Short Communication

An assessment of the zooplankton biomass in Campeche Canyon (southern Gulf of Mexico) during the "Nortes" storm season of 2011

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ABSTRACT. Biomass is a valuable indicator of biological production in any ecosystem and represents a proxy of secondary production in the case of zooplankton. This short communication aims to report zooplankton biomass values in the waters of the Campeche Canyon, southern Gulf of Mexico, during the "Nortes" storm season of 2011 and to explore their relationship with the hydrography and the circulation pattern. The results showed the presence of cyclonic and anticyclonic eddies associated with high and low water density at the base of the pycnocline. The highest values of zooplankton biomass (>40 g 100 m⁻³) were observed in regions that presented higher water density values (~26.1 kg m⁻³). In comparison, the lowest zooplankton biomass values (<5 g 100 m⁻³) were associated with low water densities (<25.6 kg m⁻³). The results presented here contribute to elucidating the role that physical forcing plays on the zooplankton biomass of the region, particularly during a season in which the passage of extreme storms is widespread.

Keywords: zooplankton biomass; spatial variability; circulation pattern; eddies; Gulf of Mexico

Zooplankton encompasses a highly diverse group of organisms, represented by practically all phyla in the marine environment, which play a pivotal role in the transfer of matter, energy, and carbon throughout the water column because they represent a fundamental link in pelagic food webs due to their position. Additionally, zooplankton represents a food source for numerous species, many of them of high commercial value, supporting important fisheries worldwide (Brierley 2017).

Biomass is considered an indicator of biological production in any marine ecosystem. In the case of zooplankton, biomass represents a proxy for secondary production and a measure to determine the rate of matter available for species in the upper trophic levels of the food web (Richardson 2008). Therefore, the quantification of zooplankton biomass is essential not only to assess the productive potential of the oceans but also represents a very valuable indicator to assess the amount of carbon that can be transferred to the oceans' interior (Irigoien et al. 2004).

It is relatively well known that zooplankton biomass and its distribution depend on multiple environmental factors and hydrodynamic processes along the water column at different spatial-temporal scales (McGillicuddy 2016). Indeed, the presence of internal waves (Woodson 2018), hydraulic jumps (Salas-Monreal et al. 2012), thermohaline fronts (Durán-Campos et al. 2019), and eddies (Eden et al. 2009) are physical forcings that play an essential role in the con-

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centration and distribution of zooplankton biomass in many marine ecosystems around the world, including Mexican waters.

Recent evidence suggests a cyclonic eddy influences the copepod zooplankton biomass in the Bay of La Paz, southern Gulf of California. This eddy generates mixing processes along the water column that support the production of organisms located at the base of the trophic web (e.g. diatoms), which ensures food availability for zooplankton filter-feeding organisms (Rocha-Díaz et al. 2022).

The influence of diverse hydrodynamic processes on the abundance and biomass of zooplankton has been evident since 2000 in the southern Gulf of Mexico (GM). Indeed, Sanvicente-Añorve et al. (2000) assessed the ichthyoplankton community structure in the southern gulf, showing that the circulation pattern, continental water discharges, eddies, and mixing processes are the main features that determine the ichthyoplankton distribution patterns and community structure. Gasca et al. (2001) also noted that cyclonic eddies in the southern GM strongly determine the community structure, euphausiids' abundance, biomass, and distribution. Espinosa-Fuentes & Flores-Coto (2004), when analyzing the community structure of the ichthyoplankton in the southern GM during an annual cycle, identified five assemblages (coastal, inner, neritic, outer neritic, oceanic) and a transitional group whose seasonal variation depends on the presence of physical processes at different scales, including mixing processes, currents, and eddies. Later, Flores-Coto et al. (2009), who conducted an extensive review of zooplankton studies in the southern GM (with emphasis on fish larvae), noted a marked spatial variability in terms of abundance and biomass of organisms; for example, the highest values occur in the coastal zone and on the continental shelf and decrease toward the oceanic zone, which is determined by the spawning period of each species, by the availability of food and by physical processes, mainly the current patterns. Espinosa-Fuentes et al. (2009) documented that the temperature and mixing of a water column are the main factors that determine zooplankton biomass in the southern GM, and they suggested that there must be marked seasonal variability in the biomass, depending on the ocean dynamics of the region. The role of the hydrographic properties of the water column on zooplankton populations was evaluated by Vera-Mendoza & Salas de León (2014), who determined that hydrographic parameters, mainly salinity, modulated zooplankton biomass. A direct relationship between zooplankton biomass and their physical environment,

