e ISSN: 0718-1957
RBMO
Revista de Biología Marina y Oceanografía
Vol. 60(1): 24-33, 2025
<https://doi.org/10.22370/rbmo.2025.60.1.5476>

OPEN ACCESS

ARTICLE

Contrasting winter and summer wet zooplankton biomass in a semi-enclosed bay in the southwestern Gulf of California

Comparación de la biomasa zooplanctónica húmeda entre verano e invierno en una bahía semi-cerrada del suroeste del Golfo de California

Karina Isabel Mariano-Peguero[1], Elizabeth Durán-Campos[2*], María Adela Monreal-Gómez[3], Erik Coria-Monter[3], David Alberto Salas-de-León[3], Franco Antonio Rocha-Díaz[4], Sarai García-Mirafuentes[4] and Benjamín Quiroz-Martínez[3]

[1]Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Estado de México, Mexico
[2]Escuela Nacional de Ciencias de la Tierra, Universidad Nacional Autónoma de México, Ciudad Universitaria, CDMX, Mexico
[3]Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, CDMX, Mexico
[4]Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, CDMX, Mexico
*Corresponding author: duranelizabethster@gmail.com

Resumen.- La biomasa del zooplancton es un indicador indirecto de producción secundaria y una medida que permite realizar estimaciones sobre la disponibilidad de materia en la trama trófica. Este estudio compara la biomasa húmeda de zooplancton dentro de la Bahía de La Paz, el cuerpo de agua costero más grande y profundo en el Golfo de California, México, en dos épocas contrastantes (invierno y verano) y analizó el papel del forzamiento físico en sus valores y distribución. Se realizaron dos cruceros oceanográficos, en febrero 2006 y agosto 2009, donde se adquirieron datos hidrográficos de alta resolución y se colectaron organismos de zooplancton. Los resultados mostraron cambios en las propiedades hidrográficas de la columna de agua. El patrón de circulación estuvo dominado por la presencia de un vórtice ciclónico bien definido con diferentes velocidades azimutales, con mayor intensidad en verano (75 cm s^{-1}) que en invierno (20 cm s^{-1}). La biomasa de zooplancton fue ligeramente menor en invierno (43,4 g 100 m^{-3}) que en verano (45,5 g 100 m^{-3}). Las biomasas de zooplancton más altas se observaron en las estaciones someras, cercanas a la costa, y en la conexión con el Golfo de California. Sin embargo, se observaron valores altos secundarios en las periferias de los vórtices, describiendo un patrón de distribución circular siguiendo su circunferencia, lo que podría atribuirse a: 1) los vórtices retienen a los organismos del zooplancton y los advectan hacia su periferia, y 2) procesos de mezcla en las periferias de los vórtices aseguran alimento (fitoplancton) para los organismos del zooplancton.

Palabras clave: Zooplancton, distribución horizontal, vórtice ciclónico, estacionalidad, Bahía de La Paz

Abstract.- Zooplankton biomass is an indirect proxy of secondary production and a measure that allows estimates to be made about the availability of matter in the food web. This study compares the wet biomass of zooplankton within the Bay of La Paz, the largest and deepest coastal water body in the Gulf of California, Mexico. It analyzes the influence of the physical forcing in zooplankton biomass and distribution. Two research cruises were conducted in February 2006 and August 2009, recording high-resolution hydrographic data and collecting zooplankton. The hydrographic properties of the seawater column changed in both seasons. The circulation pattern was dominated by a well-defined cyclonic eddy with different azimuthal velocities, being more intense in summer (75 cm s^{-1}) than in winter (20 cm s^{-1}). Zooplankton biomass showed slightly lower values in winter (43.4 g 100 m^{-3}) than in summer (45.5 g 100 m^{-3}). Its horizontal distribution showed that the highest values were observed in the shallow stations, close to the coast, and in the connection with the Gulf of California. However, high secondary values were observed at the eddy's peripheries, describing a circular distribution pattern following their circumference, which could be attributed to 1) eddies retain zooplankton organisms and advect them to their periphery, and 2) mixing processes at the eddies peripheries ensure food (phytoplankton) for zooplankton organisms.

Key words: Zooplankton, horizontal distribution, cyclonic eddies, seasonality, La Paz Bay

Article information

Received: 12/01/2024

Accepted: 25/04/2025

Editor responsible: Pilar Muñoz Muga

Peer review is the responsibility of the RBMO-UV editorial team and is conducted using a double-blind method.

How to cite in RBMO style

Mariano-Peguero KI, E Durán-Campos, MA Monreal-Gómez, E Coria-Monter, DA Salas-de-León, FA Rocha-Díaz, S García-Mirafuentes & B Quiroz-Martínez. 2025. Contrasting winter and summer wet zooplankton biomass in a semi-enclosed bay in the southwestern Gulf of California. Revista de Biología Marina y Oceanografía 60(1): 24-33. <https://doi.org/10.22370/rbmo.2025.60.1.5476>

Introduction

Biomass, classically defined as the weight of organic matter present in a given area (g 100 m^{-3}) during a given period (Odum 1963), represents an ecological indirect proxy of biological production in any ecosystem. Its quantification is an initial step to estimate the availability of organic and, sometimes, inorganic matter and energy throughout the food webs (Steinberg & Landry 2017, Drago *et al.* 2022).

Marine zooplankton is a complex and diverse group of species that inhabits the world's oceans, it is represented by practically all phyla in the marine environment playing a fundamental function in the biogeochemical cycles. The quantification of zooplankton biomass is an indirect proxy of secondary production and is a measure of matter available from the base of the food web to organisms at higher trophic levels (including species of high ecological and economic value) allowing the evaluation of the productive potential of the ocean (Irigoien *et al.* 2004, Brierley 2017, Hernández-León *et al.* 2019). The quantification of zooplankton biomass also allows the estimation of the carbon amount that can be transferred to the oceans' interior (Burd & Thomson 2022).

