

Article

Environmental Drivers of the Epipelagic Pteropod Community Structure in the Deep-Water Basin of the Southern Gulf of Mexico During Summer

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Abstract

Holoplanktonic mollusks (Mollusca: Gastropoda: Pteropoda) are vital structural and functional components of marine zooplankton communities, characterized by high sensitivity to physicochemical shifts in the water column. Consequently, multidisciplinary assessments are essential to elucidate their community dynamics. This study investigated the epipelagic pteropod community structure in the deep-water basin of the southern Gulf of Mexico (sGoM) in relation to hydrographic features and circulation patterns. During the summer (September) of 2016, we collected high-resolution hydrographic data and zooplankton samples using CTD casts and oblique bongo net tows. Hydrographic data revealed intense temperature and density gradients, including a cold-dense core associated with a well-defined cyclonic eddy. The pteropod assemblage comprised 25 species from 13 genera and 10 families. *Heliconoides inflatus* (947.5 ind 100 m⁻³) and *Limacina trochiformis* (396.8 ind 100 m⁻³) were the most abundant species, whereas *Cavolinia gibbosa* (0.4 ind 100 m⁻³) and *Cymbulia* sp. (0.3 ind 100 m⁻³) were the least abundant. Horizontal distribution analyses revealed that the peak population densities occurred within the influence of the cyclonic eddy, particularly at its periphery where strong currents (>0.5 m/s) were recorded. A Canonical Correspondence Analysis identified temperature and salinity as the primary environmental drivers of community variability, while current systems significantly influenced the horizontal distribution of key species. Although pteropod research in the sGoM spans decades, most studies have been limited to taxonomic checklists, often overlooking environmental drivers and hydrographic influences. By applying a multidisciplinary approach to examine physical–biological coupling, this study advances the ecological understanding of this group within the historically underrepresented deep-water basin of the sGoM.

Keywords: pteropod community; hydrography; cyclonic eddies; deep southern Gulf of Mexico



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1. Introduction

Marine zooplankton comprises a highly heterogeneous group distributed across all ocean basins, representing nearly every marine phylum [1]. Among this taxonomic diversity, mollusks are a numerically and functionally significant component of pelagic communities.

Within the phylum Mollusca, pteropods (Gastropoda: Pteropoda) are a diverse and abundant group that occupy a pivotal ecological role. As primarily strict herbivores [2], they function as critical intermediaries in pelagic food webs, exerting significant top-down control on phytoplankton communities [3] while serving as essential prey for various higher-order consumers [4]. Furthermore, their specialized swimming appendages facilitate diel vertical migrations, which drive the efficient vertical flux of organic matter and carbon through the water column [5].

Pteropods are notably sensitive to environmental change. Their composition, distribution, and abundance are significantly influenced by temperature fluctuations [6] and shifts in water column hydrography, often driven by ocean eddies, which serve as a critical mechanism shaping pteropod community structures [7].

Ocean eddies, classified as cyclonic, anticyclonic, or mode-water, act as keystone structures that fundamentally shape planktonic communities [8]. In the Northern Hemisphere, cyclonic eddies generate counterclockwise circulation that triggers the upwelling of nutrient-rich water masses. This influx of nitrogen fertilizers in the euphotic zone stimulates both primary and secondary production. Conversely, anticyclonic eddies exhibit clockwise rotation, inducing the downwelling of warm, oligotrophic waters that typically suppress biological productivity [9].

Ocean eddies are fundamental drivers of zooplankton population dynamics [10], particularly profound on pteropod community composition. In the North Pacific, for example, eddies propitiate high densities of species such as *Clio pyramidata* and *Limacina helicina* [7], while in the Gulf of Alaska, these features act as primary agents for the distribution of *L. helicina* [11]. Similarly, within the California Current System, eddy-linked fronts exert a strong influence on both the vertical and horizontal distribution of regional populations [12]. Recent findings confirm that this impact extends to the southern Gulf of Mexico (sGoM), where eddy activity significantly shapes local pteropod communities [13].

The sGoM is a highly productive and biodiverse ecosystem renowned for its rich zooplankton assemblages. Although research in this region dates back to the early 20th century, historical studies have primarily focused on copepods and ichthyoplankton [14]. Subsequent investigations have characterized the pteropod community by its high taxonomic richness and localized abundance. Initial inventories identified 15 species, dominated by *Creseis acicula* and *Heliconoides inflatus* (formerly *Limacina inflata*) [15]. Further analysis of the vertical distribution of five key genera (*Cavolinia*, *Diacavolinia*, *Diacria*, *Oxygyrus*, and *Clio*) revealed that adult distributions exhibit greater overlap within the water column than those of juveniles [16].

In the neritic waters of the sGoM, taxonomic inventories have registered 27 species, with nearly 95% of total abundance attributed to four dominant taxa: *C. acicula* (recorded as *C. clava*), *H. inflatus*, *Limacina trochiformis*, and *Creseis virgula* [17]. Comparative studies between continental shelf and oceanic environments have further refined this picture, identifying a total of 29 species [18]. These findings indicate higher overall abundance in the neritic zone (particularly near river mouths) while the oceanic region is characterized by the dominance of two indicator species, *H. inflatus* and *Limacina lesueurii* [18].