epicontinental water discharges, was addressed by Zavala-García et al. (2016). They determined that the biomass changes depend on the discharges, not only in terms of the annual cycle but also directly related to the size of the volume discharged into the ocean. More recently, the relationship between zooplankton distribution and hydrography in the southern GM was assessed by Färber-Lorda et al. (2019), who, based on in situ observations during autumn, summer, and winter, identified the presence of alternating cyclonic/ anticyclonic eddies and a quasi-permanent cyclonic circulation in the Bay of Campeche (their Fig. 4), which induced high nutrient concentrations and high zooplankton biomass. The authors also noted that rainfall considerably impacts the region's biomass; for example, stronger rainfall induced a strong salp bloom during summer, increasing biomass values, particularly in the Bay of Campeche.

Although the studies carried out to date represent a very valuable effort to elucidate the role that some physical variables play in the distribution of zooplankton biomass in the southern GM, there are still some gaps because the vast majority of studies have been carried out during the warm seasons of the year (spring and summer) without consideration of the high variability to which the region is subject, particularly during the cold season (November to February), in which the passage of storms, locally called "Nortes," is extremely frequent, which has a very marked influence on the dynamics of the water column and, therefore, on the distribution of zooplanktonic organisms.

This short communication aims to report zooplankton biomass values and their relationship with the physical environment in the waters of Campeche Canyon, southern GM, during the "Nortes" season of 2011. Our premise is that the zooplankton biomass is directly related to the presence of hydrodynamic processes in the region, which induce changes in the hydrographic parameters. We intend to contribute to the knowledge of zooplankton at a time of the year when direct observations are scarce due to the challenges involved in navigation when winds and wind wave conditions are extreme. These factors contribute to filling the existing gaps and, thus, continuing the advancement of scientific knowledge in terms of zooplankton ecology, which will make it possible to propose improved management actions in the southern GM, an ecosystem recognized for its high biological production and for being the habitat of numerous emblematic species, some of which are highly endangered.

The GM is a large marginal sea of North America with a variable topography (Fig. 1a) that shares waters with three countries (Mexico, Cuba, and the USA) and is characterized by its remarkable hydrodynamics as a product of different oceanic processes (e.g. internal waves, fronts, eddies) and current systems (e.g. the Loop Current) that occur in the GM. Due to these hydrodynamics, the GM supports numerous species of high economic and ecological value, which is why it has been included on the list of Large Marine Ecosystems of the World (Sherman & Hempel 2009).

In the southern GM, Campeche Canyon (Fig. 1b) is a geomorphic feature that reaches depths of >2500 m (Goff et al. 2016), in which several hydrodynamic processes take place, including internal waves, hydraulic jumps, and mesoscale eddies (both cyclonic and anticyclonic), which exert a notable influence on the entire planktonic ecosystem (Santiago-Arce & Salas de León 2012, Durán-Campos et al. 2017, Färber-Lorda et al. 2019). In climatic terms, the southern GM is characterized by three contrasting seasons: 1) dry (from March to May); 2) wet (from June to October); and 3) storm ("Nortes") from (November to February), in which extremely strong (>80 km h⁻¹) and persistent winds impact the region, exerting a marked influence on the surface waters and inducing vertical mixing and low temperatures (<22°C) (Ojeda et al. 2017).

The information used in this study comes from the oceanographic expedition "Cañon-IV" carried out on board the R/V "Justo Sierra", operated by the National Autonomous University of Mexico, from February 22-28, 2011. The expedition covered 48 hydrographic stations (+ symbols, Fig. 1c), in which a CTD probe (SeaBird 19 plus), previously calibrated by the manufacturer, was used to acquire temperature, conductivity, and pressure data. The casts extended from the surface to close to the bottom (~5 m above the bottom), acquiring data at a frequency of 24 Hz.

Immediately after each CTD cast, zooplankton organisms were collected by oblique hauls at a total of 21 stations (O symbols, Fig. 1c) using Bongo nets of 333 μ m configured with mechanical flowmeters (General Oceanics 2030R) and placed in each mouth. Zooplankton organisms were captured from a depth of 200 m to the surface for 15 min at 2 kn (1 m s⁻¹). Once on board, the nets were carefully inspected and rinsed with seawater, and the organisms collected were fixed immediately with 4% formalin buffered with borax for 24 h; after that time, the organisms were transferred to a 70% ethanol solution for their final preservation, the samples were kept in airtight bottles in dry and dark conditions. During storage, the samples were subject to

preventive maintenance, including a continuous replenishment of ethanol to avoid degradation of the organisms.

