

*Review*

## Processes and mechanisms that determine the planktonic production in the largest bay inside the Gulf of California, Mexico: a synthesis and review

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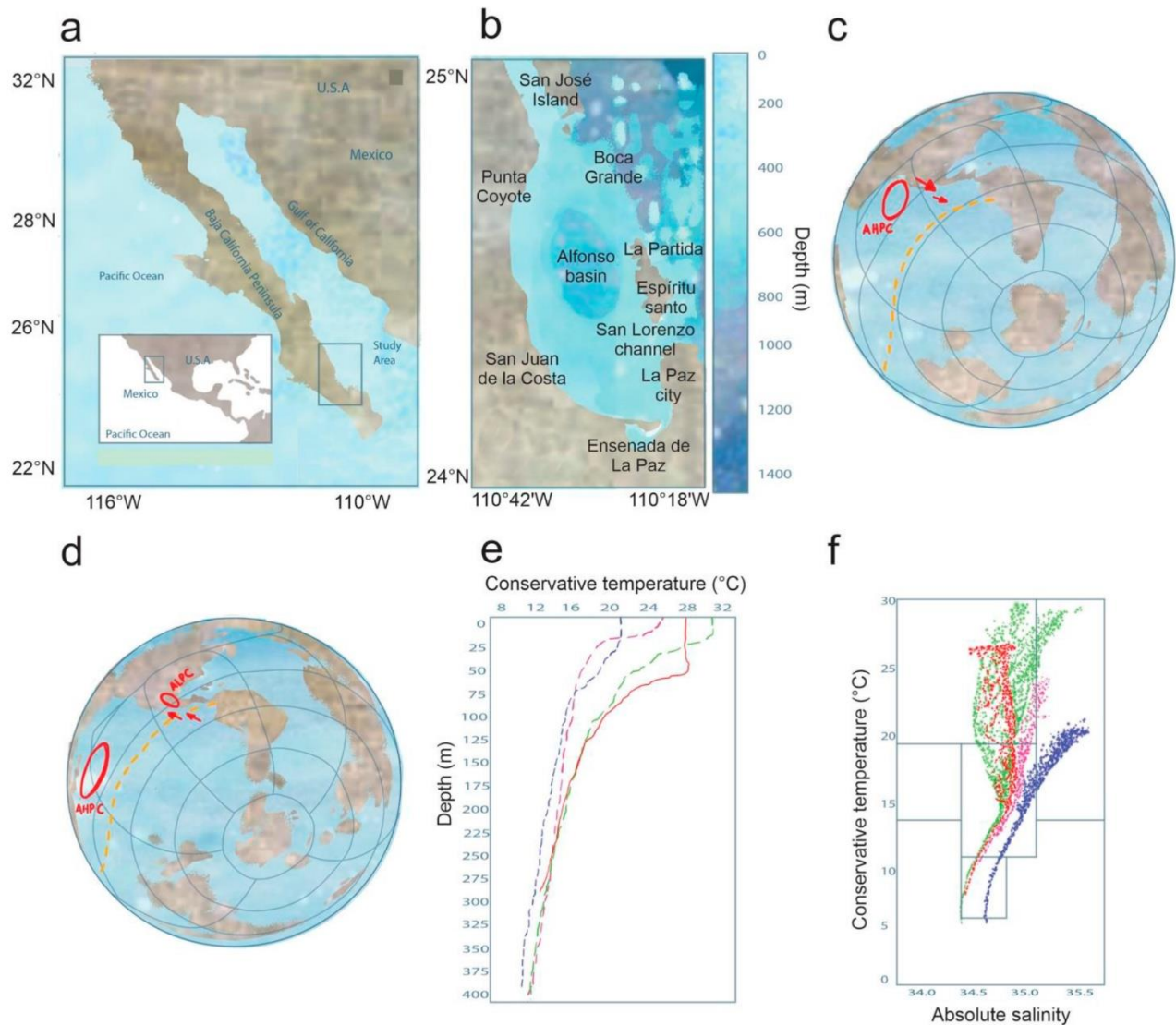
**ABSTRACT.** The Bay of La Paz (BLP) is located in the southwestern portion of the Gulf of California (GC), the largest and deepest coastal environment along the gulf. The BLP is recognized for its high biological diversity and is a place of refuge, growth, and feeding for several emblematic species, some of which are critically endangered. However, what makes the BLP productive? This paper presents a synthesis and review of the physical processes and mechanisms related to planktonic production, which are directly linked to productivity at higher trophic levels, including top predators. This review reveals that the BLP has a high richness and abundance of plankton species. Several hydrodynamic processes at different scales exert a marked influence on these organisms, including internal waves, hydraulic jumps, thermohaline fronts, the presence of a dipole eddy, and a quasi-permanent cyclonic eddy that is confined to the bay, which induces Ekman pumping that determines the availability of nutrients in the euphotic zone. This eddy induces a differential phytoplankton distribution, with a predominance of dinoflagellates in its center and the dominance of diatoms in its periphery. This arrangement is closely linked to that of zooplankton. Herbivorous zooplankton are highly abundant in the periphery of the eddy, while omnivorous zooplankton are dominant in the center. In contrast, carnivorous zooplankton are dominant in the GC. Although significant progress has been made in understanding the dynamics of the BLP over the last two decades, gaps remain unaddressed. This review highlights the areas of opportunity to continue advancing this endeavor, achieve a better scientific understanding of the region, and propose better management and conservation plans for this highly diverse area.

**Keywords:** planktonic ecosystem; diversity; hydrodynamic processes; Bay of La Paz; Gulf of California

### INTRODUCTION

The Gulf of California (GC) (Fig. 1a) is a large and elongated interior sea recognized for its extreme biodiversity. It supports numerous species of high commercial value (e.g. tuna, sardines, and sharks); is refuge, breeding, and feeding habitat of numerous emblematic species (e.g. dolphins, whales, and sea lions); and is a habitat for critically endangered species (e.g. sea turtles, the vaquita, and totoaba) (Arreguín-Sánchez et al. 2017, Villagómez-Vélez et al. 2024). In

addition, the GC is a key site for the migration, wintering, and reproduction of different species of aquatic birds (e.g. terns and skimmers) (Lluch-Cota et al. 2007). For these reasons, the GC is recognized as one of Latin America's most important large marine ecosystems (Sherman & Hempel 2009). In addition, due to its natural beauty, the GC is one of the most popular tourist sites in the world and is responsible for bringing foreign currency into the Mexican economy (Johnson et al. 2019). The high commercial value species exploitation in the GC represents 60% of the



**Figure 1.** A schematic illustration that summarizes the physical atmospheric forcing to which the Gulf of California (GC) and the Bay of La Paz (BLP) are subject. a) Location of the GC, Mexico; b) location of the BLP at the southwestern portion of the Gulf; c-d) outlines the seasonal migration of the Intertropical Convergence Zone (ITCZ; yellow line), which during the winter/spring months is located near the equator ( $\sim 2^{\circ}\text{N}$ ) and migrates latitudinally to the north as summer/fall approaches (up to  $20^{\circ}\text{N}$ ) which then induces seasonal rearrangements of the atmospheric centers of the North Pacific (high pressure, AHPC) and the Sonoran Desert (low pressure, ALPC) that cause the formation of a barometric gradient and then induce that the winds to flow along the axial axis of the gulf with different directions along an annual cycle (red arrows); e) vertical profiles of the conservative temperature ( $^{\circ}\text{C}$ ) constructed with historical CTD casts acquired in the central portion of the bay, Alfonso Basin, in different seasons of the year [winter (blue line), spring (magenta line), summer (green line) and fall (red line)]; f) temperature-salinity diagram constructed with historical CTD cast carried out in different seasons of the year: winter (blue points), spring (magenta points), summer (green points), and autumn (red points).

country's annual catches, contributing significantly to food security and the country's wealth and generating hundreds of thousands of jobs (Arreguín-Sánchez et al. 2017).