Studies of pteropods in the deepest regions of the sGoM remain scarce. Recent multidisciplinary research has begun to address this by examining how the physical environment dictates species composition. For instance, in the Campeche Canyon, a

deep thermocline at 90 m and circulation patterns driven by cyclonic and anticyclonic eddies were found to support an assemblage of 33 species [13]. Similarly, in the deep sGoM, research identified 32 species, with four dominant taxa comprising 63% of the total abundance. In this instance, an anticyclonic eddy increased water column stratification [19] and reduced chlorophyll-*a* concentrations, fostering a pteropod community specifically adapted to oligotrophic conditions [19].

Although these studies [13,19] have been important for uncovering previously unreported distribution patterns in the deep Gulf basin, they are inherently limited by their temporal and spatial focus. The former [13] was conducted in the Campeche Canyon during the coldest months (February), under the influence of an eddy dipole, while the latter [19] was restricted to the deep Gulf basin during late spring. Consequently, these findings leave significant gaps in our understanding of how this group responds to environmental variability throughout the year.

While recent studies integrating hydrographic, current, and satellite data have advanced our knowledge of pteropod composition in the deep sGoM, broader environmental drivers remain unresolved. To address these data gaps, our study examines how hydrography and circulation patterns can influence pteropod composition, distribution, and abundance in the deep-water basin of the sGoM. Utilizing in situ hydrographic data and zooplankton samples collected during summer of 2016 (September), we test the hypothesis that current patterns, specifically cyclonic eddies, regulate species composition by altering horizontal distribution.

2. Materials and Methods

2.1. Study Area

The Gulf of Mexico is a large, semi-enclosed marginal sea in North America, covering an area exceeding 1.5 million km² and bordered by Mexico, Cuba, and the United States (Figure 1A). Geomorphologically, the basin exhibits highly heterogeneous bathymetry, including extensive continental shelves, submarine canyons, and escarpments, culminating in a maximum depth of nearly 4000 m within the central abyssal plain [20].

The Gulf hydrodynamic regime is governed by a multiscale complex of physical processes, ranging from localized turbulent mixing and internal waves propagation to mesoscale eddy activity [21,22]. Central to this system is the Loop Current, a major current that enters the basin through the Yucatán Channel and exits via the Florida Straits into the North Atlantic. This circulation pattern is a primary driver of flux of heat, salt, and kinetic energy fluxes [23]. Furthermore, these physical forcing mechanisms facilitate the vertical and horizontal transport of nutrients, which are essential for sustaining primary productivity and supporting higher trophic levels [14].

Ecologically, the Gulf of Mexico serves as a vital habitat for numerous species of conservation and socio-economic importance [24]. The region maintains high taxonomic diversity within planktonic communities, including both phytoplankton and zooplankton [14]. The spatiotemporal distribution of these organisms is intricately linked to the aforementioned hydrodynamic features, which modulate nutrients availability and the overall stability of the marine food web.

2.2. Sampling

Sampling was conducted in the sGoM at depths ranging from 227 to 3774 m during the multidisciplinary “SOGOM-2” research cruise aboard the R/V Justo Sierra (UNAM) from 2 to 28 September 2016. The sampling design included 62 hydrographic stations and 27 zooplankton collection sites (Figure 1B). The number of hydrographic locations was implemented to provide a high-resolution characterization of regional circulation and

environmental conditions. Although incomplete spatial overlap between hydrographic and zooplankton sampling limits our ability to fully characterize the influence of environmental gradients on pteropod community structure, these data remain highly valuable. They provide essential insights into previously undocumented ecological dynamics within the deep-water basin of the sGoM.

