pteropoda

Order Pteropoda Cuvier, 1804

Suborder Euthecosomata Meisenheimer, 1905

Superfamily Cavoliniioidea Gray, 1850 (1815)

Family Cavoliniidae Gray, 1850 (1815)

Hyalocylis striata (Rang, 1828)

Figure 2A

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.24°N, 093.50°W; 10 m depth; 22.II.2011; E. Coria-Monter and E. Durán-Campos leg.; preservation 70% ethanol; CC2011-1.

Identification. Animal to 0.8 cm long, with a transparent, uncoiled, fragile shell. Shell cylindrical and dorsally colored, circular in cross section. Visceral mass visible through shell. Concave closing membrane punctuated on surface.

Distribution. Nova Scotia to the Gulf of Mexico.

Styliola subula (Quoy & Gaimard, 1827)

Figure 2B

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.25°N, 093.00°W; 10 m depth; 23.II.2011; E. Coria-Monter and E. Durán-Campos leg.; preservation 70% ethanol; CC2011-2.

Identification. Animal to 1.3 cm long, with a completely transparent, uncoiled, needle-like shell. Upper part of shell with a rib that projects like a cusp from aperture rim. Surface with growth lines. Shell long, tubular, not curved. Visceral mass visible through shell. Aperture width in is smaller than shell diameter just posterior to aperture. Triangular tooth may be found dorsally and a triangular incision ventrally at the aperture border.

Distribution. Circumtropical.

Creseis conica (Eschscholtz, 1829)

Figure 2C

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.25°N, 092.49°W; 10 m depth; 23.II.2011; E. Coria-Monter and E. Durán-Campos leg.; preservation 70% ethanol; CC2011-3.

Identification. Animal to 0.6 cm long, with a transparent, uncoiled shell. Shell short, narrow, tube-shaped, and not curved, and in cross section round. Aperture diameter about 1 mm.

Distribution. Circumtropical.

Creseis acicula (Rang, 1828)

Figure 2D

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.25°N, 092.25°W; 10 m depth; 23.II.2011; E. Coria-Monter and E. Durán-Campos leg.; preservation 70% ethanol; CC2011-4.

Identification. Animal to 4 cm long, with a transparent, uncoiled shell. Shell extremely long and narrow, tube-shaped, not curved, and round in cross section. Shell not perfectly straight due to many small shape aberrations caused by irregular growth. Shell surface smooth. Visceral mass visible through shell.

Distribution. Circumtropical. Atlantic, pelagic (50°N–40°S).

Creseis virgula (Rang, 1828)

Figure 2E

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 19.74°N, 093.00°W; 10 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg.; preservation 70% ethanol; CC2011-5.

Identification. Animal to 0.7 cm long, with a transparent, uncoiled shell. Shell slender, tube-shaped, and curved, and in cross-section is round. Shell surface smooth.

Distribution. Circumtropical.

Cavolinia inflexa (Lesueur, 1813)

Figure 2F

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.00°N, 092.25°W; 10 m depth; 23.II.2011; E. Coria-Monter and E. Durán-Campos leg.; preservation 70% ethanol; CC2011-6.

Identification. Animal to 0.8 cm long. Shell transparent, with a flat dorsal and ventral side. Caudal spine long and straight, and lateral spines well developed on the middle of shell. Shell sculpture consists of faint growth lines.

Distribution. Worldwide, pelagic; 45°N–45°S, 090°W–000°W.

Cavolinia uncinata (d'Orbigny, 1835)

Figure 2G

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 20.74°N, 093.50°W; 10 m depth; 24.II.2011; E. Coria-Monter and E. Durán-Campos leg.; preservation 70% ethanol; CC2011-7.

Identification. Animal about 0.6 cm long. Shell transparent, brownish. Lateral spines small, and caudal spine curved and small. Dorsal and ventral sides strongly vaulted so that shell length and shell thickness are equal.

Distribution. Virginia to Argentina.