Zooplankton biomass is highly variable in space and time. It is dependent on multiple physical factors (*e.g.*, temperature, salinity, density) and hydrodynamic processes that occur in the sea water column (*e.g.*, internal waves, fronts, eddies) (McGillicuddy 2016, Woodson 2018). Sea water temperature has been postulated as the primary physical driver of zooplankton biomass rates in the North Sea (Nicolas *et al.* 2014). Increases in sea surface temperature have been related to a long-term decline in zooplankton biomass on the Patagonian Shelf, Argentina (Cepeda *et al.* 2022), while seasonal and interannual variations in zooplankton biomass have also been associated with changes in the temperature regime related to the confluence of large-scale processes (such as the Pacific decadal oscillation in the Sea of Japan), suggesting that zooplankton biomass increases on average during the cold-water regime (Kodama *et al.* 2022). Salinity has also been postulated as one of the main physical factors controlling zooplankton biomass, mainly in the epipelagic layer in different marine environments worldwide (Drago *et al.* 2022).

The physical conditions that determine changes in zooplankton biomass have been investigated in Mexican waters during the last two decades. For example, in the southern Gulf of Mexico, Vera-Mendoza & Salas de León (2014) evaluated zooplankton biomass near the region where the Coatzacoalcos River joins the open gulf, reporting salinity as the main physical factor driving zooplankton biomass. Later, Zavala-García *et al.* (2016) analyzed the magnitude of freshwater discharge volume of the Grijalva-Usumacinta River system in the southern Gulf of Mexico, concluding that seasonal fluctuations in freshwater discharge control the zooplankton biomass in the region. Changes in the sea water column temperature regime have also been postulated as the main physical factor determining fluctuations in zooplankton biomass in the southern Gulf of Mexico (Espinosa-Fuentes *et al.* 2009). Studies on the influence of the hydrography and the circulation pattern of the southern Gulf of Mexico on zooplankton populations in the last years displayed that the presence of cyclonic eddies induced high nutrient concentrations and high values of zooplankton biomass (Färber-Lorda *et al*. 2019). In this regard, Fuentes-Martínez *et al.* (2022) assessed zooplankton biomass rates and their horizontal distribution in the Campeche Canyon, southern Gulf of Mexico, revealing a circulation pattern dominated by the presence of eddies (both cyclonic and anticyclonic) that strongly influence the distribution of zooplankton organisms inducing high biomass values in association with cyclonic eddies.

In the Gulf of California, some works have addressed the role of the physical forcing on the zooplankton populations, showing that sea water temperature (Lavaniegos-Espejo & Lara-Lara 1990), salinity levels (Farfán & Álvarez-Borrego 1992) and the presence of eddies (Salas-de-León *et al.* 2011) strongly influence the zooplankton biomass. In Cabo Pulmo, located in the southern Gulf of California, a recent study indicates that certain zooplankton populations are undergoing changes in their composition, abundance, and biomass due to extreme and unusual warming events. These warming events have resulted in a decline in these parameters and have led to a dominance of species with tropical affinities (Beltrán-Castro *et al.* 2020).

Particularly in the Bay of La Paz, the biomass, abundance and distribution of some zooplankton groups (*e.g.,* euphausiids) are influenced by the changes that exist in the temperature regime between February and August, generating higher biomass values during the coldest months (De Silva-Dávila & Palomares-García 2002).

These studies have been very valuable in elucidating some environmental variables' role in zooplankton groups distribution. However, the circulation pattern's role in the zooplankton biomass of the Gulf of California and adjacent regions, such as the Bay of La Paz, still needs to be addressed.

This study aimed to compare zooplankton biomass and its relationship with the hydrography and the circulation pattern within the Bay of La Paz during winter and summer, based on high-resolution hydrographic data and zooplankton samples that were acquired in two oceanographic cruises on board the R/V El Puma operated by Universidad Nacional Autónoma de México. This study hypothesizes that the significant climatic differences between winter and summer in the region will lead to changes in the hydrographic properties of the water column and circulation patterns. These changes are expected to affect zooplankton biomass values and their distribution patterns. By presenting wet biomass values during two contrasting seasons, this research enhances the understanding of zooplankton dynamics in Bay of La Paz, particularly highlighting the role of eddies influencing these dynamics.

Materials and methods

Study area

The Bay of La Paz is located in the southwestern portion of the Gulf of California (Fig. 1a). The bay area is about 2,400 km^2 (Durán-Campos *et al.* 2020). It is the largest and deepest bay (420 m of maximum depth) in the Gulf of California (Fig. 1b). Several groups of organisms inhabit the Bay of La Paz, including species with ecological and commercial value, some of these species are endangered (Durán-Campos *et al.* 2020). The high biodiversity has been closely related to its circulation pattern dominated by the presence of a quasi-permanent cyclonic eddy (Monreal-Gómez *et al.* 2001) that induces an Ekman pumping with nutrients fertilizing the euphotic zone to which the phytoplankton responds, triggering a bottom-up mechanism that positively impacts the upper levels of the pelagic trophic web (Coria-Monter *et al.* 2017). Additional processes such as internal waves, thermohaline fronts, and hydraulic jumps have been related to the high biological production within the Bay of La Paz (Coria-Monter *et al.* 2019a, Durán-Campos *et al.* 2019, Rocha-Díaz *et al.* 2021).

The thermohaline structure of the bay includes the presence of four main water masses: 1) the warm, salty Gulf of California Water (GCW, S > 35 and T > 12 ºC), 2) the Subtropical Subsurface Water (StSsW, 34.5 < S < 34.9 and 9 ºC < T < 18 ºC), 3) the Tropical Surface Water (TSW, S < 34.6, T > 25.1 ºC), and 4) the Pacific Intermediate Water (PIW, 34.6 < S < 34.9 and 4 ºC < T < 9 ºC) which is restricted to the region connecting the bay to the Gulf of California (Torres-Orozco 1993, Lavín *et al.* 1997, Lavín & Marinone 2003). The TSW mass is typically related to the presence of El Niño events that potentially impact the region, which also affects the trophic status of the interior of the bay and confers low phytoplankton biomass values in the bay (Monreal-Gómez *et al.* 2001, Coria-Monter *et al.* 2019b).