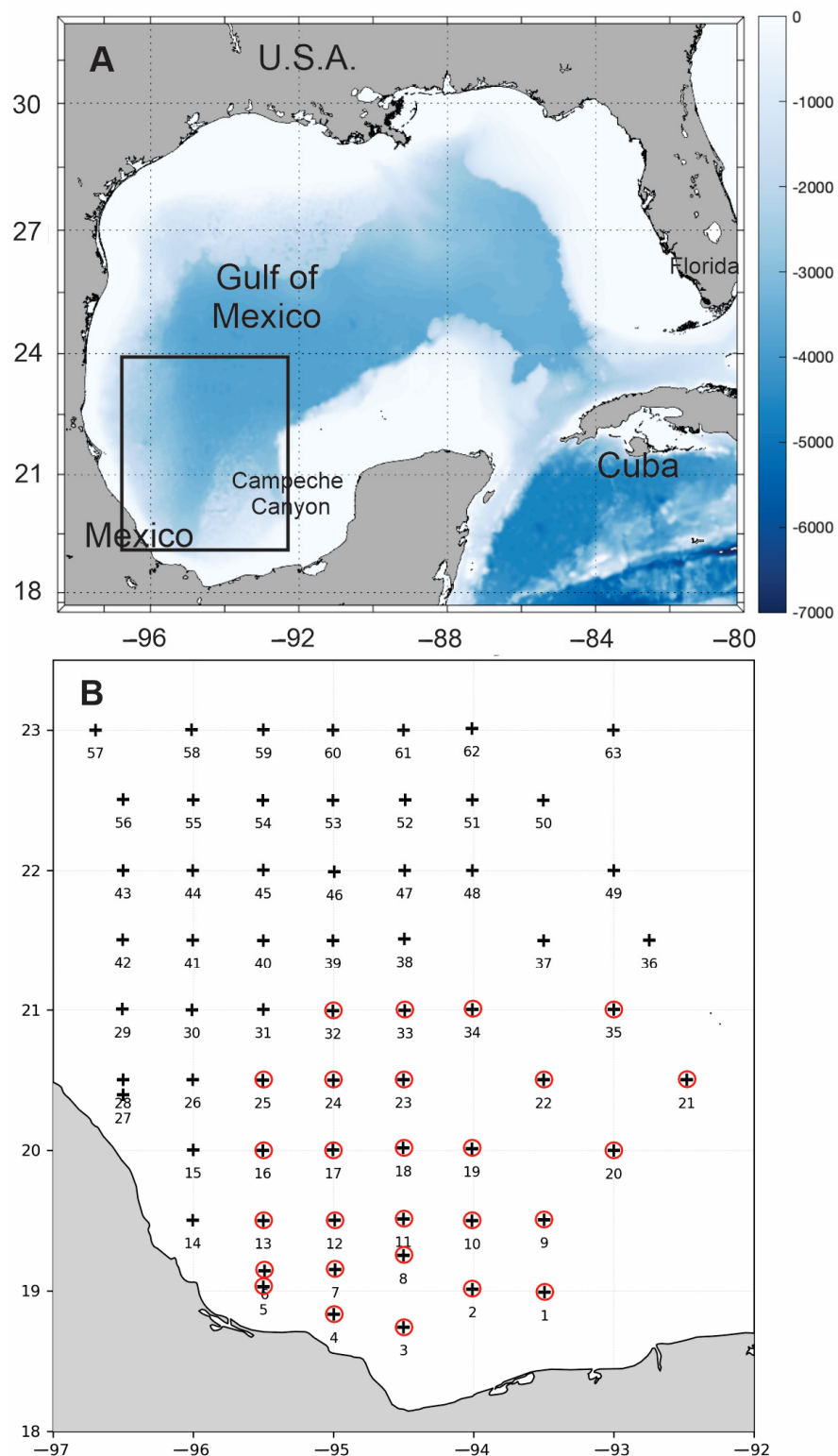


Figure 1. Study area. (A) The Gulf of Mexico showing bathymetry (depth in meters). The black square indicates the region sampled during the “SOGOM-2” research cruise. (B) Detail of the sampling area. Black plus signs (+) indicate hydrographic stations; red circles (o) indicate zooplankton collection sites.

Hydrographic profiles were acquired using a Sea-Bird SBE 9plus, Bellevue, WA, USA, CTD integrated with a General Oceanics rosette system, equipped with SBE 43 dissolved oxygen and ECO-Wet Labs chlorophyll-*a* fluorescence sensors. All sensors were calibrated by the manufacturer prior to the cruise. Vertical casts were performed from the surface to within approximately 100 m of the seafloor. To ensure optimal vertical resolution and minimize sensor lag, the instrument was lowered at a constant rate of 0.5 m/s with a sampling frequency of 24 Hz.

Following each CTD cast, zooplankton were collected using a Bongo net system (60 cm mouth diameter) equipped with 333 μm nylon mesh. A calibrated flowmeter (General Oceanics 2030R, Miami, FL, USA) was mounted in the net mouth to quantify the volume of filtered water. Oblique tows were conducted from a maximum depth of 200 m to the surface at a vessel speed of 2 knots for approximately 15 min. Upon recovery, samples were immediately fixed in 4% borax-buffered formalin. After 24 h, the organisms were transferred to 70% ethanol for long-term preservation.

2.3. Laboratory Analyses

In the laboratory, pteropods were sorted from the samples using a Zeiss Stemi 508, Oberkochen, Germany, stereomicroscope and identified to the species level using standard keys [25,26]. Identifications were verified against international biological databases, including MolluscaBase and the Tree of Life Project. Finally, organisms counts were standardized to density ($\text{ind } 100 \text{ m}^{-3}$) based on flowmeter data, following the standard protocols of Kramer et al. [27].

2.4. Data Analyses

CTD data were initially processed using standard protocols within the SBE Data Processing (v.7.26.7) software suite, with filters applied to exclude low-quality data. Following quality control, conservative temperature ($^{\circ}\text{C}$), absolute salinity (g kg^{-1}), and density ($\sigma\text{-t}$, kg m^{-3}) values were calculated using the algorithms of the thermodynamic equation for seawater (TEOS-10). The resulting data were finally averaged to 1-decibar bins.

Geostrophic velocities were then calculated from this dataset following standard methods [28], assuming a level of no motion at 1000 m depth. For calculation purposes, we define the no-motion level at a depth of 1000 m. This reference level is chosen based on the geostrophic method, which relates horizontal pressure gradients to the Coriolis force. By setting velocity to zero at 1000 m ($v = 0$), we assume that the resulting geostrophic velocities—driven by density variations in temperature and salinity—are well-represented. This depth serves as a practical baseline, as deep-water velocities are significantly lower than surface currents, effectively isolating the bulk of the wind-driven circulation. This methodology is consistent with previous studies calculating geostrophic velocities in the southern Gulf of Mexico [13]. Finally, the results were synthesized into maps of hydrographic parameters and geostrophic currents.

To evaluate the influence of environmental drivers on the pteropod community during the study period, a Canonical Correspondence Analysis (CCA) was performed. This approach yields a low-dimensional ordination space that highlights the primary ecological drivers of community structure [29].

