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Seasonal Variations of the Zooplankton Community in the Western Gulf of Mexico: is there an Influence of the Warm Eddy Jumbo?

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In the Gulf of Mexico, the Loop Current sporadically sheds warm anticyclonic eddies that travel into the gulf and whose influence on the zooplankton community of the western region is not known. This research examined the zooplankton community dynamics in the western Gulf of Mexico during three seasons: July 2010 (summer), January 2011 (winter), and October–November 2012 (fall), and the possible effect of the warm eddy called Jumbo, released from the Loop Current in the middle of 2012 and that approached the western side of the gulf at the end of the year. We hypothesized shifts in the composition and/or biomass of the zooplankton fauna collected during the fall period due to the transport of organisms from elsewhere or because of a rapid response of zooplankton to warmer environmental conditions. This could result in a greater similarity of the fall season to the summer rather than to the winter. Zooplankton samples were taken onboard the oceanographic vessel Justo Sierra and a total of 82 oceanographic stations were sampled with a Bongo net; at each sampling station, temperature and salinity were measured with a CTD profiler. Both environmental and zooplankton data were treated through a Principal Coordinate Analysis (PCO) to explore their relationship. Fourteen zooplankton groups were recognized in all three sampling periods, with seasonal variations in biomass. The PCO showed that July was characterized by high-temperature values (~27°C), low chlorophyll concentration (< 1 mg/m^3), the dominance of copepods, chaetognaths, and luciferids, as well as high biomass values of crustacean larvae (decapods stomatopods), signaling this season as the reproductive period. January was characterized by higher chlorophyll concentration (1–1.3 mg/m^3), lower temperatures (18–22°C), and a high biomass of amphipods, ostracods, and jellyfishes; October–November registered similar environmental conditions to July, but the PCO and the associated distance among centroids indicated that the zooplankton community structure was more similar to January. The occurrence of the 14 groups in all the seasons, reveals no shifts in the composition in the study area. Besides, the similarity of the fall to the winter in the zooplankton structure discarded the hypothesis. Our results suggest that the zooplankton community follows its natural seasonal dynamics and shows high resilience to eventual hydrographic phenomena, such as anticyclonic eddies.

Key words: Anticyclonic eddies, Temperature trend, Reproduction, Zooplankton resilience, Sea surface temperature (SST)

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BACKGROUND

The Gulf of Mexico is a semi-enclosed sea, where circulation patterns result from complex interactions between bathymetric mechanisms, wind forcing, atmospheric conditions, water density, and the Loop Current (Oey et al. 2005; Sturges and Kenyon 2008). In the central zone of the gulf, circulation is determined by the Loop Current and the anticyclonic eddies that shed from it. When an anticyclonic eddy sheds, its trajectory starts toward the western or west northwestern gulf, where it meets the continental shelf between the northern end of Veracruz (Mexico) and the south of Texas, and where it dissipates (Vidal and Vidal 1997; Hamilton et al. 1999; Hamilton and Berger 2002; Muller-Karger et al. 2015). In their trajectory, eddies generate currents and redistribute warm and cold water on the ocean surface to ~1000 m depth; therefore, they affect the structure and distribution of the plankton (Biggs et al. 1997; Zavala-Hidalgo and Fernández-Eguiarte 2006). Anticyclonic eddies travel toward the interior of the gulf at speeds of ~6 km/d, with residence times of about 9 to 12 months and shedding intervals from 3 to 17 months (Vidal and Vidal 1997; Sturges and Leben 2000; Oey et al. 2005; Hamilton et al. 2019).

In June 2012, a specific phenomenon occurred in the western central Gulf of Mexico: an anticyclonic eddy called 'Jumbo' was shed from the Loop Current. The eddy Jumbo was characterized by its large size and long duration. In August 2012, it reached a diameter of approximately 247 km, and lasted for about nine months. Once it collided with the continental slope, it dissipated in the northern Veracruz-southern Tamaulipas area, two Mexican states bordering the western gulf (Díaz-Maya 2018; WHG 2023). Besides this sporadic mesoscale hydrographical phenomenon, the river plumes generated in the area modify the physical, chemical, and biological conditions of the pelagic environment (Cruz-Ábrego et al. 1991; Biggs and Ressler 2001; Dagg and Breed 2003). All these mesoscale processes on the continental shelf and the open water of the western gulf drive shifts in the dynamics of the plankton communities.

A vital function of zooplankton in the pelagic ecosystem is the transmission of energy from primary producers to higher trophic levels. Since the organisms of the zooplankton have short life cycles (days, weeks, months, or occasionally years) they respond rapidly to environmental changes (Verity and Smetacek 1996; Litchman et al. 2013). Therefore, understanding the shifts in the zooplankton community structure in response to environmental changes at different scales will allow us a better understanding of the marine pelagic ecosystem of the Gulf of Mexico.

The zooplankton community on the western side of the Gulf of Mexico has been scarcely addressed, encompassing only a few zooplankton groups (López-Salgado et al. 2000; Gutiérrez-Aguirre et al. 2015; Sanvicente-Añorve et al. 2021). To continue the zooplankton exploration in this region, three field surveys were conducted during July 2010 (summer), January 2011 (winter), and October–November 2012 (fall) to examine the seasonal variations of the whole zooplankton community and the possible influence of the eddy Jumbo, that approached the western gulf at the end of 2012, on the hydrological conditions and zooplankton community. We hypothesized shifts in the zooplankton structure of the fall period due to the transport of organisms from the eastern or central gulf or because of a rapid response of zooplankton to warmer water conditions. This could cause the fall period to be more similar to the summer than to the winter.

MATERIALS AND METHODS

Field and laboratory work

The zooplankton samples were taken as part of the project "Environmental Framework of the Oceanographic Conditions in Mexico's Northwestern Exclusive Economic Zone in the Gulf of Mexico" (MARZEE). Sampling was carried out in July 2010, January 2011, and October–November 2012 (Fig. 1) onboard the oceanographic vessel Justo Sierra. In total, 82 stations were sampled using a Bongo net (333 and 505 µm mesh); in each net, a flowmeter was installed to estimate the volume of filter water. The samples were collected following oblique tows; sampling depth varied between 10 to 200 m and towing time between 4 to 25 min, both depending on the bottom depth. Samples were fixed with 4% formaldehyde and neutralized with sodium borate. In each oceanographic station, temperature and salinity were measured with an SBE 9Plus CTD profiler, and chlorophyll concentrations were measured with a Wet Labs FLRTD sensor adapted to the sonde. All measurements were read from the surface down to 1500 m depth, depending on the bottom depth of each station; however, they were graphically represented by taking the mean integrated value in the 50 m surface layer.

