Research Articles

Zooplankton abundance during summer in the Bay of La Paz (southwestern Gulf of California, Mexico)

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ABSTRACT. Marine zooplankton play key roles in the transfer of energy to higher trophic levels and the removal of CO_2 from the atmosphere through the sedimentation of inorganic and organic carbon compounds included in their fecal pellets. Therefore, differences in the zooplankton groups driven by climate variations could influence the biogeochemical cycles at large oceanic scales. As a contribution to this topic, we analyzed the zooplankton groups in the Bay of La Paz, Gulf of California, Mexico, a highly dynamic basin characterized by its high biological productivity. We used information gathered during multidisciplinary research cruises in the summers of 2008 and 2009. The results showed differences in the hydrographic parameters between both summers, with a higher temperature recorded in 2009. The zooplankton groups showed that the calanoid copepods were the most abundant; however, there were important differences in the relative abundance of the rest of the analyzed groups as an effect of the temperature distribution along the study area, which was confirmed by multivariate statistical methods. These temperature changes were associated with increased gelatinous zooplankton (Cnidaria, Chaetognatha, Appendicularia, and Ctenophora) in 2009 in a region where the temperature was higher, possibly as a result of changes in food (phytoplankton) availability.

Keywords: zooplankton community; copepods; distribution; temperature; Bay of La Paz; Gulf of California

INTRODUCTION

Zooplankton occupies key positions in the pelagic food web as either primary consumers or low-level predators. Indeed, they are also a key bottleneck of transferring the energy produced by phytoplankton to higher trophic levels, including high-commercial-value fish stocks (Richardson, 2008). Also, zooplankton contributes to removing CO_2 from the atmosphere through the sedimentation of inorganic and organic carbon compounds in their fecal pellets (Brierley, 2017).

The distribution of zooplankton in the ocean is closely related to complex arrays of factors, including the presence of hydrodynamic processes at different scales (*e.g.*, internal waves, eddies), the water column depth, the trophic status (*i.e.*, productivity) of a particular region, and, mainly, the water temperature regime, which, in turn, determines the biological cycles, growth and metabolism rates of zooplankton.

Investigations of the effects of environmental factors on zooplankton composition contribute to understanding their population fluctuations by providing clues about whether certain groups may succeed under certain environmental conditions (Estrada *et al.*, 2012).

The role of the physical environment in the distribution of zooplankton is also relatively well documented. For example, since the work of Backus *et al.* (1981), the cold-water masses associated with the cyclonic Gulf Stream rings have proven to be important for the horizontal and vertical distribution of zooplankton in the upper 800 m of the water column. Then, over the last decade, numerous studies on the role of physical forcing factors on the zooplankton community have been conducted around the globe. Among these, Estrada *et al.* (2012) analyzed the zooplankton community structure in Hudson Bay (Canada) and showed that the hydrological and hydrodynamic conditions (salinity, stratification, mixing, and temperature) could have significant effects on zooplankton

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spatial distribution. In the Gulf of California, high zooplankton biomass, mostly represented by Copepoda, Chaetognatha, and Euphausiacea, was associated with cold-water masses, where dense chlorophyll-*a* patches also support high zooplankton biomass (Salas de León *et al.*, 2011). In the southern Gulf of California, during summer, the occurrence of mesoscale structures, such as fronts and eddies, affected the sea surface temperature (SST) distribution, with values >28°C (Lavín *et al.*, 2009). In this region, the influence of different environmental variables on particular zooplankton groups was previously reported, showing that the zooplankton population dynamic and its response depends on the presence of physical structures with different scales that exert a significant influence over the euphausiids (Ambriz-Arreola *et al.*, 2017), the mesopelagic fish larvae (Contreras-Catala *et al.*, 2016), and the epipelagic copepods (Palomares-García *et al.*, 2013). In the Bay of La Paz, a relationship between the abundance of zooplankton functional groups and the cold-water masses associated with a mesoscale cyclonic eddy has been documented, showing a radial distribution from the center of the eddy to the periphery, with the highest zooplankton biomass at the center. In particular, the changes in the temperature regime induced by the eddy retain a markedly different composition of the zooplankton, with a predominance of herbivorous taxa in the center and a higher proportion of omnivorous zooplankton at the periphery. In contrast, the carnivorous zooplankton was observed to be in high abundance in connection with the Gulf (Durán-Campos *et al.*, 2015).