The CTD data were primarily converted and processed according to the routines and subroutines of the software manufacturer (SBE data processing v7.7.26.7). Before averaging to 1 dbar, a low-pass filter was applied to purge bad or low-quality data. Then, the algorithms proposed by the Thermodynamic Equation of Seawater - 2010 (TEOS-10) (IOC 2010) were used to derive water density (σ_t , kg m⁻³). These data were then used to calculate the pycnocline depth, defined as the maximum vertical density gradient ($\partial \sigma_t/\partial z$) depth. Later, geostrophic velocities relative to 1000 m depth were calculated.

The geostrophic method for calculating relative velocities between pairs of hydrographic stations A and B, separated by a distance L, is determined according to the equation for the meridional component (v_1 – v_2) = $\frac{1}{L_f} (\Delta \Phi_B - \Delta \Phi_A)$, which is the usable form of the geostrophic equation to obtain relative speeds for two levels (1 and 2), where $\Delta \Phi_B$ and $\Delta \Phi_A$ are the geopotential anomalies. The zonal (u) and meridional (v) geostrophic velocity components were calculated from the CTD data following Pond & Pickard (1995): $u = -\frac{1}{f\rho} \frac{\partial P}{\partial y}$ and $v = \frac{1}{f\rho} \frac{\partial P}{\partial x}$, where ρ is the water density, P is the hydrostatic pressure resulting from the water density, and $f = (2\Omega \sin \phi)$ represents the Coriolis parameter, which depends on the angular speed of rotation of the earth Ω and the geographic latitude ϕ . The circulation pattern was analyzed at the pycnocline depth.

In the laboratory, zooplankton biomass wet weight (ww) was calculated following the protocols described by Durán-Campos et al. (2015, 2019). This technique consists of weighing the entire sample inside a sieve after removing the excess ethanol with blotting paper and then applying the equation $ZB = \frac{NW}{FW} \times 100$, where ZB is the zooplankton biomass expressed in g 100 m⁻³ of filtered water, NW is the net weight of the sample (after removing all excess ethanol) expressed in g, and FW is the volume of filtered water during the haul (obtained from the flowmeter placed in the net) expressed in m³. To avoid bias in the biomass calculations and following standard specifications, organisms greater than 3 mm were removed from the samples (rinsed prior), including large gelatinous zooplankton (e.g. jellyfish) and juvenile fishes.

Once the ww of the zooplankton biomass was obtained, the zooplankton carbon biomass (C) was calculated according to Wiebe (1988), following the



Figure 1. Study area: a) Gulf of Mexico, bathymetry (m); b) Bay of Campeche, showing the Campeche Canyon bathymetry in the southern Gulf of Mexico; and c) Campeche Canyon. (•) Represents the hydrographic stations in which CTD casts were executed and (O) represents the stations in which zooplankton organisms were collected.

equation $Log(ww) = -1.537 + 0.852 \ Log(C)$, $\left(0; \ Log(C) = \frac{Log(ww) + 1.537}{0.852}\right)$; with ww (g m⁻³) and C (mg m⁻³). Thus, the zooplankton biomass was also reported in mg C m⁻³.

The results showed the pycnocline depth at 90 m; thus, the geostrophic circulation pattern was presented at this depth. The density values ranged from 25.2 to 26.2 kg m⁻³, and the density field at 90 m depth showed the highest values in the southern and eastern regions. In comparison, low values from 25.5 to 25.8 kg m⁻³ were observed in the central region (Fig. 2a). The geostrophic circulation pattern showed the presence of cyclonic circulation in the southern region of the domain, coinciding with the high-density core; additionally, the presence of two eddies in the central region of the domain, one cyclonic (centered at 20.9°N, and 93.2°W) and another anticyclonic eddy (centered at 20.3°N, and 92.7°W) (Fig. 2b), was observed. The zooplankton biomass values ranged from 1.29 to 49.63 g 100 m⁻³, which displayed an interesting distribution pattern along the domain. The highest value (49.63 g 100 m⁻³) was located in the southern region, where the highest density values (from 25.9 to 26.1 kg m⁻³) were recorded; the second highest zooplankton biomass values (>20 g 100 m⁻³) were observed in the eastern portion of the domain, coinciding with relatively high-density values (~25.8 kg m⁻³) (Fig. 2c). In contrast, the lowest zooplankton biomass values were observed in the regions where low-density values occurred (Fig. 2c).

A t-test was applied to analyze the existence of significant differences among our data, showing significant differences between the zooplankton biomass and water density (P = 0.0003), which means that this variable influenced the zooplankton biomass and its distribution at the time of our observations.