Diacria danae (van Leyen & van der Spoel, 1982)

Figure 2H

Material examined. MEXICO • southern Gulf of

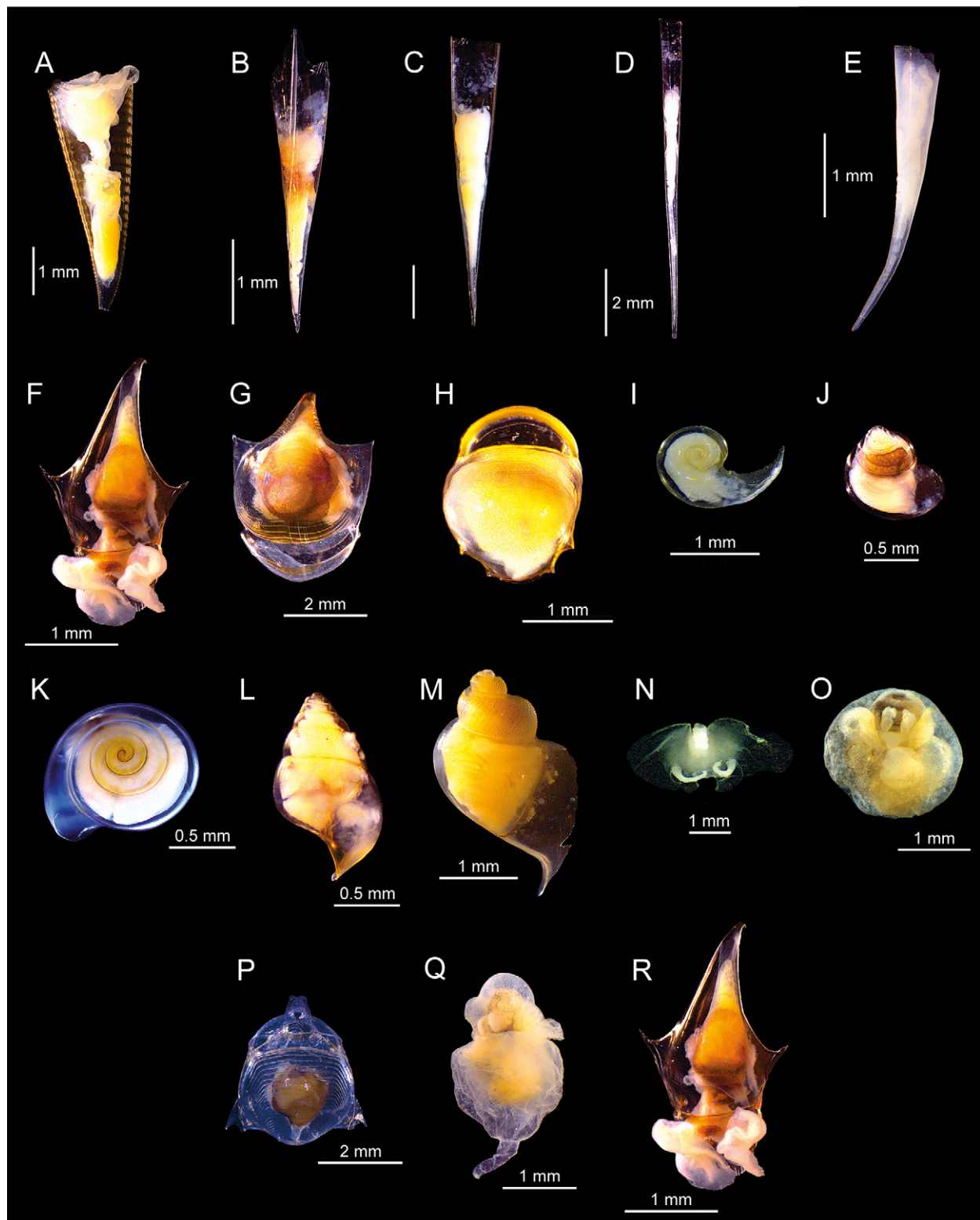


Figure 2. Pteropoda of the Campeche Canyon, southern Gulf of Mexico during winter storm ("Nortes") season. **A.** *Hyalocylis striata* (Rang, 1828). **B.** *Styliola subula* (Quoy & Gaimard, 1827). **C.** *Creseis conica* (Eschscholtz, 1829). **D.** *Creseis acicula* (Rang, 1828). **E.** *Creseis virgula* (Rang, 1828). **F.** *Cavolinia inflexa* (Lesueur, 1813). **G.** *Cavolinia uncinata* (d'Orbigny, 1835). **H.** *Diacria danae* (van Leyen & van der Spoel, 1982). **I.** *Heliconoides inflatus* (d'Orbigny, 1835). **J.** *Limacina trochiformis* (d'Orbigny, 1835). **K.** *Limacina lesueurii* (d'Orbigny, 1836). **L.** *Limacina bulimoides* (d'Orbigny, 1835). **M.** *Peracle reticulata* (d'Orbigny, 1835). **N.** *Desmopterus papilio* (Chun, 1889). **O.** *Pneumoderma violaceum* (d'Orbigny, 1835). **P.** *Diacavolinia constricta* van der Spoel, Bleeker & Kobayasi, 1993. **Q.** *Paraclione longicaudata* (Souleyet, 1852). **R.** *Cavolinia inflexa inflexa* (Lesueur, 1813).

Mexico, Campeche Canyon; 20.24°N, 092.99°W; 10 m depth; 25.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-8.

Identification. Animal small, 0.2 cm or less long. Shell red-brown, semi-transparent, and globular with rounded ventral and dorsal sides and well-developed ribs. Lateral spines small. Dorsal lip arched and borders a very narrow shell aperture. Ventral and dorsal sides heavily vaulted and with striae near aperture lips. Caudal spine mark oval.

Distribution. Circumtropical.

Superfamily Limacinoidea (Gray, 1840)
Family Heliconoididae (Rampal, 2019)

***Heliconoides inflatus* (d'Orbigny, 1835)**

Figure 2I

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 20.24°N, 092.50°W; 10 m depth; 25.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-9.

Identification. Shell small, 0.2 cm in diameter and dextrally coiled. Animal with large eyes and a single swimming fin. Shell strongly flattened and keeled, with seven whorls. Operculum monogyre.

Distribution. Tropical to subtropical.

Family Limacinidae (Gray, 1840)

***Limacina trochiformis* (d'Orbigny, 1835)**

Figure 2J

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 20.00°N, 92.25°W; 10 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-10.