In the laboratory, the samples obtained with the mesh size of 333 µm were processed with a Folsom plankton splitter; samples were divided from one to five times depending on the whole zooplankton concentration. From each fraction, the main groups of zooplankton were separated and identified according to specialized literature (Gasca and Suárez 1996; Boltovskoy 1999a b; Johnson and Allen 2012; Castellani and Edwards 2017). Since the whole zooplankton community was taken into account, organisms were classified into taxonomic groups broader than the superfamily level. Afterward, the biomass of each zooplankton group from each sampling station was estimated by removing the interstitial water between

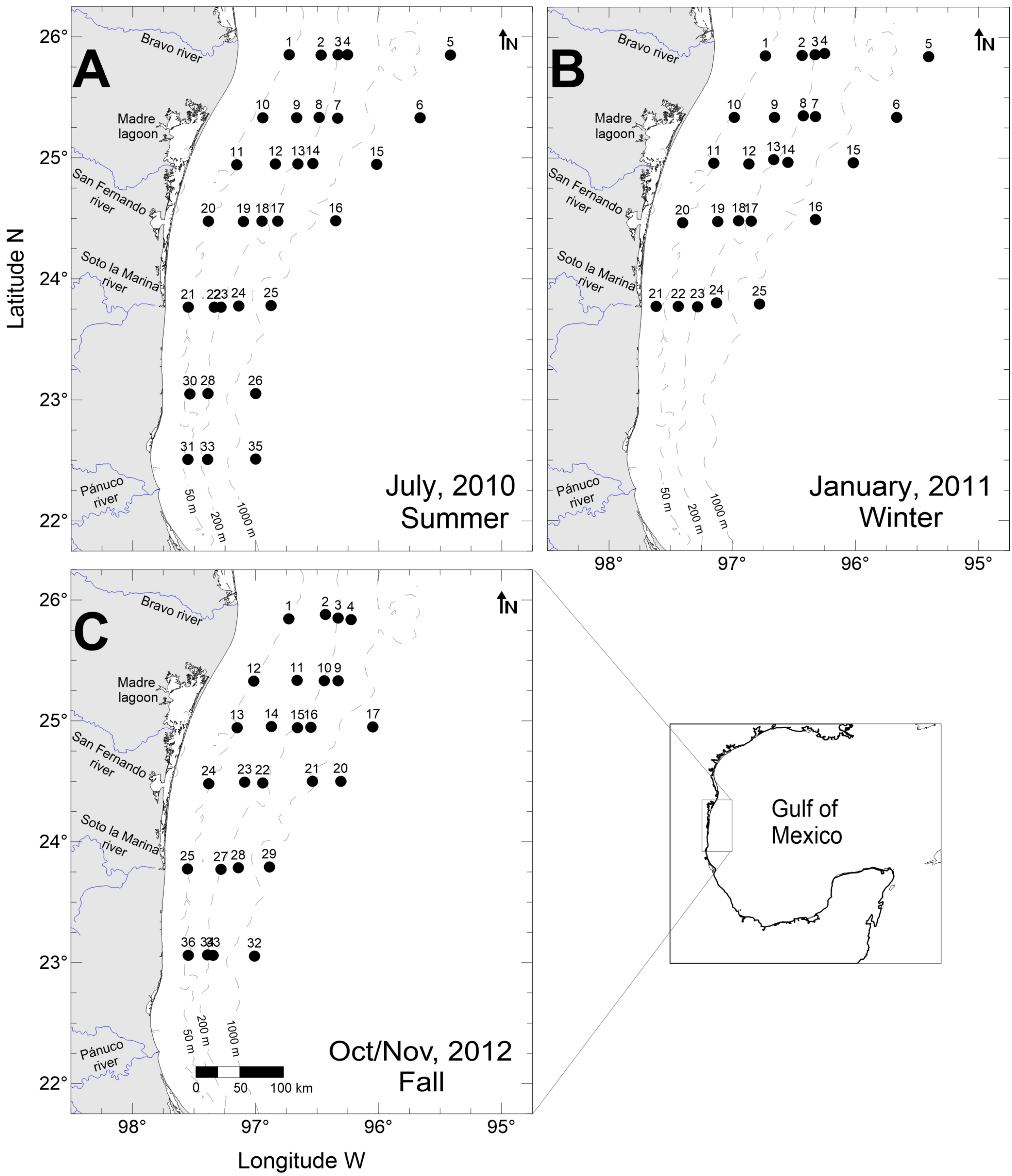

Fig. 1. Study area and sampling sites during the three seasons in the western Gulf of Mexico. A: Cruise MARZEE 1, 31 sampling stations; B: Cruise MARZEE 2, 25 sampling stations; C: Cruise MARZEE 3, 26 sampling stations.

the organisms and transferring the zooplankton to a measuring cylinder with a known volume of water; the displaced volume was standardized to 100 m^3 of water and represented the biomass of each zooplankton group in mL/100 m^3 (Sell and Evans 1982; Postel et al. 2000).

Anticyclonic eddies

Two main eddies were released from the Loop Current during the sampling period, Icarus and Jumbo. According to their size, the Icarus was categorized by scientists as a 'large' eddy (175 km in diameter approximately), whereas the Jumbo, was considered a 'huge' one (247 km in diameter approximately). The Icarus detached from the Loop Current in November 2011 and its lifetime ended in February 2013; at the end of its life, it lost strength and became part of the circulation in the southwest of the Gulf (Hamilton et al. 2016; WHG 2023) (Fig. 2). The Jumbo was released from the Loop Current in June 2012 and dissipated in February 2013; this eddy split into two quasi-separate eddies. At the end of its life, the Jumbo integrated into the circulation pattern in the southwest of the Gulf (Díaz-Maya 2018; WHG 2023) (Fig. 2). Until September 2012, the eddies Icarus and Jumbo were well differentiated, but after that date, it appears that their trajectories joined and dissipated in the southwestern Gulf.

Data analyses

A principal coordinate analysis (PCO) was performed to evaluate the temporal variation in the zooplankton community. This analysis ordinates both environmental and biological similarity matrices allowing us to visualize the proximity between them (Anderson et al. 2008).

This procedure was applied three times. The first one included only environmental parameters (temperature, salinity, and chlorophyll), using a Euclidean distance similarity algorithm with data previously transformed into Log (x+1) and normalized. The second analysis included only biological data (composition and biomass of zooplankton taxa); data was Log (x+1) transformed and the similarity matrix was constructed using the Bray-Curtis index. The third analysis included both matrices (environmental + biological) with the same data treatment mentioned above. In all the analyses, a Pearson correlation higher than 0.5 was employed.

In all the cases, a similarity analysis (ANOSIM) was applied to determine if there were significant differences among seasons. Additionally, the distance among the centroids of the seasons was calculated from the PCOs ordination diagrams to estimate the degree of similarity between each pair of seasons. All analyses were performed using the PRIMER v.7.0.13 software (Clarke and Gorley 2015).

The friction depth, or the Ekman pumping depth, was estimated in some transects to help the understanding of some hydrological characteristics. The friction depth (*De*), indicating the depth at which the wind-driven current becomes insignificant compared to velocity in surface waters, was estimated according to the following equation (Pond and Pickard 1983; Li et al. 2021).

$$D_e = \frac{4.3U_a}{\sqrt{\sin(|\theta|)}}$$

where,
U_a = wind speed (m/s)
θ = latitude (radians)

Surface wind velocities were taken from the Windy Weather Service platform (Windy 2024) for Tamaulipas, and corresponded to 2.64, 2.81, and 3.87 m/s for July, October–November and January, respectively.