The Bay of La Paz is highly variable, with two contrasting seasons. During the winter, the atmospheric circulation pattern is characterized by intense (> 12 m s^{-1}) and persistent dry and cold northwesterly winds, affecting the region from December to March. During the summer, the circulation pattern is reversed, with winds of the southeast component that are characterized by being wet, warm and low speed (< 4 m s^{-1}) associated with frequent

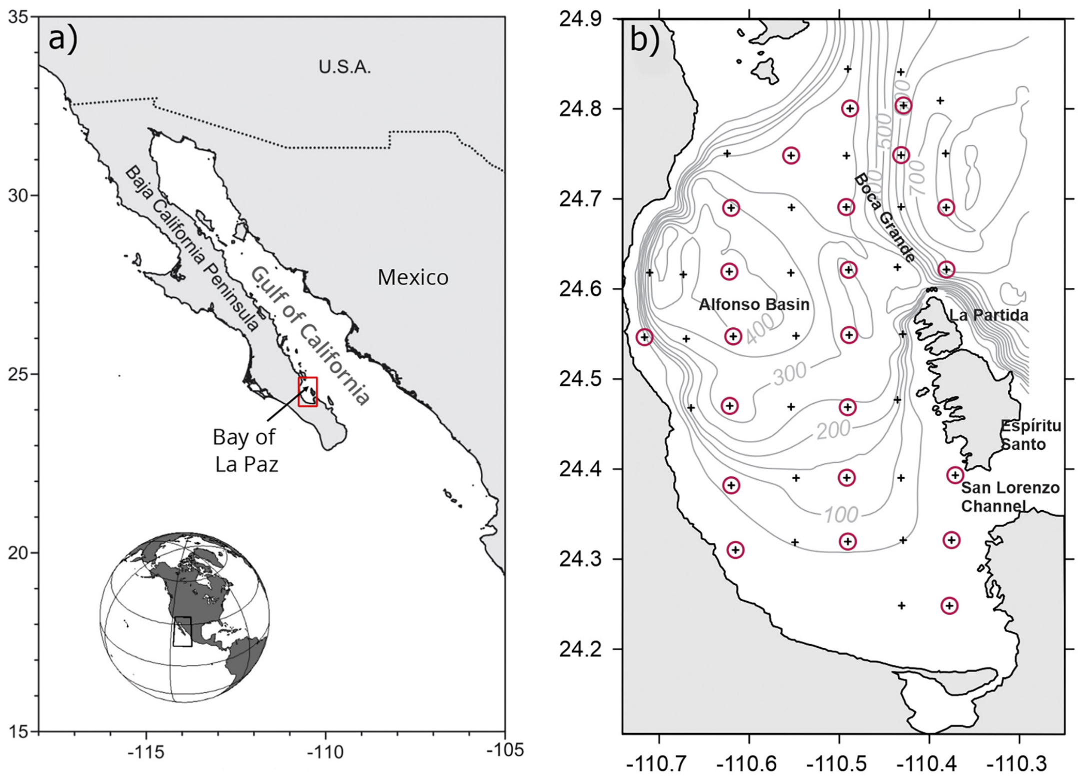

Figure 1. a) Map of the Gulf of California, Mexico and b) study area in the Bay of La Paz. The plus sign (+) represent the stations in which a CTD sonde was used to acquire hydrographic data. Circles in red represent stations in which zooplankton organisms were collected. The bathymetry is shown in meters / Mapa del Golfo de California, México, área de estudio en la Bahía de La Paz. El símbolo más (+) representa las estaciones en las que se utilizó una sonda CTD para adquirir datos hidrográficos. Los círculos rojos representan las estaciones en las que se recolectaron organismos zooplanctónicos. La batimetría se muestra en metros

calms from June to September (Monreal-Gómez *et al.* 2001). This seasonal wind pattern has a strong impact because it induces mixing of the water column during winter (which benefits phytoplankton communities, and therefore zooplankton), but also induces an alternation in the depth of the thermocline/pycnocline, being deeper during winter (> 50 m) than during summer (25-30 m) (Durán-Campos *et al.* 2020).

Sampling

This study is based on hydrographic data and zooplankton samples collected in the Bay of La Paz and its connection to the Gulf of California in two research cruises on board the R/V El Puma, carried out in two contrasting seasons, winter (February 3 to 7, 2006) and summer (August 11 to 16, 2009) (Fig. 1b). Hydrographic data were acquired in both cruises with a CTD/Rosette System on a grid of 45 hydrographic stations (Fig. 1b). The CTD was set to store data at a 24 Hz frequency. Each cast was run at a downwelling speed of ~1 m s^{-1} and ~5 m above the seafloor.

Zooplankton organisms were collected at a total of 22 oceanographic stations (Fig. 1b), both day and night, by oblique hauls using Bongo nets (333 µm mesh-size, 60 cm of diameter at the mouth) configured with calibrated mechanical flowmeters (General Oceanics) before and after the cruise. Each haul was carried out for 15 min at a speed of 1.02 m s^{-1}, from 200 m depth to the surface, but for shallow stations, hauls started near the bottom (5 m) to the surface. After each zooplankton haul, the nets were inspected and carefully rinsed with seawater. The collected organisms were immediately fixed with 4% formalin for an initial period of 24 h. A 70% ethanol solution was then used for final preservation in airtight glass containers in dark and dry conditions. During the storage time, the samples were subjected to continuous maintenance, including 1) continuous changes of the jar lids to avoid evaporation of the solvent, and 2) periodic changes of alcohol (usually every two months) to avoid degradation of the organisms.

Laboratory analyses

In the laboratory, zooplankton biomass was calculated following the protocols described by Durán-Campos *et al.* (2015, 2019). Zooplankton was weighed from the complete sample from each sampling station contained in a plastic sieve configured with a 200 µm mesh after removing the excess ethanol by blotting paper for a time between 1 and 3 h (wet weight). The zooplankton biomass value of each station (expressed in g per 100 m^{-3}) was then obtained with the equation:

$$ZB = \frac{NW}{FW} \times 100$$

Where, NW is the net weight of the sample (after complete removal of ethanol) expressed in g. FW is the volume of water filtered during hauling (obtained from the flowmeter placed on the nets) expressed in m^3. It is important to note that large organisms that could introduce bias into the calculations were removed before weighing the samples, including large gelatinous zooplankton (*e.g.,* jellyfish) and juvenile fish. Unrelated items such as marine debris, leaf litter, and small mangrove branches were removed.