The GC has been extensively reviewed in different disciplines. For example, Brinton et al. (1986) presented one of the first reviews to examine the composition and distribution of phytoplankton and zooplankton species throughout the gulf; Lluch-Cota et al. (2007) summarized the biotic and abiotic compo-

nents of the GC and discussed the vulnerability of the system to anthropogenic pressures; Álvarez-Borrego (2012) synthesized the main mechanisms of fertilization acting in the biomass and production of the phytoplankton; Páez-Osuna et al. (2016) summarized the potential risks to which the region is subject as a result of climate change; Arreguín-Sánchez et al. (2017) highlighted the importance of the GC as a large marine ecosystem, with special emphasis on the state of fisheries; and Páez-Osuna et al. (2017) analyzed contaminants in water, sediment, and some organisms and highlighted the presence of metals, persistent organic pollutants (e.g. polycyclic aromatic hydrocarbons, polychlorinated biphenyls), and other pesticides.

These reviews have been of crucial importance in understanding the dynamics of the GC; however, except for some studies that have summarized the macroalgal distribution in coastal lagoons in its interior (e.g. Piñón-Gimate et al. 2012), to date, there have been no reviews of the main coastal regions adjacent to the gulf, which are very important areas in terms of biodiversity because they are crucial for refuge, breeding, and feeding for numerous species (Whitehead et al. 2020a).

In the southwestern portion of the GC, the Bay of La Paz (BLP) stands out due to its extension and depth. It is a highly dynamic zone with diverse biotic and abiotic characteristics that make it extremely biodiverse with several ecosystems that include beaches, dunes, seagrass beds, rocky reefs, and mangroves, some of which are subject to special protection by the Mexican authorities, including the category of National Park, Flora and Fauna Protection Area, or Ramsar site (Ávila-Flores et al. 2020). The mangrove ecosystem is crucial in the southern GC and BLP because it contributes to the energy flow between land and sea and provides vital ecosystem services, including waste processing, habitat, food production, and recreation. The value of mangrove ecosystem services worldwide has been estimated at an annual global flow of US\$ 1,648 billion (Costanza et al. 1997, Hsu et al. 2020) and within the GC benefit the capture of fish and blue crab, which generates an average annual income of US\$ 19 million for fishermen (Aburto-Oropeza et al. 2008).

The BLP is located on the east coast of the Baja California Peninsula, approximately 200 km from the connection between the GC and Pacific Ocean (Fig. 1b). It has an oval shape, with a minor axis of approximately 33 km and major axis of 81 km, and a total area of over 2,600 km<sup>2</sup>. The BLP communicates directly with the GC through two openings: 1) the San Lorenzo Channel (narrow and shallow, 19 m depth) to

the south and 2) the Boca Grande (wide and deep, 250 m depth) to the north. In bathymetric terms, the BLP is characterized by a deep region called the Alfonso Basin in its northern portion, with a depth of 420 m. The depth gradually decreases toward the south until it presents an area with a gentle slope and extensive beaches (Nava 1997). An important feature is the presence of a bathymetric sill located along the Boca Grande, which partially isolates the bay from the GC and inhibits the exchange of surface water masses between the two basins (Molina-Cruz et al. 2002) (Fig. 1b).

Owing to the extreme diversity that it supports, the BLP has been subjected to intense multidisciplinary research in the last two decades, focused on understanding the mechanisms that generate it. The present review summarizes the efforts made so far, from a physical point of view, and their effects on the planktonic ecosystem. It also points out the uncertainties, gaps, and areas of opportunity necessary to continue advancing the scientific understanding of the region.

The objectives of this study are to 1) present the state-of-the-art knowledge of the BLP in terms of physical-biological coupling, 2) summarize the processes and mechanisms involved in the high biological production focused on the planktonic ecosystem, 3) discuss the gaps and windows of opportunity that exist, and 4) propose strategies that allow further progress in the scientific understanding of the region. We believe that 1) and 2) could serve as a baseline that allows the establishment of current ecosystem conditions and thus have elements of comparison in the face of the potential threats to which the region is subjected. For example, increasing anthropogenic loads through overfishing and tourist activities seriously threaten this ecosystem. Finally, the objectives 1) to 4) would allow progress in the scientific understanding of the region, from which more and better management actions could be implemented to achieve the sustainable use of the bay's resources.

The remainder of this paper is organized as follows. The first part presents a synthesis of the knowledge of atmospheric aspects and hydrographic/hydrodynamic processes at different scales inside the bay and in connection with the GC. Subsequently, we analyze and discuss how the physical environment determines planktonic production. Although the physical environment affects the upper trophic levels, the main intention of this review was not to present their effect on top predators; however, some evidence shows how bottom-up control affects the distribution of emblematic species, such as hammerhead sharks and whales.

During the writing process of this paper, a deep search was carried out (until October 2023) in different databases, including Web of Science, Scopus, ScienceDirect, Google Scholar, and PubMed, with a series of keyword combinations (in both English and Spanish) such as "Bay of La Paz", "La Paz Bay", "Bahía de la Paz", "eddies", "hydrography", "hydrodynamic", "chlorophyll-*a*", "phytoplankton", "fitoplancton", "zooplankton", "zooplancton", "biomass", "productivity", "primary production", "secondary production", "nutrients", "diversity", "abundance", and others. More than 100 citations, including research articles, short communications, and research notes, were retrieved, reviewed, and examined one by one, and repeated references were discarded. Although this review focused on scientific articles published in indexed journals with high impact factors, some relevant works recognized as "gray literature" (e.g. graduate and undergraduate thesis, articles, and chapter books with local distribution, as well as Mexican workshops booklets) were considered. Gray literature was retrieved from local repositories, such as the National Autonomous University of Mexico (UNAM, by its Spanish acronym), the National Commission for the Knowledge and Use of Biodiversity (CONABIO, by its Spanish acronym), the Metropolitan Autonomous University (UAM, by its Spanish acronym), and the National Polytechnic Institute (IPN, by its Spanish acronym). Additionally, this review includes historical hydrographic data acquired from CTD casts conducted during research cruises in different seasons onboard the R/V El Puma operated by the UNAM to show the wide seasonal variability to which the region is subject.

## Physical scenario

### Atmospheric forcing and their influence on the water column

The BLP follows, in general terms, the atmospheric pattern described for the GC, with a marked seasonal variability derived from three main factors: 1) the irradiance on the surfaces layers of the water column that presents its maximum incidence in the northern hemisphere during the summer months (from June to September) and minimum in the winter months (from December to March) which induces heating/cooling of the surface layer (Durán-Campos et al. 2020); 2) the annual migration of the Intertropical Convergence Zone (ITCZ), which during the winter months is located near the equator ( $\sim 2^{\circ}\text{N}$ ) (yellow line in Fig. 1c) and moves latitudinally to the north as summer approaches (up to  $20^{\circ}\text{N}$ ) (Pérez-Cruz 2013) (yellow

line in Fig. 1d); and 3) the seasonal rearrangements of the atmospheric centers of the North Pacific (high pressure) and the Sonoran Desert (low pressure) that induce the formation of a barometric gradient and then stimulate that the winds to flow along the axial axis of the gulf with different directions along an annual cycle (Lluch-Cota et al. 2007) (red arrows in Figs. 1c-d). Overall, 1), 2), and 3) define the patterns of winds, precipitation, and changes in atmospheric flows with two well-defined seasonal phases, giving rise to a monsoon climate characterized by a change in wind direction. During winter, dry, cold, intense ( $>12\text{ m s}^{-1}$ ), and persistent winds present a northwesterly component. In contrast, the wind pattern is reversed during summer, with southeasterly winds characterized as warm, wet, and weak ( $<5\text{ m s}^{-1}$ ) and associated with frequent calms (Barry & Chorley 2003, Obeso-Nieblas et al. 2004).

The seasonal cycle of the wind field over the BLP was analyzed by Turrent & Zaytzev (2014), who, from numerical simulations, identified two distinct breeze flows: a nocturnal and morning breeze closely related to the regional sea surface temperature between the Pacific Ocean and the GC and a mid to late afternoon sea breeze associated with the regional daily cycle of insolation heating. More recently, based on satellite information obtained from July 2002 to December 2013, Herrera-Cervantes (2019) analyzed the monthly sea surface temperature and chlorophyll-*a* (Chl-*a*) climatologies and their relationship with the rotational wind inside the BLP. They found that the annual signal is dominant, corresponding to the seasonal warming/cooling cycle in the bay associated with the advection of nutrient-rich waters that generate Chl-*a* enrichments, which are also associated with the annual cycle of the wind stress curl.