Identification. Animal small, 0.1 cm in diameter. Shell sinistral, 1 mm high × 0.8 mm wide. Spire highly coiled and last whorl increases quickly in diameter. Shell with five rapidly growing whorls separated by a clear suture. Apical angle 75–96° (average 84°). Shell color white to light purple; thicker parts along columella and upper apertural lip purple-brown. Aperture relatively small. Wing protrusions absent.

Distribution. Massachusetts to Brazil.

***Limacina lesueurii* (d'Orbigny, 1836)**

Figure 2K

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 19.74°N, 093.00°W; 10 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-11.

Identification. Shell small, 0.1 cm in diameter, and sinistral. Spire depressed. Last whorl increases very quickly in diameter. Whorls 4½, colorless, and transparent. Umbilicus narrow and deep. Spiral striation around umbilicus, but remaining parts of shell smooth.

Distribution. Massachusetts to Brazil.

***Limacina bulimoides* (d'Orbigny, 1835)**

Figure 2L

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 19.74°N, 093.49°W; 10 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-12.

Identification. Shell small, 0.2 cm in diameter, sinistral. Spire blunt, highly coiled. Whorls more than six, colorless and transparent. Thicker parts of shell near aperture brownish. No umbilicus. Shell smooth except for faint growth lines.

Distribution. Bermuda; New York to Florida; Quintana Roo, Mexico; Venezuela, Cuba, and Brazil.

***Peracle reticulata* (d'Orbigny, 1835)**

Figure 2M

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.24°N, 93.50°W; 10 m depth; 22.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-13.

Identification. Shell 0.6 cm long, sinistral. Whorls five. Suture deep suture. Spire not depressed. Keel present but does not form a at the aperture. Aperture wide and oval, with its pointed towards the keeled rostrum. Shell surface with regular reticulate sculpture, without radial ridges. Wings fused into a swimming plate.

Distribution. Circumtropical.

***Desmopterus papilio* (Chun, 1889)**

Figure 2N

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.25°N, 92.25°W; 10 m depth; 22.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-14.

Identification. Animal shell-less, very small; diameter of swimming disc only 0.4 cm. Wings disc-shaped and transparent except for a few muscle fibers. Visceral mass forms an opaque appendix curved around the swimming disc. Besides median lobe, disc has two long tentacles. No separate proboscis.

Distribution. Circumtropical.

