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ORIGINAL RESEARCH ARTICLE

Impact of a dipole on the phytoplankton community in a semi-enclosed basin of the southern Gulf of California, Mexico

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Summary The present study assesses the impact of a dipole on the abundance and distribution of phytoplankton groups as well as the chlorophyll-*a* concentration in the Bay of La Paz, Gulf of California, Mexico. Based on *in situ* observations obtained in a multidisciplinary research cruise during the summer of 2008, a mesoscale dipole (cyclone-anticyclone) was observed; the cyclone had ~25 km diameter and tangential speed of ~45 cm s^{-1}, while the anticyclone had ~15 km diameter and tangential speed of ~40 cm s^{-1}. Strong gradients in conservative temperature and density were observed between both structures, suggesting the presence of an oceanic thermohaline front. Differences in phytoplankton distribution showed minimum abundance of diatoms in the southern bay and close to Roca Partida Island, and maximum in the periphery in the northern cold core. The maximum abundance of dinoflagellates and silicoflagellates occurred at the frontal zone. The chlorophyll-*a* concentration was high in the region associated with the frontal zone.

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Although mesoscale eddies are ubiquitous processes in the Bay of La Paz, this study represents the first observational report of the impacts of a dipole on the phytoplankton structure and chlorophyll-*a* in the region. The observations presented here indicate the existence of a strong association between the mesoscale processes and the phytoplankton community in the study area. This study highlights the value of efforts to improve projections of physical forcing and its influence on the planktonic ecosystem.

1. Introduction

Phytoplankton are the primary source of the marine food chain, which contributes to the major fishery resources around the world and play a pivotal role in the marine ecosystem due to their contribution in mitigating climate change and global warming, by reducing global CO_2 levels (Vajravelu et al., 2017). Numerous studies highlight the fact that the phytoplankton community structure, composition, and distribution are determined by several physicochemical variables, as well as hydrodynamic processes such as mesoscale eddies (McGillicuddy, 2016). Mesoscale eddies (with radius scales of 10—100 km) are responsible for a major portion of ocean circulation energy (Gaube et al., 2013; Liu et al., 2013). Three types of ocean eddies are described: cyclonic, mode-water and anticyclonic. Cyclonic and mode-water eddies contribute significantly to the transport of nutrients affecting both the horizontal and vertical distribution of phytoplankton community (McGillicuddy et al., 2007) while the anticyclonic are related to a reduction of primary productivity by the fact that they induce convergent movements, sinking surface waters below the euphotic zone (McGillicuddy, 2016; McGillicuddy and Robinson, 1997).

To date, it is increasingly common to find reports in the scientific literature on the role of mesoscale eddies on the phytoplankton community in different domains. In the Sea of Japan, the timing and initiation mechanisms of the spring phytoplankton blooms is associated with the presence of mesoscale anticyclonic and cyclonic eddies (Maúre et al., 2017). The phytoplankton community in the Western South China Sea is highly influenced by the presence of a cyclonic eddy owing to the doming isopycnal within the eddy supplied nutrients gently into the upper mixing layer, and there is a remarkable enhancement in phytoplankton biomass at the surface layer (Wang et al., 2016). Eddies originating in the eastern South Indian Ocean are unique in that anticyclones, usually associated with reduction of primary productivity, contain elevated levels of chlorophyll, enhanced primary production and phytoplankton communities generally associated with nutrient-replete environments (Gaube et al., 2013).

Despite the fact that extensive observations of individual structures (cyclonic or anticyclonic) have appeared in the literature, dipole structures, consisting of two with opposite signs of vertical component of relative vorticity, are less frequent. Some studies showed that the vertical distribution of phytoplankton, in terms of community and physiology, in a dipole consisting of one warm-core and one cold-core formed off Western Australia varied between both; the warm-core eddy had a vertically dispersed photoautotrophic community dominated by large diatoms and coccolithophorids, while the cold-core had a shallower and more consistent mixed-layer depth with a deep chlorophyll maximum well-developed throughout the field (Thompson et al., 2007). In the North Pacific, an elevated chlorophyll-*a* and particle concentrations have been reported in the frontal region within an anticyclone-cyclone dipole, which is consistent with the mesoscale and submesoscale physical processes; the horizontal stirring in the region appears to have caused surface convergence within the mesoscale frontal zone, which in turn increased concentrations of buoyant particles (Guidi et al., 2012).

Mesoscale eddies are ubiquitous processes in the southern Gulf of California (GC) and in the Bay of La Paz (BoP). In the BoP, they are frequently generated in the deepest region and have been well described, mainly regarding the cyclonic structure. These studies have included the genesis and characteristics (Monreal-Gómez et al., 2001), the effects in nutrient, chlorophyll-*a* and phytoplankton distribution (Coria-Monter et al., 2014) as well as the zooplankton assemblages (Durán-Campos et al., 2015). Recent research indicated that the presence of a cyclonic circulation inside the bay induces a nutrient Ekman pumping with vertical velocities of $\sim$0.4 m d^{-1} rising up the nutricline. The fertilization of the euphotic zone is stimulating the phytoplankton to grow, resulting then in higher levels of chlorophyll-*a* within the center (Coria-Monter et al., 2017).