Data analyses

The CTD data were subject to different levels of processing. Initially, the raw data acquired at each station were converted with the manufacturer's software and processed following its routines and subroutines, applying filters to discard low-quality data. The Thermodynamic Equation of Seawater-2010 (TEOS-10) algorithms were used to obtain the conservative temperature (Θ, °C), absolute salinity (S_A, g kg^{-1}), and density (kg m^{-3}) (IOC *et al.* 2010). These data were used to construct Temperature-Salinity diagrams to analyze the proportion of sea water masses, analyze the horizontal distribution of hydrographic parameters, determine the depth of the thermocline, which was obtained according to the depth of the maximum vertical temperature gradient ($\delta T/\delta z$), and finally calculate the geostrophic velocities following the standard protocols described in Pond & Pickard (1995).

A Wilcoxon signed-rank test was conducted to determine whether the differences in biomass between the two contrasting seasons were statistically significant. This test does not assume a normal distribution and is suitable for paired measures where the same subjects are assessed under two different conditions (Legendre & Legendre 2012).

Results

Hydrographic structure

During winter, the T-S diagram showed the presence of three water masses, PIW, StSsW, and GCW, and during the summer were detected four water masses, GCW, StSsW, PIW, and TSW (Fig. 2). TSW was absent during the winter (Fig. 2). The thermocline depth obtained was different for each season. It was observed at a 50 m depth during winter, while during summer, it was observed at a 30 m depth.

The horizontal distribution of the conservative temperature (at 50 m depth) in winter showed a cold-core that decreased from 17.7 °C at its periphery, to 16.5 °C at the center (Fig. 3a). The winter horizontal density distribution showed a core with higher density values, which reached 25.7 kg m^{-3} at the center (Fig. 3a). The horizontal distribution of the conservative temperature (at 30 m depth) in summer, also showed the presence of a cold-core that decreases from 24 °C at its periphery, reaching 22 °C at its center (Fig. 3c). The density distribution showed a core with density values from 23.7 kg m^{-3} at its periphery and higher values at its center, with 24.2 kg m^{-3} (Fig. 3d). The cold and dense cores were observed in the central portion of the bay, in Alfonso Basin region, during the two contrasting seasons (Fig. 3a-d). The cold and dense cores shown in Figure 3 evidenced the presence of a cyclonic eddy confirmed with geostrophic velocity calculations (Fig. 4a, b). In both seasons, a well-defined counterclockwise circulation pattern with different diameters and velocities was observed (Fig. 4a, b). The

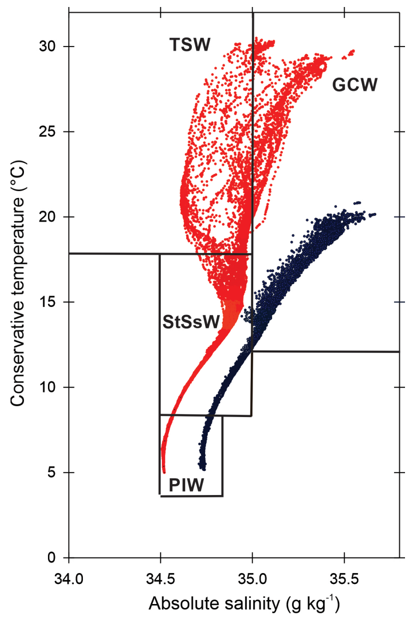

Figure 2. Conservative temperature (°C) and absolute salinity (g kg^{-1}) diagram of the Bay of La Paz in winter (blue points) and summer (red points). PIW: Pacific Intermediate Water, StSsW: Subtropical Subsurface Water, TSW: Tropical Surface Water, and GCW: Gulf of California Water / Diagrama de temperatura conservativa (°C) y salinidad absoluta (g kg^{-1}) de la Bahía de La Paz en invierno (puntos azules) y verano (puntos rojos). PIW: Agua Intermedia del Pacífico, StSsW: Agua Subtropical Subsuperficial, TSW: Agua Tropical Superficial y GCW: Agua del Golfo de California

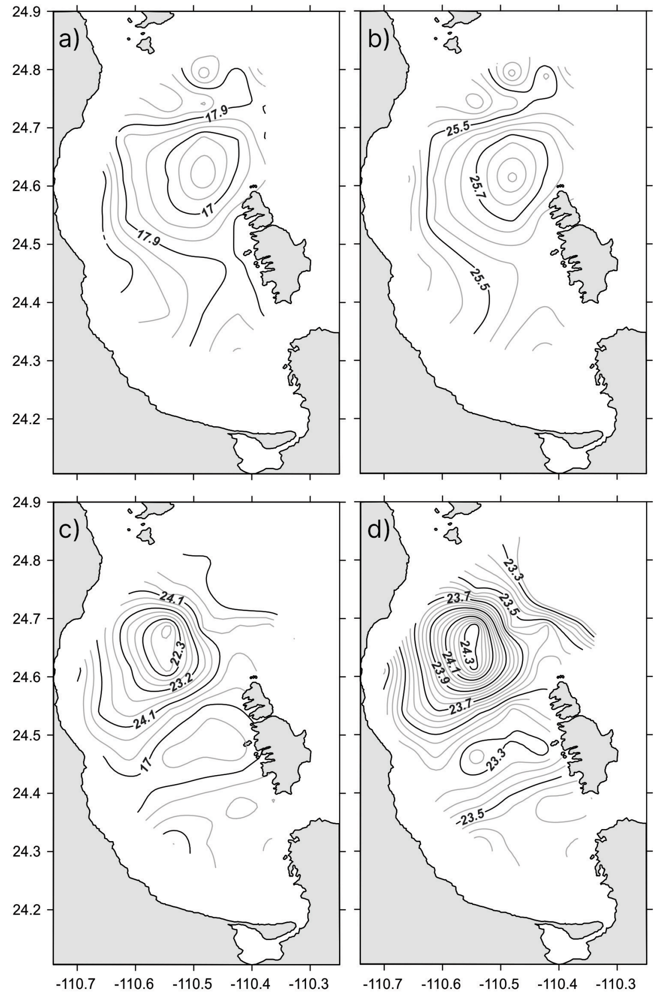

Figure 3. Horizontal distribution at the thermocline depth of hydrographic parameters in the Bay of La Paz. A) Conservative temperature (°C) for winter, B) density (σt, kg m^{-3}) for winter, C) conservative temperature (°C) for summer, D) density (σt, kg m^{-3}) for summer / Distribución horizontal en la profundidad de la termoclina de los parámetros hidrográficos en Bahía La Paz. A) Temperatura conservativa (°C) para el invierno, B) densidad (σt, kg m^{-3}) para el invierno, C) temperatura conservativa (°C) para el verano D) densidad (σt, kg m^{-3}) para el verano

diameter of the eddy in winter was about 30 km, and a mean velocity of 20 cm s^{-1} at its periphery (Fig. 4a). The diameter of the eddy during summer was similar to that observed during winter. Still, in this case, the geostrophic velocity was considerably higher, reaching values of 75 cm s^{-1} (Fig. 4b). In both seasons, intense currents were observed from the Gulf of California towards the interior of the bay through Boca Grande region, as well as outflow currents heading north through San José Island region (Fig. 4b). Intense north-south direction currents were observed flowing near the coast (Fig. 4a, b).