***Pneumoderma violaceum* (d'Orbigny, 1835)**

Figure 2O

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 20.24°N, 092.50°W; 10 m depth; 25.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-15.

Identification. Animal shell-less, to 1.3 cm long, purplish, with rather transparent cylindrical body. Visceral mass visible through body wall.

Distribution. Circumtropical.

***Diacavolinia constricta* van der Spoel, Bleeker & Kobayasi, 1993**

Figure 2P

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 19.74°N, 093.00°W; 10 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-16.

Identification. Animal to 0.6 cm long. Shell with a flat dorsal side with moderately developed ribs. Ventral side vaulted. Caudal spine not present, and no caudal spine mark present where ventral and dorsal sides grow together. Lateral spines small.

Distribution. Circumtropical.

***Paraclione longicaudata* (Souleyet, 1852)**

Figure 2Q

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 20.75°N, 092.49°W; 10 m depth; 24.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-17.

Identification. Animal shell-less, to 1 cm long, with a slender, oval, mainly transparent body. Visceral mass visible through body wall. Posterior foot lobe small or absent. Two pairs of buccal cones present.

Distribution. Worldwide.

***Cavolinia inflexa inflexa* (Lesueur, 1813)**

Figure 2R

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 20.74°N, 093.50°W; 10 m depth; 24.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-18.

Identification. Animal to 0.8 cm long. Shell with flat dorsal and ventral sides. Caudal spine long and straight. Lateral spines well developed on middle of shell. Shell transparent and sculptured with faint growth lines.

Distribution. Worldwide.

Pterotrachoidea

Order Littorinimorpha Golikov & Starobogatov, 1975

Superfamily Pterotracheoidea

Family Atlantidae Rang, 1829

***Oxygyrus inflatus* (Benson, 1835)**

Figure 3A

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.25°N, 092.49°W; 10 m depth; 23.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-19.

Identification. Shell large, 1 cm in diameter, dextral, brown, and rounded with a broad, flat keel. Keel and teleoconch not calcareous but formed of cartilage-like substance. Only one whorl visible, other whorls visible in umbilicus. Nucleus of operculum strongly eccentric. Animal with large eyes and a single swimming fin.

Distribution. Atlantic, Indian, and Pacific Oceans.

Family Carinariidae

***Carinaria pseudorugosa* (Vayssière, 1904)**

Figure 3B

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 20.00°N, 092.25°W; 10 m depth; 26.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-20.

Identification. Animal to 4 cm long, with a distinctive ventral pair of reddish-brown hemispherical structures. Body cannot be withdrawn into shell. Shell low-conical with a high keel. Only broad triangular visceral nucleus darkly pigmented. Eyes large, with black retina. Mouth organs clearly seen. Intestine frequently full and visible. Body long, cylindrical, and with one swimming fin.

Distribution. Atlantic, west of the Azores, surface water.

Family Pterotracheidae

***Firoloida desmarestia* (Lesueur, 1817)**

Figure 3C

Material examined. MEXICO • southern Gulf of Mexico, Campeche Canyon; 21.24°N, 093.50°W; 10 m depth; 22.II.2011; E. Coria-Monter and E. Durán-Campos leg; preservation 70% ethanol; CC2011-21.

Identification. Animal to 4 cm long, with body almost completely transparent. Visceral nucleus terminal on long trunk, followed by a very short ventral tail and either a permanent egg string (in females) or a tail filament (in males). Prominent tentacles and a fin sucker present in males but absent in females.

Distribution. Cosmopolitan. Tropical to subtropical waters.

Discussion

Our study showed high species richness (18 species of Pteropoda, and three species of Pterotrachoidea) and densities of the holoplanktonic mollusks in waters of the Campeche Canyon. In terms of relative density, three species of pteropods (*Creseis conica*, *Heliconoides inflatus*, *Limacina trochiformis*) dominated the holoplanktonic mollusk fauna. Our findings agree with investigations by Lemus-Santana et al. (2014a, 2014b) and López-Arellanes et al. (2018), who studied Pteropoda and Pterotrachoidea in neritic waters on the continental shelf of the southern Gulf of Mexico in different climatic seasons.

