

Review Article

Phytoplankton studies in the southern Gulf of Mexico: what we know and what we don't

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ABSTRACT. The Gulf of Mexico is a large, semi-enclosed sea on the North American continent, known for its high biological diversity. Among the diverse organisms, phytoplankton, microscopic species that inhabit the euphotic zone, play a crucial role and provide numerous ecological and economic benefits. This work offers a critical review of the current state of research on phytoplankton in the Gulf of Mexico, with a primary focus on the southern portion, the Mexican waters. While research on phytoplankton communities in the northern Gulf of Mexico has explored several aspects, including taxonomy, genetics, modeling, and photosynthetic rates, among others, studies in the southern gulf have adopted different approaches. This variation stems from factors such as infrastructure and specific environmental issues faced in each portion. In the southern Gulf of Mexico, a significant proportion of studies concentrate on specific groups of phytoplankton, particularly diatoms and dinoflagellates. Conversely, other important groups, like silicoflagellates and coccolithophores, have been largely overlooked despite their ecological significance. Moreover, much of the research on phytoplankton in the southern gulf has focused on coastal areas and on morphological descriptions and taxonomic inventories. The influence of gulf oceanic dynamics on phytoplankton communities, however, remains largely unexplored. This review highlights gaps in the study of phytoplankton in the southern Gulf of Mexico. Given the context of global change, multidisciplinary research is crucial, making it imperative to evaluate the impact of large-scale hydrodynamic processes on phytoplankton communities.

Keywords: phytoplankton; species richness; biomass; distribution patterns; southern Gulf of Mexico

INTRODUCTION

The Gulf of Mexico (GM) is a large, semi-enclosed sea on the North American continent, spanning more than 1.5 million square kilometers and extending across more than 10° of latitude. It has complex bathymetry, including escarpments, submarine canyons, abyssal plains, and an extensive continental shelf (Fig. 1) (Goff et al. 2016).

The gulf is characterized by strong hydrodynamics driven by oceanic processes at various scales, resulting in significant seasonal variability (Morey et al. 2024). One of the most important processes in the gulf is the Loop Current, which is the flow of warm water that enters the gulf through the Yucatan Channel and exits toward the Atlantic Ocean through the Straits of Florida. The Loop Current transports energy, heat, salt, and organisms throughout the GM (Sturges et al. 2005, Coria-Monter & Durán-Campos 2025).

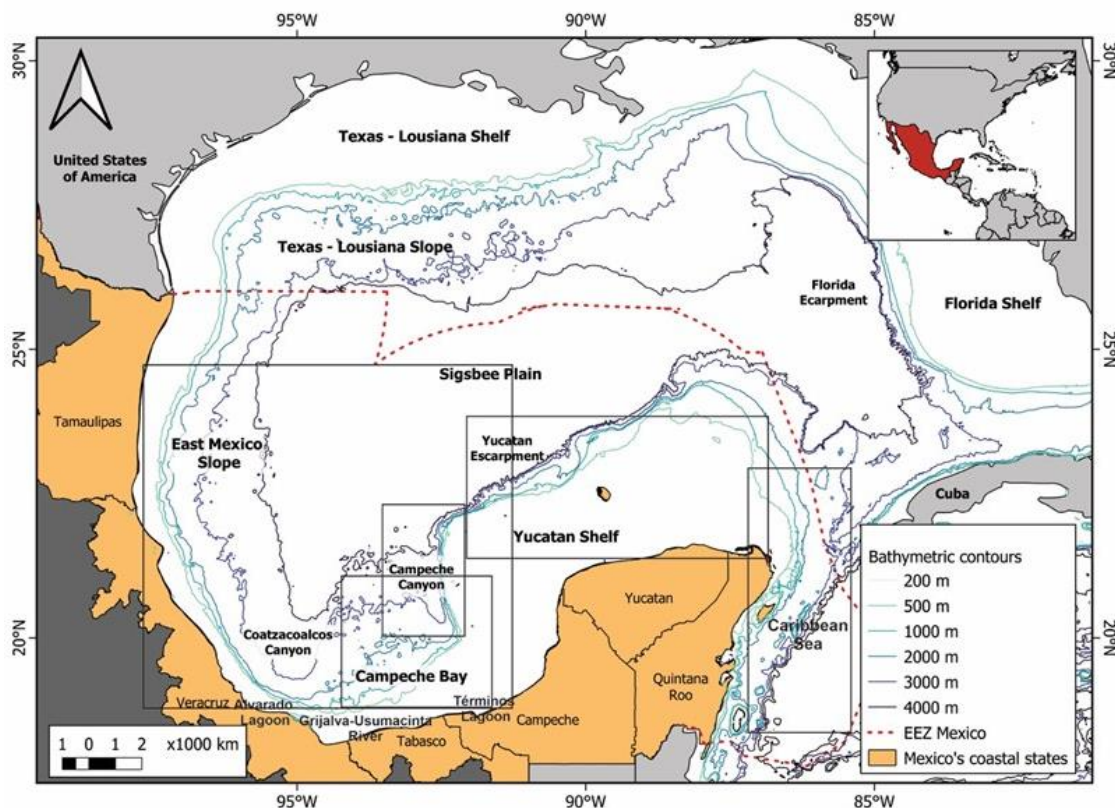


Figure 1. The Gulf of Mexico is a large marine ecosystem on the North American continent. The bathymetric contours are displayed in meters. The black boxes indicate areas with historical sampling coverage, including the Yucatan Shelf, the Campeche Canyon, the Campeche Bay, and, most recently, the deepwater regions of the gulf. Refer to the main text and Table 1 for a comprehensive overview of these sampling locations.

As the Loop Current enters the gulf, it releases a series of eddies, particularly anticyclonic ones, that propagate throughout the region (Thoppil et al. 2025). Additionally, other processes affect the gulf's biological productivity. For example, a semi-permanent cyclonic circulation occurs in the Campeche Bay (Vázquez de la Cerda et al. 2005). Also, there are dipole eddies comprised of cyclonic and anticyclonic movements in the Campeche Canyon region (Salas-de-León et al. 2004), along with the propagation of internal waves (Santiago-Arce & Salas-de-León 2012).

These hydrodynamic features are fundamental to structuring phytoplankton communities because they govern nutrient availability in the euphotic zone. While anticyclonic eddies generally suppress vertical mixing, often leading to oligotrophic (nutrient-poor) conditions, their edges and the interactions with cyclonic features facilitate intense upwelling and the uplift of nutrient-rich deeper waters. This localized enrichment triggers phytoplankton blooms, sustains primary production, and determines the spatial distribution and taxonomic

composition of these communities (Durán-Campos et al. 2017).

Phytoplankton is a highly diverse and abundant group of microorganisms found throughout the euphotic layer of the world's oceans. As primarily photosynthetic organisms, they play a crucial role in releasing oxygen into the atmosphere and capturing carbon dioxide in the oceans (Diaz et al. 2023), which led to their classification as an "Essential Climate Variable" (Grigoratou et al. 2025). Moreover, phytoplankton is vital not only for this reason but also because they form the base of the marine food chain, supporting important fisheries, many of which have significant commercial value (Stock et al. 2017).

Phytoplankton research in the GM has been conducted for more than a century. The earliest observations of phytoplankton in the gulf were made by Schmidt et al. (1874), who illustrated diatoms from the southern region. Some years later, Agassiz (1888) documented long chains of blue-green algae, now identified as *Trichodesmium*, as well as the presence of

Coccolithophoridae in the central gulf. This work inspired further studies of phytoplankton communities in the northern portion, particularly among the Florida populations (Taylor 1928) and those near the mouth of the Mississippi River (Riley 1937).

Some years later, interest in phytoplankton studies in the gulf was stimulated by the disastrous red tide (now called harmful algal blooms) outbreaks that occurred along Florida's west coast in 1946 and 1947 (Galtsoff 1948).