Although the effect of the cyclone inside the BoP is relatively well documented, the way in which anticyclonic eddies affect the phytoplankton structure remains uncertain. More uncertain is the dynamics of a dipole structure (cyclone-anticyclone) and its effect on the phytoplankton distribution as well as the chlorophyll-*a* concentration. Additionally, the effects of eddies on the biological communities and biogeochemical cycles have been mostly studied in open ocean environments and far less in semi-enclosed areas such as bays.

The aim of this study was to assess the impacts of a dipole structure on the phytoplankton abundance, distribution, and composition in the BoP during the summer of 2008. We hypothesize changes in the hydrographic/thermal structure of the water column due to the presence of the dipole structure with opposite rotation movement, resulting in differences in the phytoplankton community as well as in the chlorophyll-*a* concentration.

2. Material and methods

2.1. Study area

The BoP is the largest basin within the GC and is one of the most important ecological ecosystems, due to it is representing a place for refuge and growth of different organisms (Pardo et al., 2013). It is located in the southwestern portion of the GC, approximately 200 km from the connection with the Pacific Ocean (Fig. 1a); the bay connects with the GC through two openings: Boca Grande to the northeast (wide and deep) and the San Lorenzo Channel in the south (narrow and shallow); the bay has a maximum depth of 420 m in the Alfonso Basin. An important feature is the presence of a bathymetric sill along the Boca Grande, which partially isolates the BoP from the GC (Molina-Cruz et al., 2002). The wind in the region presents seasonal changes with northwest winds during the winter and southeast winds during the summer (Monreal-Gómez et al., 2001), however westerly winds were reported during the late spring of 2004 (Coria-Monter et al., 2017).

2.2. Sampling

High-resolution hydrographic records, fluorescence measurements and water samples for phytoplankton cell count were obtained during the oceanographic cruise "DIPAL-II" carried out on board the R/V "El Puma" of the National Autonomous University of Mexico (UNAM) from September 3 to 9, 2008 along a grid of stations covering both the bay as well as its connection with the GC at Boca Grande to the northeast (Fig. 1b).

A conductivity-temperature-depth probe (CTD) Sea Bird 19 plus was used to record conductivity, temperature, and pressure at 56 stations (Fig. 1b). The CTD casts extended almost to the bottom (~2 m above the seafloor) while the ship maintained its position on station, with accuracy not worse than 200 m. The temperature and conductivity accuracy resolution of the equipment was 0.005°C and 0.0005 S/m, respectively, and it was lowered at a rate of 1 m/s, acquiring data at 24 Hz. Chlorophyll fluorescence measurements were made using a WET Labs fluorometer sensor (range 0.00—125 mg m^{-3}) on the CTD/Rosette system, calibrated by the manufacturer prior to the cruise.

A General Oceanics rosette equipped with 10 L Niskin bottles was used to take surface water for phytoplankton count cells at 49 stations (Fig. 1b). Aliquots of 500 mL were preserved with Lugol solution in glass bottles. Samples were kept in the dark until cell counting, following the recommendations of Edler and Elbrächter (2010).

2.3. Data reduction

The CTD measurements were initially processed by the standard package from the manufacturer (SBE Data Processing V.7.26.7) and averaged to 1 dbar, and then conservative temperature (Θ, °C), absolute salinity (S_A, g kg^{-1}) and density (σ_t, kg m^{-3}) values were calculated from *in situ* temperature and practical salinity according to the Thermodynamic Equation of Seawater-2010 (IOC et al., 2010). The geostrophic velocities were calculated by standard geostrophic analysis, using CTD data to calculate the specific volume anomalies, in order to estimate the dynamic height (ΔD) at each oceanographic station relative to the bottom, then these were differentiated between pairs of stations, to obtain the relative velocity by mean the practical form of the geostrophic equation $\left(v_1 - v_2 = \frac{10}{Lf}[\Delta D_B - \Delta D_A]\right)$, which represents the difference between the geostrophic current at level p_1 from that at level p_2 averaged between the stations A and B, which are separated by a distance L, and f represents the Coriolis parameter (Pond and Pickard, 1983) and then compared with the distribution of the hydrographic parameters.

The phytoplankton biomass, expressed as chlorophyll-*a* concentration [mg m^{-3}], was estimated indirectly using the manufacturer's nominal conversion factor from the *in situ* fluorescence, and then was vertically integrated from 0 to 50 m depth.

Eight-day composite satellite images of chlorophyll-*a* and sea surface temperature from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensors on board the satellite Aqua for the period when the research cruise took place (September 05 to 12, 2008) were used to compare with the *in situ* measurements. The images, with a spatial resolution of 3.5 km (Local Area Cover (LAC)), were processed using SeaDAS, version 7.4, with standard algorithms. These algorithms return the near-surface concentration of CHLA (in mg m^{-3}), calculated using an empirical relationship derived from *in situ* measurements of CHLA and remote sensing reflectance in the blue-to-green region of the visible spectrum; the algorithm employs the standard OC3/OC4 (OCx) band ratio algorithm merged with the color index (CI) of Hu et al. (2012).