In one of the earliest studies on this group of organisms in the southern Gulf of Mexico, Suárez and Gasca (1992) highlighted the scarcity of data from oceanic waters of the Gulf during the coldest months of the year; they reported 15 species collected in January. In this month, *Creseis acicula* was the predominant species (42.0% relative density), followed by *Limacina inflata* (now called *Heliconoides inflatus*) (32.2%), *L.*

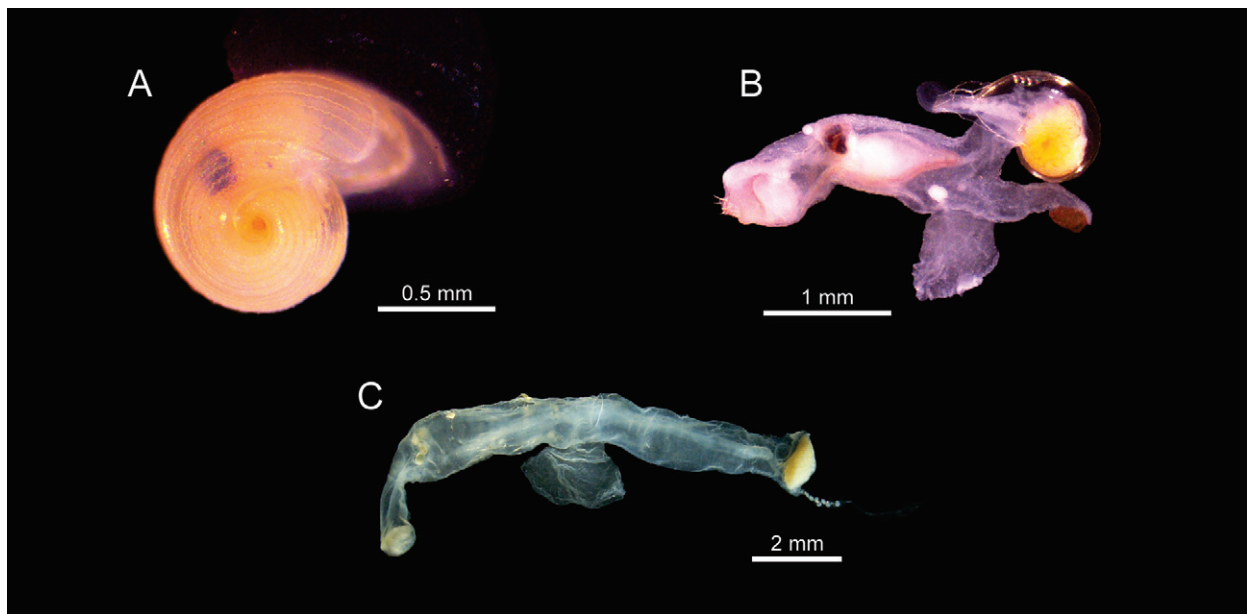


Figure 3. Pterotracheoidea of the Campeche Canyon, southern Gulf of Mexico during a winter storm (“Nortes”) season. **A.** *Oxygyrus inflatus* (Benson, 1835). **B.** *Carinaria pseudorugosa* (Vayssi re, 1904). **C.** *Firoloida desmarestia* (Lesueur, 1817).

trochiformis (9.81%), and *Cavolinia longirostris longirostris* (now called *Diacavolinia longirostris*) (4.47%).

Later, Su  rez (1994) confirmed a high number of species of the genus *Cavolinia* (13 species), followed by *Limacina* and *Creseis* (five species). More recently, Sanvicente-A  n  rve et al. (2013) documented the vertical distribution of five genera of holoplanktonic mollusks inhabiting the upper layer of neritic waters (<200 m depth) of the southern Gulf of Mexico during May and November (*Cavolinia*, *Diacavolinia*, *Diacria*, *Oxygyrus*, and *Clio*), showing that adults had a greater overlap in their distribution in the water column than juveniles. In the southern Gulf of Mexico, Flores-Coto et al. (2013) studied the community structure in coastal waters influenced by river discharges during the summer and reported that three pteropod species, *Creseis acicula* f. *acicula*, *C. acicula* f. *clava*, and *Limacina trochiformis*, constituted more than of 90% of the total density.