The heating/cooling events and wind patterns mentioned above significantly influenced the water column. Some main effects are the modulation of the thermocline/pycnocline, the thickness of the mixing layer, and the water column's stratification, which influences phytoplankton communities.

In this regard, based on *in situ* hydrographic measurements, Reyes-Salinas et al. (2003) quantified the Simpson-Hunter stratification index ( $\Phi$ ), which is defined as the mechanical energy required to mix the water column; lower values indicate a well-mixed column and higher values reflect a stratified water column. Their results showed that a well-mixed, almost homogeneous water column is present during the winter/spring transition (February-March). At the same time, during the warmer months (June to September),

very high values of the  $\Phi$  index ( $>300 \text{ J m}^{-3}$ ) indicate a very high stratification of the water column.

The stratification of the water column is directly related to the development of the thermocline throughout the annual cycle. A well-defined thermocline generally implies a strong pycnocline that inhibits vertical mixing between the surface and subsurface layers. In Molina-Cruz et al. (2002) there are two clear examples of the seasonal variability of the thermocline inside the BLP (in their Fig. 3), which is shallower during April to June and becomes deeper between November and February, the cold season; year-round, the thermocline exhibits a steep vertical gradient ( $\sim 1^\circ\text{C}$  every 4 m).

In this review, Figure 1e displays vertical temperature profiles from historical CTD cast inside the BLP in different seasons. The thermocline is deeper ( $>60 \text{ m}$  depth) during autumn (red line) and winter (blue line) because of vertical convective mixing that pushes the thermocline downwards, coupled with the fact that strong and persistent winds during these seasons (mainly in winter) contribute to the deepening of the thermocline. In the spring and summer approaches (magenta and green lines), the water column becomes warmer, causing the thermocline to move up, and the weak winds during these seasons prevent the mixing of the water column. The strengthening of the thermocline/pycnocline during the summer has been closely related to the maximum concentration of nutrients (particularly nitrate) and the formation of maximum Chl-*a* peaks due to the existence of the optimal conditions (e.g. light and nutrients) for its maintenance (Durán-Campos et al. 2019a); these authors noted that, as winter approaches and the thermocline/pycnocline becomes deeper, phytoplankton organisms could be advected to greater depths, and then be light-limited, below the compensation depth, or the critical depth.

### Water masses

One of the earliest classifications of the water masses inside BLP was proposed by Torres-Orozco (1993), who, based on former 1980 International Equation of State (EOS-80) and by historical *in situ* hydrographic measurements acquired in 38 research cruises from 1939 to 1986, documented three main water masses at the interior of BLP: 1) Gulf of California Water (GCW), 2) Subtropical Subsurface Water (StSsW), and 3) Equatorial Surface Water, the latter redefined some years later by Lavín et al. (2009) as the Tropical Surface Water (TSW). Monreal-Gómez et al. (2001) confirmed the presence of the three water masses initially reported

by Torres-Orozco (1993). However, they reported the presence of an additional water mass, the Pacific Intermediate Water (PIW), which is restricted to the Boca Grande region, in connection with the GC because of its depth range (Table 1).

By analyzing an annual cycle with hydrographic data acquired in February, May, July, and October, Obeso-Nieblas et al. (2007) concluded that the surface and subsurface layers inside the BLP and its connection with the GC present a similar structure in terms of water masses, with the most significant difference in the presence of the PIW that does not penetrate the bay because of the presence of the bathymetric sill along Boca Grande, which partially isolates the bay from the open gulf.

The authors noted that there must be a notable difference in the presence and proportion of water masses depending on the season. Figure 1f shows a temperature-salinity diagram constructed from historical CTD data acquired during different seasons of the year inside the BLP and its connection with the GC. The diagram shows significant differences in terms of the proportion of water masses between each season; for example, TSW and StSsW are observed in all four seasons of the year but with different proportions, whereas the GCW is observed predominantly in the warmer months (spring and summer) and is absent during autumn and winter. The PIW is observed throughout the year but is restricted to the connection with the open gulf.

In Portela et al. (2016), the limits of the water masses of the southern GC and adjacent regions were refined in terms of absolute salinity ( $S_A$ ) and conservative temperature ( $\Theta$ ) according to the Thermodynamic Equation of Seawater 2010 (TEOS-10). Regarding the TSW, the conversion of their limits to TEOS-10 suggested an increase in  $\Theta$  and a slight change in  $S_A$  ranges regarding the former EOS-80. After the conversion to TEOS-10, no changes were made in the definition of the GCW, StSsW, and PIW in terms of  $\Theta$  (Table 1).

In general, the study of water masses within the BLP is complex because their borders and limits change throughout the year, even in the presence of extraordinary events, such as the El Niño Southern Oscillation (ENSO) (Obeso-Nieblas et al. 2014, Coria-Monter et al. 2019a). In this sense, the proportion of water masses inside the BLP presents marked seasonal and interannual changes, whose dynamics are governed by the (1) heating/cooling processes that occur throughout the year, (2) dynamics of the winds that generate the advection of water masses, and (3) high solar radiation that induces evaporation processes,

**Table 1.** Water masses inside the Bay of La Paz. The limits correspond to the classification of Torres-Orozco (1993), based on EOS-80, and the new limits in TEOS-10, based on Portela et al. (2016) (see main text for details).

Water mass	Abbreviation	EOS-80		TEOS-10		Mean depth range (m)
		Temperature (°C)	Salinity	Conservative temperature (°C)	Absolute salinity	
Tropical Surface Water	TSW	>18	<34.9	>25.1	<34.6	0-50
Gulf of California Water	GCW	>12	>34.9	>12	>35.1	0-150
Subtropical Subsurface Water	StSsW	9-18	34.5-35	9-18	34.6-35.1	75-400
Pacific Intermediate Water	PIW	4-9	34.5-34.8	4-9	34.6-34.9	400-1000

coupled with the fact that the discharge of freshwater into the interior of the bay is null.

In terms of its presence inside the bay, the GCW is attributed to two main processes: 1) it forms inside the bay from the modification of the TSW, or 2) it penetrates the bay with its thermohaline characteristics from the GC through the Boca Grande (Monreal-Gómez et al. 2001). The presence of the TSW inside the bay can be explained as follows: during winter, it is located close to the mouth of the GC in response to the pattern of winds from the northwest; in summer, when the wind pattern reverses, the TSW penetrates the GC and thus the BLP. Once in the bay, owing to evaporation processes, its temperature and salinity increase, thus acquiring the characteristics of the GCW. StSsW can be explained similarly to TSW (Obeso-Nieblas et al. 2014).

In terms of the relationship between the presence of the water masses inside the BLP and the concentration of Chl-*a*, as an indicator of phytoplankton biomass, the incursion of the TSW during the summer can confer an oligotrophic status to the bay with low values of Chl-*a* (<0.5 mg m<sup>-3</sup>) (Lavín et al. 1997). Similarly, Monreal-Gómez et al. (2001) reported that the incursion of the GCW during the summer season induces low Chl-*a* values (<0.5 mg m<sup>-3</sup>) inside the bay.

### Hydrodynamics

To date, different hydrodynamic processes have been documented inside the BLP. These occur at different spatial-temporal scales, from the microscale to the mesoscale and macroscale, considerably affecting planktonic productivity inside the BLP.