2.4. Laboratory analyses

The phytoplankton cell count was assessed by the Utermöhl method, with 100 mL chamber sedimentation for 48 h following the protocols and recommendation by Edler and Elbrächter (2010). A Zeiss Axiovert 25A inverted microscope was used to count and identify the organisms by group (diatoms, dinoflagellates, and silicoflagellates) following Tomas (1997).

3. Results

3.1. Hydrography and geostrophic circulation

The surface conservative temperature distribution (contour interval 0.1°C) showed the presence of a cold core located at the central portion of the bay, reaching values of 29.4°C, whereas the distribution over the Boca Grande showed higher values (>30.3°C). Moreover, the isolines shown temperature gradients at the connection between the bay and the gulf, the temperature gradient was ~0.01°C/km (Fig. 2a). The density surface distribution (σ_t, contour interval of 0.1 kg m^{-3}) showed the presence of a high-density core at the central portion, in coincidence with the cold core, and low-density values over the Boca Grande region (Fig. 2b). The eight-day composite sea surface temperature satellite image (Fig. 2c), except in the southern BoP, matched well with the *in situ* measurements of conservative temperature, showing a relatively low temperature coincident with the *in situ*

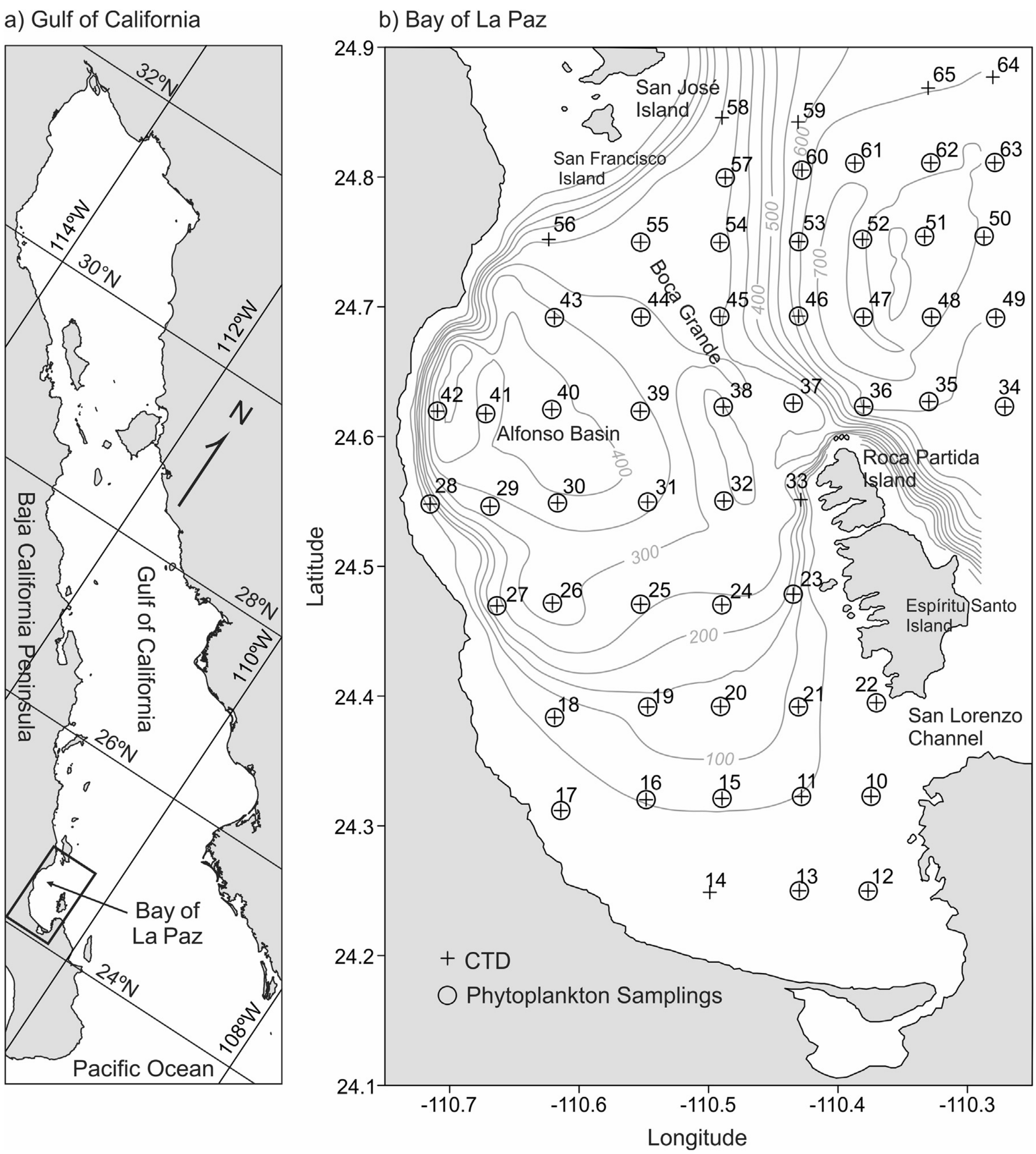

Figure 1 Location of: (a) Gulf of California and (b) Bay of La Paz and sampling stations. '+' represents CTD stations, 'O' represents phytoplankton samplings. Bathymetry (thin gray line) is shown in m.