The first systematic review of this group was published in the 1950s (Davis 1954). Since then, the study of gulf phytoplankton has expanded significantly. Research in the northern GM has explored a range of topics, from taxonomy to numerical modeling. In contrast, studies in the southern portion have focused on different issues, influenced by specific infrastructural needs and environmental challenges unique to each area.

In the following lines, we provide a critical review of the current state of phytoplankton research in the GM, with a particular focus on the southern region, specifically the waters surrounding Mexico. We identify critical knowledge gaps that must be addressed amid ongoing environmental changes, while highlighting opportunities to advance our understanding of this essential group of organisms.

To conduct this review, we searched across high-impact databases, including Web of Science, Scopus, ScienceDirect, Google Scholar, and PubMed, using targeted keyword strings. This initial search phase retrieved more than 280 documents. The resulting dataset underwent a rigorous multi-stage processing workflow: first, duplicate entries were computationally removed, followed by a thematic screening of titles and abstracts to ensure relevance.

The review primarily synthesized peer-reviewed literature from indexed journals with established impact factors. However, to mitigate publication bias and capture regional nuances, we performed a secondary manual search to incorporate significant "grey literature", such as doctoral theses, technical reports, and conference proceedings. Each source was critically appraised for its methodological soundness before being integrated into the final synthesis.

Phytoplankton studies in the southern Gulf of Mexico

What we know

The first report on phytoplankton in the southern GM, specifically in the waters of the Campeche Bay, was

published by Schmidt et al. (1874). This report included illustrations of local species, with a particular focus on diatoms. Following this initial publication, subsequent taxonomic lists were generated, identifying a total of 78 diatom species, notably featuring a significant presence of the genus *Campylodiscus* (Mann 1925). The author observed that this taxonomic list bore many similarities to the flora of other regions of the world, which was attributed to parallel development and dispersal of species across different ocean basins.

After several years without systematic studies on phytoplankton, the importance of these organisms in the southern GM was recognized again in the 1940s. A notable observation was the complete lack of organized research in this area (Osorio-Tafall 1942).

During the 1960s, important studies on phytoplankton, particularly dinoflagellates from the Caribbean, emerged. These studies contributed significantly to our understanding of the spatial distribution patterns of this group. Additionally, valuable taxonomic lists were presented, including 30 taxa primarily from the genera *Ceratium* (now referred to as *Tripos*), *Diplopelta*, *Dinophysis*, *Protoperidinium*, *Ceratocorys*, *Gonyaulax*, and *Ornithocercus* (Balech 1967a,b).

The 1960s and 1970s were a period of significant advancement in the study of phytoplankton in the southern GM, especially in shallow coastal waters and coastal lagoons. During this time, initial research on the hydrography and phytoplankton productivity of the Alvarado Lagoon in Veracruz was published (Villalobos et al. 1966). The first taxonomic lists of the Alvarado Lagoon reported 27 phytoplankton species, predominantly from the genera *Skeletonema*, *Chaetoceros*, and *Bacteriastrum* (Margalef 1975). In Términos Lagoon, researchers documented 19 phytoplankton genera, with *Rhizosolenia* as the dominant genus, comprising over 90% of the population (Gómez-Aguirre 1965). Additional studies revealed a high abundance of phytoplankton, including 44 diatom genera and 5 dinoflagellate genera (Suárez-Cabroo & Gómez-Aguirre 1965), totaling 123 diatom species (Loyo-Rebolledo 1966). Furthermore, in the coastal area off Veracruz, taxonomic lists identified 15 genera, with *Nitzschia* and *Asterionella* being the most representative (Vega-Rodríguez & Arenas-Fuentes 1965).

Between 1964 and 1984, Cuban-Soviet expeditions onboard Soviet research vessels marked a significant advancement in the study of phytoplankton in the southern GM. These studies focused on oceanic rather than coastal waters and collected samples from over

2,000 stations. The findings were published in a comprehensive book, more than 25 scientific articles, and several technical reports (Okolodkov 2003). This wealth of information was valuable not only from a taxonomic perspective but also from an oceanographic standpoint, as the research cruises adopted a multidisciplinary approach. They identified previously unknown hydrodynamic factors and linked them to phytoplankton populations.

For instance, it was first discovered that circulation patterns in Campeche Bay fertilize the euphotic zone, thereby enhancing phytoplankton biomass in the region (Zernova 1969). Additionally, researchers found that phytoplankton populations in the Campeche Bank exhibit significant diel variability; specifically, dinoflagellates are most abundant at noon, while diatoms peak at dawn (Zernova 1970).

From these investigations, initial taxonomic lists were developed, identifying 700 species from two major areas: the southern GM and the Caribbean Sea (Roujiyaynen et al. 1971). A few years later, new taxonomic lists emerged, increasing the total number of species to over 1,500 in both the southern gulf and the Caribbean region, primarily consisting of diatoms and dinoflagellates (Zernova & Krylov 1974). Decades later, using information from these expeditions, López-Baluja et al. (1992) compiled a list of 529 species, with dinoflagellates (264 species) and diatoms (230 species) predominating.

Before the National Autonomous University of Mexico acquired the oceanographic R/V Justo Sierra, significant research was conducted onboard Mexican Navy vessels. This research produced invaluable insights into the composition of phytoplankton species in the southern gulf. Consequently, the first taxonomic lists for the Yucatan continental shelf region were published, documenting 85 species. Among these, diatoms were dominant, comprising 75% of the recorded species, followed by dinoflagellates at 20% and coccolithophores at 5% (Luna-Soria 1979). Additionally, hydrographic aspects related to the distribution and abundance of phytoplankton were identified (Santoyo & Signoret 1973). For example, diatoms from the genera *Thalassiosira*, *Chaetoceros*, *Lauderia*, *Skeletonema*, and *Nitzschia* were commonly identified in the Cape Catoche upwelling zone (Licea 1992).

The arrival of the R/V Justo Sierra in Mexico in 1982 marked a pivotal moment in the study of phytoplankton in the southern GM. It enabled Mexican researchers to expand their sampling areas to include oceanic zones beyond the continental shelf and

establish long-term monitoring programs. As a result, the first oceanographic research cruise, "PROGMEX-I," was conducted in April 1983. This expedition collected samples for phytoplankton identification, reporting 175 taxa. The genus *Chaetoceros* was the most diverse diatom genus, with 30 species identified, followed by *Ceratium* (now referred to as *Tripes*) and *Oxytoxum*. Overall, dinoflagellates were represented by 44 species, primarily thecate forms (Licea et al. 2017).

Monitoring programs conducted between the mid-1980s and the early 2000s, specifically the "OGMEX" and "SGM" projects, enabled the collection of organisms from over 600 stations in both the continental shelf and deep waters of the southern GM. These efforts resulted in taxonomic lists comprising over 250 species of dinoflagellates, with a particular dominance of species from the genera *Ceratium* (now classified as *Tripes*) with 47 species, *Protoperidinium* (28 species), *Dinophysis* (26 species), *Oxytoxum* (19 species), and *Prorocentrum* (15 species) (Licea et al. 2004). From the generated taxonomic list, more than 10 potentially toxin-producing species were identified, including *Karenia brevis*, *Amphidinium carterae*, *Dinophysis acuta*, *D. caudata*, *D. fortii*, *D. mitra* (now known as *Phalacroma mitra*), *D. rotundata* (currently referred to as *Phalacroma rotundatum*), *D. tripes*, *Prorocentrum mexicanum*, *P. micans*, and *P. minimal* (now recognized as *P. cordatum*) (Licea et al. 2004). Additionally, these monitoring projects generated databases that documented the presence of 255 diatom species. The most commonly observed genera included *Chaetoceros* (36 species), *Thalassiosira* (20 species), *Nitzschia* (18 species), and *Rhizosolenia* (14 species) (Licea et al. 2011).

Parallel oceanographic research cruises carried out between 1983 and 1989, including the "Yucatan" and "J.S." projects, significantly advanced our understanding of diatoms. These campaigns documented 38 species of *Chaetoceros* in the oceanic and neritic waters of the Yucatan Shelf (Hernández-Becerril & Flores-Granados 1998).