### Internal waves

Internal waves are highly energetic structures caused by vertical variations in the density of seawater that propagate at the interface between layers at different temperatures (Morozov 2018). These structures generate changes in the biogeochemical properties of the water

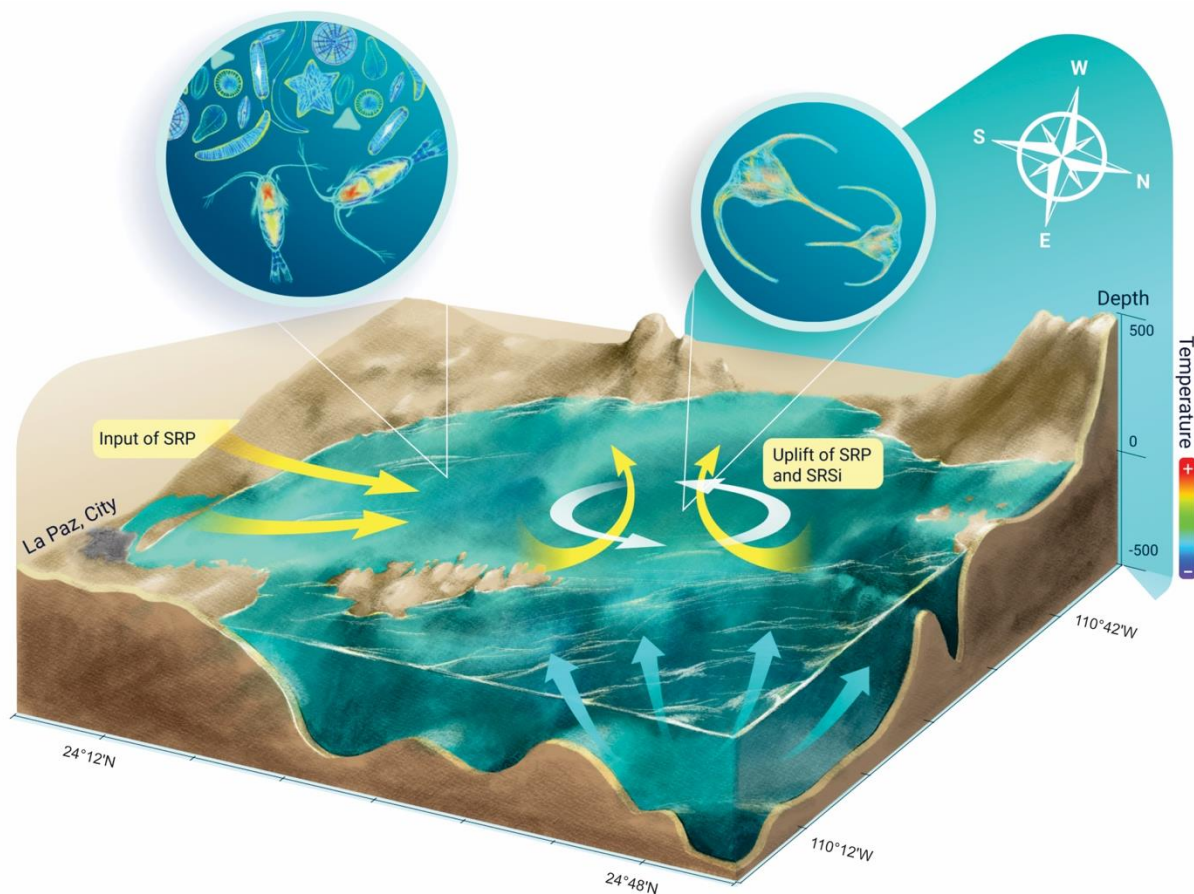
column. They are responsible for transporting phytoplankton in the vertical light gradient and displacement of nutrients towards the euphotic layer, which induces Chl-*a* enhancement by turbulent mixing (Sangra et al. 2001).

Some studies have evaluated the propagation of internal waves within the GC, particularly in its central and northern portions (Gaxiola-Castro et al. 2002, Filonov & Lavín 2003). These studies indicate that internal waves propagate particularly during the summer because of the strong pycnocline that occurs and that the waves are generated locally by the interaction of strong tidal currents, differences in bathymetry, and the geometry of the coast.

The propagation of internal waves from the GC through the Boca Grande was documented inside the BLP (Fig. 2). In recent research, Coria-Monter et al. (2019b) documented from fluctuating records of temperature and Chl-*a* and by satellite images acquired during the summertime of 2004, strong variations (in terms of minutes) between the downcasts and upcasts profiles of the CTD records, with marked changes in the depth of the thermocline and the depth of the Chl-*a* maximum; they found that the displacements in the depth of the thermocline were 8.7 m, while the displacements in the maximum of Chl-*a* were 4.4 m, in an average period of 11.6 min.

From the satellite images, the authors reproduced the internal wave structure and calculated that the wavelength in the northern and southern parts of the bay was 3.11 km, whereas that in the central part was 15.56 km. Regarding the mechanisms of generating these internal waves, the authors discussed the association between currents from the GC and the bathymetric sill in connection with the gulf, as well as the strong summer stratification, representing an ideal scenario for their propagation.

At the bay's interior, the presence of these internal waves suggests strong repercussions in the phytoplanktonic organisms of the BLP, moving them in the



**Figure 2.** A schematic illustration summarizes the physical processes at different scales that affect the planktonic ecosystem inside the Bay of La Paz (BLP). The blue arrows indicate the input of water from the Gulf of California through the Boca Grande region, which rubs against the bathymetric sill of the area, generating a hydraulic jump and, therefore, the resuspension of nutrients. Besides, from Boca Grande, trains of internal waves are generated and dissipated and move towards the bay's interior, towards the southwest. As they travel along the bay, internal waves perturb the thermocline, moving it vertically, moving phytoplankton in the vertical light gradient, and generating changes in the depth of the chlorophyll-*a* maximum. The yellow arrows indicate the input of nutrients into the BLP. The allochthonous nutrients are derived from the mining activity in the southern region, and the autochthonous nutrients are derived from the uplift of subsurface waters caused by the cyclonic eddy at Alfonso Basin. The white arrows indicate the counterclockwise circulation pattern induced by the semi-permanent cyclonic eddy that occurs in the deepest region of the bay, the Alfonso Basin. This eddy induces a nutrient Ekman pumping, benefiting phytoplankton and generating a differential distribution of diatoms and dinoflagellates from the center to the periphery. The mixing processes at the eddy's periphery generate a predominance of diatoms, while dinoflagellates dominate the eddy's center. The above impacts the zooplankton organisms, generating a differential distribution of herbivorous and carnivorous organisms according to their feeding habits. SRP: soluble reactive phosphorus, SRSi: soluble reactive silica.

vertical light gradient with a consequent change in their biomass. The authors noted that during the upcast record, the Chl-*a* was slightly lower compared to the downcast profile, which could be related to a light acclimatization effect; however, further studies on the propagation of internal waves in the region, their possible seasonal and interannual variability, and their impact on the rates of primary production are needed.

### Circulation pattern

Circulation patterns inside BLP have attracted considerable attention since the 90s. Pioneering studies using numerical models presented the first scenario of surface and subsurface circulation in the region. Indeed, Obeso-Nieblas et al. (1993) simulated the pattern of tidal currents using a hydrodynamic model adapted for shallow waters, showing that during ebb and flow, tidal

currents were in the range of 3-8 cm s<sup>-1</sup>, whereas currents in the San Lorenzo Channel were of considerable magnitude (20-25 cm s<sup>-1</sup>). Later, the circulation pattern was simulated by a model for wind-driven currents, showing evidence of a shallow coastal current with cyclonic rotation in the southern portion of the bay, which ends in a current that drives water towards the GC through the San Lorenzo Channel, resulting in the most important mechanism for renewing the surface waters of the bay (Jiménez-Illescas et al. 1997).

Subsequent observational studies on the circulation pattern in regions adjacent to the BLP in connection with the GC, particularly in the El Bajo Espiritu Santo Seamount, showed evidence of a cyclonic eddy with a diameter close to 100 km and speed of 56 cm s<sup>-1</sup> at its periphery. Due to its diameter, this eddy exerts a notable influence on the BLP, particularly in its northern portion in Boca Grande (Emilsson & Alatorre 1997).

Table 2 summarizes the studies related to the circulation pattern inside the BLP in different seasons and with varying methods of study, both direct and indirect. The first observational report of the circulation pattern inside the BLP was the work of Monreal-Gómez et al. (2001), who, based on hydrographic data from CTD casts acquired in summer (June), analyzed the horizontal distribution of temperature, isotherm topographies, and geostrophic velocities, documenting the presence of a cyclonic eddy with an elliptical shape and a diameter of ~20 km, with a major axis in a west-east direction, located in the central portion of the bay in the Alfonso Basin. In addition, their observations showed a highly stratified water column, resulting in a shallow pycnocline (25 m depth) and surface water exchange between the bay and the gulf, which occurs predominantly through Boca Grande.