Zooplankton ecology studies have progressively become crucial to understanding and predicting the impact of current (climate-driven) changes of the oceans, particularly in regions with high biological diversity, such as the Gulf of California and the Bay of La Paz. This area has been considered one of the most diverse and productive seas in the world, with a high number of emblematic endemic species, such as the totoaba (*Totoaba macdonaldi*), the mystery anchovy (*Anchoviella parri*), and the vaquita (*Phocoena sinus*). This high biodiversity is close related with the confluence of several hydrodynamic processes at different scales; for this reason, the region has been considered one of the largest marine ecosystems of the world (Páez-Osuna *et al.*, 2016; Mercado-Santana *et al.*, 2017; Coria-Monter *et al.*, 2018), and, since 2005, it is entitled as a UNESCO World Heritage site (Silverberg *et al.*, 2014). Not only the Gulf is unique in terms of biodiversity, but it also has economic importance due to its support of high-value commercial species for the fishery industry, including tuna, sardines, squid, and shrimp, together totaling 60% of

Mexico's annual catch (Arreguín-Sánchez *et al.*, 2017). Additionally, due to the pristine beaches, reefs, and wildlife, the Gulf draws over a million tourists each year (Johnson *et al.*, 2019). It is an important ecological region, as it represents a site for either the refuge or feeding of several species (Pardo *et al.*, 2013). The climate is semiarid, with evaporation (300 mm yr^{-1}) that exceeds precipitation (180 mm yr^{-1}), and the rivers discharge is practically nil. The weather temperature during summer reaches 37°C, while it is ~10°C in winter. The bay interchanges water masses with the Gulf through two openings: Boca Grande, a broad and deep region located at the northern portion, and the San Lorenzo Channel, a narrow and shallow region in the south (Monreal-Gómez *et al.*, 2001). The sea surface temperature field inside the bay presents an apparent seasonal variability (Durán-Campos *et al.*, 2020), with values of ~30°C during summer (Durán-Campos *et al.*, 2019) and values of ~19°C during winter (García-Mirafuentes, 2010). The circulation pattern inside the bay is dominated by the presence of a mesoscale cyclonic eddy (Monreal-Gómez *et al.*, 2001), which induces a nutrient Ekman pump, fertilizing the euphotic zone (Coria-Monter *et al.*, 2017). A phytoplankton differential distribution between diatoms and dinoflagellates has been observed in the eddy field (Coria-Monter *et al.*, 2014), with a consequent differential zooplankton aggregation, mainly due to the food availability (Durán-Campos *et al.*, 2015).

This study aims to assess the zooplankton groups during the summer of 2008 and 2009 in the Bay of La Paz, southern Gulf of California, Mexico. We focused our study over two consecutive summers to compare and explore any patterns in zooplankton distribution along the bay, with the hypothesis that there will be changes in the zooplankton groups due to changes in the temperature.

MATERIALS AND METHODS

Study area and sampling

The Gulf of California and adjacent areas (Fig. 1a), such as the Bay of La Paz, have high importance in terms of the planktonic species' productivity, abundance, and diversity. The Bay of La Paz (maximum depth 420 m) is located at the southwestern portion of the Gulf of California, between 24°06'-24°54'N and 110°18'-118°48'W, of which represents the biggest basin (Fig. 1b).

The hydrographic measurements and zooplankton samples were gathered during the oceanographic expedition's DIPAL-II and DIPAL-III, carried out from September 3 to 9, 2008, and August 13 to 17, 2009, respectively, onboard the R/V El Puma owned by the
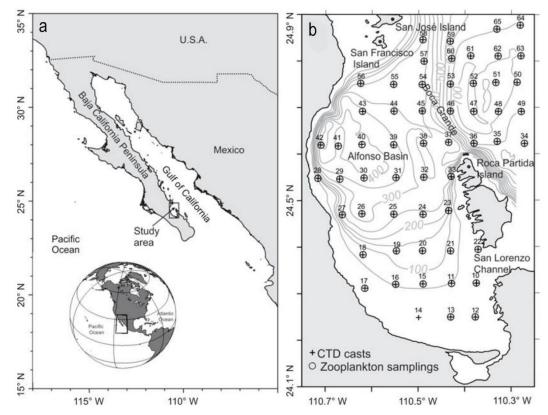
Figure 1. Study area: a) the Gulf of California, and b) Bay of La Paz. [+]Represents the hydrographic stations; o represents stations where oblique zooplankton hauls were performed. Bathymetry is shown in meters.