Finally, the web resource Atlantic Oceanographic and Meteorological Laboratory of the NOAA (NOAA-AOML 2023) was consulted to complete the temperature data for the hydrological analyses. This web includes monthly and annual time series of the sea surface temperature in the Gulf of Mexico since 1985. All median annual temperatures from 1985–2022 were taken and graphed to visualize the temperature trend in the study area.

RESULTS

The zooplankton in their natural environment

The temperature values in July and October-November were high, around 27°C (Fig. 3A, 3C); the highest values were recorded in July in the northern end of the study area and, two colder patches (26°C) were also observed (Fig. 3A). In January, the temperature showed a clear coastal-ocean gradient, with the lowest values (18.7°C) recorded in the coastal area and the highest (22.8°C) in the oceanic zone (Fig. 3B). Vertical temperature profiles of transects 2 and 5 (from north to south) in July showed an upwelling of colder subsurface water to the surface (Fig. 4) and, estimations of the friction depth in those transects were 17.4 and 17.9 m, respectively. As seen, the friction depth values nearly correspond to the height of the dome resulting from the upwelling of subsurface waters (Fig. 4). This could explain the colder patches observed in July in the temperature horizontal planes (Fig. 3A). Considering a greater temporal scale, and treating the NOAA historical records, the temperature in the Gulf of Mexico had a mean increase of 0.48°C from 1985 to 2022 (*i.e.*, an increase rate of 0.013°C per year) (Fig. 5).

The salinity was less variable. In July it ranged from 36 to 36.5 psu, with the lowest values in the northern study area and off the Soto la Marina River discharge. January recorded the greatest gradient, with the lowest values (33 to 35 psu) on the continental shelf and the highest (36 psu) in the oceanic zone. Finally, October–November had small salinity variations (36.3 to 36.6 psu) (Fig. 6).

The chlorophyll concentration was low in the

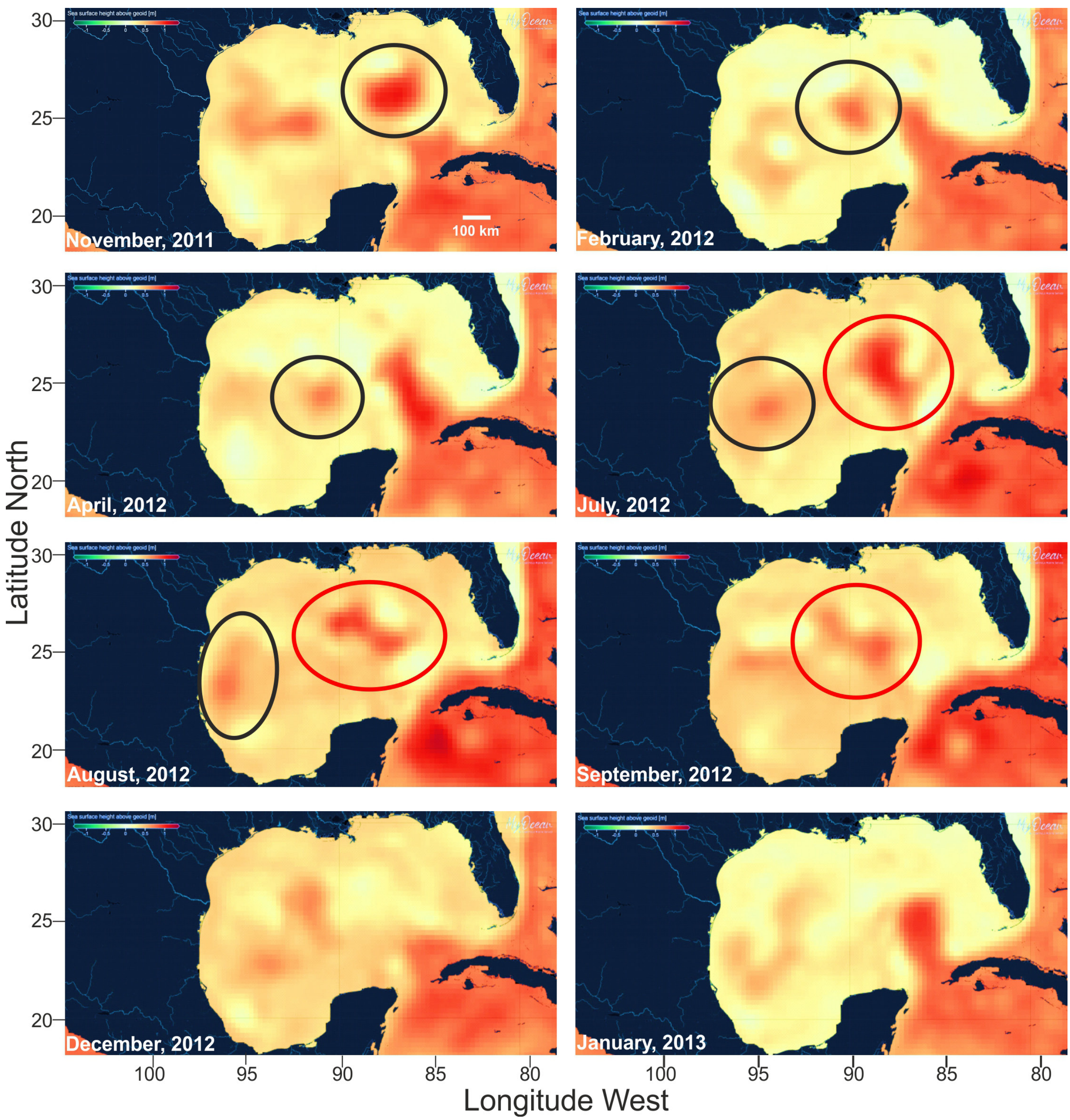

Fig. 2. Trajectories of the eddies Icarus (black circle) and Jumbo (red circle) between 2011–2013 in the Gulf of Mexico. Images taken and modified from an animation from the Copernicus (2024) website.

three sampled seasons (< 1.3 mg/m^3). In January, the highest values of chlorophyll concentration (1 to 1.3 mg/m^3) were recorded near the mouth of the Soto la Marina River. During July and October–November, the chlorophyll values ranged from 0.09 to 1 mg/m^3 (Fig. 7).