Since the late 1990s and throughout the 2000s, extensive monitoring programs in the southern GM have not only generated taxonomic lists but also examined the role of the physical environment in the composition, distribution, and abundance of phytoplankton species.

During multidisciplinary research cruises conducted under the project "PROMEBIO", hydrographic and current data were collected, along with water samples at different depths in Campeche Bay and the Campeche Canyon. This research identified three distinct ecological regions: the inner shelf where phytoplankton

biomass increases near the seafloor, associated with the thermocline, and the euphotic layer extends throughout the entire water column; the middle shelf that shows a sharp maximum of phytoplankton biomass at mid-depths, strongly linked to the thermocline; and the outer region, above the continental slope where a deeper phytoplankton biomass is observed, correlated with low-light conditions (Signoret et al. 2006).

Additionally, a total of 180 species were identified, including 114 diatoms, 32 dinoflagellates, 32 coccolithophores, and 2 silicoflagellates. The distribution of these species is closely related to the region's hydrographic conditions, including a thermohaline front formed by freshwater from the Grijalva-Usumacinta River flowing into the southern GM, as well as the cyclonic and anticyclonic circulation patterns in the area (Hernández-Becerril et al. 2008). Furthermore, it was observed that the vertical distribution of species differs between the Canyon and Campeche Bay waters. In Canyon, the highest abundance of organisms occurs at the base of the euphotic layer and is dominated by dinoflagellates and coccolithophores. In contrast, in the Campeche Bay, the highest abundance occurs at the thermocline and is dominated by silicoflagellates (Durán-Campos et al. 2017).

Other phytoplankton groups received attention through these multidisciplinary research cruises. In particular, studies on picophytoplankton have shown that the abundance of *Prochlorococcus* and *Synechococcus* is higher in shallow continental shelf waters than in oceanic waters of the Campeche Canyon (Aquino-Cruz et al. 2013). Additionally, it was documented that the abundance of the nitrogen-fixing cyanobacterium *Trichodesmium* spp. increases in the Campeche Canyon region, attributed to eddy activity and the formation of thermohaline fronts (Aldeco et al. 2009). Another group was the unarmored dinoflagellates, with reports identifying 65 species (Zamudio et al. 2013). Notably, there is a high abundance of *Noctiluca scintillans* (Escobar-Morales & Hernández-Becerril 2015).

While progress in the study of phytoplankton in oceanic waters, thanks to the aforementioned monitoring programs, was highly valuable, research in coastal areas of the southern GM continued to emerge. For example, in the waters of the Veracruz Reef Park (southwestern GM), 46 species of dinoflagellates of the genus *Protoperidinium*, 33 species of the genus *Ceratium* (now called *Tripes*), and 38 species of the order Dinophysiales were reported, providing keys for the correct taxonomic identification of these organisms

(Okolodkov 2008, 2010, 2014). Likewise, studies in the region reported 275 phytoplankton species, with marked seasonal variability in species richness, highest in June and October and lowest in April, November, and December (Okolodkov et al. 2011). The study of benthic dinoflagellates also gained relevance in coastal areas. That is the case in the coastal zone of Yucatan, where 20 species belonging to 12 genera were identified, with *Prorocentrum* being the most abundant (Okolodkov et al. 2014). Similarly, in the Veracruz Reef Park, 17 species belonging to 11 genera were reported, with *Amphidinium* being the most abundant (Okolodkov et al. 2007).

Motivated by the Deepwater Horizon disaster in the northern GM in 2010, a series of research cruises (e.g. "Ueyatl") was conducted to assess the impact of this event on the marine ecosystem in the southern GM. During these cruises, samples were collected for various analyses, including phytoplankton studies. As a result, a total of 29 species and 6 subspecies of heterotrophic dinoflagellates belonging to the genus *Protoperidinium* were identified, with their abundance linked to the current patterns in the central region of the GM (González-Fernández 2018).

In 2015, following the Deepwater Horizon disaster, a highly ambitious project funded by the Mexican government established a consortium dedicated to monitoring the environmental health of the southern GM, particularly in its deep zones. As part of this initiative, 18 oceanographic expeditions were conducted to collect water samples at various depths for various purposes, including identifying phytoplankton (Herzka 2021).

This project uncovered several ecological aspects in the deepest areas that had not been documented before. For instance, in the central portion of the GM, researchers found that dinoflagellates dominated over other phytoplankton groups. This abundance is closely linked to nutrient-rich cores induced by cyclonic eddies (González-Fernández et al. 2025). In the Yucatan region, a total of 215 phytoplankton species were identified, including 104 diatoms and 111 dinoflagellates, of which 27 have the potential to form harmful blooms (Medina-Gómez et al. 2019). Additionally, for the first time, researchers identified the numerical importance of smaller phytoplankton fractions, such as the carbon biomass of picoplankton (including *Prochlorococcus*, *Synechococcus*, and pico-eukaryotes) and heterotrophic (heterotrophic bacteria) communities in the deep portions of the gulf. This study revealed spatial and temporal patterns in their distribution (Linacre et al. 2019). Furthermore, thanks to these

multidisciplinary cruises, some aspects related to the impact of large-scale processes, such as the El Niño Southern Oscillation (ENSO), on phytoplankton populations in the Yucatan Shelf region were identified. Thus, previously undocumented patterns were identified, for example, an increase in phytoplankton biomass related to substantial precipitation during the late rainy season in the ENSO warm phase, and the increase in cold-front activity that took place in winter during ENSO's warm phase, leading to different coastline-marine chlorophyll-*a* levels (Medina-Gómez et al. 2020).

In the past decade, algal bloom-causing species have generated significant environmental concerns and have become the focus of numerous studies in the southern GM. Among dinoflagellates, *Peridinium quadridentatum* has been identified as a common species in the waters off Veracruz (Okolodkov et al. 2016, Rodríguez-Gómez et al. 2019). Meanwhile, species from the genera *Kryptoperidinium* and *Durinskia* have been reported in high abundance along the Yucatan coast (Okolodkov et al. 2020). In the coastal area of Campeche, species from the genera *Akashiwo*, *Karenia*, *Pyrodinium*, and *Prorocentrum* have been observed (Poot-Delgado et al. 2015).

A recent review on toxic dinoflagellates in Mexican waters highlights that species from the genera *Gambierdiscus*, *Fukuyoa*, *Prorocentrum*, *Amphidiniopsis*, and *Bysmatrum* are also frequently found in the southern GM (Okolodkov et al. 2022). Moreover, it has been documented that domoic acid-producing diatoms of the genus *Pseudo-nitzschia* are often abundant in the southwestern GM (Parsons et al. 2012). Additionally, cyanobacteria from the genera *Anabaena*, *Merismopedia*, *Oscillatoria*, and *Cylindrospermopsis* frequently generate algal blooms along the coasts of Campeche (Poot-Delgado et al. 2018, Poot-Delgado & Pérez-Morales 2023). Furthermore, it has been reported that in the coastal waters of Campeche, the cyanobacterium *Trichodesmium* can produce significant blooms, exceeding 2.6×10^5 cells L^{-1} (Poot-Delgado et al. 2022), with maximum abundance during the rainy season (Poot-Delgado et al. 2025).

While Table 1 provides a historical context of phytoplankton research in the southern GM, Figure 2 illustrates the key mechanisms driving phytoplankton production.

The schematic traces the influence of nutrient-rich discharge from the Grijalva-Usumacinta River, which fosters a distinct phytoplankton assemblage compared with that of oceanic waters. Additionally, it highlights how cyclonic eddies trigger the upwelling of essential

nutrients (specifically nitrogen, phosphorus, and silicon) into warm, oligotrophic surface layers, fueling significant phytoplankton blooms. The figure also captures localized upwelling events, which further enrich the water column. Finally, it emphasizes the role of major currents, notably the Loop Current, in transporting heat, salt, energy, and organisms throughout the region. Ultimately, this synthesis integrates multiscale spatiotemporal processes to provide a comprehensive view of phytoplankton dynamics in the southern GM.