measurements, and the highest temperature (~31.5°C) outside the bay. In addition, the image showed a relatively high temperature close to the Roca Partida Island, outside the bay. The geostrophic circulation was dominated by the presence of a dipole structure (cyclone-anticyclone). The cyclone was located at 24.5°N, 110.6°W, had ~25 km diameter and tangential speed of ~45 cm s^{-1}, while the anticyclone was located at 24.7°N, 110.4°W, with ~15 km diameter and tangential speed of ~40 cm s^{-1} extending out of the bay, reaching the Boca Grande region (Fig. 2d). According to Simpson and Lynn (1990), the classical hydrodynamic dipole (vortex pair) consists of two eddies of equal and opposite strength whose centers are separated by a distance small enough that the two structures interact, consistent with our observations.

3.2. Phytoplankton

The abundance of phytoplankton (diatoms, dinoflagellates, and silicoflagellates) analyzed in this study showed interesting variations. The diatom abundance ranged from 70 to 2800 cells L^{-1}, the dinoflagellates from 550 to 5060 cells L^{-1} while the maximum abundance of silicoflagellates was 50 cells L^{-1}. Dinoflagellates represented 64% of all organisms and diatoms 35%, while silicoflagellates represented only 1%.

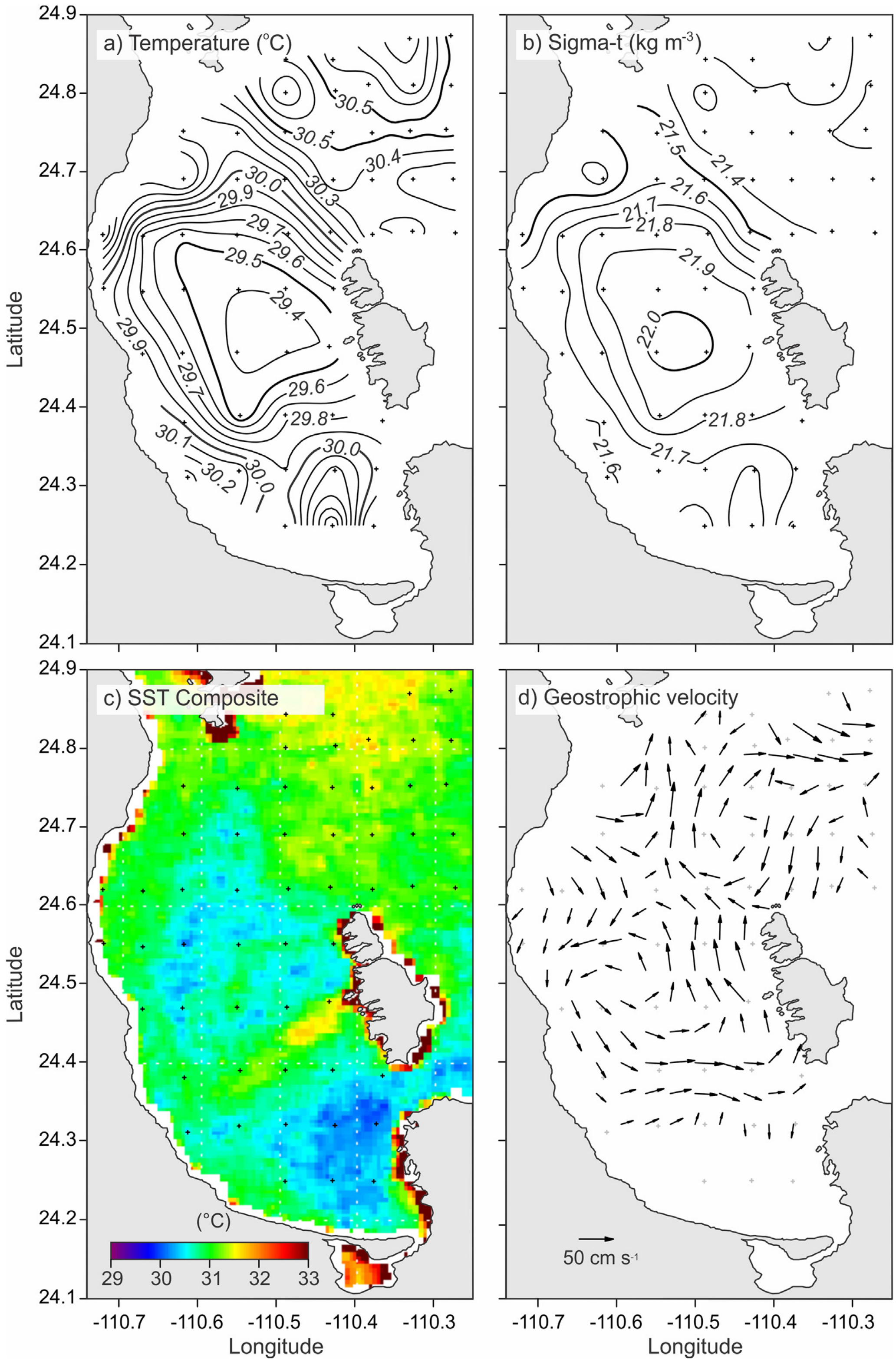

Figure 2 Surface horizontal distribution of: (a) conservative temperature [°C] (contour interval 0.1°C), (b) density [σ_t: kg m^{-3}] (contour interval 0.1 kg m^{-3}), (c) eight-day composite sea surface temperature satellite image (MODIS-AQUA) and (d) geostrophic circulation [cm s^{-1}].

Differences in their horizontal distributions were clearly observed along the dipole structure field. In order to visualize their distribution pattern, the same scale was used to compare the abundance of diatoms (Fig. 3a), dinoflagellates (Fig. 3b), and silicoflagellates (Fig. 3c). On the other hand, using different scales in order to easily visualize their patterns, the lower abundance of diatoms (~70 cells L^{-1}) was found on the southern bay and close to Roca Partida Island,

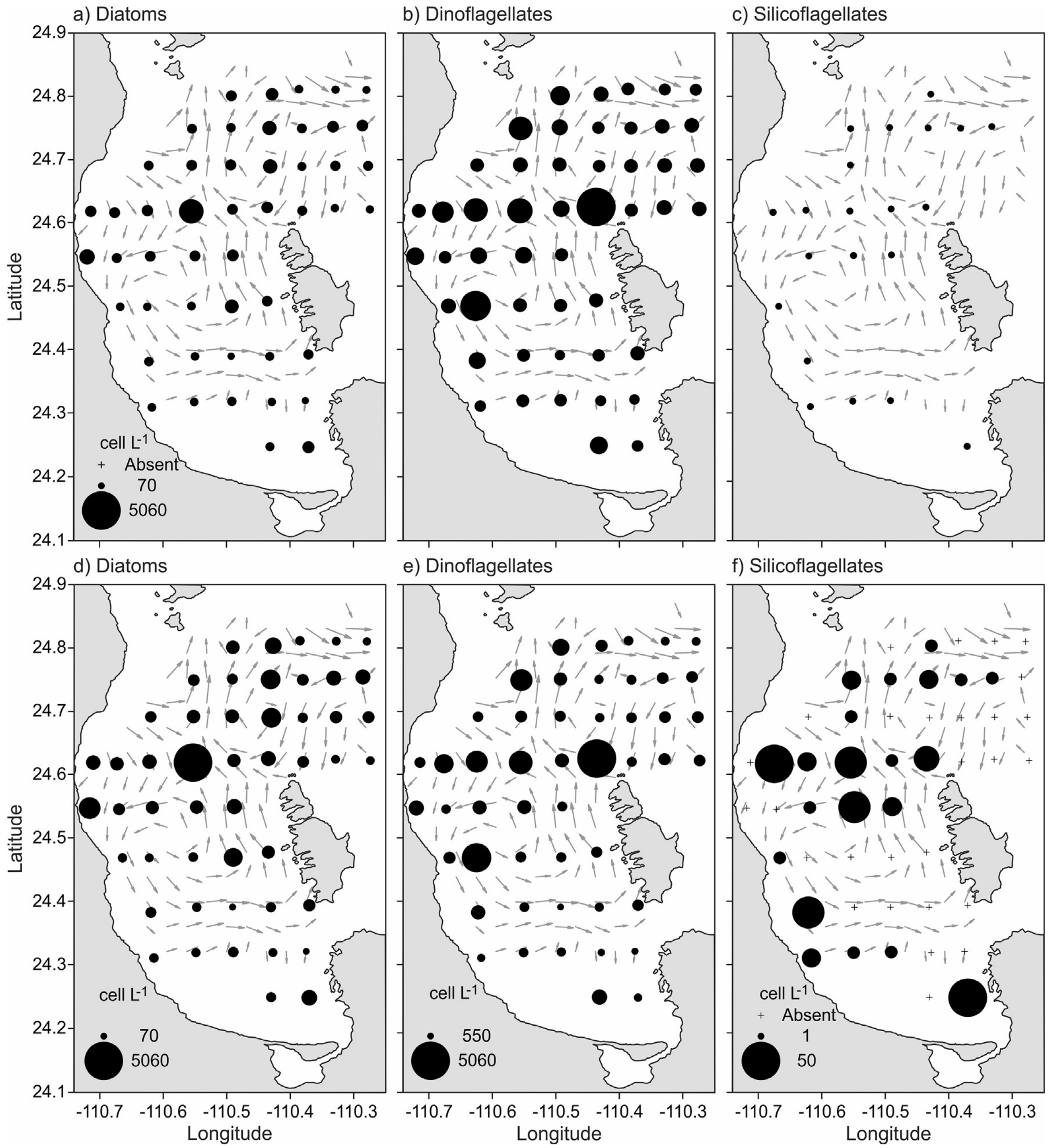

Figure 3 Horizontal distribution of phytoplankton [cells L^{-1}] at the surface: (a) diatoms, (b) dinoflagellates and (c) silicoflagellates, with same scales to compare the abundance between three groups, and (d) diatoms, (e) dinoflagellates, (f) silicoflagellates, using different scales in order to easily visualize their patterns.