National Autonomous University of Mexico (UNAM). A total of 56 hydrographic stations were sampled, covering both the Bay of La Paz and the adjacent area in the Gulf of California (Fig. 1b).

At all stations, a conductivity, temperature, and depth probe (CTD, SeaBird 19 plus), equipped with a fluorescence sensor (ECO-Wet Labs) attached to a General Oceanics rosette system, was used to obtain high-resolution hydrographic records. The CTD casts were ~5 m above the seafloor. The probe was lowered at a rate of 1 m s^{-1} to acquire data at 24 Hz, with a temperature of 0.005°C and conductivity sensitivities of 0.0005 S m^{-1}, respectively.

Immediately following the rosette cast, oblique zooplankton hauls (day and night-time) were carried out using bongo nets (60 cm diameter in mouth and a 333 μm mesh size) for 15 min at ~2 knots (Fig. 1b). In the 2008 oceanographic expedition, 48% of the stations sampled were carried out under light (day) conditions, and 52% were under dark (night) conditions; in 2009, 45% of the stations sampled were carried out under light conditions, and 55% under dark conditions. With the use of nets with a 60 cm diameter in mouth and 333 μm mesh size, we assumed good representability of the mesozooplankton fraction in our samples, and we avoid the ease clogging of the net by phytoplankton or

organic matter (MacGowan & Fraundorf, 1996). After each tow, the nets were carefully inspected and washed with seawater. Zooplankton organisms were collected from 200 m depth to the surface. Calibrated General Oceanics mechanical flowmeters were used to calculate the water volume filtered. Onboard, the organisms were fixed with a solution of formalin with sodium borate at 4% for 24 h and then preserved in 70% ethanol into airtight glass bottles and in dark conditions. The samples consisted of a great variety of organisms, including mollusks, crustaceans, cnidarians, doliolids, appendicularians, ctenophores, chaetognaths, larval squids, larval fishes, among others.

Data reduction

The data obtained by the CTD probe were firstly processed with the manufacturer software (SBE Data Processing v.7.26.7) and averaged to 1 dbar. Finally, standard algorithms were used to derive the temperature (°C), salinity, and density (kg m^{-3}).

Satellite images of the SST and chlorophyll-*a* (Chl-*a*) concentration from the Moderate-Resolution Imaging Spectroradiometer (MODIS) were obtained during the dates when both research cruises took place for a comparison with the *in situ* measurements. Images with a 1 km/pixel spatial resolution were obtained from the

NASA Ocean Color Group browser (https://ocean-color.gsfc.nasa.gov/). The processing method was as follows: First, using level 2 (before mapping), values of both variables were extracted with SeaDAS v.7.4. In order to screen insufficient -or low- quality data when generating the images, the flags/masks CLDICE, HILT, LAND, and STRAYLIGHT were applied following the protocols by Pieri *et al.* (2015).

Laboratory analyses

Each zooplankton sample was initially split sequentially using a Folsom splitter until reaching the curve's point with less variation, to count and identify organisms obtained at 1/32 of the total sample (Kramer *et al.*, 1972). Then, using a Carl Zeiss microscope, the organisms were identified according to the major zooplankton groups following Trégouboff & Rose (1957) and Boltovskoy (1999) using a Petri glass dish to observe under the microscope. The abundance of the collected material was standardized to 100 m^3 following the protocols by Kramer *et al.* (1972) with the expression $N = {Nm}/{V} \times 100$, where N is the zooplankton abundance per 100 m^3 water strained, Nm is the zooplankton collected in net tow, and V is the cubic meters of water strained. We then calculated the relative abundance for each zooplankton group, which is the number of samples collected per group over the total number of organisms collected, expressed as a percentage.

Data analyses

Diversity is one of the most important parameters used to describe ecosystems. In this study, we computed the Shannon-Weaver diversity index (H'), which is one widely used index for comparing diversity between habitats, and it is enough to distinguish by groups (Magurran, 2004). The index was computed with the expression $H' = -\sum_{n=1}^{n}(pi \times ln\,pi)$ where H' is the diversity index, pi is the proportion of each group in the sample, and $ln\,pi$ is the natural logarithm of the proportion (Ortiz-Burgos, 2016). This index's value ranges from 1.0 to 4.0, and its principal objective is to obtain a quantitative estimate of the biological variability and then compare this variability both in space and time (Ortiz-Burgos, 2016).