What we don't know

The monitoring programs implemented in the southern GM have been successful in enhancing our understanding of phytoplankton species by identifying their spatial distribution patterns and some of the physical processes that influence their production. However, there are still many opportunities to further our knowledge of this important group.

Different approaches have been employed in the northern GM to understand better how phytoplankton species are distributed and the factors that influence their distribution.

To substantially advance the current understanding of phytoplankton ecology in Mexican waters, it is essential to prioritize the following research objectives:

Expanding taxonomic focus in phytoplankton research

As established in the preceding section, the current literature on phytoplankton assemblages in the southern GM exhibits a significant taxonomic bias, favoring diatoms and dinoflagellates. This skew underscores a critical knowledge gap that warrants a more comprehensive investigation of other ecologically vital yet understudied fractions, specifically silicoflagellates and coccolithophores.

Coccolithophores are pivotal components of marine ecosystems, distinguished by their intricate calcium carbonate ($CaCO_3$) plates, known as coccoliths. These organisms are essential drivers of the global carbon cycle, facilitating the transport of carbon to the deep ocean via both the organic pump and the carbonate counter-pump. Currently, ocean acidification, driven by increased anthropogenic CO_2 absorption, poses an existential threat to this group by reducing the availability of carbonate ions. This chemical shift significantly impairs calcification, often resulting in structural malformations or a marked decline in biomass (Doney et al. 2009).

Table 1. Historical progression of phytoplankton research in the southern Gulf of Mexico (GM).

Period	Scope / Region	Taxonomic focus & diversity	Key ecological/oceanographic findings	References
1874-1925	Campeche Bay (neritic waters)	78 diatom species (notably <i>Campylodiscus</i>)	Initial taxonomic descriptions and illustrations	Schmidt et al. (1874), Mann (1925)
1960s	Caribbean & Southern GM	Dinoflagellates (30 taxa: notably <i>Ceratium</i> (now <i>Tripos</i>), <i>Dinophysis</i> , <i>Protoperidinium</i>)	Spatial distribution patterns in both regions	Balech (1967a,b)
1960s-1970s	Coastal lagoons	Diatom dominance: 27 spp. (Alvarado); 123 spp. (Términos)	<i>Rhizosolenia</i> dominance (>90%) in Laguna de Términos; hydrography of Alvarado Lagoon.	Villalobos (1966), Gómez-Aguirre (1965)
1964-1984	Oceanic southern GM	High diversity: >1,500 species	Discovery of fertilization via Campeche Bay circulation; diurnal biomass peaks.	Cuban-Soviet Expeditions, Zernova (1969, 1970)
1980s (early)	Yucatan Continental shelf	85 species (75% diatoms, 20% dinoflagellates)	Phytoplankton composition linked to Cape Catoche upwelling.	Luna-Soria (1979), Licea (1992)
1983-2000s	Deep water & Oceanic zones	>250 dinoflagellates; 255 diatoms.	Long-term monitoring (OG-MEX/SGM); identification of >10 toxin-producing species	Licea et al. (2004, 2011, 2017)
Late 1990s-2017	Campeche Bay & Canyon	180 species; Picophytoplankton (<i>Synechococcus</i>).	Identification of three ecological regions (inner/middle/outer shelf) based on biomass verticality.	Signoret (2006); Hernández-Becerril (2008)
2010-Present	Deep GM & Yucatan shelf	215 species; Carbon biomass of pico-eukaryotes.	Assessment of Deepwater Horizon impact: biomass fluctuations linked to ENSO warm phases.	Herzka (2021), Medina-Gómez (2019, 2020)
Last decade	Coastal southern GM	Harmful algal bloom (HAB) species.	Recurrence of <i>Peridinium quadridentatum</i> and blooms of <i>Trichodesmium</i> and <i>Pseudo-nitzschia</i>	Okolodkov (2022), Poot-Delgado (2025)

In the southern GM, research addressing these taxonomic groups remains notably sparse. Evaluating the population dynamics of these organisms is therefore imperative to establish a robust baseline. Such data are essential for characterizing the sensitivity of regional marine biota to declining pH levels and for predicting the broader implications for the southern gulf's biogeochemical resilience.

Silicoflagellates are highly sensitive bioindicators, as their distribution and community structure are intrinsically linked to the physicochemical properties of the water column, including temperature, salinity, and nutrient availability (Dumitrica 2014). Shifts in their species composition within a given region often serve as a diagnostic proxy for environmental variations, accurately reflecting modifications in water mass structure or the influence of localized oceanographic phenomena, such as thermohaline fronts and upwelling events (Herrera & Escribano 2006).

Despite their ecological significance, studies concerning silicoflagellates in the southern GM remain notably scarce. Given their utility as environmental proxies, it is imperative to broaden the scope of phytoplankton research to include this group. Establishing baseline data on their population dynamics is essential for detecting ecological responses to regional hydrographic variability and anthropogenic climate stressors.

Numerical modeling

Numerical modeling transforms large sets of observational data and theoretical knowledge into a predictive and analytical tool. This process uncovers the interconnections between physics, chemistry, and biology, making it essential for the effective management of marine resources and for understanding global biogeochemical cycles (Miller 2007).

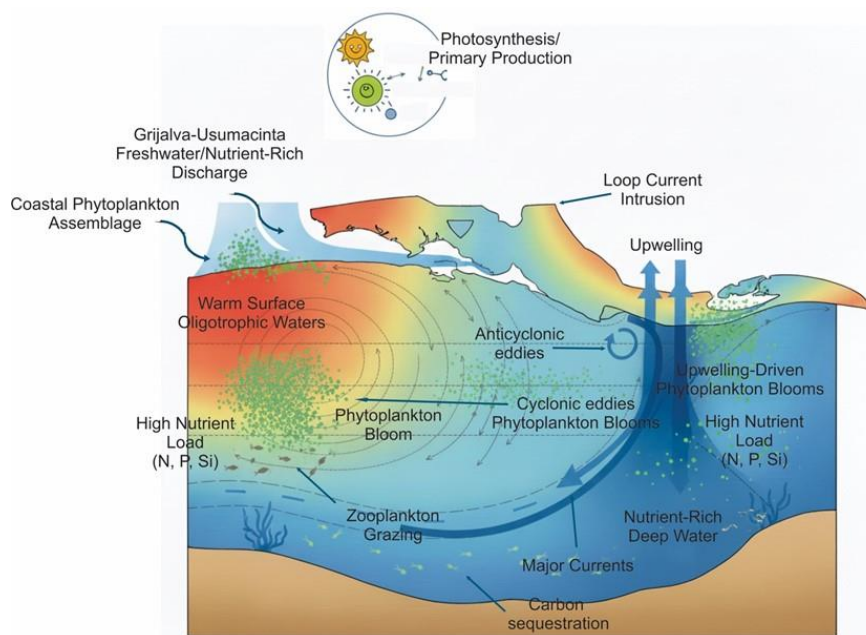


Figure 2. Schematic illustration of the key mechanisms driving phytoplankton production in the southern Gulf of Mexico. See main text for details.

In the case of phytoplankton, numerical modeling is crucial for understanding its dynamics and its vital role in global aquatic ecosystems. As the base of the marine food web and a key participant in the global carbon cycle, phytoplankton is intrinsically linked to its physicochemical environment. Then, numerical modeling allows us to simulate these interactions, providing a comprehensive view of these systems that observation alone cannot achieve (Sakar et al. 2025).

Numerous studies in the northern GM have employed numerical models to examine the distribution and variability of phytoplankton species in relation to climate fluctuations. Biogeochemical models have been used to investigate the spatial distribution of phytoplankton functional groups in relation to nutrient availability. For instance, these models suggest that diatom growth is limited by silica in the deep GM during winter and near the Mississippi Delta in spring (Gomez et al. 2018).