while the maximum abundance occurred in the periphery in the northern cold core (Fig. 3d). The dinoflagellates distribution was found in three cores with different abundances along the bay; the first one located on the southwest portion near the coast, which is coincident with the core of the cyclone observed with an abundance of ~3200 cells L^{-1}; a second core located at the central BoP with an abundance of 2400 cells L^{-1} and a third core with the highest values located near Roca Partida Island on the Boca Grande with an abundance of 5060 cells L^{-1}, associated to the thermohaline front. Considering the abundance of the last two cores, the highest concentration of dinoflagellates was observed at the zone along the transect crossing the bay on latitude 24.6°N (Fig. 3e). The silicoflagellates distribution was similar to that of dinoflagellates, with highest abundance over the same transect and one core in the southwestern region close to the coast (Fig. 3f).

Although the organisms were not identified to species level, these results contributed to the knowledge of their ecology and contributed information on the patterns of distribution into a dipole system.

3.3. Chlorophyll-*a*

The surface chlorophyll-*a* concentration rose in a range from 0.02 to 0.18 mg m^{-3}. The maximum values inside the bay were located over the southern region. The central zone of the bay showed concentrations (~0.1 mg m^{-3}) in a core close to the Roca Partida Island (Fig. 4a). The region outside the bay, in the GC, showed the lowest concentrations with ~0.02 mg m^{-3}. The eight-day composite satellite image for the period when the oceanographic cruise took place matched well with the *in situ* measurements (Fig. 4b) with maximum values located in the southern bay (~0.18 mg m^{-3})