To explore the effect of the environmental variables measured by the CTD probe on the zooplankton groups analyzed, a canonical correspondence analysis (CCA) was performed. Following the protocols by Ter Braak (1986) and the standard routines for Canoco v.4.5 software, two matrices were implemented: one containing the square-root transformed abundance data for each zooplankton group by sampling station, and another one with the surface hydrographic data (*e.g.*, temperature, salinity, density, Chl-*a* concentration) obtained for each hydrographic station.

RESULTS

The hydrographic parameters and their distribution in the bay varied between the two sampling periods. During the summer of 2008, at 2 m depth, the temperature showed values between 29.4 and 30.2°C, while during 2009, values ranged from 28.4 to 30.6°C. The horizontal distribution of sea surface temperature also varied between the two study periods. More in detail, during 2008, there was a cold-core situated in the central part of the bay, reaching values of 29.4°C at its center, and high temperatures (>30°C) were observed outside the bay (Fig. 2a). In 2009 fragmented cold cores occurred in the bay's central region with values of ~29.3°C but characterized by slightly higher values than those observed in 2008. The surface temperature presented values of ~28.4°C, particularly in the southern part of the bay, close to the Gulf (Fig. 2b).

The patterns in surface temperature were confirmed by SST satellite images (Figs. 3a,c), while Chl-*a* surface concentrations were characterized by clear north-to-south and cost-to-offshore gradients in both sampling periods, with higher values, observed close to the Gulf and in coastal areas (>1 mg m^{-3}). In 2008, the relatively higher values of Chl-*a* were observed in the central part of the bay (Fig. 3b), in coincidence with the cold core; in 2009, the distribution of the Chl-*a* values followed a circular shape in the central part of the bay with values of ~0.9 mg m^{-3} and the maximum values again observed close to the southern coast, reaching values of 1.3 mg m^{-3} associated to cold water (Fig. 3d).

Sixteen zooplankton groups were identified from the zooplankton samplings; these are summarized in Table 1. In terms of their relative abundance, the calanoid copepods were the most abundant group in both summers, representing 49 and 38% of total zooplankton abundance in 2008 and 2009, respectively, followed by cyclopoid copepods (24 and 37%). The remaining taxa represented less than 10% cumulatively in both summers, with ctenophores as the least abundant group (<1%).

Gelatinous zooplankton as cnidarians, chaetognaths, appendicularians, and ctenophores, were more abundant in 2009 than in 2008; these gelatinous organisms accounted for more than 11% in 2009 and only 6.8% in 2008 of the total zooplankton groups analyzed (Fig. 4). Based on their feeding behavior (except for appendicularians, mostly herbivores), the gelatinous organisms were carnivores. The Shannon-Weaver index calculation showed a value of 1.67 in 2008 and 1.58 in 2009.
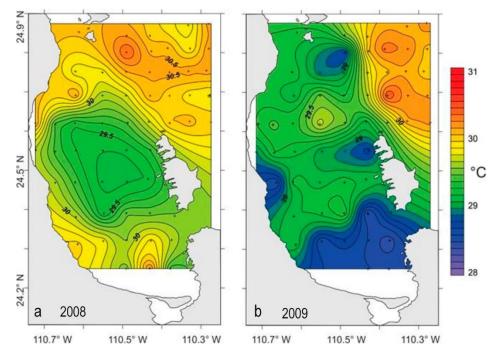
Figure 2. Surface distribution (at 2 m depth) of the temperature (°C) during: a) summer of 2008, and b) summer of 2009. Contour interval: 0.1°C.

The differences presented in the spatial distribution of two target groups in this study (calanoid copepods and cnidarians) showed changes along the bay and between both summers analyzed (Fig. 4). During 2008, the calanoid copepods' maximum abundance (3,900 ind 100 m^{-3}) was observed at the southern portion of the bay (Fig. 5a), while during 2009, the maximum abundances (7,520 ind 100 m^{-3}) were located at the central portion of the bay (Fig. 5b). An interesting pattern of distribution was observed for the cnidarians. In contrast, during 2008, the horizontal distribution showed their maximum values (470 ind 100 m^{-3}) in the northern portion of the bay (Fig. 5c); during 2009, their abundances showed an increase, with the maximum values (>500 ind 100 m^{-3}) observed close to the connection with the Gulf of California (Fig. 5d). In this region, the temperature distribution was higher during 2009.