Later studies on the circulation pattern of the BLP, based on geostrophic velocity calculations during summer, confirmed the presence of a cyclonic eddy. Indeed, from hydrographic data acquired during May and July, Sánchez-Velasco et al. (2004) documented the presence of a cyclonic eddy in the central portion of the bay with velocities of up to 30 cm s<sup>-1</sup> that connects the northern bay with the adjacent gulf. They showed that half of the eddy is located outside the bay in July, representing an advection mechanism for planktonic organisms between the gulf and bay. Later, using hydrographic data acquired in summer (August), Coria-Monter et al. (2014) reported a cyclonic eddy with a diameter of 30 km and geostrophic velocities >20 cm s<sup>-1</sup> at a depth of 60 m, with a maximum of 70-80 cm s<sup>-1</sup>

at a depth of 20 m. More recently, Sánchez-Mejía et al. (2020), based on *in situ* hydrographic observations acquired during August, documented the presence of a cyclonic eddy with a diameter of 20 km and maximum geostrophic velocity (95 cm s<sup>-1</sup>) in the periphery.

Studies on the circulation pattern during the spring season have documented, by geostrophic velocities, the presence of the cyclonic eddy confined to the interior of the bay in Alfonso Basin, with velocities reaching 50 cm s<sup>-1</sup>, with a mechanism of generation closely related to the wind stress and with the topography of the basin (Coria-Monter et al. 2017); these authors argue that the presence of this eddy in conjunction with the wind stress, induce an upwelling with a vertical velocity of ~0.4 m d<sup>-1</sup>, which represents the main fertilization mechanism inside the BLP which induce a higher nutrient concentration (nitrate, phosphate, and silicate) in the center of the eddy, where a rise in the nutricline contributed to the nutrients enhancement to the euphotic layer as a result of an Ekman pumping, which then results in maximum concentrations of Chl-*a*, up to 2 mg m<sup>-3</sup>.

The presence of cyclonic eddies has been reported during the winter. Indeed, using hydrographic data obtained in February and applying the geostrophic method, Sánchez-Velasco et al. (2006) documented the presence of a weak cyclonic eddy with velocities lower than 20 cm s<sup>-1</sup>, which exerted a marked influence on the dynamics of circulation not only inside the bay but also in connection with the gulf. More recently, Rocha-Díaz et al. (2021), by analyzing a dataset of hydrographic measurements obtained in winter (February) and applying the geostrophic method, documented the presence of a cyclonic eddy confined in the Alfonso Basin, with a diameter of 30 km and velocity of 20 cm s<sup>-1</sup>, which extended 110 m in depth.

Although there are few observational reports on the circulation pattern inside the BLP during autumn, it is known that during October, the circulation pattern is dominated by the presence of a well-defined cyclonic eddy that practically covers the entire central portion of the BLP with geostrophic velocities greater than 30 cm s<sup>-1</sup> (Sánchez-Velasco et al. 2006).

These studies, based on geostrophic velocity calculations, motivated studies that directly measured the circulation pattern within the bay, such as lowered acoustic profiles and drifters, which confirmed the presence of cyclonic eddies in the north-central part of the bay during the warmest months of the year. Indeed, Beier et al. (2023) analyzed lowered ADCP profiles and tracking of surface drifters from June to October of 2004, confirming the cyclonic circulation; however, the



**Table 2.** Surface and subsurface circulation patterns within the Bay of La Paz are documented within different seasons through different study methods.

Circulation pattern	Diameter (km)	Velocity (cm s <sup>-1</sup> )	Applied method	Season	Authors
Cyclonic	40	--	Isotherm topography analyses	Summer (June)	Monreal-Gómez et al. (2001)
Cyclonic	30	35	Geostrophic velocities	Summer (July)	Sánchez-Velasco et al. (2006)
Cyclonic	30	80	Geostrophic velocities	Summer (August)	Coria-Monter et al. (2014)
Cyclonic	20	98	Geostrophic velocities	Summer (August)	Sánchez-Mejía et al. (2020)
Cyclonic	16	25	LADCP/Drifters	Summer (June-August)	Beier et al. (2023)
Cyclonic	8	20	Drifters	Summer (August)	Torres-Hernández et al. (2022)
Cyclonic	26	50	Geostrophic velocities	Spring (early June)	Coria-Monter et al. (2017)
Cyclonic	30	15	Geostrophic velocities	Winter (February)	Sánchez-Velasco et al. (2006)
Cyclonic	30	20	Geostrophic velocities	Winter (February)	Rocha-Díaz et al. (2021)
Cyclonic	40	30	Geostrophic velocities	Fall (October)	Sánchez-Velasco et al. (2006)
Anticyclonic	40	--	Isotherm topography analyses	Summer (August)	Salinas-González et al. (2003)
Dipole eddy (cyclonic)	25	45	Geostrophic velocities	Summer (September)	Durán-Campos et al. (2019b)
Dipole eddy (anticyclonic)	15	40	Geostrophic velocities	Summer (September)	Durán-Campos et al. (2019b)

authors noted that the magnitudes previously reported from the geostrophic method are overestimated in terms of the orbital velocity.

For example, the speed calculations (20-25 cm s<sup>-1</sup>) were ~25-40% lower than those estimated from geostrophic balance because the centrifugal force cannot be neglected; however, the authors agreed with the presence of an intense surface cyclonic circulation with considerable interaction between the bay and the GC. The mean rotation period during their observations in August 2004 was ~1.4 days but varied in the time that surface drifters were inside the bay, from ~1-2 days in June-July to ~2.5-3 days in September-October. In a collateral study using the same surface drifter dataset, Torres-Hernández et al. (2022) confirmed the presence of a cyclonic eddy with a complete life cycle of up to 30 days.

Anticyclonic eddies have also been reported in the BLP. Salinas-González et al. (2003) evaluated the formation of a thermohaline structure inside the bay based on hydrographic measurements obtained in summer (August) and autumn (October-November). Their results showed that the three-dimensional distribution of density showed concave isopycnics towards the central portion of the bay, suggesting the existence of an anticyclonic eddy and the important role played by the heating/cooling processes of the water column in the formation of the mixed layer.

Dipole eddies have been documented in the interiors of bays. Based on hydrographic observations acquired during summer (September), Durán-Campos et al. (2019b) reported that the surface circulation pattern was dominated by a cyclonic eddy associated with an anticyclonic eddy located inside the bay and in the

connection region with the GC, with diameters of 20 and 32 km, respectively. The authors also documented strong temperature and density gradients at the periphery of both eddies, suggesting the formation of a thermohaline front that notably influenced both phytoplankton and zooplankton.

The authors pointed out that the exchange of surface and subsurface waters between the open gulf and BLP throughout Boca Grande would have a marked effect on the generation of this dipole eddy. In this sense, if the current flows into the bay close to the Roca Partida or San José Island, the eddy may be cyclonic or anticyclonic, and once formed, could give rise to another with different rotation pattern by energy transfer; additional aspects, such as the presence of the bathymetric sill along Boca Grande could be important mechanisms of generation, stemming from the bathymetrically induced instability of a baroclinic current. Another hydrodynamic process related to the bay's surface and subsurface circulation patterns is the presence of hydraulic jumps, which have been reported in the Boca Grande region, where the bathymetric sill is located.

The interaction of the currents that enter the bay from the gulf, as well as the abrupt change in depth, generates friction with the sill, which resuspends organic matter and sediments towards the euphotic zone, benefiting phytoplankton and zooplankton communities, particularly copepods (Rocha-Díaz et al. 2021).

## Planktonic ecosystem

### Phytoplankton

Phytoplankton studies inside the BLP have addressed three main aspects: 1) taxonomic listings, 2) studies of their biomass (expressed as Chl-*a* concentration) and its relationship with the physical environment, and 3) primary production rates.

Pioneering studies on the taxonomic composition of phytoplankton inside BLP appeared in the 1980s. These studies were mainly focused on presenting taxonomic listings. However, some of them considered the role of the physical environment, primarily the changes in temperature that affect the composition and distribution of these organisms.