Zooplankton biomass

The zooplankton biomass recorder in both seasons showed small differences in terms of its magnitude and its horizontal distribution throughout the study area.

Zooplankton biomass ranged between 10.6 and 43.4 g 100 m^{-3} in winter, showing changes in its horizontal distribution with the highest values in the stations near the coast and high secondary values in connection with the adjacent gulf, and a circular area described by the circumference of the cyclonic circulation observed (Fig. 5a).

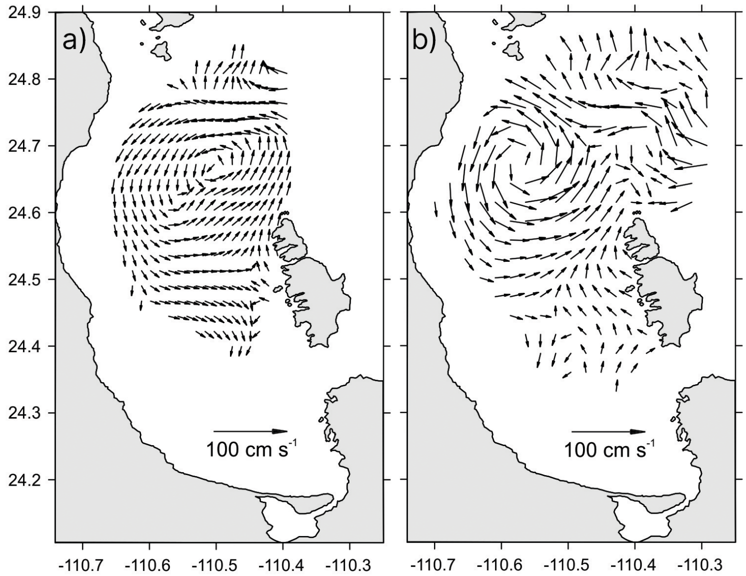

Figure 4. Geostrophic velocity calculated (cm s^{-1}) at the depth of the thermocline in the Bay of La Paz during winter (a) and summer (b) / Velocidad geostrófica calculada (cm s^{-1}) en la profundidad de la termoclina en la Bahía de La Paz durante invierno (a) y verano (b)

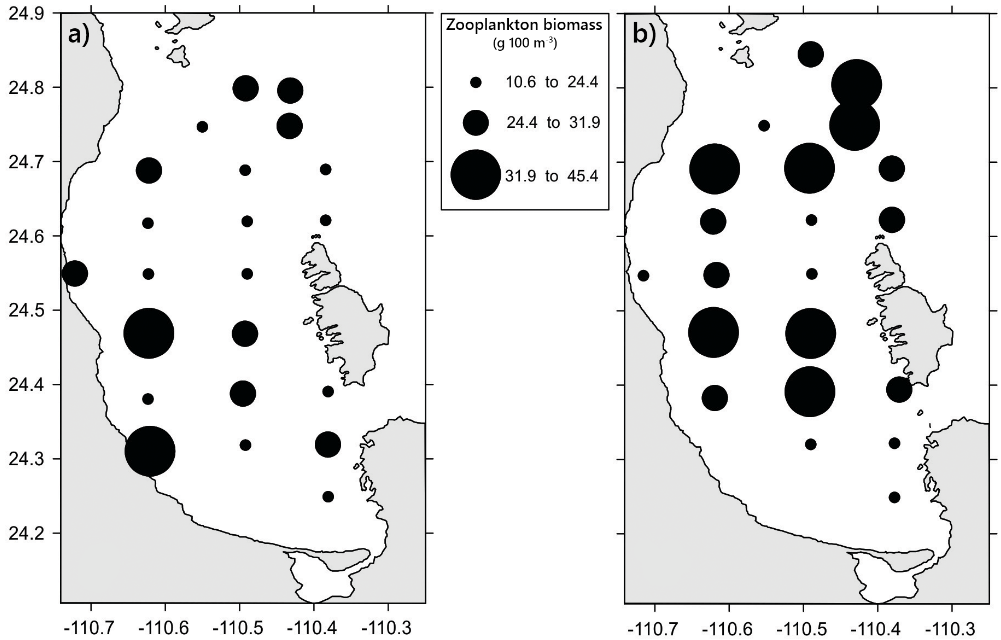

Figure 5. Horizontal distribution of wet zooplankton biomass (g 100 m^{-3}) in the Bay of La Paz in winter (a) and summer (b) / Distribución horizontal de la biomasa húmeda del zooplancton (g 100 m^{-3}) en la Bahía de La Paz en invierno (a) y verano (b)

Zooplankton biomass during the summer was slightly higher than those calculated in winter, ranging between 13.2 and 45.4 g 100 m^{-3}, showing two areas with higher values: one located at the bathymetric sill situated at the connection between the bay and the gulf, and another area of high values that described the circumference of the eddy, on its periphery, similar to that observed in the winter season (Fig. 5b).

The Wilcoxon's sign-ranked tests showed that biomass significantly differed between the two contrasting seasons (W= 167, $P < 0.05$).

Discussion

The use of high-resolution hydrographic data allowed us to determine the water column's thermohaline structure and confirm the presence of well-defined cyclonic eddies, agreeing with previous reports on the circulation pattern in the Bay of La Paz.

The water masses showed a higher proportion of TSW and StSsW during the summer, associated with the seasonal warming processes of the sea surface layer that occur during summer, enhanced by a southeast wind that induces the StSsW to have a greater incursion into the Gulf of California and, therefore, into the Bay of La Paz. These observations agree with previous reports (*e.g.,* Coria-Monter *et al.* 2019b, Durán-Campos *et al*. 2020, Rocha-Díaz *et al*. 2021) showing the wide seasonal variability to which the region is subject.