Additionally, models have been applied to understand the factors influencing phytoplankton biomass variability, carbon export, nutrient cycling, and fluctuations in bottom hypoxia in the Mississippi River plume (Green et al. 2008). More complex three-dimensional models have been developed that consider ammonium, nitrate, phytoplankton, chlorophyll, zooplankton, and different types of detritus as state variables. These models indicate that zooplankton

grazing plays a significant role in shaping changes in phytoplankton biomass and suggest that physical transport of phytoplankton could influence seasonal variations in biomass (Fennel et al. 2011).

In the southern GM, few studies employ numerical modeling, and those that do have generally focused on specific aspects. For instance, research using the coupled physical-biogeochemical model NEMO-PISCES has shown that phytoplankton production in anticyclonic eddies detaching from the Loop Current is higher than the average rate in the surrounding open waters of the GM. This increase in production is attributed to the mixed-layer response to winter convective mixing, which extends deeper into nutrient-rich waters (Damien et al. 2021). While this finding is significant, applying numerical models to understand better how other physical processes influence phytoplankton dynamics would be beneficial. For example, investigating the impact of ENSO events and the Atlantic Multidecadal Oscillation (AMO) on nutrient and phytoplankton dynamics would greatly enhance our knowledge in this area.

Recent literature indicates that ENSO events are shifting toward greater duration, intensity, and stochasticity, thereby decoupling from historical periodicity (Coquereau et al. 2025). This emergent unpredictability necessitates the deployment of advanced numerical models to quantify the influence of

these large-scale oscillations on the structure and productivity of phytoplankton assemblages in the southern GM.

Metabarcoding studies

Environmental DNA (eDNA) metabarcoding is a rapid and effective method for investigating microplankton community composition and species diversity (Gaonkar & Campbell 2023). The development of molecular-based methods and high-throughput sequencing has provided powerful tools for characterizing phytoplankton diversity (Nagai et al. 2016) and for differentiating cryptic species (de Luca et al. 2021).

In the northern GM, molecular techniques have significantly impacted the study of species that cause harmful algal blooms. For instance, this technique has enabled the identification of species previously undescribed by conventional methods, thereby enhancing our understanding of their dynamics (Gaonkar & Campbell 2023). Unfortunately, there are very few studies applying metabarcoding techniques to analyze phytoplankton communities in the southern GM.

The implementation of metabarcoding techniques is imperative for advancing our understanding of phytoplankton assemblages in the southern GM, as it overcomes the systemic limitations of traditional morphological taxonomy by providing high-throughput, accurate identification of cryptic taxa and picoplankton fractions that have historically been underestimated (Taberlet et al. 2018). Beyond superior taxonomic resolution, this molecular approach facilitates the early detection of potentially harmful algal bloom-forming species, serving as a critical diagnostic tool. Furthermore, metabarcoding enables the establishment of a robust genetic baseline, which is essential for correlating community dynamics with physicochemical stressors at unprecedented spatial and temporal scales (Pawlowski et al. 2018). Ultimately, integrating these genomic data is a strategic necessity for mapping regional marine biodiversity and predicting the resilience of the trophic web in the face of escalating anthropogenic pressures.

Studies on the role of large-scale processes: the case of ENSO and the AMO

ENSO is recognized as a significant ocean-atmospheric process that profoundly impacts various aspects of nature, including phytoplankton communities (Monreal-Gómez et al. 2025). While extensive research has been conducted in the northern GM on the effects of ENSO on phytoplankton, there is a notable lack of studies in the southern GM.

In the northern GM, studies suggest that ENSO is a primary driver of interannual variability in salinity and plankton biomass during winter and spring (Gomez et al. 2019). Generally, El Niño leads to increased river runoff into the GM, while La Niña results in decreased river runoff (Munoz & Dee 2017). However, this phenomenon has not yet been adequately explored in Mexican waters.

As for the AMO, it has been well documented that this process influences USA precipitation patterns and, consequently, river discharge into the northern GM (Enfield et al. 2001, Tootle & Piechota 2006), thereby affecting phytoplankton populations. Yet, studies examining this relationship in the southern GM are practically nonexistent.

Assays for determining phytoplankton growth limitation

In the northern GM, several studies have focused on identifying the optimal conditions for photosynthesis, thereby enhancing primary production rates. For instance, bioassays conducted on the Louisiana continental shelf have shown that in waters with salinity below 20, light limitation is prevalent. In contrast, at higher salinities, phytoplankton growth is primarily limited by nitrogen or by a combination of nitrogen and phosphorus (Turner & Rabalais 2013). Furthermore, studies have shown that adding nitrate can alter phytoplankton community structure, increasing the proportions of diatoms and prasinophytes while decreasing the abundances of cyanobacteria and prymnesiophytes (Zhao & Quigg 2014). In Florida Bay, nutrient-limitation bioassays conducted across various climatic seasons showed that phosphorus additions more strongly stimulated phytoplankton growth than nitrogen additions. This finding suggests a reduced potential for nutrient limitation during the cooler months, when nutrient demand is typically low, and supply is generally high (Murrell et al. 2002). In the deep waters of the northern GM, in situ observations have shown that net primary production is higher in the upper euphotic zone than at the deep chlorophyll maximum, a pattern primarily driven by recycled nutrients. Additionally, productivity tends to decrease with depth (Yingling et al. 2021).

Although previous research has made significant strides in understanding the photosynthetic dynamics and light-availability requirements of phytoplankton in Mexican waters (e.g. Coria-Monter et al. 2019, 2021), these efforts remain spatially and temporally constrained. Current data are largely confined to subma-

rine canyon regions and Campeche Bay, and observations are restricted to the summer months. This narrow focus fails to capture the pronounced seasonal cycles, driven by atmospheric forcing, riverine discharge, and transient mesoscale features, that define the hydrography of the southern GM.

Addressing these knowledge gaps is a matter of regional urgency. The southern GM is a complex, high-productivity environment that sustains vital fisheries and essential ecosystem services. Yet, it faces intensifying anthropogenic pressures, including hydrocarbon exploration and the accelerating effects of ocean acidification and climate-driven thermal anomalies (Osborne et al. 2022). Given this susceptibility, expanding our understanding of phytoplankton community responses beyond the summer window is a strategic necessity for establishing a robust baseline. Such comprehensive data are vital for elucidating the mechanisms governing primary productivity and predicting the resilience of the regional trophic web under a changing climate.

Final remarks

The study of phytoplankton in the southern GM has a long and rich history that spans over a century. During this time, numerous valuable studies have produced extensive taxonomic lists and documented species distribution patterns. Initially, research focused on coastal regions, but later expanded to include open waters, even reaching the deepest parts of the GM, thanks to improved oceanographic monitoring infrastructure in Mexico.

While monitoring programs have provided invaluable information, many have lacked the necessary continuity and have often been limited in both spatial and temporal scope. Therefore, the implementation of long-term multidisciplinary oceanographic monitoring is essential, particularly in light of global change.

Global change, encompassing warming, ocean acidification, and shifts in ocean circulation patterns, presents a complex array of simultaneous stressors. To understand how these stressors affect phytoplankton, a sustained, comprehensive monitoring approach with a long-term perspective is required. This strategy enables the creation of long-term time series, which are crucial for understanding how seasonal, annual, and interannual climate fluctuations affect phytoplankton populations in the southern GM.

In this context, the investigations must be multidisciplinary and encompass a range of measurements, including oceanographic variables such as

temperature, salinity, stratification, and circulation, as well as biogeochemical variables such as nutrient concentrations (nitrates, nitrites, phosphates, silicates), dissolved oxygen, pH, and CO₂ levels. Additionally, biological variables, including phytoplankton species composition, primary productivity, and food web structure (such as zooplankton), are crucial.

Furthermore, integrating *in situ* data (obtained through sampling and buoys), remote sensing (satellite data), and numerical models is essential for developing a comprehensive three-dimensional understanding of phytoplankton community structure in the southern GM.