In one of the first studies, Signoret & Santoyo (1980) documented a clear seasonal variability in the phytoplankton composition based on sampling gathered between 1975 and 1976. For example, even though diatoms were dominant throughout the year, the authors noted changes in their abundance depending on the

season. During the spring season, more than 70% of the relative abundance of phytoplankton was dominated by diatoms of the genera *Chaetoceros*, *Rhizosolenia*, and *Nitzschia*, followed by dinoflagellates. In contrast, the diatom species represented only 40% of the relative abundance in autumn. Wide fluctuations in the phytoplankton population throughout the year have been reported, ranging from 140,000 cells L<sup>-1</sup> in spring to more than 1,708,950 cells L<sup>-1</sup> in winter. The authors argue that these variations are largely due to changes in surface temperature and the horizontal transport of water masses due to the tides and point out that the extreme values observed during the winter may be related to the upwelling events that occur during this time in the eastern portion of the GC; however, the distance between both coasts (>200 km) makes this mechanism unlikely. In Ensenada de La Paz, in the southern BLP, the predominance of diatoms throughout the year has also been documented, with *Nitzschia closterium* being the dominant species (García-Pámanes 1987).

The structure of the phytoplankton community in the San Lorenzo Channel during an annual cycle was analyzed by Lavaniegos & López-Cortés (1997), who documented the predominance of diatoms throughout the year (with a total of 16 species), followed by dinoflagellates (7 species) and silicoflagellates (2 species). The authors documented changes in the relative abundance of diatoms throughout the year. For example, during autumn, they observed the maximum values of diatoms with a predominance of *Chaetoceros*. In contrast, during spring and summer, *Nitzschia* were dominant, possibly related to the input of nutrients in the coldest months.

In a more recent study, from monthly samples (from June 2001 to June 2022) collected at different depths, Verdugo-Díaz & Gárate-Lizárraga (2018) analyzed the annual variation of the phytoplankton community structure in a fixed point located in the central portion of the bay; they reported a total of 62 taxa, belonging to 45 species of diatoms, 11 species of dinoflagellates, 3 species of silicoflagellates, 1 ciliate, 1 cyanophyte, and 1 coccolithophorid. Diatoms were dominant during the annual cycle, followed by dinoflagellates. Regarding the vertical distribution of all taxa, diatoms were dominant at the surface, and dinoflagellates were observed at high densities at depths related to 10% of the incident irradiance. Simultaneously, silicoflagellates were abundant in euphotic zones. This heterogeneity was associated with the temporal evolution of the mixed-layer depth.

As one of the main phytoplankton groups inside the BLP, dinoflagellates have drawn attention in recent years, not only because of their abundance and diversity but also because some species that occur in the region induce harmful algal blooms that are potentially toxic, representing a potential risk to the ecosystem and human health. In a review of the state of knowledge regarding harmful algal blooms in Mexico by Band-Schmidt et al. (2011), it was pointed out that the BLP is a region in which multispecies harmful algal blooms are recurrent, including the dinoflagellates *Cochlodinium polykrikoides*, *Gymnodinium catenatum*, and *Noctiluca scintillans*. However, harmful algal blooms caused by dinoflagellates have been reported, and diatoms of the genera *Chaetoceros* and *Pseudonitzschia* generate blooms inside the BLP, which represent a serious threat to species, particularly crustaceans and fishes (Núñez-Vázquez et al. 2011).

Multidisciplinary studies focused on understanding the role of physical forcing on the distribution, composition, and phytoplankton have appeared in the last decade. Since the publication of the work of Monreal-Gómez et al. (2001), the role that the circulation pattern inside the bay exerts on phytoplankton populations began to become relevant.

As mentioned above, Coria-Monter et al. (2014) reported the presence of a cyclonic eddy in the Alfonso Basin. They analyzed the composition and distribution of phytoplankton (at the group level) within the field of action of this eddy. They identified a differential distribution of phytoplankton from the center to the periphery, with a predominance of diatoms on the periphery (with values ranging from 300 to 1,420 cells L<sup>-1</sup>) and a predominance of dinoflagellates in the center of the eddy (with values ranging from 340 to 2,430 cells L<sup>-1</sup>). Likewise, they reported that the concentration of Chl-*a* differed in the field of action of the eddy, with maximum values in the periphery and lower values in the center. The authors argued that there are different mechanisms associated with this differential phytoplankton distribution, including 1) the rise of the nutricline by the eddy, which fertilizes the euphotic zone to which phytoplankton respond; 2) mobility by dinoflagellates that causes these organisms to present migrations/aggregations towards favorable areas (in this case, with the center of the eddy), in contrast to the null mobility of diatoms; and 3) grazing by heterotrophic dinoflagellates present in the center of the eddy, which could explain the low values of diatoms there.

Coria-Monter et al. (2017) documented that the presence of the cyclonic circulation pattern inside the

bay during early spring induces an elevation of the nutricline by an Ekman pumping, which shows vertical velocities of ~0.4 m d<sup>-1</sup>, fertilizing the surface layer (particularly with nitrate) and then induces high Chl-*a* concentrations (>2 mg m<sup>-3</sup>) in the central portion of the eddy. A similar pattern was documented by Sánchez-Mejía et al. (2020), who observed the highest Chl-*a* concentrations (> 3 mg m<sup>-3</sup>) in the center of the eddy during the summer of 2017 in a layer between 20 and 30 m depth, with absolute maximum values located at a depth of 20 m because of nutrient pumping.

The presence of dipole eddies inside the bay is also related to the phytoplankton communities. Based on hydrographic observations made during the summer season, Durán-Campos et al. (2019b) documented the presence of a dipole eddy (cyclonic-anticyclonic), which in turn generates a thermohaline front that exerts a notable influence on the distribution and abundance of phytoplankton groups. Dinoflagellates represented 64% of all organisms, diatoms 35%, and silicoflagellates only 1%, with clear differences in their horizontal distribution along the dipole structure showing the highest concentration of dinoflagellates and silicoflagellates in the region where the thermohaline front is present.

Understanding Chl-*a* distribution patterns (as an indicator of phytoplankton biomass) and their seasonal variability is essential for evaluating the productive potential of the BLP and its possible implications for food webs. Some studies have focused on assessing the vertical distribution of phytoplankton biomass. Indeed, based on high-resolution *in situ* observations, Durán-Campos et al. (2019a) assessed the vertical distribution of Chl-*a* inside the bay during summer, showing high values (>3 mg m<sup>-3</sup>) and a vertical distribution consistent with two patterns: 1) a peak closely related to the seafloor at stations in the shallow area close to the coast and 2) a peak related to the thermocline and pycnocline, either above or below, in the central region of the bay. Both patterns have several implications for food webs, particularly grasslands. The authors also proposed marine zoning, in which a trend would be expected for summer based on the two vertical patterns described.

In a recent study based on field and satellite observations, Durán-Campos et al. (2020) documented the Chl-*a* seasonal variability in the central part of the bay, showing the highest values (>9 mg m<sup>-3</sup>) during winter and the lowest values (1.17 mg m<sup>-3</sup>) during summer. Spring and fall represent transitional seasons. This wide seasonal variability is closely related to the different mechanisms acting in the region, including local atmospheric forcing, which induces wind-driven

mixing and changes in the heating/cooling of the water column.

Some studies have addressed the possible relationship between large-scale processes like El Niño and phytoplankton biomass inside the BLP. During 2015-2016, an extreme El Niño event (named "Godzilla") occurred in the Pacific Ocean, impacting different ecosystems worldwide. Using high-resolution observations acquired during November 2016 (post-Godzilla), Coria-Monter et al. (2019a) evaluated the possible impact of this event on phytoplankton inside the BLP. Their results showed that, contrary to expectations, Godzilla did not dramatically impact phytoplankton biomass. Although warm water masses were reported, they did not appear to negatively impact phytoplankton populations, at least in the surface layer, suggesting that the circulation pattern inside the bay, together with the confluence of different hydrodynamic processes at different scales, can "mask" the negative effects of El Niño within the BLP. However, controversies remain regarding the impact of the El Niño 2015-2016 event inside the BLP. For example, recent research has reported anomalously low Chl-*a* values ( $<1.2 \text{ mg m}^{-3}$ ) associated with extreme sea surface temperature changes, together with changes in wind field patterns (Herrera-Cervantes et al. 2023).