The CCA ordination diagrams varied between both summers analyzed. In 2008, the dominant groups (calanoid and cyclopoid copepods) showed a relationship with the density values along the bay (which ranged from 21.5 to 22.5 kg m^{-3}), as well as with the Chl-*a* concentrations (which ranged from 0.2 to 1.3 mg m^{-3}), suggesting an elevated food concentration in the region that may influence the distribution of these organisms (Fig. 6a). During 2009, the CCA ordination diagram presented substantial changes concerning

2008, showing that the gelatinous zooplankton (Cnidaria, Chaetognatha, Appendicularia, and Ctenophora) was related with the temperature (Fig. 6b), which rose into a range from 28.4 to 30.4°C and confirms the distribution patterns observed (Fig. 5).

DISCUSSION

Copepods are probably the most numerous multicellular organisms on Earth. In the marine ecosystem, they play an essential role due to the position that they occupy in the trophic webs, and by their contribution to the removal of CO_2 from the atmosphere through the sedimentation of inorganic and organic carbon compounds included in their fecal pellets, contributing to the appropriate functioning of the biological or carbon pump, which is why they have been the subject of interest in recent years (Richardson, 1980; Vidal, 1980; Mauchline *et al.*, 1998; Durán-Campos *et al.*, 2019). Calanoid copepods are of prime importance because many of them are herbivorous, feeding on phytoplankton to form a direct link between phytoplankton and the higher trophic levels pelagic food web, including commercially important fish (Mauchline *et al.*, 1998). Although cyclopoid copepods are strictly carnivores, some species at some stages could feed phytoplankton, particularly diatoms (Turner, 1986; Paffenhöfer, 1993). Particularly in the southern Gulf of
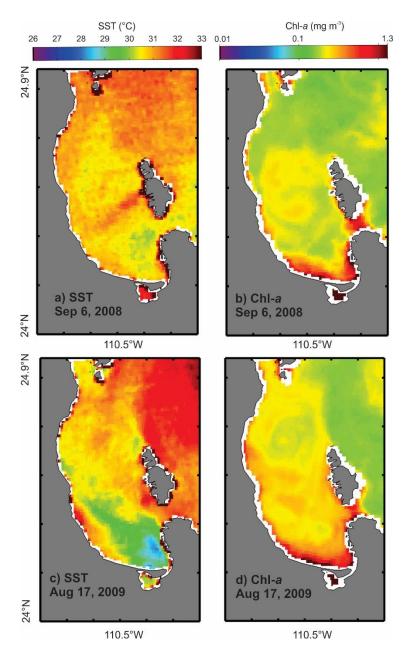
Figure 3. Satellite images from MODIS: on September 6, 2008 a) sea surface temperature (°C), and b) chlorophyll-*a* (mg m⁻³); on August 17, 2009, c) sea surface temperature (°C), d) chlorophyll-*a* (mg m⁻³).

California, calanoid copepods have been reported as the dominant group (Durán-Campos *et al.*, 2015), and studies have evaluated their composition and distribution about hydrographic properties, as well as hydrodynamic processes. For example, Cruz-Hernández *et al.* (2018) evaluated the distribution of calanoid copepods concerning the water column's thermal structure, showing that the most propitious conditions for their feeding occur in the thermocline. Those authors also revealed a clear relationship with the water column stratification and interpreted it as an adaptation strategy to survive there.

Our results revealed that calanoid copepods were the most abundant group during both summers, representing 49 and 38% of total zooplankton abundance in 2008 and 2009. However, significant differences ($R^2 = 0.87$, $P < 0.005$) emerged in their relative abundances, not only for the Calanoid Copepods but also for the rest of the analyzed groups. We contend that such differences can be related to the hydrographic properties, and, particularly with the surface temperature distribution along the study area, which showed statistical significance ($R^2 = 0.97$, $P < 0.005$) and an increment of ~1.00°C during 2009, parti-

Table 1. Total abundance and their relative abundance of each analyzed zooplankton group during the summers of years 2008 and 2009.