Credit author contribution

E. Coria-Monter & E. Durán-Campos: conceptualization, methodology, formal analysis, writing-original draft, review and editing. Both authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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REFERENCES

- Agassiz, A. 1888. Three cruises of the U.S. coast and geodetic survey steamer Blake. Bulletin of the Museum of Comparative Zoology at Harvard College, 14: 1-314.
- Aldeco, J., Monreal-Gómez, M.A., Signoret, M., et al. 2009. Occurrence of a subsurface anticyclonic eddy, fronts, and *Trichodesmium* spp. over the Campeche Canyon region, Gulf of Mexico. Ciencias Marinas, 35: 333-344.
- Aquino-Cruz, A., Hernández-Becerril, D.U., Signoret-Poillon, M., et al 2013. Studies on picophytoplankton in the southern Gulf of Mexico: recognition of picoprokaryotes and abundances of picophytoplankton during "dry season". Brazilian Journal of Oceanography, 61: 265-276.

- Balech, E. 1967a. Microplankton of the Gulf of Mexico and Caribbean Sea. Texas A&M Research Foundation, 67-10-T: 1-144.
- Balech, E. 1967b. Dinoflagelados nuevos o interesantes del Golfo de Mexico y Caribe. Revista Museo Argentino de Ciencias Naturales "B. Rivadavia" - Hidrobiologia, 2: 77-126.
- Coquereau, A., Sévellec, F., Huck, T., et al. 2025. Increase in ENSO frequency and intensity under 20th and 21st century warming: Insights from CMIP6 large ensembles. Geophysical Research Letters, 52: e2025 GL116541. doi: 10.1029/2025GL116541
- Coria-Monter, E. & Durán-Campos, E. 2025. Research trends on marine zooplankton in the southern Gulf of Mexico: A short review. Latin American Journal of Aquatic Research, 53: 541-559. doi: 10.3856/vol53-issue4-fulltext-3362
- Coria-Monter, E., Gracia, A., Salas De León, D., et al. 2021. Optical characterization of the deepwaters of the Gulf of Mexico by *in situ* PAR during summer. Latin American Journal of Aquatic Research, 49: 654-662. doi: 10.3856/vol49-issue4-fulltext-2668
- Coria-Monter, E., Salas De León, D., Monreal-Gómez, M., et al. 2019. Optical properties of the waters of the southern Gulf of Mexico during summer. Latin American Journal of Aquatic Research, 47: 568-574. doi: 10.3856/vol47-issue3-fulltext-18
- Damien, P., Sheinbaum, J., Pasqueron de Fommervault, O., et al. 2021. Do Loop Current eddies stimulate productivity in the Gulf of Mexico? Biogeosciences, 18: 4281-4303. doi: 10.5194/bg-18-4281-2021
- Davis, C.C. 1954. Phytoplankton of the Gulf of Mexico. In: Fish and Wildlife Service (Ed.). Gulf of Mexico: Its origins, waters, and marine life. United States Government Printing Office, Washington, D.C., pp. 163-169.
- de Luca, D., Piredda, R., Sarno, D., et al. 2021. Resolving cryptic species complexes in marine protists: phylogenetic haplotype networks meet global DNA metabarcoding datasets. ISME Journal, 15: 1931-1942. doi: 10.1038/s41396-021-00895-0
- Diaz, B.P., Zelzion, E., Halsey, K., et al. 2023. Marine phytoplankton downregulate core photosynthesis and carbon storage genes upon rapid mixed layer shallowing. ISME Journal, 17: 1074-1088. doi: 10.1038/s41396-023-01416-x
- Doney, S.C., Fabry, V.J., Feely, R.A., et al. 2009. Ocean acidification: The other CO₂ problem. Annual Review of Marine Science, 1: 169-92. doi: 10.1146/annurev.marine.010908.163834
- Dumitrica, P. 2014. Double skeletons of silicoflagellates: Their reciprocal position and taxonomical and paleobiological values. Revue de Micropaléontologie, 57: 57-74. doi: 10.1016/j.revmic.2014.04.001
- Durán-Campos, E., Salas de León, D.A., Monreal-Gómez, M.A., et al. 2017. Patterns of chlorophyll-a distribution linked to mesoscale structures in two contrasting areas, Campeche Canyon and Bank, southern Gulf of Mexico. Journal of Sea Research, 123: 30-38. doi: 10.1016/j.seares.2017.03.013
- Enfield, D.B., Mestas-Núñez, A.M. & Trimble, P.J. 2001. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental U.S. Geophysical Research Letters, 28: 2077-2080.
- Escobar-Morales, S. & Hernández-Becerril, D.U. 2015. Free-living marine planktonic unarmoured dinoflagellates from the Gulf of Mexico and the Mexican Pacific. Botanica Marina, 58: 9-22. doi: 10.1515/bot-2014-0049
- Fennel, K., Hetland, R., Feng, Y., et al. 2011. A coupled physical-biological model of the northern Gulf of Mexico shelf: model description, validation and analysis of phytoplankton variability. Biogeosciences, 8: 1881-1899. doi: 10.5194/bg-8-1881-2011
- Galtsoff, P.S. 1948. Red tide. A report on the investigations of the cause of the mortality along the west coast of Florida conducted by the United States Fish and Wildlife Service and cooperative organizations. U.S. Department of the Interior Fish and Wildlife Service Special - Scientific Report, 46: 1-39.
- Gaonkar, C.C. & Campbell, L. 2023. Metabarcoding reveals high genetic diversity of harmful algae in the coastal waters of Texas, Gulf of Mexico. Harmful Algae, 121: 102368. doi: 10.1016/j.hal.2022.102368
- Goff, J.A., Gulick, S.P.S., Pérez-Cruz, L., et al. 2016. Solution pans and linear sand bedforms on the bare-rock limestone shelf of the Campeche Bank, Yucatán Peninsula, Mexico. Continental Shelf Research, 117: 57-66. doi: 10.1016/j.csr.2016.02.005
- Gomez, F.A., Lee, S-K., Hernandez Jr., F.J., et al. 2019. ENSO-induced co-variability of salinity, plankton biomass and coastal currents in the northern Gulf of Mexico. Scientific Reports, 9: 178. doi: 10.1038/s41598-018-36655-y
- Gomez, F.A., Lee, S-K., Liu, Y., et al. 2018. Seasonal patterns in phytoplankton biomass across the northern and deep Gulf of Mexico: a numerical model study. Biogeosciences, 15: 3561-3576. doi: 10.5194/bg-15-3561-2018
- Gómez-Aguirre, S. 1965. Algunas consideraciones acerca del fitoplancton primaveral en la Boca de Paso Real, Campeche. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, 36: 65-69.