Additional large-scale processes, such as the Pacific Decadal Oscillation (PDO), are related to the Chl-*a* levels inside the BLP. For example, Guevara-Guillén et al. (2018) analyzed the variability in Chl-*a* levels from 116 monthly averaged composite satellite images with a spatial resolution of 1.1 km from 2000 to 2009, a period in which PDO was one of the most important phenomena. They identified two main Chl-*a* concentration periods: a higher one ( $>1.2 \text{ mg m}^{-3}$ ) from December to March and a lower one ( $<0.4 \text{ mg m}^{-3}$ ) from April to November.

In addition to studies focused on understanding the role of physical forcing in the composition and phytoplankton biomass inside the BLP, several studies have focused on evaluating phytoplankton primary production and the ideal bio-optical conditions for photosynthesis. For example, Reyes-Salinas et al. (2003) estimated primary production values from natural fluorescence in different months of the year. They reported that the highest values ( $16 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) occurred in spring. In contrast, the lowest values ( $2\text{-}5 \text{ mg C m}^{-3} \text{ h}^{-1}$ ) occurred in summer and autumn due to the high stratification of the water column that occurs during the warmer months. A seasonal model of primary production in the central portion of the BLP estimated from natural fluorescence was presented by

Cervantes-Duarte et al. (2005), who showed two main seasons in the primary production cycle, one of the high values ( $>2.26 \text{ g C m}^{-2} \text{ d}^{-1}$ ) from March to August and the other with low values ( $<0.74 \text{ g C m}^{-2} \text{ d}^{-1}$ ) from September to February, which depend on the light intensity available for phytoplankton populations and also on the water column stratification variability throughout the year. Verdugo-Díaz et al. (2014) presented primary production estimates based on  $^{14}\text{C}$  assimilation in the central portion of the bay (in the Alfonso Basin). They pointed out high production in the bay, reaching integrated values of  $>300 \text{ g C m}^{-2} \text{ yr}^{-1}$ . More recently, Coria-Monter et al. (2019c) showed primary production values estimated from natural fluorescence during late spring (June), whose integrated vertical values ranged from 0.02 to  $2.45 \text{ g C m}^{-2} \text{ d}^{-1}$ , agreeing with previous observations carried out during the same month.

The smallest fraction of phytoplankton, picophytoplankton, has also been studied in the BLP. Hernández-Becerril & Pastén-Miranda (2005) analyzed the abundance and distribution of *Synechococcus* in the central portion of the bay, as well as their connection with the GC during June, showing values ranging from  $9.1 \times 10^4$  to  $7.7 \times 10^7 \text{ cells L}^{-1}$  which are comparable with some observations made in the northern GC and the California Current region (Díaz & Maske 2000). In a recent study, Pajares (2021) showed evidence that a cyclonic eddy inside the BLP strongly influenced *Synechococcus*'s abundance and vertical distribution.

### Zooplankton

The extreme diversity of organisms, including marine zooplankton, in the southern GC and BLP has led to the publication of several taxonomic studies. Among the first annotated species lists of the gelatinous zooplankton (e.g. medusae, chaetognaths, and siphonophores) of the southern GC, including the BLP region, were those of Mass (1897) and Bigelow (1909), who listed the species collected in scientific expeditions on board the US Fish Commission steamer "Albatross". Subsequently, Alvariño (1965, 1969, 1971) contributed to the species description of these groups in the southern portion of the gulf, particularly in the first 150 m of the water column. These pioneering observations generated intriguing questions about the species that can reach coastal regions as refuges and feeding areas.

In particular, inside the BLP, one of the earliest taxonomic lists that included several groups collected in different climatic seasons (winter, spring, summer, and autumn) was presented by Signoret & Santoyo (1980), who identified 13 phyla, 55 genera, and 36

species, with copepods (15 genera and 16 species) being the most abundant group. In contrast, foraminifera, radiolaria, tintinnids, ctenophores, and other crustaceans (e.g. ostracods, cladocerans, and amphipods) showed low abundance values. The authors noted a wide range of variability according to each season, with variations in their abundance and, in many cases, the substitution of some species related to changes in the hydrographic properties of the water column, mainly temperature. The authors noted that while copepods were observed in all climatic seasons, medusae and ctenophores were only observed during spring, and holoplanktonic mollusks (pteropods and heteropods) were only observed in summer and fall. Later, Lavaniegos & González-Navarro (1999a) confirmed the dominance of copepods, followed by chaetognaths and appendicularia, with marked interannual changes related to the confluence of ENSO events that impacted the region. Recent studies have documented eight major zooplankton groups, with a marked dominance of copepods, followed by chaetognaths (Whitehead et al. 2020b).

In this sense, as one of the most conspicuous groups and because they have marked ecological importance, copepods have been subject to intense research in the BLP and its adjacent regions, including an annotated listing of species and environmental aspects. The number of species reported in the BLP is indeed high, reaching a total of 146 species (Lavaniegos & González-Navarro 1999a, González-Armas et al. 2002, Palomares-García et al. 2018) with marked changes according to the season, physical environment (including ENSO events), and regions inside the bay. For example, Palomares-García (1996) reported a high number of species (126 species) in the southern portion of the bay, Lavaniegos & González-Navarro (1999b) reported in the San Lorenzo channel, a total of 93 species during the ENSO event of 1992-1993, while Aceves-Medina et al. (2007) reported 45 species in waters of the Ensenada de La Paz (southern BLP). The differences in the total number of species have been attributed mainly to hydrographic changes in the water column and to different sampling strategies; for example, the mesh sizes varied from 333 to 500  $\mu\text{m}$ , thus capturing species of different sizes, making robust comparisons among populations difficult.

The circulation pattern of the BLP has been identified as an important mechanism regulating the distribution of copepods and their biomass. In a recent study, Rocha-Díaz et al. (2021) reported that the presence of the cyclonic eddy in the central portion of the bay during winter induces the formation of a

"copepod belt-shaped area" around the eddy attributed to the affinity of the organisms for waters with favorable temperature and the availability of food for copepods due to the mixing processes by the eddy which promotes the growth of phytoplankton at the eddy periphery. In addition, the seasonal variability in copepod biomass between summer and winter appears to be regulated by the maturity stages of the cyclonic eddy inside the bay (Rocha-Díaz et al. 2022). Mojica-Ramírez et al. (2023) analyzed the dynamic population of the calanoid copepod *Centropages furcatus* (from copepodites to adult stages) under the influence of a cyclonic eddy in the interior of the BLP, documenting a differential distribution from the center to the periphery of the eddy, with a high abundance of the first copepodite stage in the center of the eddy related to high Chl-*a* values in this region. Copepods within the BLP are ecologically important, with some estimates suggesting that they consume 17% of the daily phytoplankton production, making them vital in transferring matter and energy along the pelagic food web (Hernández-Trujillo et al. 2007).

Another important group of crustaceans inside the BLP is euphausiids, which are highly abundant and have relatively high species richness, with seven reported species (De Silva-Dávila & Palomares-García 2002). Based on data collected during seven oceanographic expeditions, the larval growth production of the neritic euphausiid *Nyctiphanes simplex* in the BLP was analyzed by de Silva-Dávila & Palomares-García (1998), showing high values that can be compared with upwelling regions, highlighting the importance of the BLP as a nursery and feeding area. Another euphausiid species reported to be highly abundant in the BLP is *Nematoscelis difficilis*, whose population dynamics are closely related to the current and wind patterns of the bay (De Silva-Dávila et al. 2004). It is important to remember that euphausiids represent the main food resource for emblematic organisms such as whales; therefore, their recurring presence inside the bay could be related to the high abundance of these small crustaceans.

Gelatinous zooplankton are also highly abundant inside the BLP. For example, Ketchum et al. (2013) reported that after copepods, cnidarians, and chaetognaths were the major groups of zooplankton assemblages, chaetognaths were a potential source of food for whale sharks in the region. Cnidarians are a conspicuous but relatively unknown component of the BLP, whose populations fluctuate widely, with high temporal and spatial variability in abundance with the temperature regime inside the bay (Coria-Monter et al.