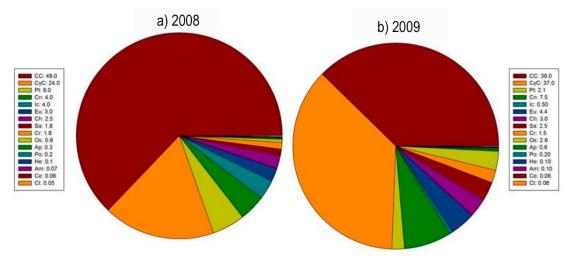| Zooplankton group	Total abundance (ind 100 m^{-3})	Relative abundance (%)	Total abundance (ind 100 m^{-3})	Relative abundance (%)
	Summer 2008		Summer 2009	
Calanoid copepods	74028	49	74064	38
Cyclopoid copepods	38525	24	72343	37
Pteropods	12648	8	3838	2.1
Cnidarians	10339	4	14380	7.5
Ichthyoplankton	6323	4	1054	0.5
Euphausiids	5361	3	8594	4.4
Chaetognaths	5321	2.5	5444	3.0
Crustaceans (shrimps, crabs, and lobsters larvae)	2994	1.8	3036	1.5
Salps	3003	1.8	5387	2.5
Ostracods	1300	0.8	5258	2.6
Appendicularians	571	0.3	571	0.6
Polychaetes	365	0.2	359	0.2
Heteropods	214	0.1	252	0.1
Amphipods	121	0.07	160	0.1
Cephalopods	103	0.06	130	0.06
Ctenophores	95	0.05	121	0.06

Figure 4. Relative abundance (%) of each analyzed zooplankton group in the a) summer of 2008, and b) summer of 2009. CC: calanoid copepods, CyC: cyclopoid copepods, Pt: pteropods, Cn: cnidarians, Ic: ichthyoplankton, Eu: euphausiids, Ch: chaetognaths, Sa: salps, Cr: crustaceans, Os: ostracods, Ap: appendicularians, Po: polychaetes, He: heteropods, Am: amphipods; Ce: cephalopods, Ct: ctenophores.

cularly in the stations close to the connection with the Gulf of California. For example (Table 1, Fig. 4), it is clear that gelatinous organisms (cnidarians, chaetognaths, appendicularians, and ctenophores) showed an increment (>3.5, 0.5, 0.3, and 0.01%, respectively) in their relative abundance in 2009, concerning 2008, associated with the increment in SST values in 2009, which was confirmed with the CCA ordination diagram (Fig. 6).

In this regard, it is widely known that both the vertical and horizontal compositions and the distribution of marine zooplankton depend on the temperature of the water column (which in turn determine movements of the water masses) as well as depend on the light intensity over a 24 h cycle, inducing diel vertical migrations of zooplankton in the ocean. Particularly, the temperature is strongly related to the biological cycles, growth, and metabolism of zooplankton orga-
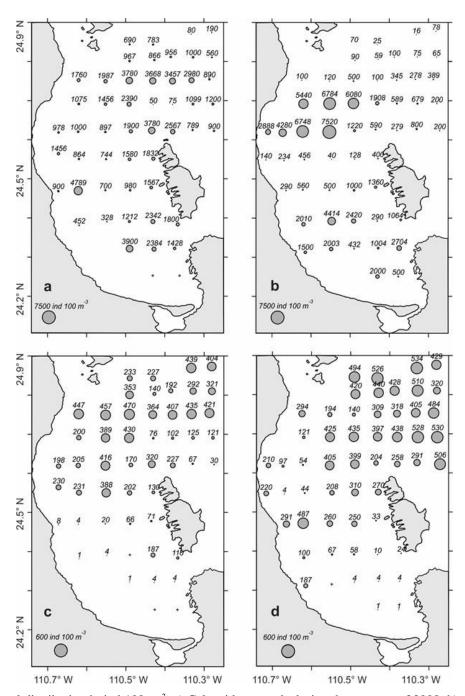
Figure 5. Horizontal distribution in ind 100 m^{-3}. a) Calanoid copepods during the summer of 2008, b) calanoid copepods during the summer of 2009, c) cnidarians during the summer of 2008, and d) cnidarians during the summer of 2009.