All statistical routines were implemented using CANOCO v5.10 software [30]. To stabilize variance and reduce the influence of the most abundant species, data were square-root-transformed prior to analysis [31]. In CCA, the square-root-transformation is a standard preprocessing technique used to stabilize variance and mitigate the disproportionate influence of highly abundant species. This transformation is particularly beneficial for ecological datasets; by addressing the positive skewness common in zero-inflated, highly

peaked count data, it prevents ordination axes from being driven solely by a few dominant taxa. Consequently, this method helps normalize count distributions while ensuring that meaningful ecological signals are preserved [31].

The final plot was used to visualize the positioning of species relative to the vectors of the measured physical and chemical variables.

3. Results

3.1. Environmental Drivers

The surface horizontal distribution of the hydrographic parameters and the circulation pattern observed during our study showed interesting features. The conservative temperature (Figure 2A) showed a clear gradient with warmer waters (up to 31 °C) in the northeastern and northwestern sections of the sampled area. A distinct core of cooler water (<29.5 °C) was visible in the south–central region (centered around 20° N, 94° W), which likely suggests the presence of a cyclonic eddy. The absolute salinity distribution (Figure 2B) remained relatively uniform, with most of the region characterized by typical marine values near 36.4 g kg⁻¹. However, localized high-salinity patches (>37 g kg⁻¹) were observed in the northern sector, likely resulting from evaporation-driven concentration. In terms of density (Figure 2C), this parameter reflects the temperature patterns, the highest density values (>22.8 kg m⁻³) coincided with the cooler regions, which reinforced the idea of a physical feature bringing denser, deeper water toward the surface. Finally, the geostrophic velocity (Figure 2D) revealed a well-defined cyclonic (counterclockwise) circulation in the south–central region. This feature aligns with the low temperatures and high densities shown in Figure 2A,C. Notably, strong peripheral currents reached velocities of 0.5 m/s, flowing from northeast toward southwest and extending into coastal waters.

The dissolved oxygen distribution (Figure 3A) showed moderate to high oxygenation, with a maximum core (>4.5 mL/L) located in the central region. Interestingly, this high-oxygen patch sits just above the cooler, denser water mass noted in previous figures. The chlorophyll-*a* distribution showed a clear contrast between the northern and southern regions (Figure 3B). The southeastern region exhibited high biomass (>1.2 mg m⁻³); in contrast, the northern area remained oligotrophic, with values below 0.3 mg m⁻³.

3.2. Pteropod Community Structure

The pteropod community structure identified in this study comprised 25 species of 13 genera and 10 families. *Heliconoides inflatus* (947.5 ind 100 m⁻³) and *Limacina trochiformis* (396.8 ind 100 m⁻³) were the most abundant taxa, whereas *Cavolinia gibbosa* (0.4 ind 100 m⁻³) and *Cymbulia* sp. (0.3 ind 100 m⁻³) were the least frequent.

The horizontal distribution analyses of the most abundant species revealed significant spatial variability (Figure 4). Note that bubble scales were adjusted individually for each species to enhance visual clarity. *Heliconoides inflatus* (Figure 4A) and *Limacina trochiformis* (Figure 4B) exhibited similar patterns, with peak abundances concentrated in the central and southern regions. In contrast, *Cavolinia gibbosa* (Figure 4C) was primarily restricted to the southern sector, while *Cymbulia* sp. (Figure 4D) peaked in the westernmost portion. Broadly, the highest concentrations of these four species align with the cyclonic circulation and intense currents identified in Figure 2D, suggesting a strong biological response to the regional dynamics.