The mean zooplankton biomass values varied among the seasons, with the highest records (14.94 mL/100 m^3) in July and the lowest in October–

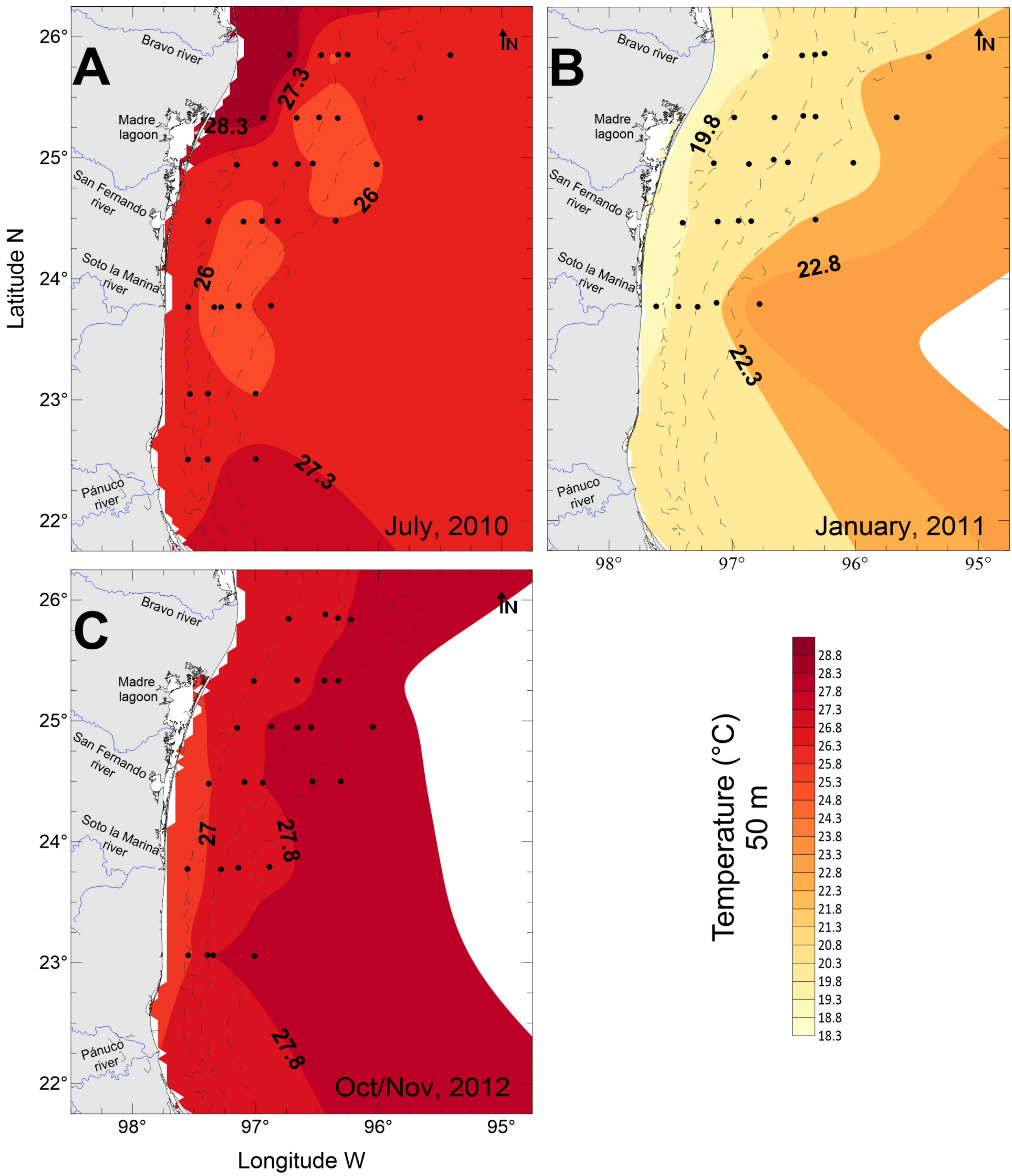

Fig. 3. Mean integrated values of temperature (°C) in the upper 50 m layer in the western Gulf of Mexico. A: July 2010, summer; B: January 2011, winter; C: Oct/Nov 2012, fall.

November (4.83 mL/100 m^3) (Table 1). The zooplankton was classed into fourteen major groups broader than the superfamily level (amphipods, chaetognaths, copepods, decapod larvae in megalopa stage, fish larvae, jellyfishes, luciferids, mollusks, ostracods, polychaetes, salps, shrimp-like decapod larvae, siphonophores, stomatopod larvae). All the groups occurred in all the sampling seasons and most taxa were more abundant

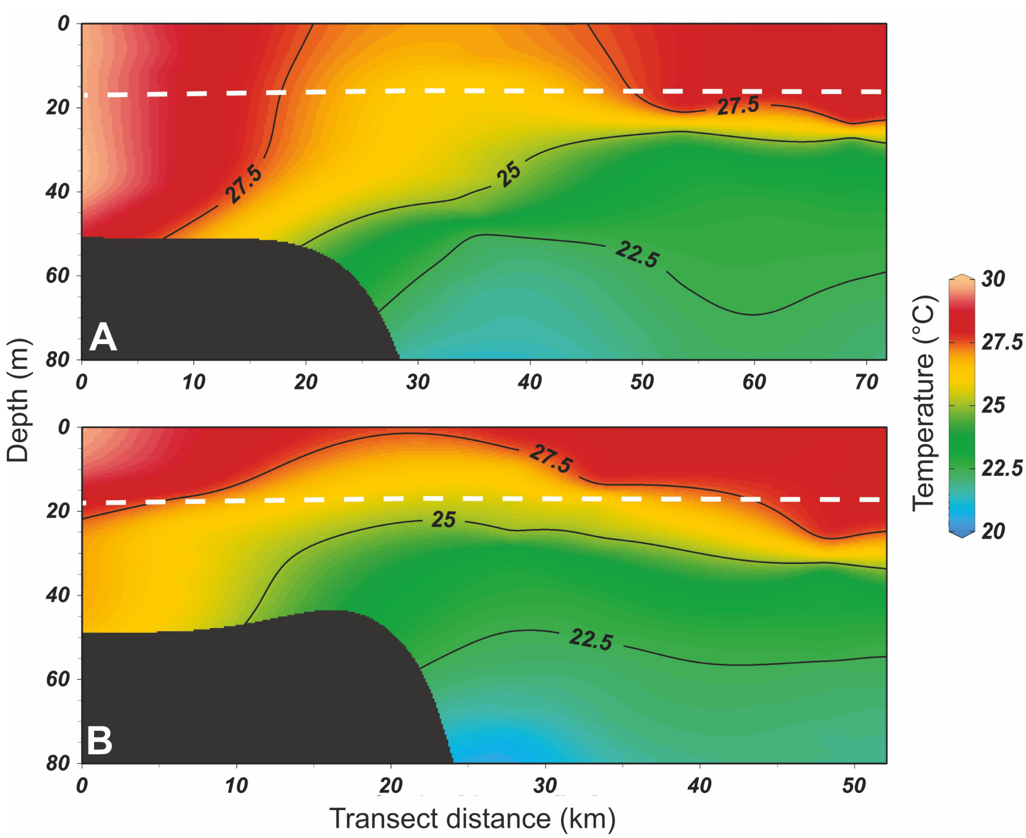

Fig. 4. Vertical temperature profiles of the transects 2 (A) and 5 (B) (from north to south) in July 2010, summer. The dotted lines indicate the friction depth.