nisms and the availability of food (phytoplankton) for zooplankton. Indeed, Youngbluth *et al.* (2008) observed an affinity of gelatinous zooplankton (medusae, ctenophores, siphonophores, appendicularians, and tunicates) that persist in specific water masses in the Mid-Atlantic Ridge; this agrees with our observations, in which differences in the SST between both summers were observed and associated with an increase in the relative abundance of the gelatinous zooplankton. Previous research on the effects of temperature on jellyfish has shown increased growth associated with higher temperatures (Webster & Lucas, 2012). Similar observations were made by Riascos *et al.* (2013), who documented that increments in the temperature regimes may favor asexual reproduction (budding) and podocyst formation in jellyfish, with
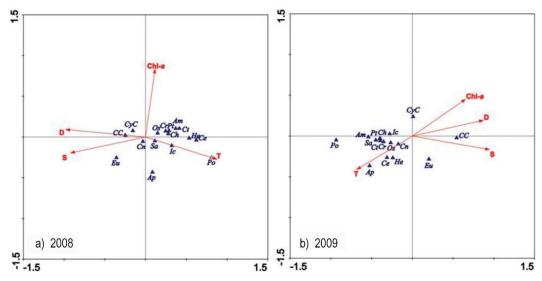
Figure 6. Canonical correspondence analysis diagrams. Red vectors indicate environmental variables: T: temperature (°C); S: salinity; D: density (kg m^{-3}); Chl-*a*: chlorophyll-*a* (mg m^{-3}); blue triangles represent the abundance for each zooplankton group (ind 100 m^{-3}). The abbreviations are described in Figure 4.

strong impacts on the abundance of the medusa stage. In the Northern Adriatic Sea, high jellyfish's high abundances coincided with hot temperatures (Kogovsek *et al*., 2010). In the Mediterranean Sea, several holoplanktonic jelly species also have been unusually abundant in warm waters (Molinero *et al*., 2008). In the Chesapeake Bay, temperature changes have been associated with jellyfish blooms (Decker *et al*., 2007).

Cnidarians are not the only group to have been studied about increased temperatures. Field-based evidence has shown that the abundance of copepods (either calanoids or cyclopoids) changes with the water temperature in Port Phillip Bay, southern Australia (Jenkins & Black, 2019). The composition and biomass of copepods from the Gulf of Gdansk (southern Baltic Sea) are also directly affected by water temperature, showing variations in biomass values as the tempera-ture increases, which, in turn, determines the biological processes and affects variability, including the distri-bution, abundance, and biomass of copepods (Musialik-Koszarowska *et al*., 2019). The mesozoo-plankton fraction (mostly euphausiids and salps) was studied along a transect with high-temperature gradients in the eastern South Pacific Ocean, showing that these groups increase with temperature (González *et al*., 2019). A progressive migration across a thermal gradient was observed into the California Current, where the zooplankton groups, particularly euphau-siids, benefit from favorable environments due to the temperature regime (Mackas *et al*., 1991). The Shannon-Weaver index results showed a slight

difference between both summers, with lower values during 2009. This difference could be related to the increment in the temperature values, which could negatively affect the food availability (phytoplankton) for the herbivorous organisms.

The results presented here are also consistent with previous reports for the southern Gulf of California region, where a high variability in the zooplankton populations has been documented due to changes in the water column structure. For example, Palomares-García *et al*. (2013) documented that the epipelagic copepods distribution is closely related to the water column's temperature, showing the highest abundances during the summertime (July). Contreras-Catala *et al*. (2016) evidenced a strong relationship between the mesopelagic fish larvae populations and the water column's stratification, which depends on the tempe-rature distribution. More recently, Ambriz-Arreola *et al*. (2017) documented that the distribution of some euphausiids species is strongly related to the water column's thermal structure, with their maximum abundance close to the thermocline.

CONCLUSIONS

The observational evidence showed differences in the hydrographic parameters between both summers, with a higher temperature recorded in 2009. The zooplank-ton groups showed that the calanoid copepods were the most abundant group; however, there were important differences in the relative abundance of the rest of the

analyzed groups due to the temperature distribution along the study area.

Based on the evidence presented here, gathered over consecutive summers from the Bay of La Paz, it is possible to envisage that, during the summer season, the zooplankton group composition will be dominated by copepods, calanoids, and cyclopoids. Then, depending on the temperature, some groups' predominance would be expected as a function of the heating; under this scenario, gelatinous zooplankton would be dominant.

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