A growing body of scientific evidence suggests that zooplankton biomass is strongly related to the physical environment and the presence of several hydrodynamic processes at different spatial and temporal scales (Steinberg & Landry 2017, Drago *et al.* 2022). Cyclonic eddies perturb the thermocline/pycnocline and induce changes in the vertical temperature distribution (McGillicuddy 2016, Sánchez-Mejía *et al.* 2020). Cyclone eddies lead to changes in zooplankton populations. This study confirmed that a quasi-permanent and well-defined cyclonic eddy located in the central portion of the bay altered the hydrographic structure. It generated cold and dense cores during both winter and summer, consistent with previous observations (Coria-Monter *et al.* 2017, Sánchez-Mejía *et al.* 2020). However, clear differences were observed regarding the seasonal azimuthal velocity. In winter, the mean velocity was 20 cm s^{-1}, while in summer, it increased to approximately 75 cm s^{-1}, which is roughly four times faster. This pattern can be attributed to the upper layer having higher internal energy during summer, resulting in a greater rotational speed in the circulation pattern. Another possible reason to explain the differences found in the azimuthal velocity of both seasons could be the maturation age. Previous studies on the temporal evolution of the cyclonic eddy inside the Bay of La Paz suggest an intensification stage that starts from spring, reaches maturity in early summer, decays in late autumn, and starts the cycle again towards the end of winter (Coria-Monter *et al.* 2014). This temporal changing pattern explains that the eddy's highest azimuthal speeds occurred in summer, corresponding to a mature eddy stage.

Evidence has emerged since the late 1980s about the influence of cyclonic eddies on zooplankton biomass in different regions of the world (Backus *et al.* 1981). In the Mediterranean Sea, cyclonic eddies have been documented to represent one of the main mechanisms promoting high zooplankton biomass values, particularly during summer (Belkin *et al.* 2022). In the China Sea, the presence of cyclonic (cold core) eddies has been related to increases in zooplankton biomass, which contributes significantly to the energy transfer chain from primary producers to higher trophic levels of the food web in the region (Chen *et al*. 2020).

Biggs *et al.* (1988) observed that a cyclonic eddy in the Gulf of Mexico induced the upwelling of nutrient-rich cold waters to the euphotic zone, benefiting phytoplankton and then induced high levels of zooplankton biomass. Later, Biggs *et al*. (1997) confirmed the role of cyclonic eddies on zooplankton biomass in the Gulf of Mexico by retaining and transporting zooplankton in the eddy's influence and then moving them to the periphery, as was observed in the present study.

Recent evidence in the Bay of La Paz suggests that the presence of eddies (mainly cyclonic) can act as independent habitats for zooplankton populations in the region, as suitable conditions are present within the physical structure (in terms of temperature) to benefit the metabolism of some zooplankton taxonomic groups (Durán-Campos *et al.* 2019). The results presented here indicate that the zooplankton biomass was associated with the cyclonic eddy in both seasons, with moderately high values following their circumference, considering that eddies retain the organisms and move them towards the periphery. Another possible explanation for this distribution of zooplankton is the predominance of diatoms at the periphery of the cyclonic eddy in La Paz Bay (Coria-Monter *et al.* 2014). Phytoplankton is the food for herbivorous, omnivorous, and filter-feeding zooplankton, such as copepods, which are known to be the most abundant taxonomic group in the bay, contributing the largest proportion of zooplankton assemblage biomass (Rocha-Díaz *et al.* 2021).

In conclusion, the horizontal distribution patterns of zooplankton biomass were consistent, showing the highest densities in the periphery of the cyclonic eddy in both winter and summer. Notably, the biomass values were somewhat lower in winter compared to summer. The summer months exhibited the peak zooplankton biomass, likely due to the mature stage of the cyclonic eddy during this time of year. Furthermore, the elevated biomass observed in Boca Grande region during summer can be directly linked to the strong currents entering the bay, which create drag against the area's bathymetric sill. This drag induces a resuspension of nutrients that benefits phytoplankton and consequently enhances zooplankton biomass.

Although considerable efforts have been invested in recent years in unraveling the mechanisms and physical processes that influence the planktonic ecosystem inside the Bay of La Paz, a complete characterization is still far from being completed, Therefore, it is necessary to continue focusing efforts on long-term monitoring programs that analyze both seasonal and interannual variability, taking into account that the geographical position of La Paz Bay means that the processes that occur in the Pacific Ocean are manifested within it. For example, ENSO events, and marine heat waves that impact phytoplankton and zooplankton but are not yet completely well known.

Statements

Acknowledgments

We are grateful for the assistance of the captain and his crew in all maritime activities, as well as the many volunteers who participated in the expeditions. Sergio Castillo-Sandoval and Francisco Ponce Núñez provided technical support during the analyses. Constructive comments from two anonymous reviewers improved this study.

Author contributions

Karina Isabel Mariano-Peguero: methodology, investigation, data curation, writing—original draft preparation.

Elizabeth Durán-Campos: conceptualization, methodology, software, validation, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—review and editing, supervision, funding acquisition.

María Adela Monreal-Gómez: conceptualization, methodology, software, validation, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—review and editing, supervision, funding acquisition.

Erik Coria-Monter: conceptualization, methodology, software, validation, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—review and editing, supervision, funding acquisition.

David Alberto Salas-de-León: conceptualization, methodology, software, validation, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—review and editing, supervision, funding acquisition.

Franco Antonio Rocha-Díaz: methodology, investigation, data curation, writing—original draft preparation.

Sarai García-Mirafuentes: methodology, investigation, data curation, writing—original draft preparation.

Benjamín Quiroz-Martínez: methodology, software, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—review and editing, supervision.

All authors have read and agreed to the published version of the manuscript.

Funding

This study was supported by DGAPA-PAPIIT-UNAM Project #IG100421 "Análisis de las interacciones entre aguas continentales y marinas en el Golfo de California bajo el enfoque de la fuente al mar como base para su gestión sustentable". Additional funding was provided by the Institute of Marine Sciences and Limnology of the National Autonomous University of Mexico (UNAM) with the projects #144, 145, and 627. The ship time of the research cruises aboard the R/V El Puma was funded by UNAM.