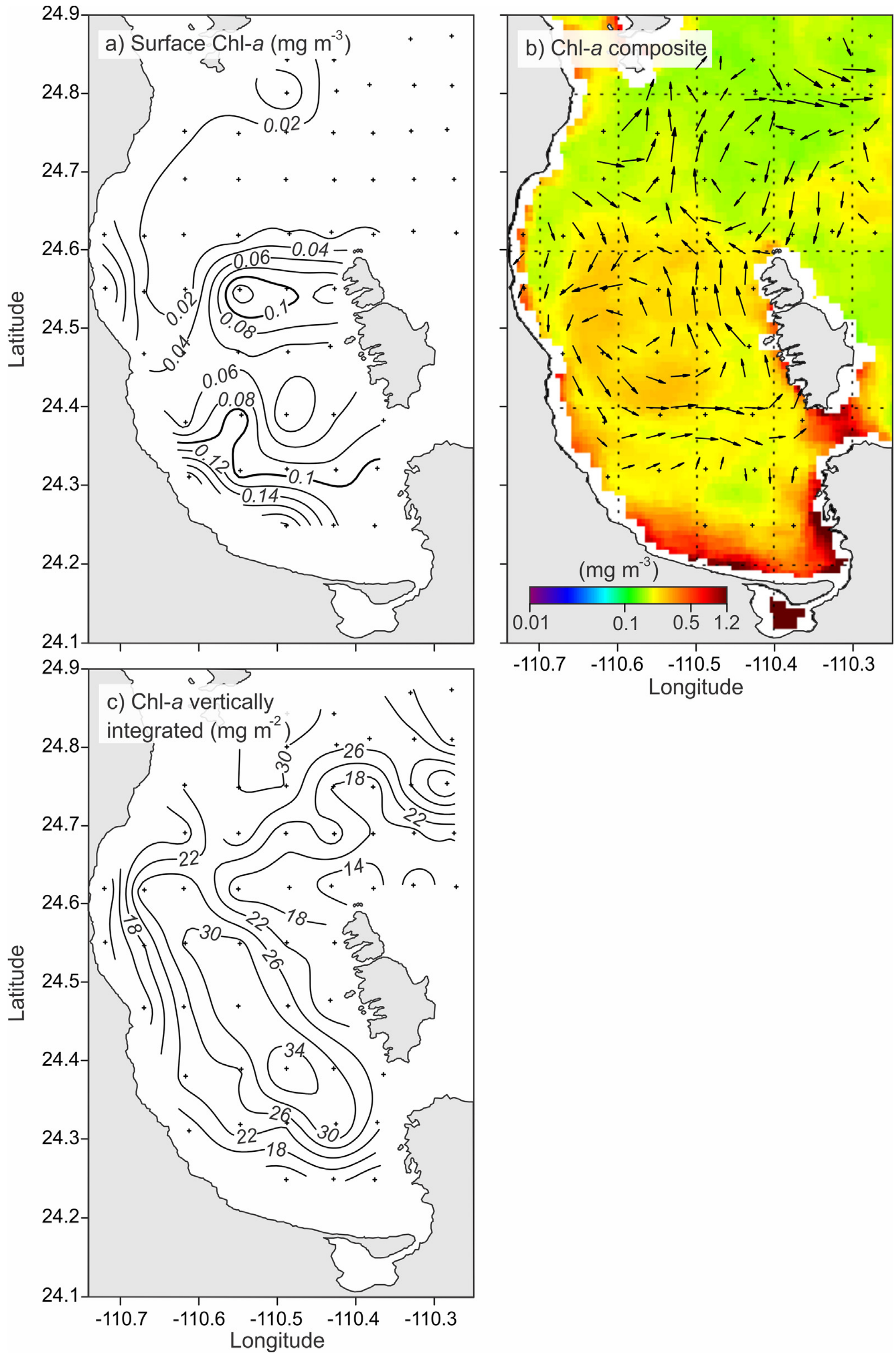

Figure 4 Surface horizontal distribution of chlorophyll-*a*: (a) *in situ* measurements [mg m^{-3}], (b) derived from eight-day composite satellite image [mg m^{-3}] (MODIS-AQUA) with geostrophic velocity field, and (c) horizontal distribution of chlorophyll-*a* vertically integrated from surface to 50 m depth [mg m^{-2}].

and relatively high concentrations in the central region (~0.10 mg m^{-3}), which coincided with phytoplankton cell counts. The vertically integrated values rose to a range of 10—34 mg m^{-2}; the maximum values occurred in a core in the southern region, with values between 30 and 34 mg m^{-2} and the pattern of distribution showed a tongue extended along the central part of the bay reaching the zone were the front is present, with values of 26 mg m^{-2} (Fig. 4c). The images also show a low-relative chlorophyll-*a* value (≈14 mg m^{-2}) in the region close to the Roca Partida Island, a region with high-temperature values.

4. Discussion

The generation of mesoscale eddies inside the GC and adjacent areas have received special attention in recent years. An important number of observational and numerical studies have contributed to elucidate their forcing mechanisms (Lavín et al., 2013; Salas de León et al., 2011). Particularly within the BoP, a quasi-permanent cyclonic circulation induced by the wind stress and by the interaction with the bottom topography and the currents between the GC and BoP has been well described (Coria-Monter et al., 2017; Monreal-Gómez et al., 2001). The information in the BoP described the presence of a single mesoscale cyclonic eddy; however, in this study, our observations showed a circulation pattern not previously reported for the region as the presence of a dipole structure consistent in a cyclone-anticyclone. In this regard, the polarity for each structure could be explained by the interaction of the currents between the BoP and the GC through the Boca Grande; if the entrance of the current to the bay is close to the Roca Partida or to the San José Island, the polarity may be cyclone or anticyclone, and once formed, this might originate another with a different rotation movement due to energy transfer, which could explain our results.

The presence of dipole structures (cyclone-anticyclone) can induce the generation of a front exerting a noticeable effect on chlorophyll-*a* levels and suspended particulate matter (Salas de León et al., 2004). A front could be represented as a linear zone that defines an axis of laterally convergent flow, below or above which vertical flows are induced and are regions of strong horizontal temperature and/or salinity contrast (Franks, 1992). Fronts not only promote fertilization by nutrients also may result in downward export of particles and organisms toward the adjacent areas, and account for the persistence of large animal populations at depth (Sournia, 1994). Erga et al. (2014) showed that a front in the Norwegian Sea is an area of higher production due to the vertical circulation bringing nutrients into the euphotic zone. In our particular case, the front was confirmed by the presence of strong gradients of both conservative temperature and density (Fig. 2a and b). Numerous studies have shown phytoplankton aggregations to be closely related to fronts in the ocean. That fronts are typically sites of enhanced phytoplankton biomass suggesting that there may be processes common to various types of fronts that support such aggregations (Franks, 1992). In the Catalan front (northwest Mediterranean), high chlorophyll-*a* concentrations and diatom dominance were observed during winter-spring, while a high abundance of coccolithophorids was observed to be offshore of the front (Estrada et al., 1999). Lehahn et al. (2007) showed that fronts in the Northeast Atlantic clearly separate regions of different chlorophyll-*a* concentration and produce chlorophyll filaments due to sub-mesoscale vertical nutrient injection. Fronts occur over a wide range of scales and are ubiquitous throughout the ocean, being formed by a persistent wind stress curl or by spatially nonuniform surface fluxes of heat which in turn sustain the vertical advective transport of nutrients from the subsurface into the euphotic layer (Mahadevan, 2016). In the northeastern Arabian Sea, fronts are active biological spots owing to injection of subsurface nutrients into the surface layer where the plankton response depended on the age of the front as well as with the initial or background conditions under which a front forms (Sarma et al., 2018). Fronts are prominent structures that organize transport and dispersion of coastal waters in the Ibiza channel (Western Mediterranean), impacting physical and biological coupled processes at regional scales (Hernández-Carrasco et al., 2018).