2020). From samples collected from the eastern margin of the BLP during the summer season, Mendoza-Becerril et al. (2020) reported 16 species comprising 15 genera of cnidarians (Medusozoa), emphasizing the need to direct research efforts towards this group of organisms, considering the ecological services provided by this group. There are many different ecosystem services that cnidarians offer; for example, this group exerts important effects owing to its role as a predator of zooplankton, fish eggs, and ichthyoplankton, as well as providing food for some species of juvenile fish, which in turn ensures the correct operation of the biological or carbon pump. Some cnidarians benefit humans in this region, especially by providing food (López-Martínez et al. 2020).

In general, the abundance of gelatinous zooplankton in the BLP seems to be strongly influenced by changes in the temperature regime; it has been documented that the proportion of cnidarians, chaetognaths, appendicularians, and ctenophores is high when the surface temperature increases, possibly as a result of changes in food (phytoplankton) availability along the water column (Coria-Monter et al. 2020).

Because of their ecological importance and high abundance, studies on other specific zooplankton groups, such as ichthyoplankton, have appeared in the literature. Sánchez-Velasco et al. (2004) documented the summertime richness, abundance, and spatial distribution of this group, identifying more than 90 species with high abundance values ( $>4000$  ind  $100$  m<sup>-3</sup>), with spatial variations depending on the sea surface temperature regime inside the bay, in association with the exchange of water masses between the bay and the GC and related to the wind pattern that induces mixing of the water column, particularly in the shallow region inside the bay. Some years later, Sánchez-Velasco et al. (2006) analyzed the spatial and temporal distribution of this group and its relationship with geostrophic surface currents using data and samples collected in months representative of each climatic season of the year (May, July, October, and February). Their results showed a high total abundance (32,728 ind) of 289 taxa distributed across 86 families, with the largest species number (230) recorded in October. The authors argued that species with oceanic affinity enter the interior of the bay because of the presence of a cyclonic eddy, which advects organisms from one site to another. The circulation pattern inside the bay and its vicinity greatly influences the ecology of this group of organisms.

Information on zooplankton distribution in terms of trophic or functional groups (herbivores, carnivores, and omnivores, assigned according to their main

feeding habits and the classification proposed by Le Quéré et al. (2005)), and their relationship to the circulation pattern has appeared in the literature in the last decade. For example, Durán-Campos et al. (2015) documented that the zooplankton trophic group distribution inside BLP depends on different mechanisms related to the presence of the cyclonic eddy, which induces a vertical displacement of the nutricline. This benefits phytoplankton, representing a potential food resource for herbivorous zooplankton such as calanoid copepods, doliolids, pteropods, salps, and others. The authors noticed that the cyclonic eddy induced a differential zooplankton aggregation in the eddy influence. While herbivorous zooplankton was dominant inside the eddy, the periphery was dominated by carnivorous zooplankton (e.g. chaetognaths, ctenophores, siphonophores, and jellyfish). In a later study, Durán-Campos et al. (2019c) suggested that the presence of the eddies inside BLP may serve as important habitats for the zooplankton trophic groups; for example, using information collected in September, they documented the presence of a dipole eddy (cyclonic-anticyclonic) in which carnivores (e.g. jellyfish, cyclopoid copepods, amphipods, ctenophores) were more abundant inside the anticyclonic (warm) eddy and herbivores (e.g. calanoid copepods, pteropods, appendicularians) were predominant at the center of the cyclonic (cold) eddy. They also noted that an eddy dipole induced the formation of a thermohaline front at the periphery between both eddies, representing a mechanism of zooplankton biomass accumulation.

### Final remarks

The BLP is a highly dynamic region as a product of the processes and mechanisms that it presents at different scales; it exerts a notable influence on the entire ecosystem, including changes in picophytoplankton, phytoplankton, and zooplankton, and even seems to regulate the genes that participate in the nitrogen cycle (Ramos-de-la-Cruz et al. 2021).

Even though the number of studies and scientific publications has increased in the last two decades, there are still many opportunities to continue advancing the knowledge of this productive ecosystem. We then present some considerations for future research, particularly on physical-biological coupling.

1) Observational studies. As can be seen in this review, much of the information available to date comes from specific "snapshots" for certain times or seasons, so it is necessary to implement long-term monitoring programs that allow a deep evaluation of the seasonal and interannual variability to which the region is

subjected, with the following research questions: how is the evolution of the eddies throughout the year? What generates them? What other hydrodynamic processes are involved? What generates them? What are the effects of these processes on nutrient dynamics and transport? What are the responses of phytoplankton and zooplankton? What are the ecological implications of the findings? Naturally, the above represents a significant challenge owing to the high costs involved in the execution and implementation of oceanographic expeditions onboard research vessels; however, oceanographic expeditions onboard research vessels are imperative.

2) Numerical modeling. Numerical modeling is a tool that allows progress and coverage of existing gaps. Some works have appeared in the GC that have used numerical models to evaluate the circulation pattern and its effect on the region's biogeochemistry (e.g. Marinone 2003, Salas de León et al. 2011). These studies have been very helpful in understanding the system's behavior; these models could be adapted to BLP conditions to obtain valuable information.

3) Satellite imagery. Technological progress in satellite products has made it possible to advance the scientific understanding of oceans globally and locally because it allows synoptic observations to be obtained with very high spatial (1 km or less) and temporal resolution (1-2 days). The analysis of long time series to monitor environmental changes in both coastal and oceanic environments by *in situ* observations involves important challenges owing to the high operational and logistical costs of oceanographic research vessels. Therefore, alternative and affordable methodologies, such as satellite imagery, are essential to analyze pivotal parameters in marine ecosystems. This need is particularly important for environments recognized for their high biological diversity and regions that, owing to their geographical location, are subject to the influence of extreme phenomena (e.g. ENSO and PDO) that have repercussions for the entire marine ecosystem. This new methodology is particularly important in global warming, where model simulations have shown that the consequences of ENSO events will increase, with a global trend of a decline in Chl-*a* levels linked to changes in oceanographic conditions and climate variability.

4) Emergent tools. Modern times have brought significant advances in generating robust measuring devices such as gliders, surface drifters, ROVs, and drones. The use of alternative technologies is essential for monitoring pivotal aspects of the BLP, such as the eddy life cycle, which could also allow the estimation

of associated parameters, including the mass of water trapped, fluxes, and eddy dissipation, with the consequent response of phytoplankton/zooplankton. In recent years, drones have proven very useful for monitoring mangroves, beach topography changes, and marine animal populations (jellyfish, sharks, sea turtles, birds, and whales) (Hsu et al. 2020). Drones have proven useful for monitoring harmful algal blooms (Bilyeu et al. 2022, Hanlon et al. 2022).

5) Pollutant studies. Another important aspect that needs to be considered is the constant and growing anthropogenic load the region is subjected to; therefore, research on how pollutants could affect marine species inhabiting the BLP is needed. To date, the area is increasingly affected by different activities, including tourist development, urbanization (with more than 250,000 inhabitants), and agriculture, which increase wastewater discharge and port activities from La Paz City, representing a potential risk for the species. Recent research in the southern portion of the BLP documented the composition, distribution, and sources of 16 polycyclic aromatic hydrocarbons in surface sediments and tissues of the mussel *Modiolus capax*, showing that polycyclic aromatic hydrocarbons in mussels were higher than those in sediments and like those in mussels from other contaminated sites (Roldán-Wong et al. 2020). Another environmental threat to the region is contamination by plastics and microplastics. Plastic debris is one of the most abundant anthropogenic wastes, classified as a contaminant of emerging concern, and virtually no studies have yet covered this topic. This research will help to answer key knowledge gaps regarding the effect of microplastics on recruitment, species populations, and, ultimately, broader economic consequences, such as impacts on shell and finfish stocks. Understanding the potential effects of microplastics across all biological levels is the key to developing effective risk assessments (Galloway et al. 2017). Research on this topic within the BLP has begun to appear in the scientific literature, focusing on filter feeder megafauna (Galli et al. 2023); however, studies on organisms at the lowest trophic levels, such as zooplankton, are still scarce.

#### **Credit author contribution**

All authors contributed equally to this review paper. All authors have read and accepted the published version of the manuscript.

#### **Conflict of interest**

The authors declare no potential conflict of interest in this manuscript.

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