Lemus-Santana et al. (2014a, 2014b) identified 14 species of heteropod mollusks in samples collected in the neritic epipelagic layer of the southern Gulf of Mexico during May and November. In their study *Atlanta lesueurii*, *A. gaudichaudi*, *Firoloida desmarestia*, *A. selvagensis* were dominant; in terms of pteropods, they recorder 27 species with *Creseis clava*, *Heliconoides inflatus*, *L. trochiformis* and *C. virgula* being the most abundant. Other studies undertaken in the shelf waters of the southern Gulf of Mexico during 2006 and 2010 springs found over 30 species, with *Creseis conica*, *Limacina trochiformis*, *Creseis acicula* and *Heliconoides inflatus* the most abundant species (L  pez-Arellanes et al. 2018). The number of species reported in these previous studies are higher than that reported by us; however, our sampling strategy was different. For example, they used Bongo nets hauls to collect organisms at the surface to a depth of 200 m, so they sampled a larger water column, which could explain the differences in

the species collected. Another difference is that we carried out our study in oceanic waters, instead of in shelf waters.

Recent studies (e.g. Peijnenburg et al. 2020; Wall-Palmer et al. 2021) have pointed out the importance of the holoplanktonic mollusks in the marine ecosystem and have highlighted the need for more study given the potential risk posed by anthropogenic threats. Ocean acidification is one such serious threat, as it has a direct negative effect on the fragile aragonite shells of holoplanktonic mollusks (Mekkes et al. 2021).

It is important to keep in mind that the species composition and densities reported by us only represent collections made at 10 m deep. This substantially differs from commonly used methods elsewhere around the world (e.g. Burrige et al. 2017) and in the southern Gulf of Mexico waters (e.g. L  pez-Arellanes et al. 2018) and does not allow robust comparisons between our study and those of other authors. Nonetheless, our results significantly contribute to the knowledge of holoplanktonic mollusks in waters of the Campeche Canyon at a depth of 10 m. Depth-specific sampling, such as ours, cannot be obtained with the traditional Bongo net method that samples the whole water column (surface to 200 m depth) and does not accurately provide data on vertical distributions of holoplanktonic mollusks. Holoplanktonic mollusks undergo daily vertical migrations down to 200 m, so future studies should contemplate collecting these organisms in the mesopelagic zone to get better data on their vertical distribution. Density values for some species in our study (Table 1) seem higher (even despite not having considered species in the genus *Atlanta*, *Clio*, *Cymbulia*, and *Corolla* which usually are an important component of the community structure of the holoplanktonic mollusks) compared to other regions of the world, such as the Atlantic Ocean (e.g. Burrige et al. 2017). These

differences may be due to differing hydrodynamic processes in the Gulf of Mexico at different scales, including internal waves, fronts, meanders, and eddies, which promote higher biological productivity. During the winter storm “Nortes” season, when we did our sampling, strong northerly winds generate intense mixing of the water column, which ensures the supply of nutrients in the surface layers, generating a high phytoplankton production. This can trigger a bottom-up mechanism that benefits multiple organisms at different trophic levels (including holoplanktonic mollusks) and may explain the high density values reported here.

In terms of composition, our results agree with Suárez and Gasca (1992) and Suárez (1992), who reported between 15 and 18 species of pteropods in the southern Gulf of Mexico. However, our study show a lower species richness than by other researchers, who reported a more than 25 species in neritic waters of the continental shelf (Lemus-Santana et al. 2014 a, 2014b; López-Arellanes et al. 2018). These differences in species richness may be influenced by: the sampling method and the greater water column sampled, the greater number of research cruises and sampling stations, and the location in neritic waters having freshwater discharges and higher organic matter.

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Authors' Contributions

Conceptualization: DASL, ZLC, MAMG, ECM, AG, EDC. Data curation: ECM, ZLC. Formal analysis: ZLC, AG, ECM, MAMG, DASL, EDC. Funding acquisition: EDC, DASL, AG, MAMG, ECM.