Studies have shown that the presence of a mesoscale dipole structure has an important effect over the distribution of particulate organic matter and plays an important ecological role in enhancing pelagic production and transporting coastal production offshore (Kolasinski et al., 2012). High phytoplankton abundance and chlorophyll-*a* values have been associated with a thermal front induced in the boundary zone between a dipole in the south of the Gulf of Mexico (Aldeco-Ramírez et al., 2009). Abundances of phytoplankton are frequently higher near the edges of a dipole in the Gulf of Alaska compared to the center or outside waters (Batten and Crawford, 2005), demonstrating that enhanced primary production is capable of supporting higher trophic levels. These edge regions may, therefore, represent excellent forage areas for fish, birds and marine mammals. Indeed, larval fish are often associated with high standing stocks of chlorophyll *a*nd zooplankton found at the edges of eddies in the northwest of the Gulf of Alaska, suggesting that frontal regions may play important roles in the survival or growth of some species (Peterson et al., 2011).

Our observations evidenced that phytoplankton group distribution is closely related to the front formed between both cyclone-anticyclone structures considering the high abundance of the three phytoplankton groups analyzed and relatively high values of chlorophyll-*a* were found in that region. Additionally, a higher concentration of the phytoplankton groups was observed at the zone along the transect crossing the bay on latitude 24.6°N which can be associated with other processes and not only with the front.

High phytoplankton abundances at the surface and high concentrations of chlorophyll-*a* were observed in regions considered to be frontal zones between a dipole with high horizontal shear rates (Thompson et al., 2007).

Using two high-resolution ocean transects across a pair of mesoscale eddies (cyclone—anticyclone) in the North Pacific Ocean, Guidi et al. (2012) showed that horizontal turbulent stirring has a dominant control on the spatial distribution of some planktonic organisms around this feature, considering that the horizontal stirring associated with mesoscale eddies affects the distribution of plankton blooms and may even determine phytoplankton community structure and dominant groups by creating fluid dynamical niches within scales of a few kilometers; in this way, buoyant phytoplankton cells are advected into the frontal zone and accumulated in regions of convergent flow, enhancing chlorophyll-*a* concentrations there.

The high biomass values commonly seen at fronts are often explained by a physiological response of the organisms to the frontal environment. However, some intuitive idea of the physiological response of the organisms to their new environment can be obtained by consideration of the physical processes affecting the organisms during swimming and accumulation (Franks, 1992).

Because they are not under the influence of the ambient vertical velocities, strong swimmers are very likely to create accumulation zones. Weak swimmers may not always create such zones, but their swimming behavior will alter the amount of time they spend in any given region of the flow (Persson et al., 2013). Due to the absence of turbulence measurements in the front during the time of our observations, we assume it to be high; under this scheme the tolerance to high turbulence by dinoflagellates, which is often accompanied by high swimming speeds, could explain the abundance of this group, which in consequence could serve as pelagic seed stock for subsequent plankton aggregations (Smayda, 2002). The ability of dinoflagellate species to tolerate the vertical velocities of frontal zones has suggested that fronts may serve as "pelagic seed banks" (Smayda, 2002). Although there are no nutrient measurements for the time of our observations, it is well known that in BoP, the presence of mesoscale cyclonic eddies modulate the pulses of fertilization to the euphotic zone due to an Ekman pumping (Coria-Monter et al., 2017), then a differential distribution of phytoplankton has been observed, with a predominance of diatoms in the periphery of the eddy due to a high concentration ($>10\ \mu$M) of soluble reactive Si (Coria-Monter et al., 2014). Under this scheme the surface layer divergence by eddies may be transporting the upwelled subsurface nutrient-rich water to the eddy field at a rate similar as it takes for the diatoms and silicoflagellates to flourish.

The stretching of the isolines in the frontal region between the cyclone-anticyclone has dynamical consequences, as it intensifies the existing lateral subsurface temperature and density gradient, as reported in mesoscale fronts created by a dipole in the North Pacific Ocean (Guidi et al., 2012).

5. Conclusions

The dipole and its front associated can be the dominant physical features influencing the horizontal distribution of phytoplankton in the BoP. To date, the information available in the area showed the presence of a quasi-permanent cyclonic eddy, which originates fertilization in the euphotic zone and a differential phytoplankton distribution, with a high abundance of dinoflagellates at its center and a high abundance of diatoms at the periphery. The results presented in this study showed the presence of a dipole structure (cyclone-anticyclone), which induced a frontal region between both structures, prompting a high accumulation of phytoplankton. Additionally, a high abundance of diatoms was observed close to the center of the anticyclonic pole. Many aspects of the influence of physical forcing on the phytoplankton community remain uncertain, then more detailed observations are required in order to enable the evaluation of many aspects of eddies, such as differences and variations in hydrographic properties, seed populations, and food-web dynamics.

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