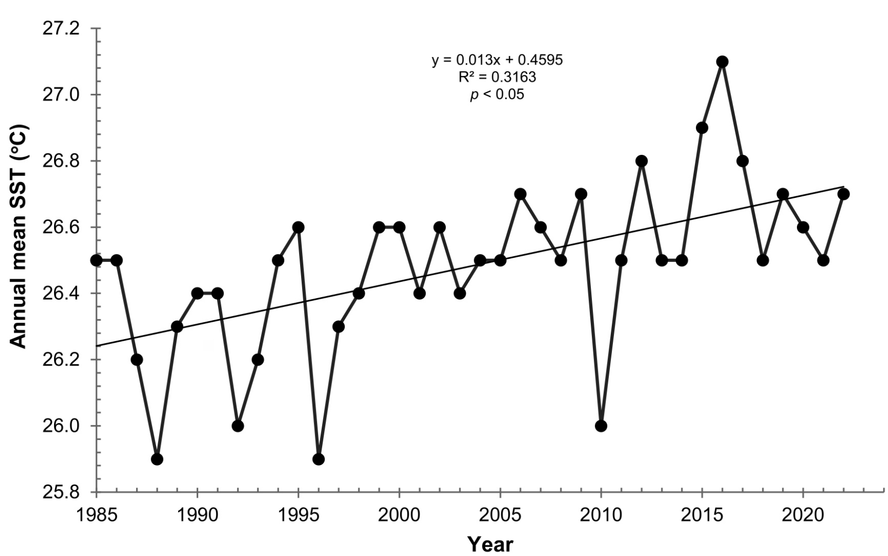

Fig. 5. Variations in the mean Sea Surface Temperature (SST) in the Gulf of Mexico (1985 to 2022) based on data recorded by the Atlantic Oceanographic and Meteorological Laboratory of the NOAA (NOAA-AOML 2023).

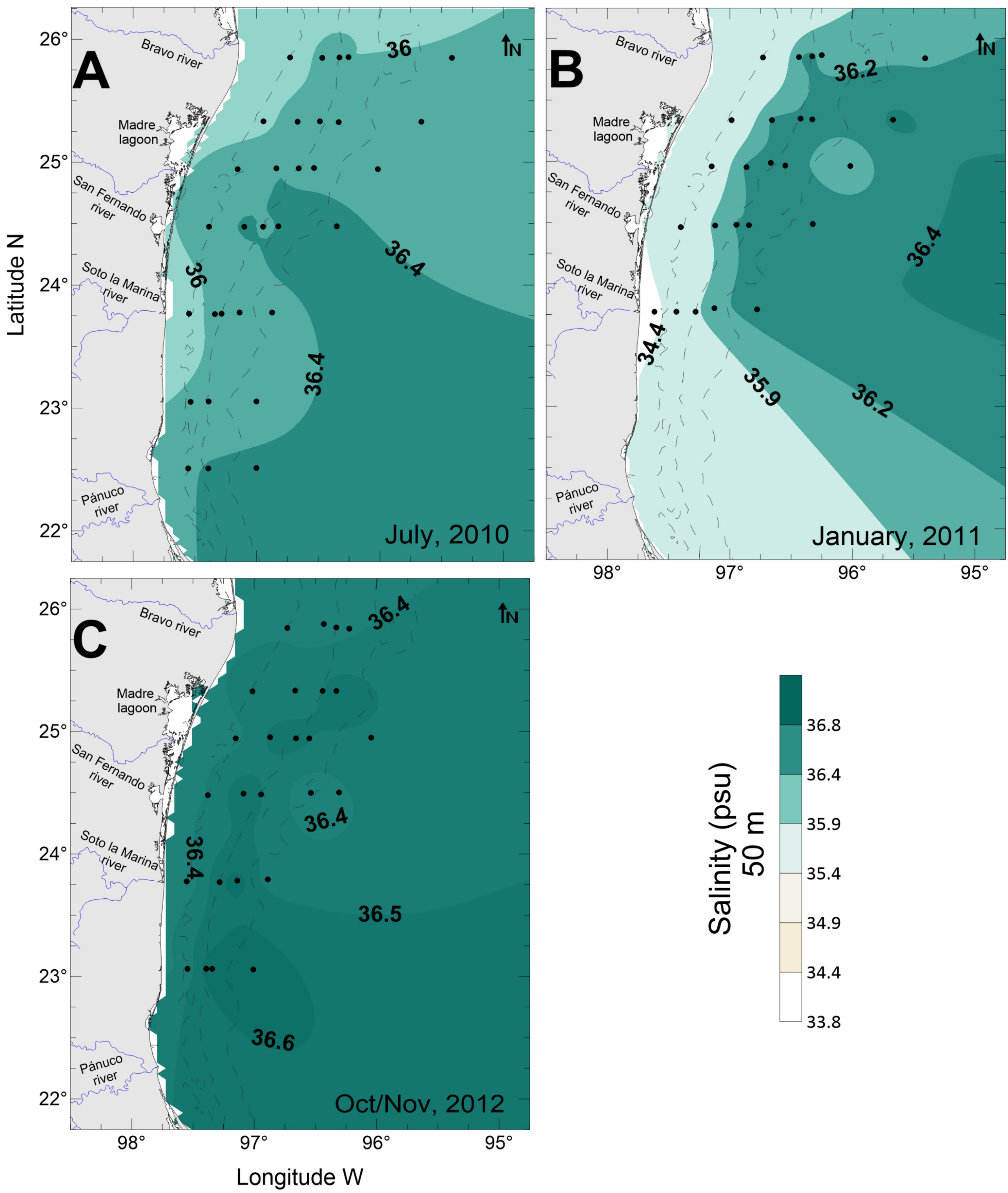

Fig. 6. Mean integrated values of salinity (psu) in the upper 50 m layer in the western Gulf of Mexico. A: July 2010, summer; B: January 2011, winter; C: Oct/Nov 2012, fall.