- González-Fernández, J.M. 2018. Análisis de la composición, abundancia y distribución de *Protoperdinium* Bergh (Dinophyceae) en la región central del Golfo de México. M.Sc. Thesis, Universidad Nacional Autónoma de México, Ciudad de México.
- González-Fernández, J.M., Luna-Soria, R., Alexander-Valdés, H., et al. 2025. Influence of mesoscale eddies on the spring phytoplankton groups in the southern Gulf of Mexico. *Botanica Marina*, 68: 85-99. doi: 10.1515/bot-2024-0042
- Green, R.E., Breed, G.A., Dagg, M.J., et al. 2008. Modeling the response of primary production and sedimentation to variable nitrate loading in the Mississippi River plume. *Continental Shelf Research*, 28: 1451-1465. doi: 10.1016/j.csr.2007.02.008
- Grigoratou, M., Menden-Deuer, S., McQuatters-Gollop, A., et al. 2025. The immeasurable value of plankton to humanity. *BioScience*, 0: 1-16. doi: 10.1093/biosci/biaf049
- Hernández-Becerril, D.U. & Flores-Granados, C. 1998. Species of the diatom genus *Chaetoceros* (Bacillariophyceae) in the plankton from the southern Gulf of Mexico. *Botanica Marina*, 41: 505-519.
- Hernández-Becerril, D.U., García-Resendiz, J.A., Salas-de-León, D.A., et al. 2008. Nanoplankton fraction in the phytoplankton structure in the southern Gulf of Mexico (April 2000). *Ciencias Marinas*, 34: 77-90.
- Herrera, L. & Escribano, R. 2006. Factors structuring the phytoplankton community in the upwelling site off El Loa River in northern Chile. *Journal of Marine Systems*, 61: 13-38. doi: 10.1016/j.jmarsys.2005.11.010
- Herzka, S.Z. 2021. Hidrografía, biogeoquímica, ecología y biología. In: Herzka, S.Z., Zaragoza-Álvarez, R.A., Peters, E.M., et al. (Eds.). *Atlas de línea base ambiental del golfo de México* (tomo III, segunda parte). Gulf of Mexico Research Consortium, Ensenada.
- Licea, S. 1992. Especies de diatomeas seleccionadas del sur del Golfo de México, estudiadas en microscopio de luz y electrónico. Ph.D. Thesis, Universidad Nacional Autónoma de México, Ciudad de México.
- Licea, S., Luna, R., Okolodkov, Y.B., et al. 2017. Phytoplankton abundance and distribution on the Yucatan shelf (June 1979 and April 1983). *Novosti Sistematiki Nizaikh Rastenii*, 51: 121-144.
- Licea, S., Zamudio, M.E., Luna, R., et al. 2004. Free-living dinoflagellates in the southern Gulf of Mexico: Report of data (1979-2002). *Phycological Research*, 52: 419-428.
- Licea, S., Zamudio, M.E., Moreno-Ruiz, J.L., et al. 2011. A suggested local regions in the southern Gulf of Mexico using a diatom database (1979-2002) and oceanic hydrographic features. *Journal of Environmental Biology*, 32: 443-453.
- Linacre, L., Durazo, R., Camacho-Ibar, V.F., et al. 2019. Picoplankton carbon biomass assessments and distribution of *Prochlorococcus* ecotypes linked to loop current eddies during summer in the southern Gulf of Mexico. *Journal of Geophysical Research: Oceans*, 124: 8342-8359. doi: 10.1029/2019JC015103
- López-Baluja L., Zernova, V.V. & Semina, H.J. 1992. *Phytoplankton of Cuban waters and the Gulf of Mexico*. Ed. Academia, Moscow.
- Loyo-Rebolledo, M.E. 1966. Sistemática y distribución de las diatomeas del plancton de la Laguna de Términos, Campeche, Mexico. B.Sc. Thesis, Universidad Nacional Autónoma de México, Ciudad de México.
- Luna-Soria, R. 1979. Algunos aspectos del fitoplancton de la plataforma continental de Yucatán (7-12 de junio 1979). B.Sc. Thesis, Universidad Nacional Autónoma de México, Ciudad de México.
- Mann, A. 1925. Diatoms of Campeche Bay, Gulf of Mexico. In: Mann, A. (Ed.). *Marine diatoms of the Philippine Islands*. United States National Museum, Smithsonian Institution, Washington, D.C., pp. 5-8.
- Margalef, R. 1975. Fitoplancton invernal de la Laguna Costera de Alvarado (México). *Anales del Instituto Botánico A.J. Cavanilles*, 32: 381-387.
- Medina-Gómez, I., Aguilar-Trujilli, A., Mariño-Tapia, I., et al. 2019. Phytoplankton responses under a joint upwelling event and an algal bloom scenario in the southeast Gulf of Mexico. *Continental Shelf Research*, 184: 30-43. doi: 10.1016/j.csr.2019.07.006
- Medina-Gómez, I., Cahuich-López, M., Aguilar-Trujillo, A., et al. 2020. Spatio-temporal patterns of Chlorophyll-*a* in a wide and low-relief shelf sea of the Gulf of Mexico: Insights of interannual climatic patterns on the phytoplankton biomass varying behavior. *Continental Shelf Research*, 205: 104174. doi: 10.1016/j.csr.2020.104174
- Miller, R.N. 2007. *Numerical modeling of ocean circulation*. Cambridge University Press, Cambridge.
- Monreal-Gómez, M.A., Pérez-Cruz, L., Durán-Campos, E., et al. 2025. Phytoplankton communities in the eastern tropical Pacific Ocean off Mexico and the southern Gulf of California during the strong El Niño of 2023/24. *Plants*, 14: 1375. doi: 10.3390/plants14091375
- Morey, S.L., He, R., Chassignet, E.P., et al. 2024. Editorial: Understanding and predicting the Gulf of Mexico ocean dynamics. *Frontiers in Marine Science*, 11: 1400560. doi: 10.3389/fmars.2024.1400560
- Munoz, S.E. & Dee, S.G. 2017. El Niño increases the risk of lower Mississippi River flooding. *Scientific Reports*, 7: 6. doi: 10.1038/s41598-017-01919

- Murrel, M.C., Stanley, R.S., Lores, E.M., et al. 2002. Evidence that phosphorus limits phytoplankton growth in a Gulf of Mexico estuary: Pensacola Bay, Florida, USA. *Bulletin of Marine Science*, 70: 155-167.
- Nagai, S., Urusizaki, S., Hongo, Y., et al. 2017. An attempt to semi-quantify potentially toxic diatoms of the genus *Pseudo-nitzschia* in Tokyo Bay, Japan, by using massively parallel sequencing technology. *Plankton and Benthos Research*, 12: 248-258. doi: 10.3800/pbr.12.248
- Nagai, S., Miyamoto, S., Ino, K., et al. 2016. Easy detection of multiple *Alexandrium* species using DNA chromatography chip. *Harmful Algae*, 51: 97-106. doi: 10.1016/J.HAL.2015.10.014
- Okolodkov, Y.B. 2003. A review of Russian plankton research in the Gulf of Mexico and the Caribbean Sea in the 1960-1980s. *Hidrobiológica*, 13: 207-221.
- Okolodkov, Y.B. 2008. *Protoperdinium* Bergh (Dinophyceae) of the National Park Sistema Arrecifal Veracruzano, Gulf of Mexico, with a key for identification. *Acta Botanica Mexicana*, 84: 93-149.
- Okolodkov, Y.B. 2010. *Ceratium* Schrank (Dinophyceae) of the National Park Sistema Arrecifal Veracruzano, Gulf of Mexico, with a key for identification. *Acta Botanica Mexicana*, 93: 41-101.
- Okolodkov, Y.B. 2014. Dinophysiales (Dinophyceae) of the National Park Sistema Arrecifal Veracruzano, Gulf of Mexico, with a key for identification. *Acta Botanica Mexicana*, 106: 9-71.
- Okolodkov, Y.B., Campos-Bautista, G. & Gárate-Lizárraga, I. 2016. Circadian rhythm of a red-tide dinoflagellate *Peridinium quadridentatum* in the port of Veracruz, Gulf of Mexico, its thecal morphology, nomenclature, and geographical distribution. *Marine Pollution Bulletin*, 108: 289-296. doi: 10.1016/j.marpolbul.2016.04.047
- Okolodkov, Y.B., Aké-Castillo, J.A., Gutiérrez-Quevedo, M.G., et al. 2011. Annual cycle of the plankton biomass in the National Park Sistema Arrecifal Veracruzano, southwestern Gulf of Mexico. In: Kattel, G. (Ed.). *Zooplankton and phytoplankton: Types, characteristics and ecology*. Nova Science Publishers, New York, pp. 63-88.
- Okolodkov, Y.B., Campos-Bautista, G., Gárate-Lizárraga, I., et al. 2007. Seasonal changes of benthic and epiphytic dinoflagellates in the Veracruz reef zone, Gulf of Mexico. *Aquatic Microbial Ecology*, 47: 223-237.
- Okolodkov, Y.B., Durán-Riveroll, L.M., Band-Schmidt, C.J., et al. 2022. A review on marine benthic dinoflagellates in Mexico. *Hidrobiológica*, 32: 183-210. doi: 10.24275/uam/izt/dcbh/hidro/2022v32n3/Okolodkov
- Okolodkov, Y.B., Merino-Virgilio, F.C., Aké-Castillo, J.A., et al. 2014. Seasonal changes in epiphytic dinoflagellate assemblages near the northern coast of the Yucatan peninsula, Gulf of Mexico. *Acta Botanica Mexicana*, 107: 121-151.
- Okolodkov, Y.B., Merino-Virgilio, F.C., Huerta-Quintanilla, D.A., et al. 2020. A Kryptoperidiniaceae species (Dinophyceae: Peridiniales) blooming in coastal Yucatan waters, Gulf of Mexico. *Protistology*, 14: 58-69.
- Osborne, E., Hu, X., Hall, E.R. 2022. Ocean acidification in the Gulf of Mexico: Drivers, impacts, and unknowns. *Progress in Oceanography*, 209: 102882. doi: 10.1016/j.pocean.2022.102882
- Osorio-Tafall, B.F. 1942. Estudios sobre el plancton de México. *Ciencia*, 3: 114-119.
- Parsons, M.L., Okolodkov, Y.B. & Aké-Castillo, J.A. 2012. Diversity and morphology of the species of *Pseudo-nitzschia* (Bacillariophyta) of the National Park Sistema Arrecifal Veracruzano, SW Gulf of Mexico. *Acta Botanica Mexicana*, 98: 51-72.
- Pawlowski, J., Kelly-Quinn, M., Altermatt, F., et al. 2018. The future of biotic indices in the ecogenomic era: Integrating (e)DNA metabarcoding in biological assessment of aquatic ecosystems. *Science of the Total Environment*, 637-638: 1295-1310. doi: 10.1016/j.scitotenv.2018.05.002
- Poot-Delgado, C.A. & Pérez-Morales, A. 2023. Spatio-temporal variation of harmful phytoplankton in recreational beaches in Campeche, southeastern Gulf of Mexico. *Ciencias Marinas*, 49: e3389. doi: 10.7773/cm.y2023.3389
- Poot-Delgado, C.A., Okolodkov, Y.B. & Rendón-von Osten, J. 2022. Spatio-temporal variation of harmful planktonic microalgae and cyanobacteria along the central coast of Campeche, southeastern Gulf of Mexico. *Bulletin of Environmental Contamination and Toxicology*, 108: 15-23. doi: 10.1007/s00128-021-03203-w
- Poot-Delgado, C.A., Okolodkov, Y.B., Aké-Castillo, J.A., et al. 2015. Annual cycle of phytoplankton with emphasis on potentially harmful species in oyster beds of Términos Lagoon, southeastern Gulf of Mexico. *Revista de Biología Marina y Oceanografía*, 50: 465-477. doi: 10.4067/S0718-19572015000400006
- Poot-Delgado, C.A., Okolodkov, Y.B., Aké-Castillo, J.A., et al. 2018. Potentially harmful cyanobacteria in oyster banks of Términos lagoon, southeastern Gulf of