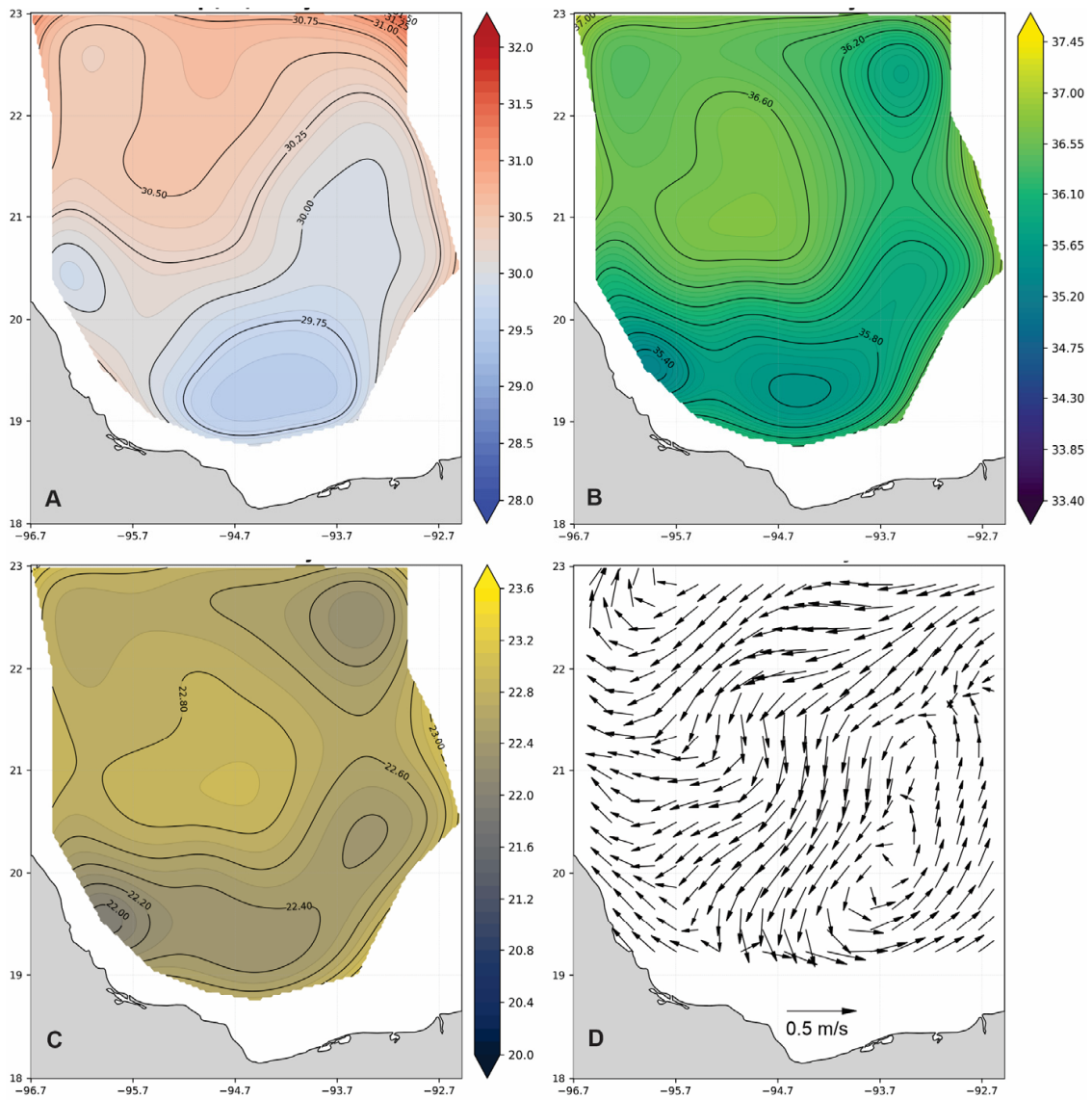


Figure 2. Horizontal distribution at the surface (5 m depth) of (A) conservative temperature (°C), (B) absolute salinity (g kg⁻¹), (C) density (kg m⁻³) and (D) geostrophic velocities (m/s).

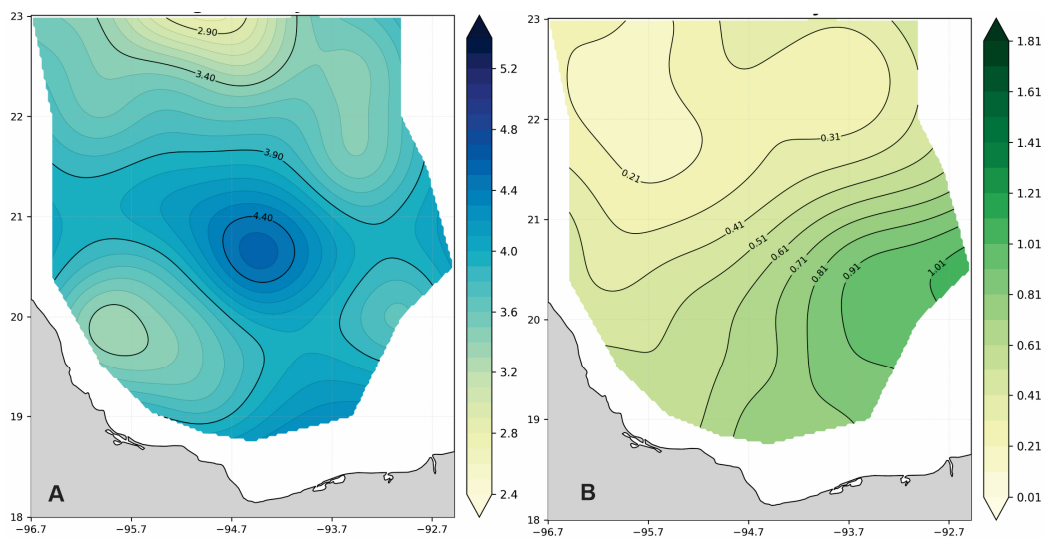


Figure 3. Horizontal distribution at the surface (5 m depth) of (A) dissolved oxygen (ml/L) and (B) chlorophyll-a (mg m⁻³).