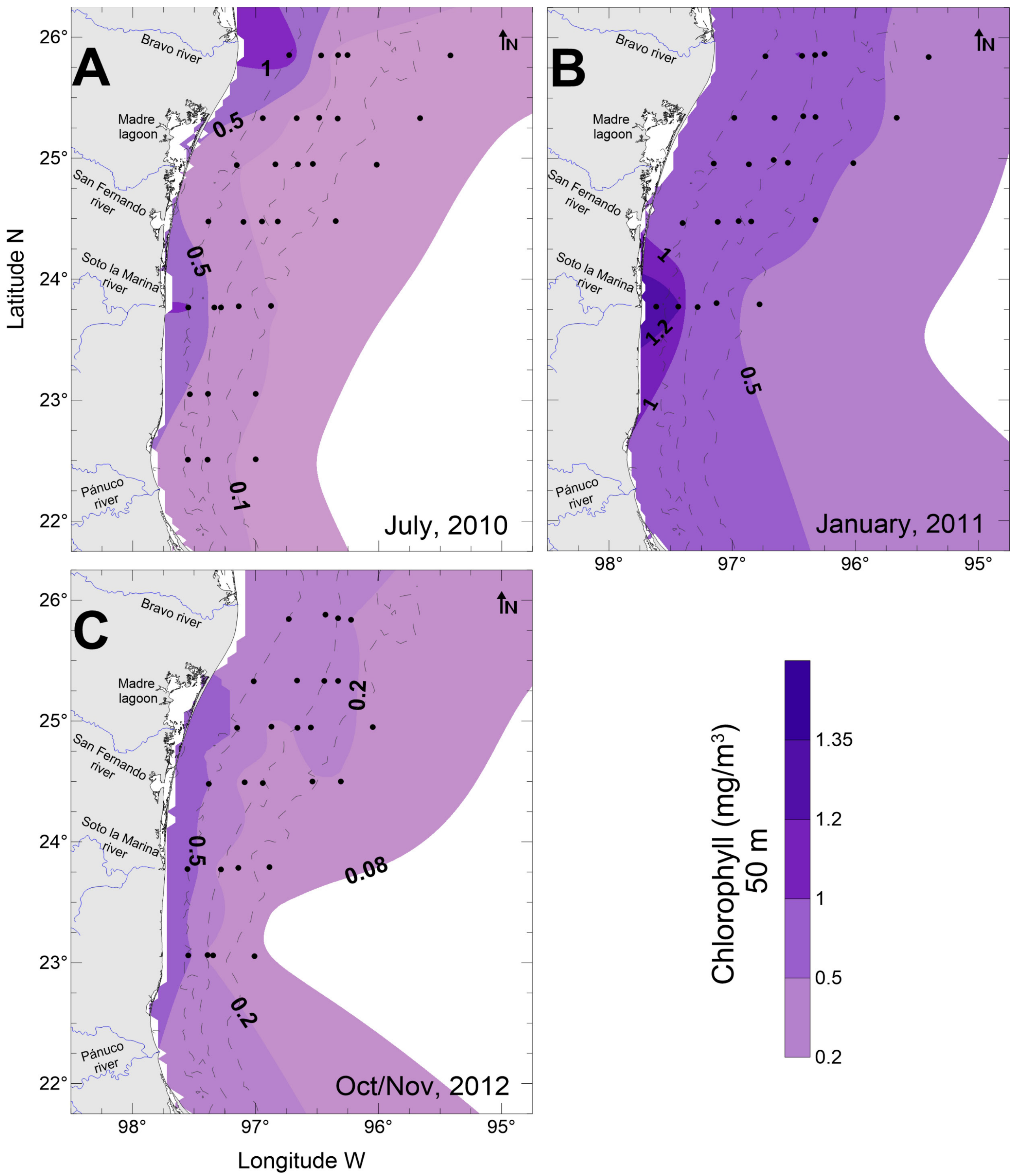

Fig. 7. Mean integrated values of chlorophyll (mg/m^3) in the upper 50 m layer in the western Gulf of Mexico. A: July 2010, summer; B: January 2011, winter; C: Oct/Nov 2012, fall.

during July; the chaetognaths, copepods, and luciferids stand out due to their high biomass (Table 1).

Seasonal variation of environmental and biological data

The PCO applied to the environmental variables (temperature, salinity, and chlorophyll) showed a clear separation of the three sampled seasons. The first two axes explained 88.5% of the total variation (Fig. 8). Furthermore, the ANOSIM test indicated significant differences among the seasons ($p < 0.05$) (Table 2). The highest values of temperature and salinity were associated with July and October–November. Meanwhile, chlorophyll's highest values were related to January (Fig. 7). The distance among centroids showed a closer distance between July and October-November; January showed a clear separation from the other months (Fig. 8; Table 3).

The PCO applied to biological variables also evidenced a separation of the three seasons analyzed; the first two axes explained 49.7% of the total variability (Fig. 9). Furthermore, the ANOSIM test showed significant differences ($p < 0.05$) between sampling seasons (Table 2). The zooplankton taxa associated with July were decapod larvae, stomatopod larvae, decapod larvae in the megalopa stage, luciferids, chaetognaths, copepods, and siphonophores; in January, ostracods, jellyfish, and amphipods (Fig. 9). The distance among centroids of the seasons showed a high biological affinity between October–November and January (Table 4).

Finally, the PCO applied to both the environmental and biological variables showed a high similarity between July and October–November, and the first two axes explained 49.3% of the total variation (Fig. 10; Table 5). The ANOSIM test revealed significant differences ($p < 0.05$) among seasons and the association of environmental and biological data to the seasons was as the previous analyses (Table 2).

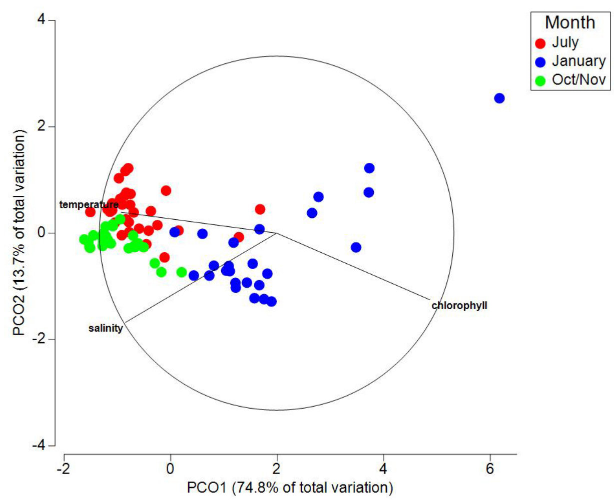

Fig. 8. Principal Coordinates Analysis (PCO) ordination plot applied to the data of environmental variables (temperature, salinity, chlorophyll), based on the Euclidean Distance index.

Table 1. Mean biomass (X, mL/100 m^3) and standard deviation (SD) of zooplankton groups in the three seasons in the western Gulf of Mexico

Taxonomic categories	Zooplankton group	Abbreviation	July, 2010			January, 2011			Oct/Nov, 2012		
			X		SD	X		SD	X		SD
Order	Amphipods	amp	0.10	±	0.21	0.44	±	0.56	0.12	±	0.14
Phylum	Chaetognaths	cha	3.40	±	3.29	1.68	±	1.33	1.25	±	1.50
Class	Copepods	cop	2.95	±	2.84	2.55	±	1.39	1.35	±	0.56
Order	Decapod larvae in megalopa stage	meg	0.37	±	0.84	0.05	±	0.13	0.04	±	0.08
Superclass	Fish larvae	fishl	0.64	±	0.69	0.36	±	0.95	0.22	±	0.16
Subphylum	Jellyfishes	jel	0.25	±	0.41	0.34	±	0.40	0.13	±	0.21
Superfamily	Luciferids	luc	2.48	±	3.92	0.68	±	1.12	0.12	±	0.14
Phylum	Mollusks	mol	0.58	±	1.22	0.38	±	0.48	0.30	±	0.19
Class	Ostracods	ost	0.31	±	0.43	0.67	±	0.93	0.27	±	0.28
Class	Polychaetes	pol	0.06	±	0.12	0.15	±	0.20	0.08	±	0.06
Class	Salps	salp	0.46	±	0.64	0.16	±	0.27	0.19	±	0.29
Order	Shrimp-like decapod larvae	decl	0.96	±	1.60	0.12	±	0.35	0.10	±	0.12
Order	Siphonophores	siph	1.25	±	1.39	0.96	±	1.17	0.57	±	0.40
Order	Stomatopod larvae	stoml	1.14	±	4.45	0.09	±	0.26	0.10	±	0.13
	Total biomass		14.94	±	15.58	8.63	±	5.41	4.83	±	2.37