References

- Arriola-Pizano JG, Aldeco-Ramírez J, Salas-de León DA, Pagano M, Mendoza-Vargas L (2022) Distribution, abundance, and diversity of euphausiids and their relationships with hydrodynamic processes in Campeche Canyon, Gulf of Mexico. *Revista Mexicana de Biodiversidad* 93: e933723. <https://doi.org/10.22201/ib.20078706e.2022.93.3723>
- Brierley AS (2017) Plankton. *Current Biology* 27 (11): R478–R483. <https://doi.org/10.1016/j.cub.2017.02.045>
- Burridge AK, Goetze E, Wall-Palmer D, Le Double SL, Huisman J, Peijnenburg KTCA (2017) Diversity and abundance of pteropods and heteropods along a latitudinal gradient across the Atlantic Ocean. *Progress in Oceanography* 158: 213–223. <https://doi.org/10.1016/j.pocean.2016.10.001>
- Durán-Campos E, Salas de León DA, Monreal-Gómez MA, Coria-Monter E (2017) Patterns of chlorophyll-a distribution linked to mesoscale structures in two contrasting areas Campeche Canyon and Bank, southern Gulf of Mexico. *Journal of Sea Research* 123: 30–38. <https://doi.org/10.1016/j.seares.2017.03.013>
- Flores-Coto C, Arellanes HL, Sánchez-Robles J, López-Serrano A (2013) Composición, abundancia y distribución de Pteropoda (Mollusca: Gastropoda) en la zona nerítica, del sur del Golfo de México (Agosto, 1995). *Hidrobiológica* 23 (3): 348–364.
- Gasca R, Janssen AW (2014) Taxonomic review, molecular data and key to the species of Creseidae from the Atlantic Ocean. *Journal of Molluscan Studies* 80 (1): 35–42. <https://doi.org/10.1093/mollus/eyt038>
- Goff JA, Gulick SPS, Pérez-Cruz L, Stewart HA, Davis M, Duncan D, Sastrup S, Sanford J, Urrutia-Fucugauchi J (2016) Solution pans and linear sand bedforms on the bare-rock limestone shelf of the Campeche Bank, Yucatán Peninsula, Mexico. *Continental Shelf Research* 117: 57–66. <https://doi.org/10.1016/j.csr.2016.02.005>
- Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley M (2000) ICES zooplankton methodology manual. Academic Press, San Diego, USA, 684 pp.
- Lalli CM, Gilmer RW (1989) Pelagic snails. The biology of holoplanktonic gastropod mollusks. Stanford University Press, Stanford, USA, 259 pp.
- Le Quéré C, Harrison SP, Prentice IC, Buitenhuis ET, Aumont O, Bopp L, Claustre H, Cotrim Da Cunha L, Geider R, Giraud X, Klaas C, Kohfeld KE, Legendre L, Manizza M, Platt T, Rivkin RB, Sathyendranath S, Uitz J, Watson AJ, Wolf-Gladrow D (2005) Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology* 11 (11): 2016–2040. <https://doi.org/10.1111/j.1365-2486.2005.1004.x>
- Lemus-Santana E, Sanvicente-Añorve L, Hermoso-Salazar M, Flores-Coto C (2014a) The holoplanktonic Mollusca from the southern Gulf of Mexico. Part 1: heteropods. *Cahiers de Biologie Marine* 55: 229–239.
- Lemus-Santana E, Sanvicente-Añorve L, Hermoso-Salazar M, Flores-Coto C (2014b) The holoplanktonic Mollusca from the southern Gulf of Mexico. Part 2: pteropods. *Cahiers de Biologie Marine* 55: 241–258.
- López-Arellanes H, Funes-Rodríguez R, Flores-Coto C, Zavala-García F, Espinosa-Fuentes ML (2018) Comparison of pteropod assemblages and their relationship with environmental variables in the southern Gulf of Mexico.