Data availability statement

The datasets generated during this study are available from the corresponding author on request.

Conflicts of interest

The authors declare no conflicts of interest.

Ethical approval

Not applicable.

Use of AI

No Artificial Intelligence methods were used in this manuscript.

Literature cited

Backus RH, GR Flierl, DR Kester, DB Olson, PL Richardson, AC Vastano, PH Wiebe & JH Wormuth. 1981. Gulf Stream Cold-core rings: their physics, chemistry, and biology. Science 212(4499): 1091-1110. <https://doi: 10.1126/science.212.44 99.1091>

Belkin N, T Guy-Haim, M Rubin-Blum, A Lazar, G Sisma-Ventura, R Kiko, AR Morov, T Ozer, I Gertman, B Herut & E Rahav. 2022. Influence of cyclonic and anticyclonic eddies on plankton in the southeastern Mediterranean Sea during late summertime. Ocean Science 18: 693-715. <https://doi: 10.5194/os-18-693-2022>

Beltrán-Castro JR, S Hernández-Trujillo, J Gómez-Gutiérrez, A Trasviña-Castro, E González-Rodríguez & O Aburto-Oropeza. 2020. Copepod species assemblage and carbon biomass during two anomalous warm periods of distinct origin during 2014-2015 in the southern Gulf of California. Continental Shelf Research 207, 104215. <https://doi.org/10.1016/j.csr.2020.104215>

Biggs DC, AC Vastano, A Ossinger, A Gil-Zurita & A Pérez-Franco. 1988. Multidisciplinary study of warm and cold cores rings in the Gulf of Mexico. Memorias de la Sociedad Ciencias Naturales de Venezuela 48(3): 11-31.

Biggs DC, RA Zimmerman, R Gasca, E Suárez-Morales, I Castellanos & RR Leben. 1997. Note on plankton and cold-core rings in the Gulf of Mexico. Fishery Bulletin 95(2): 369-375.

Brierley AS. 2017. Plankton. Current Biology 27: R478-R483. <https://doi:10.1016/j.cub.2017.02.045>

Burd BJ & RE Thomson. 2022. A review of zooplankton and deep carbon fixation contributions to carbon cycling in the dark ocean. Journal of Marine Systems 236, 103800. <https://doi:10.1016/j.jmarsys.2022.103800>

Cepeda GD, AJ Jaureguizar, H Fenco, R Reta & ME Sabatini. 2022. Long-term zooplankton variability in the southern Patagonian shelf, Argentina. Journal of Marine Systems 235, 103782. <https://doi: 10.1016/j.jmarsys.2022.103782>

Chen Y, S Lin, C Wang, J Yang & D Sun. 2020. Response of size and trophic structure of zooplankton community to winter marine environmental conditions in the northern South China Sea. Journal of Plankton Research 42(3): 378-393. <https://doi:10.1093/plankt/fbaa022>

Coria-Monter E, MA Monreal-Gómez, DA Salas-de-León, J Aldeco-Ramírez & M Merino-Ibarra. 2014. Differential distribution of diatoms and dinoflagellates in a cyclonic eddy confined in the Bay of La Paz, Gulf of California. Journal of Geophysical Research Oceans 119: 6258-6268. <https://doi:10.1002/ 2014JC009916>

Coria-Monter E, MA Monreal-Gómez, DA Salas-de-León & E Durán-Campos. 2017. Wind driven nutrient and chlorophyll-*a* enhancement at a cyclonic circulation in Bay of La Paz, Gulf of California, Mexico. Estuarine Coastal and Shelf Science 196: 290-300. <https://doi:10.1016/j.ecss.2017.07.010>

Coria-Monter E, DA Salas-de-León, MA Monreal-Gómez & E Durán-Campos. 2019a. Internal waves in the Bay of La Paz, Southern Gulf of California, Mexico. Vie et Milieu 69 (2-3): 115-122.

Coria-Monter E, MA Monreal-Gómez, DA Salas-de-León & E Durán-Campos. 2019b. Water masses and chlorophyll-*a* distribution in a semi-enclosed bay of the southern Gulf of California, Mexico, after the "Godzilla El Niño". Arabian Journal of Geosciences 12, 473. <https://doi: 10.1007/s12517-019-4636-1>

De Silva-Dávila R & R Palomares-García. 2002. Distributional patterns of the euphausiid community in Bahía de La Paz, B.C.S., México. In: Hendrickx ME (ed). Contribution to the study of East Pacific crustaceans 1: 109-125. Universidad Nacional Autónoma de México, Ciudad de México.

Drago L, T Panaïotis, J-O Irisson, M Babin, T Biard, F Carlotti, L Coppola, L Guidi, H Hauss, L Karp-Boss, F Lombard, AMP McDonnell, M Picheral, A Rogge, AM Waite, L Stemmann & R Kiko. 2022. Global distribution of zooplankton biomass estimated by *in situ* imaging and machine learning. Frontiers in Marine Science 9, 894372. <https://doi:10.3389/fmars.2022.894372>

Durán-Campos E, DA Salas-de-León, MA Monreal-Gómez, J Aldeco-Ramírez & E Coria-Monter. 2015. Differential zooplankton aggregation due to relative vorticity in a semi-enclosed bay. Estuarine, Coastal and Shelf Science 164: 10-18. <https://doi:10.1016/j.ecss.2015.06.030>

Durán-Campos E, MA Monreal-Gómez, DA Salas-de-León & E Coria-Monter. 2019. Zooplankton functional groups in a dipole eddy in a coastal region of the southern Gulf of California. Regional Studies in Marine Science 28, 100588. <https://doi:10.1016/j.rsma.2019.100588>

Durán-Campos E, MA Monreal-Gómez, DA Salas-de-León & E Coria-Monter. 2020. Field and satellite observations on the seasonal variability of the surface chlorophyll-*a* in the Bay of La Paz, Gulf of California, Mexico. International Journal of Oceans and Oceanography 14(1): 157-167. <https://doi:10.37622/IJOO/14.1.2020.157-167>

Espinosa-Fuentes ML, C Flores-Coto, L Sanvicente-Añorve & F Zavala-García. 2009. Vertical distribution of zooplankton biomass and ichthyoplankton density during an annual cycle on the continental shelf of the southern Gulf of Mexico. Revista de Biología Marina y Oceanografía 44(2): 477-488.