Figure 2. Horizontal distribution at 90 m depth of a) sigma-t (kg m^{-3}), b) geostrophic circulation pattern (cm s^{-1}), c) zooplankton biomass in wet weight (g 100 m^{-3}), and d) zooplankton biomass (mg C m^{-3}).

Regarding carbon units, the results showed zooplankton biomass values from 1 to 28 mg C m⁻³ (Fig. 2d) with a similar distribution pattern to those previously described.

During our observations, the surface and subsurface geostrophic circulation patterns in the waters of Campeche Canyon revealed the presence of cyclonic and anticyclonic eddies, which were previously reported during the warmest months of the year. Indeed, Salas de León et al. (2004) reported that during August, the circulation pattern is characterized by the presence of a subsurface dipole eddy (cyclone/ anticyclone), which has a positive impact on the planktonic ecosystem; the authors also noticed that during this season, the mixed layer averaged 40 m in depth. More recently, with a dataset acquired in June, Durán-Campos et al. (2017) reported the presence of a cyclonic eddy associated with an anticyclonic eddy, which exerted an important effect on the phytoplankton population, inducing the formation of a deep chlorophyll-a layer (>90 m depth) due to the displacement of the thermocline and the pycnocline in the field of action of the cyclonic eddy; these chlorophyll-a values then have repercussions on zooplankton organisms, in particular herbivorous and filter-feeding organisms, such as copepods. Our results agree with these previous reports regarding the circulation pattern, confirming the existence of eddies (cyclonic and anticyclonic), which can provide clues about the permanent or quasi-permanent circulation pattern to which the region is subject.

One of the earliest studies that pointed out the influence of physical forcing on zooplankton biomass in the waters of the GM was that of Biggs et al. (1988), who hypothesized that the presence of cyclonic eddies induced high values of zooplankton biomass because these physical structures promoted the rise of coldwater masses rich in nutrients and then generated fertilization in the euphotic zone, benefiting the phytoplankton and, therefore, the zooplankton populations. In a later study, Biggs et al. (1997) confirmed that cyclonic (cold core) eddies north of the GM benefited zooplankton stocks and suggested that these structures could act as organism retention zones. They could subsequently be transported several hundred kilometers in the GM.

In the southern GM, some previous reports have noted that in areas close to a river discharge, the zooplankton biomass is modulated particularly by salinity (Vera-Mendoza & Salas de León 2014); however, our results suggest that the zooplankton biomass values at the time of our observations were determined by the temperature, which in turn determines the density. It is important to keep in mind that our samples came from a region that is not under the influence of river discharges, unlike the results by Vera-Mendoza & Salas de León (2014), who presented zooplankton biomass values from a region close to the discharge of the Coatzacoalcos River in the southern GM. In a subsequent study that analyzed the relationship between zooplankton biomass and the continental water discharges in the southern GM at different seasons of the year, Zavala-García et al. (2016) reported zooplankton biomass values of 19.2 g 100 m⁻³ on average during the winter season, which is lower than those reported in our study, suggesting that the circulation pattern of the Campeche Canyon positively influences zooplankton organisms. It has a greater influence than the possible contribution of organic matter and food availability for river zooplanktonic organisms. Additionally, Espinosa-Fuentes et al. (2009) reported very low values of zooplankton biomass (<5 g 100 m⁻³) during the winter season in a region close to the Grijalva-Usumacinta River system.

In summary, the results presented here suggest that the circulation pattern observed in the waters of Campeche Canyon during the storm "Nortes" season of 2011 determines the distribution of zooplankton organisms and, therefore, influences biomass values. In comparative terms, the values reported in our study are twice as high as those reported in regions under the influence of epicontinental water discharge from the main rivers in the southern GM, which highlights the fact that the presence of eddies in the Campeche Canyon can be a decisive factor that had not been considered previously and supports the need to focus more efforts on the execution of monitoring programs that cover both seasonal and interannual periods. Some recently published works have addressed the role that cyclonic and anticyclonic eddies play in the distribution of zooplankton organisms in the southern GM in different climatic seasons (autumn, summer, and winter), identifying that the presence of these structures largely determines the secondary production rates of the region (Färber-Lorda et al. 2019). However, for the Campeche Canvon in particular, most of the sampling expeditions have been carried out during the warm seasons, for example, during August 1999 when the thermocline and pycnocline were located at a depth of 40 m (Salas de León et al. 2004), while during the "Nortes" season, the winds induce the thermocline to sink up to 90 m, so it is necessary to direct efforts to acquire data from the storm season, which represents enormous challenges, both logistically and financially.

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