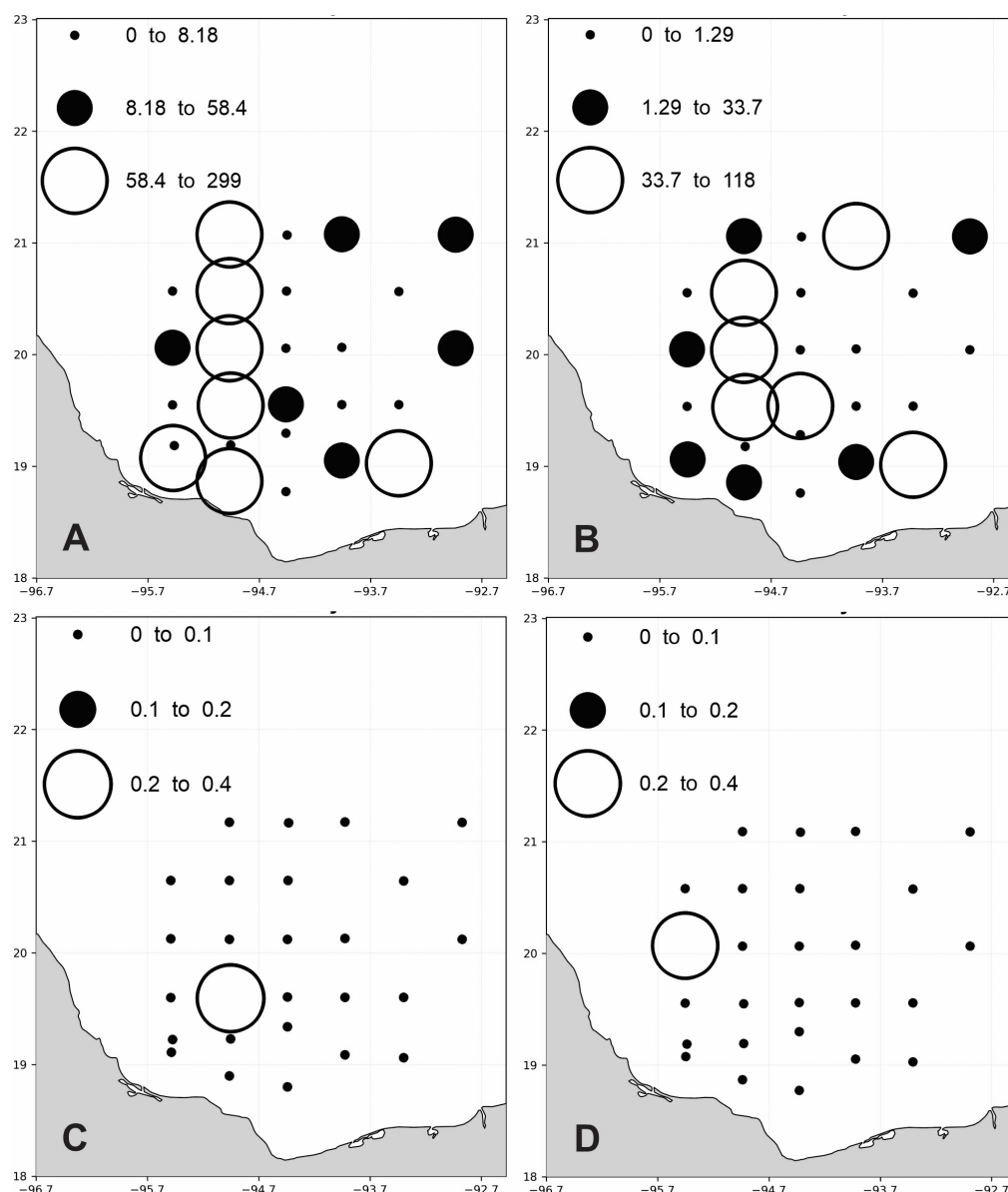


Figure 4. Horizontal distribution of the density (ind 100 m⁻³) of (A) *Heliconoides inflatus*, (B) *Limacina trochiformis*, (C) *Cavolinia gibbosa* and (D) *Cymbulia sp.*

3.3. Statistical Analysis

The CCA showed that the first two axes explain 75.4% of the cumulative variance in the pteropod–environment relationship, reflecting a robust coupling between the community structure and environmental forcing (Figure 5). Axis 1 (59.2%) represents a primary hydrographic gradient defined by temperature (T) and salinity (S). Species positioned along the positive end of this axis, such as *Cavolinia uncinata* (*C. unc*), *Clio sp.* (*Cl. sp.*), and *Cavolinia inflexa* (*C. inf*), present a strong affinity for warmer, more saline water masses. Conversely, species like *Clio pyramidata* (*C. pyr.*), *Peracle reticulata* (*P. ret.*), and *P. diversa* (*P. div*) were negatively correlated with these parameters, likely indicating their distribution in cooler, less saline, or deeper layers.