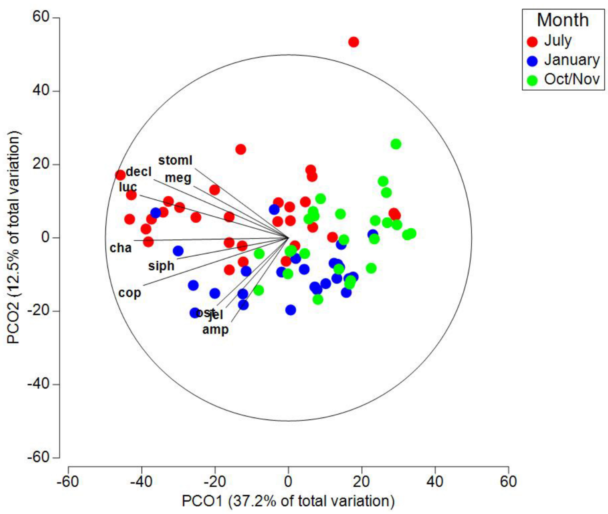

Fig. 9. Principal Coordinates Analysis (PCO) ordination plot applied to biological data (zooplankton abundance and composition) based on the Bray-Curtis similarity index, showing vectors that contributed the most to the variation among seasons (Pearson's correlation > 0.5). Abbreviations are in table 1.

Table 2. Results of ANOSIM permutation-based hypothesis test for environmental, biological, and environmental/biological

Pairwise test	R statistic	*p*-value
Environmental variables		
July, January	0.694	0.0001
July, Oct/Nov	0.413	0.0001
January, Oct/Nov	0.801	0.0001
Biological variables		
July, January	0.18	0.0001
July, Oct/Nov	0.294	0.0001
January, Oct/Nov	0.191	0.0001
Environmental/biological variables		
July, January	0.217	0.0001
July, Oct/Nov	0.123	0.006
January, Oct/Nov	0.403	0.001

Table 3. Distance among centroids of the PCO applied to environmental variables (temperature, salinity, chlorophyll)

Month	July	January	Oct/Nov
July	-	-	-
January	2.55	-	-
Oct/Nov	0.78	2.91	-

DISCUSSION

Temperature and salinity showed similar values in July and October-November (Figs. 3 and 6), which was evidenced by the PCO (Fig. 8) and the smallest distance between centroids (Table 3). In the Gulf of Mexico, the temperature during the summer shows a uniform warming at the sea surface (around 27°C) and is maintained for a period of three to four months (Müller-

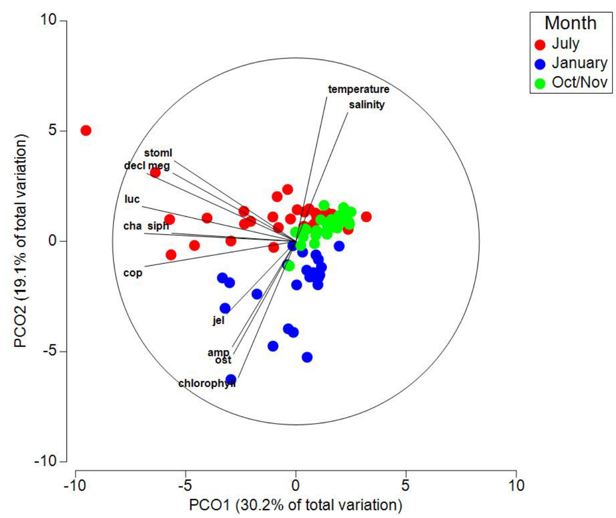

Fig. 10. Principal Coordinates Analysis (PCO) ordination plot applied to environmental/biological variables based on the Euclidean Distance index, showing vectors that contributed the most to the variation among seasons (Pearson's correlation > 0.5). Abbreviations are in table 1.

Table 4. Distance among centroids of the PCO applied to the biological variables

Month	July	January	Oct/Nov
July	-	-	-
January	22.11	-	-
Oct/Nov	28.24	20.85	-

Table 5. Distance among centroids of the PCO applied to environmental/biological variables

Month	July	January	Oct/Nov
July	-	-	-
January	3.51	-	-
Oct/Nov	2.62	3.36	-

Karger et al. 1991; Sturges and Leben 2000; Chassignet et al. 2005); in the center of the Gulf of Mexico the temperature reaches 29–30°C (Muller-Karger et al. 2015). Higher temperatures observed in this season may also cause a strong stratification of the water column leading to a reduction of nutrients in the euphotic zone (Lalli and Parsons 1993; Gargett and Marra 2002); this could explain the low levels of chlorophyll recorded in July (Fig. 6A). The colder oval patches (26°C) observed in July (Fig. 3A) were probably a consequence of an isothermal doming that resulted from an eddy-Ekman pumping induced by the wind (Fig. 4).

Considering the wind and rainy seasonal regime, the region is characterized by three meteorological periods: 'dry' season, from February to May; 'rainy' season from June to September, and 'nortes' season, from October to February, characterized by cold north winds and occasional strong storms (Yáñez-Arancibia and Day 1982). The cold air outbreaks during the nortes season affect the shelves in the western Gulf (Martínez-López and Zavala-Hidalgo 2009); then, one could expect that the beginning of the nortes period could result in a decrease in the sea surface temperature; however, the temperature recorded in this study in October–November 2012 was high (~27°C). This could be due to two factors: 1) the influence of the anticyclonic eddy Jumbo shed from the Loop Current in June 2012 (WHG 2023) and, 2) the trend in the increase in temperature of the Gulf of Mexico, in which October usually shows the maximum rate of increase (Li et al. 2022). The eddies detached from the Loop current have a warm core and during their movement through the gulf they affect the hydrographic properties of surface and subsurface waters (Sturges et al. 2003). However, the eddies are not the only causes affecting these properties, but also the global increase in temperature in the oceans. In the particular case of the Gulf of Mexico, the rate of increase is less than 1/50 of a degree (Fig. 5).

January recorded the lowest temperatures (18.7 to 22.8°C); these values are comparable to those observed in the central Gulf of Mexico during winter (Müller-Karger et al. 1991). Also, January recorded the highest values of chlorophyll (0.5 to 1.3 mg/m^3), which could result from the transport of waters from the north, off the Mississippi and Atchafalaya rivers, which induce an increase in primary productivity (Zavala-Hidalgo et al. 2006).

The PCO applied to the biological variables (Fig. 9) and the corresponding ANOSIM test, evidenced differences between the seasons (Table 2). In July, the high biomass of copepods, chaetognaths, luciferids, and larvae (stomatopods, decapods, and megalops) stood out, which is a sign of the reproduction season. Previous studies indicated that reproduction in zooplankton organisms is continuous in tropical regions (Alvariño 1990; Bauer 1992). For most of the aforementioned groups, the studies in the southern Gulf of Mexico indicated that the greatest reproductive activity occurs during the warm season (Gómez-Ponce and Gracia 2003; Maynou et al. 2004; Sanvicente-Añorve et al. 2021; Sierra-Zapata 2021). In temperate regions, high temperatures trigger marked breeding events in comparison with low latitudes (Bauer 1992; Landeira and Lozano-Soldevilla 2018).