- Journal of Molluscan Studies 84 (4): 386–396. <https://doi.org/10.1093/mollus/eyy029>
- Lunden JJ, McNicholl CG, Sears CR, Morrison CL, Cordes EE** (2014) Acute survivorship of the deep-sea coral *Lophelia pertusa* from the Gulf of Mexico under acidification, warming, and deoxygenation. *Frontiers in Marine Science* 78 (1): <https://doi.org/10.3389/fmars.2014.00078>
- Mekkes L, Renema W, Bednaršek N, Alin SR, Feely RA, Huisman J, Roessingh P, Peijnenburg KTCA** (2021) Pteropods make thinner shells in the upwelling region of the California Current Ecosystem. *Scientific Reports* 11: 1731. <https://doi.org/10.1038/s41598-021-81131-9>
- Moreno-Alcántara M, Giraldo A, Aceves-Medina G** (2017) Heteropods (Gastropoda: Pterotracheoidea) identified along a coastal-oceanic transect in the Colombian Pacific. *Bulletin of Marine and Coastal Research* 46(2): 175–181. <https://doi.org/10.25268/bimc.invenmar.2017.46.2.733>
- Ojeda E, Appendini CM, Mendoza ET** (2017) Storm-wave trends in Mexican waters of the Gulf of Mexico and Caribbean Sea. *Natural Hazards Earth System Sciences* 17: 1305–1317. <https://doi.org/10.5194/nhess-17-1305-2017>
- Peijnenburg KTCA, Janssen AW, Wall-Palmer D, Goetze E, Maas AE, Todd JA, Marlétaz F** (2020) The origin and diversification of pteropods precede past perturbations in the Earth's carbon cycle. *Proceedings of the National Academy of Sciences of the United States of America* 117 (41): 25609–25617. <https://doi.org/10.1073/pnas.1920918117>
- Richter G, Seapy RR** (1999) Heteropoda. In: Boltovskoy D (Ed.) *South Atlantic Zooplankton*. Backhuys Publishers, Leiden, the Netherlands, 621–647.
- Santiago-Arce T, Salas de León DA** (2012) Vorticity and internal waves in the Campeche Canyon, Gulf of Mexico. In: Klapp J, Cros A, Velasco Fuentes O, Stern C, Rodríguez Meza M. (Eds.) *Experimental and theoretical advances in fluid dynamics*. Springer, Berlin, Germany, 163–169. https://doi.org/10.1007/978-3-642-17958-7_11
- Sanvicente-Añorve L, Lemus-Santana E, Flores-Coto C, Alatorre-Mendieta M** (2013) Vertical segregation of holoplanktonic molluscs in the epipelagic layer, southern Gulf of Mexico. *Helgolander Marine Research* 67: 397–405. <https://doi.org/10.1007/s10152-012-0331-2>
- Sherman K, Hempel G** (2009) Perspectives on regional seas and the large marine ecosystem approach. In: Sherman K, Hempel G (Eds.) *The UNEP large marine ecosystem report: a perspective on changing conditions in LMEs of the world's regional seas*. UNEP Regional Seas Report and Studies. United Nations Environment Programme, Nairobi, Kenya, 3–22.
- Suárez M E, Gasca R** (1992) Pterópodos (Gastropoda: Thecosomata y Pseudothecosomata) de aguas superficiales (0–50 m) del sur del Golfo de México. *Anales del Instituto de Ciencias del Mar y Limnología UNAM* 19: 199–207.
- Suárez M. E** (1994) Distribución de los pterópodos (Gastropoda: Thecosomata y Pseudothecosomata) del Golfo de México y zonas adyacentes. *Revista de Biología Tropical* 42 (3): 523–530.
- Van der Spoel S, Dadon JR** (1999) Pteropoda. In: Boltovskoy D (Ed.) *South Atlantic zooplankton*. Backhuys Publishers, Leiden, the Netherlands, 649–706.
- Vaske T Jr., Travassos PE, Hazin FHV, Tolotti MT, Barbosa TM** (2012) Forage fauna in the diet of bigeye tuna (*Thunnus obesus*) in the western tropical Atlantic Ocean. *Brazilian Journal of Oceanography* 60 (1): 89–97.
- Wall-Palmer D, Smart CW, Kirby R, Hart MB, Peijnenburg KTCA, Janssen AW** (2016) A review of the ecology, palaeontology and distribution of atlantid heteropods (Caenogastropoda: Pterotracheoidea: Atlantidae). *Journal of Molluscan Studies* 82 (2): 221–234. <https://doi.org/10.1093/mollus/eyv063>
- Wall-Palmer D, Burridge AK, Goetze E, Stokvis FR, Janssen AW, Mekkes L, Moreno-Alcántara M, Bednaršek N, Schiøtte T, Sørensen MV, Smart CW, Peijnenburg KTCA** (2018) Biogeography and genetic diversity of the atlantid heteropods. *Progress in Oceanography* 160: 1–25. <https://doi.org/10.1016/j.pocean.2017.11.004>
- Wall-Palmer D, Mekkes L, Ramos-Silva P, Dämmer LK, Goetze E, Bakker K, Duijm E, Peijnenburg KTCA** (2021) The impacts of past, present and future ocean chemistry on predatory planktonic snails. *Royal Society Open Science* 8: 202265. <https://doi.org/10.1098/rsos.202265>