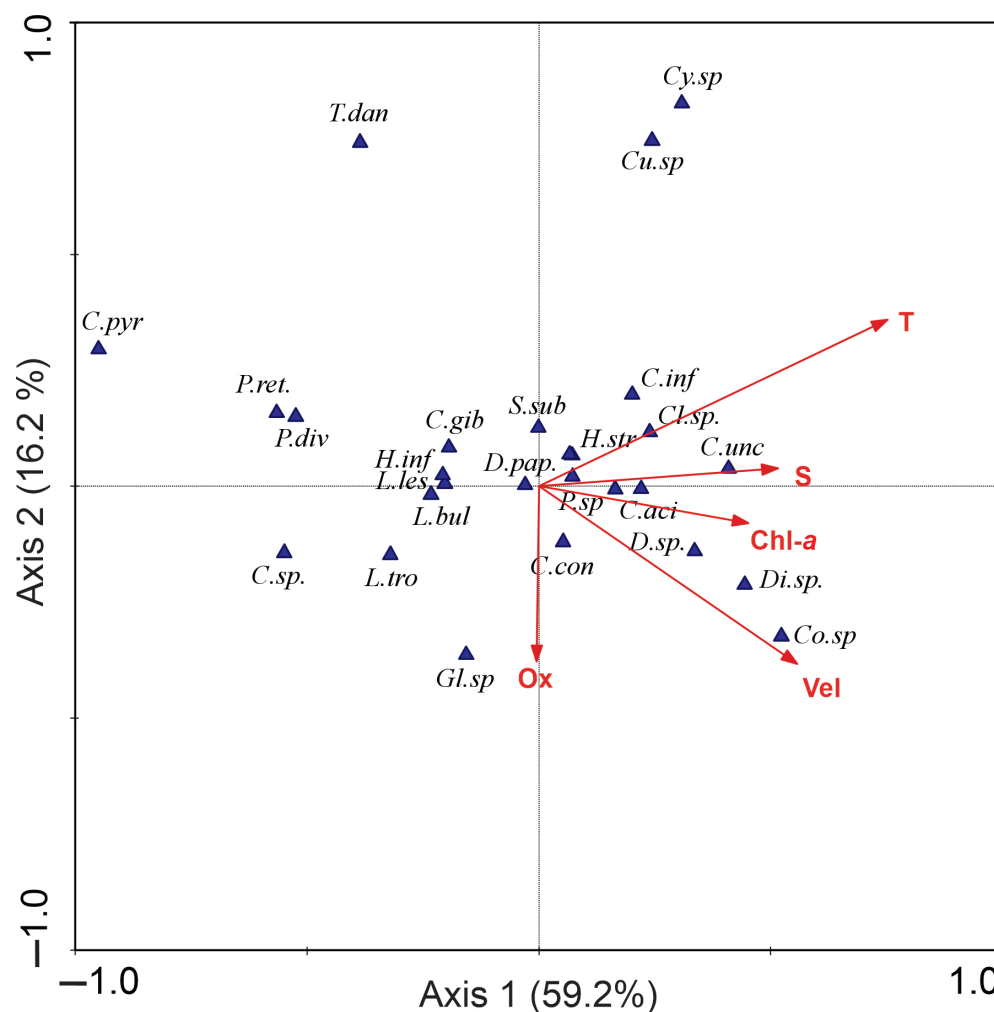


Figure 5. Canonical Correspondence Analysis biplot. The vectors in red represent environmental variables. T: temperature; S: salinity; Chl-a: chlorophyll-a; Vel: current velocities; Ox: dissolved oxygen. Purple triangles indicate the distribution of pteropod species within the ordination space. Specific species names corresponding to the abbreviations detailed in Table 1. The two first axes accounted for 75.4% of the total variance.

Table 1. Pteropod community structure and its density (ind 100 m⁻³) in the deep southern Gulf of Mexico during summer. Total density represents the sum of all stations.

Family	Genus	Species	Abbreviation	Total Density (ind 100 m ⁻³)
Limacinidae	<i>Limacina</i>	<i>Limacina bulimoides</i> (A. d’Orbigny, 1835)	<i>L. bul.</i>	82.1
		<i>Limacina trochiformis</i> (A. d’Orbigny, 1835)	<i>L. tro.</i>	396.8
		<i>Limacina lesueuri</i> (A. d’Orbigny, 1836)	<i>L. les.</i>	131.5
Heliconoididae	<i>Heliconoides</i>	<i>Heliconoides inflatus</i> (A. d’Orbigny, 1835)	<i>H. inf.</i>	947.5
Cavoliniidae	<i>Cavolinia</i>	<i>Cavolinia</i> sp.	<i>C. sp.</i>	4.2
		<i>Cavolinia gibbosa</i> (A. d’Orbigny, 1835)	<i>C. gib</i>	0.4
		<i>Cavolinia inflexa</i> (Lesueur, 1813)	<i>C. inf.</i>	55.3

Table 1. Cont.

Family	Genus	Species	Abbreviation	Total Density (ind 100 m ⁻³)
		<i>Cavolinia uncinata</i> (A. d’Orbigny, 1835)	<i>C. unc.</i>	3.1
		<i>Diacavolinia</i> sp.	<i>D. sp.</i>	15.5
		<i>Diacria</i> sp.	<i>Di. sp.</i>	108.7
		<i>Telodiacria danae</i> (van Leyen & van der Spoel, 1982)	<i>T. dan.</i>	2.3
Cliidae	<i>Clio</i>	<i>Clio</i> sp.	<i>Cl. sp.</i>	5.9
		<i>Clio pyramidata</i> Linnaeus, 1767	<i>C. pyr.</i>	2.1
Creseidae	<i>Creseis</i>	<i>Creseis acicula</i> (Rang, 1828)	<i>C. aci.</i>	177.6
		<i>Creseis conica</i> Eschscholtz, 1829	<i>C.con.</i>	256.0
	<i>Styliola</i>	<i>Styliola subula</i> (Quoy & Gaimard, 1827)	<i>S. sub.</i>	107.3
Hyalocylidae	<i>Hyalocylis</i>	<i>Hyalocylis striata</i> (Rang, 1828)	<i>H. str.</i>	120.2
Cuvierinidae	<i>Cuvierina</i>	<i>Cuvierina</i> sp.	<i>Cu. sp.</i>	0.7
Cymbuliidae	<i>Cymbulia</i>	<i>Cymbulia</i> sp.	<i>Cy. sp.</i>	0.3
	<i>Corolla</i>	<i>Corolla</i> sp.	<i>Co. sp.</i>	0.7
	<i>Gleba</i>	<i>Gleba</i> sp.	<i>Gl. sp.</i>	1.6
Desmopteridae	<i>Desmopterus</i>	<i>Desmopterus papilio</i> Chun, 1889	<i>D. pap.</i>	155.1
Peraclidae	<i>Peraclis</i>	<i>Peraclis</i> sp.	<i>P. sp.</i>	60.2
		<i>Peraclis diversa</i> (Monterosato, 1875)	<i>P. div.</i>	3.1
		<i>Peraclis reticulata</i> (A. d’Orbigny, 1835)	<i>P. ret.</i>	6.2