In January, the amphipods, ostracods, and jellyfish were associated with low temperatures (< 20°C) and a high concentration of chlorophyll (Fig. 9). Previous studies showed that these groups inhabit high-productivity areas due to their wide feeding habits (*i.e.*, omnivores, detritivores, and carnivores) which allowed them to feed from a wide variety of particles and organisms (Alvariño 1985; Gasca et al. 2009; Gutiérrez-Aguirre et al. 2015). The high concentration of chlorophyll in the zone could be due to the Mississippi and Atchafalaya rivers discharges (Zavala-Hidalgo et al. 2006).

Previous studies showed clear seasonal variations of the aforementioned groups in the southern Gulf and other world areas, supporting the results of this study. For copepods, the most abundant group in the zooplankton realm, seasonal changes in their structure, abundance, and dominance of species have been observed at several latitudes (Ortner et al. 1989; Magalhães et al. 2009; Dzierzbicka-Glowacka et al. 2018). Regarding the chaetognaths, Nagai et al. (2008) found a replacement of dominant species as a result of inter-specific responses to environmental conditions in the Japan Sea, and Sierra-Zapata (2021) observed that the main difference between seasons was the abundance of organisms rather than the dominance of species, in the southern Gulf of Mexico. Also, in the southern Gulf, the luciferids showed marked seasonal differences in abundance and size structure of individuals (Sanvicente-Añorve et al. 2021). As stated, the ostracods have been related to low temperatures; in the Adriatic Sea, Brautović et al. (2006) observed a major abundance of ostracods during the cold period probably related to a higher abundance of gelatinous and semi-gelatinous zooplankton in the area.

The October–November (fall) sampling period showed intermediate conditions: it was more similar to July (summer) taking into account only the environmental characteristics (Fig. 8; Table 3), but more similar to January (winter), considering only biological data (Fig. 9; Table 4), and both environmental and biological data (Fig. 10; Table 5). Regarding zooplankton biomass values, October–November was more similar to January (Table 1). The seasonal variability of zooplankton biomass recorded in this study was on the same order of magnitude as the NOAA historical records (1982–2020) of annual mean zooplankton biomass in the Gulf of Mexico (NOAA-NMESW 2024). Even if the 14 zooplanktonic groups were recorded in the three sampled seasons, the main difference in the community structure during the annual cycle was their relative biomass values (Table 1); this result discards shifts in the composition during the fall period. Low zooplankton biomass recorded in October–November (Table 1) were probably influenced by low-productivity waters coming from the deep oceanic zone (Salmerón-García et al. 2011). Besides, our hypothesis stated more biological resemblance between the fall and the summer due to similarities in environmental conditions, especially temperature (Fig. 3) due to the proximity of the eddy Jumbo; however, results indicated that the fall was more similar to the winter (Fig. 9; Table 4). The origin of organisms over neritic and oceanic waters in October–November is difficult to prove; however, a supposed shift in the composition, *i.e.*, the presence of euphausiids, would indicate a transport of these organisms from the central Gulf where they are very common (Biggs and Ressler 2001), but this was not the case. Cyclonic and anticyclonic eddies can drive different zooplankton communities relative to the surrounding waters and regions (Belkin et al. 2022). Often, cold cyclonic eddies upwell nutrient-rich water increasing biological productivity (Huggett 2014); however, certain hydro-meteorological conditions may cause a strong stratification that suppresses the rise of nutrients (Mikaelyan et al. 2023). In contrast, anticyclonic eddies deepen nutrients and are relatively unproductive (Dufois et al. 2014); nevertheless, a warm-core eddy could contain high zooplankton biomass if it originated in slope or shelf-productive waters (Strzelecki et al. 2007; Liu et al. 2020). Moreover, Cummings (1983) observed that an anticyclone was not biologically different from a cyclone, in the western Gulf of Mexico. Similarly, our findings suggest that higher temperatures presumably caused by the anticyclonic eddy Jumbo in the fall (Díaz-Maya 2018) and/or the trend in the temperature increase did not influence the zooplankton biomass. In fact, the rate of temperature increase in the last 38 years is only 0.013 degrees per year ($p < 0.05$) (Fig. 5), perhaps not enough to detect changes in the zooplankton structure in about four decades. Several studies have suggested that zooplankton show slow and gradual responses to climate change (Stegert et al. 2010; Reygondeau and Beaugrand 2011). In marine systems, physical phenomena manifest in spatial and temporal scales of continuous and overlapped dimensions; these features interact with biological processes at the same scales and drive the patterns of plankton distribution (Haury et al. 1978; Sanvicente-Añorve et al. 2000). Therefore, we think that the evolutionary reproductive cycles of zooplankton communities are stable and difficult to disrupt, especially by occasional oceanographic phenomena, such as eddies.

CONCLUSIONS

In the Gulf of Mexico, the Loop Current sheds large warm anticyclonic eddies that move towards the west and eventually dissipate near the western Mexican slope. As an anticyclonic eddy approach to the western margin, it modifies the water properties, but with unknown consequences for the planktonic fauna. In the middle of 2012, the warm core eddy Jumbo detached from the Loop Current and approached the Mexican side at the end of the year. In this research we examined seasonal dynamics of the zooplankton during three sampling periods (July 2010, summer; January 2011, winter; October–November 2012, fall) under the hypothesis of a shift in the zooplankton structure during the fall period due to the transport of foreign organisms or a rapid response of zooplankton to warmer conditions induced by the eddy Jumbo; this would cause a more resemblance between the fall to the summer, instead to the winter. We recognized fourteen zooplankton groups, all of them present in the three sampling periods, with variations in their relative biomass values; this result discards a shift in the zooplankton composition. The multivariate analysis applied in three steps (environmental data, biological data, both of them) indicated an intermediate position of the fall period: it was more similar to the summer in environmental conditions, but considering the zooplankton community structure, it showed a greater resemblance to the winter. These findings reject our hypothesis and lead us to suggest that the zooplankton community in the western gulf is resilient to sporadic changes in water conditions, such as the arrival of warm eddies. Besides the influence on zooplankton biodiversity, researches incentive the study of the Loop Current because its importance on fisheries productivity, hurricane prediction and safety of oil rig operations in the Gulf.

List of abbreviations

amp, amphipods.
cha, chaetognaths.
cop, copepods.
meg, decapod larvae in megalopa stage.
fishl, fish larvae.
jel, jellyfishes.
luc, luciferids.
mol, mollusks.

ost, ostracods.
pol, polychaetes.
salp, salps.
decl, shrimp-like decapod larvae.
siph, siphonophores.
stoml, stomatopod larvae.

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Authors' contributions: ELS and LSA carried out the fieldwork; ELS made laboratory analysis; ELS, LSA, and MAM analyzed the data; ELS and LSA wrote the manuscript. All authors revised and approved the manuscript.

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Availability of data and materials: The material analyzed is available at the Laboratorio de Ecología de Sistemas Pelágicos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. The zooplankton dataset generated and analyzed in this study is available in a SEANOE repository (Lemus Santana and Sanvicente Añorve 2024).

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