Farfán C & S Álvarez-Borrego. 1992. Zooplankton biomass of the northernmost Gulf of California. Ciencias Marinas 18(3): 17-36. <https://doi: 10.7773/cm.v18i3.905>

Färber-Lorda J, G Athié, V Camacho-Ibar, LW Daessle & O Molina. 2019. The relationship between zooplankton distribution and hydrography in oceanic waters of the Southern Gulf of Mexico. Journal of Marine Systems 192: 28-41. <https://doi:10.1016/j.jmarsys.2018.12.009>

Fuentes-Martínez RM, E Coria-Monter, MA Monreal-Gómez, E Durán-Campos & DA Salas-de-León. 2022. An assessment of the zooplankton biomass in Campeche Canyon (southern Gulf of Mexico) during the "Nortes" storm season of 2011. Latin American Journal of Aquatic Research 51(3): 435-442. <https://doi: 10.3856/vol51-issue3-fulltext-3014>

Hernández-León S, MP Olivar, ML Fernández de Puelles, A Bode, A Castellón, C López-Pérez, VM Tuset & JI González-Gordillo. 2019. Zooplankton and micronekton active flux across the Tropical and Subtropical Atlantic Ocean. Frontiers in Marine Science 6: 535. <https://doi: 10.3389/fmars.2019.00535>

IOC, SCOR & IAPSO. 2010. The international thermodynamic equation of seawater – 2010. Calculation and use of thermodynamic properties. Intergovernmental Oceanographic Commission, Manual and Guides 56: 1-196. UNESCO, Paris.

Irigoien X, J Huisman & RP Harris. 2004. Global biodiversity patterns of marine phytoplankton and zooplankton. Nature 429: 863-867. <https://doi: 10.1038/nature02593>

Kodama T, Y Igeta & N Iguchi. 2022. Long-term variation in mesozooplankton biomass caused by top-down effects: A case study in the coastal Sea of Japan. Geophysical Research Letters 49, e2022GL099037. <https://doi: 10.1029/2022GL099037>

Lavaniegos-Espejo BE & R Lara-Lara. 1990. Zooplankton of the Gulf of California after the 1982-1983 El Niño event: biomass distribution and abundance. Pacific Science 44(3): 297-310.

Lavín MF & SG Marinone. 2003. An overview of the physical oceanography of the Gulf of California. In: Velasco-Fuentes OU, J Sheinbaum & J Ochoa (eds). Nonlinear processes in geophysical fluid dynamics, pp. 173-204. Springer. Dordrecht.

Lavín MF, E Beier & A Badan. 1997. Estructura hidrográfica y circulación del Golfo de California: Escalas estacional e interanual. In: Lavín MF (ed). Contribuciones a la Oceanografía Física en México, Monografía 3: 141-171. Unión Geofísica Mexicana, Ciudad de México.

Legendre P & LF Legendre. 2012. Numerical ecology, 990 pp. Elsevier, Amsterdam.

McGillicuddy DJ Jr. 2016. Mechanisms of physical-biological-biogeochemical interactions at the Oceanic mesoscale. Annual Review of Marine Science 8: 125-159. <https://doi:10.1146/annurev-marine-010814-015606>

Monreal-Gómez MA, A Molina-Cruz & DA Salas de León. 2001. Water masses and cyclonic circulation in Bay of La Paz, during June 1998. Journal of Marine Systems 30: 305-315. <https://doi: 10.1016/S0924-7963(01)00064-1>

Nicolas D, S Rochette, M Llope & P Licandro. 2014. Spatio-temporal variability of the North Sea cod recruitment in relation to temperature and zooplankton. PLoS ONE 9(2), e88447. <https://doi:10.1371/journal.pone.0088447>

Odum EP. 1963. Ecology, 141 pp. Modern Biology Series, Holt Rinehart & Winston, New York.

Pond S & GL Pickard. 1995. Introductory dynamical oceanography, 329 pp. Butterworth-Heineman, Oxford.

Rocha-Díaz F, MA Monreal-Gómez, E Coria-Monter, DA Salas-de-León, E Durán-Campos & M Merino-Ibarra. 2021. Copepod abundance distribution in relation to a cyclonic eddy in a coastal environment in the southern Gulf of California. Continental Shelf Research 222, 104436. <https://doi:10.1016/j.csr.2021.104436>

Salas-de-León DA, N Carbajal, MA Monreal-Gómez & A Gil-Zurita. 2011. Vorticity and mixing induced by the barotropic M2 tidal current and zooplankton biomass distribution in the Gulf of California. Journal of Sea Research 66(2): 143-153. <https://doi:10.1016/j.seares.2011.05.011>

Sánchez-Mejía JM, MA Monreal-Gómez, E Durán-Campos, DA Salas-de-León, E Coria-Monter, MG Contreras-Simuta & M Merino-Ibarra. 2020. Impact of a mesoscale cyclonic eddy on the phytoplankton biomass of Bay of La Paz in the southern Gulf of California. Pacific Science 74(4): 331-344. <https://doi:10.2984/74.4.2>

Steinberg DK & MR Landry. 2017. Zooplankton and the ocean carbon cycle. Annual Review of Marine Science 9: 413-444. <https://doi:10.1146/annurev-marine-010814- 015924>

Torres-Orozco E. 1997. Análisis volumétrico de las masas de agua del Golfo de California. Tesis de Maestría, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, México, 80 pp.

Vera-Mendoza R & DA Salas-de-León. 2014. Effect of environmental factors on zooplankton abundance and distribution in river discharge influence areas in the southern Gulf of Mexico. In: Amezcua F & B Bellgraph (eds). Fisheries management of Mexican and Central American Estuaries, pp. 93-112. Springer, Dordrecht.

Woodson CB. 2018. The fate and impact of internal waves in nearshore ecosystems. Annual Review of Marine Science 10: 421-441. <https://doi:10.1146/annurev-marine-121916-063619>

Zavala-García F, C Flores-Coto & ML Espinoza-Fuentes. 2016. Relationship between zooplankton biomass and continental water discharges in the southern Gulf of Mexico (1984-2001). Revista de Biología Marina y Oceanografía 51(1): 21-31.