Axis 2 (16.2%) identifies a secondary ecological gradient characterized by dissolved oxygen (Ox), which appears largely independent of the thermohaline properties of the first axis. A distinct assemblage including *Corolla* sp. (*Co.sp.*), *Diacria* sp. (*Di.sp.*), and *Diacavolinia* sp. (*D.sp.*) showed a strong relationship with current velocity (Vel) and chlorophyll-*a* (Chl-*a*), suggesting that their presence is modulated by water movement and food availability. Furthermore, the vertical orientation of the oxygen vector indicates that taxa such as *Gleba* sp. (*Gl.sp.*) and *Creseis conica* (*C.con.*) are primarily influenced by oxygen concentration. Finally, species clustered near the origin, including *Desmopterus papilio* (*D.pap.*) and *Styliola subula* (*S.sub.*), exhibit a more generalist distribution with less specialization relative to the measured environmental gradients. Eigenvalues of the axes obtained from the CCA are summarized in Table 2.

Table 2. Eigenvalues of the axes obtained from the Canonical Correspondence Analysis.

Axes	1	2	3	4	Total Inertia
Eigenvalues	0.114	0.031	0.022	0.015	0.777
Species–environment correlations	0.720	0.715	0.691	0.679	
Cumulative percentage variance					
Of species data	14.7	18.7	21.5	23.4	

Table 2. Cont.

Axes	1	2	3	4	Total Inertia
Of species–environment relation	59.2	75.4	86.6	94.5	
Sum of all eigenvalues					0.777
Sum of all canonical eigenvalues					0.193

4. Discussion

During our sampling, the water column exhibited pronounced hydrographic and biochemical gradients, reflecting the region’s intense hydrodynamic activity. Local circulation was characterized by a cyclonic eddy that drove strong northeast–southwest currents toward the coastline.

Since the late 1980s, the sGoM, specifically the Bay of Campeche, has been recognized as a highly dynamic region. This dynamism is driven by density gradients from the Grijalva–Usumacinta freshwater discharge, which sustains surface currents of up to 0.12 m/s [32]. Historical hydrographic data from 1958 to 1991 first suggested the presence of a permanent cyclonic circulation in the upper 800 m of the Bay [33]. This feature was subsequently confirmed by surface drifters, satellite altimetry, and direct ADCP measurements [34,35], which identified that its influence extends to a depth of 1000 m. Despite this established physical framework, the role of this circulation in shaping planktonic distribution has only been addressed within the last decade.

The cyclonic circulation in the sGoM facilitates the shoaling of isotherms and isopycnals, a process that pumps nutrient-rich subsurface water into the euphotic zone. This localized enrichment promotes an increase in phytoplankton biomass, dominated by diatoms, coccolithophores, and dinoflagellates [22], which in turn shapes higher trophic levels. Consequently, larval fish assemblages are closely associated with this cyclonic feature, with peak densities concentrated within its area of influence [36]. Recent findings further confirm that high biological diversity in this region coincides with the elevated nutrient and chlorophyll-*a* concentrations intrinsically linked to the regional cyclonic eddy [37]. Although direct nutrient measurements were not available for this study, we infer that concentrations were elevated within the eddy’s area of influence, consistent with the nutrient-pumping mechanism described above.

Pteropod research in the sGoM has long established the region’s high biodiversity, with historical inventories identifying up to 51 species [38,39]. These studies also highlighted substantial seasonal fluctuation richness, with reported counts ranging from 15 species in winter to 29 in spring, 18 in summer, and 27 in autumn [15,17,18,38,40]. Our summer sampling aligns with these historical records, reinforcing the significance of the sGoM as a key habitat for pteropod communities.

Research exploring how circulation patterns in the sGoM influence pteropod communities has only recently emerged. For instance, a dipole eddy (cyclonic–anticyclonic) identified in the Campeche Canyon is now known to fertilize the surface layer, supporting a diverse assemblage of 33 species. While maximum species richness occurs just below the thermocline (at 100 m depth), peak population densities are concentrated in surface waters [13].

Similar patterns were recently documented in the deeper sGoM during the summer, where 32 species were observed under warm (>27.5 °C) and oligotrophic conditions (chlorophyll-*a* < 0.5 mg m⁻³) [19]. In that study, four species (*Heliconoides inflatus*, *Creseis*

conica, *Limacina trochiformis*, and *Creseis acicula*) accounted for 63% of total abundance, a distribution that closely aligns with our observations.

Our findings are consistent with observations from other highly dynamic marine environments where physical forcing dictates pteropod composition, distribution, and abundance. For example, in the South China Sea, 24 species reach peak abundance during summer, primarily within the influence of cyclonic eddies [41]. Similarly, in the California Current System, eddy-associated fronts create sharp hydrographic gradients that foster favorable habitats for regional species [12] and high concentrations have been documented in the Alaska Gyre, particularly for *Clio pyramidata* [7].

As final remarks, the integration of our findings with existing historical and contemporary data confirms that the sGoM is a region of high biodiversity. The transition from early taxonomic inventories to recent mechanistic studies highlights the pivotal role of cyclonic circulation in sustaining pteropod communities. By facilitating nutrient enrichment and creating favorable hydrographic gradients, these eddies act as ecological anchors for pteropods. Our study reinforces the global consensus that cyclonic eddies are essential habitats, providing a critical framework for predicting how these sentinel organisms may respond to future shifts in ocean dynamics. Nevertheless, further investigations are required to evaluate seasonal and interannual variability of these physical parameters and their subsequent influence on zooplankton communities, particularly pteropods.

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