- Mexico. *Acta Biológica Colombiana*, 23: 51-58. doi: 10.15446/abc.v23n1.65809
- Poot-Delgado, C.A., Rendon-von Ostén, J. & Okolodkov, Y.B. 2025. Annual cycle of potentially harmful phytoplankton in the coastal waters of Campeche, southern Gulf of Mexico. *Regional Studies in Marine Science*, 89: 104392. doi: 10.1016/j.rsma.2025.104392
- Riley, G.A. 1937. The significance of the Mississippi River drainage for the biological conditions in the northern Gulf of Mexico. *Journal of Marine Research*, 1: 60-74.
- Rodríguez-Gómez, C.F., Vázquez, G., Aké-Castillo, J.A., et al. 2019. Physicochemical factors related to *Peridinium quadridentatum* (F. Stein) Hansen (Dinophyceae) blooms and their effect on phytoplankton in Veracruz, Mexico. *Estuarine Coastal and Shelf Science*, 230: 106412. doi: 10.1016/j.ecss.2019.106412
- Roujyaynen, M.I., Senichkina, L.G. & Georgieva, L.V. 1971. Review of the taxonomic composition of phytoplankton in the Central American seas. *Studies on the Central-American Seas*, 3: 16-49.
- Salas-de-León, D.A., Monreal-Gómez, M.A., Signoret, M., et al. 2004. Anticyclonic-cyclonic eddies and their impact on near-surface chlorophyll stocks and oxygen supersaturation over the Campeche Canyon, Gulf of Mexico. *Journal of Geophysical Research*, 109: C05012. doi: 10.1029/2002JC001614
- Santiago-Arce, T. & Salas de León, D.A. 2012. Vorticity and internal waves in the Campeche Canyon, Gulf of Mexico. In: Klapp, J., Cros, A., Velasco-Fuentes, O., et al. (Eds.). *Experimental and theoretical advances in fluid dynamics, environmental science and engineering*. Springer-Verlag, Berlin, pp. 163-169.
- Santoyo, H. & Signoret, M. 1973. Hidrología y fitoplancton en un transecto en la plataforma continental de la Bahía de Campeche, México (agosto 1972). *Revista Latinoamericana de Microbiología*, 15: 207-215.
- Sarkar, K., Nieto, J.J., Khajanchi, S., et al. 2025. Modeling the influence of global warming on carbon, phytoplankton, and zooplankton dynamics. *Scientific Reports*, 15: 17911. doi: 10.1038/s41598-025-01623-w
- Schmidt, A., Schmidt, M., Fricke, F., et al. 1874. *Atlas der Diatomea-Kunde*. Forgotten Books, Berlin.
- Signoret, M., Monreal-Gómez, M.A., Aldeco, J., et al. 2006. Hydrography, oxygen saturation, suspended particulate matter, and chlorophyll-*a* fluorescence in an oceanic region under freshwater influence. *Estuarine Coastal and Shelf Science*, 69: 153-164.
- Stock, C.A., John, J.G. & Rykaczewski, R.R. 2017. Reconciling fisheries catch and ocean productivity. *Proceedings of the National Academy of Sciences*, 114: E1441-E1449. doi: 10.1073/pnas.1610238114
- Sturges, W., Lugo-Fernández, A. & Shargel, M.D. 2005. Introduction to circulation in the Gulf of Mexico. In: Sturges, W. & Lugo-Fernández, A. (Eds.). *Circulation in the Gulf of Mexico: Observations and models*. American Geophysical Union, Washington, D.C., pp. 1-10.
- Suárez-Cabroo, J.A. & Gómez-Aguirre, S. 1965. Observaciones sobre el plancton de la Laguna de Términos, Campeche, México. *Bulletin of Marine Science*, 15: 1072-1120.
- Taberlet, P., Bonin, A., Zinger, L., et al. 2018. *Environmental DNA: For biodiversity research and monitoring*. Oxford University Press, Oxford.
- Taylor, W.R. 1928. The marine algae of Florida, with special reference to the Dry Tortugas. *Papers from the Tortugas Laboratory*, 25: 1-219.
- Thoppil, P.G., Rowley, C.D., Hogan, P.J., et al. 2025. Evaluating the performance of an ensemble forecast system in predicting Loop Current Eddy separation in the Gulf of Mexico. *Progress in Oceanography*, 237: 103529. doi: 10.1016/j.pocean.2025.103529
- Tootle, G.A. & Piechota, T.C. 2006. Relationships between Pacific and Atlantic Ocean Sea surface temperatures and U.S. streamflow variability. *Water Resources Research*, 42: 1-14. doi: 10.1029/2005WR004184
- Turner, R.E. & Rabalais, N.N. 2013. Nitrogen and phosphorus phytoplankton growth limitation in the northern Gulf of Mexico. *Aquatic Microbial Ecology*, 68: 159-169. doi: 10.3354/ame01607
- Vázquez-de la Cerda, A.M., Reid, R.O., DiMarco, S.F., et al. 2005. Bay of Campeche Circulation: An update. In: Sturges, W. & Lugo-Fernández, A. (Eds.). *Circulation in the Gulf of Mexico: Observations and models*. American Geophysical Union, Washington, D.C., pp. 279-293.
- Vega-Rodríguez, F. & Arenas-Fuentes, V. 1965. Resultados preliminares sobre la distribución del plancton y datos hidrográficos del arrecife "La Blanquilla", Veracruz, Ver. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, 36: 53-59.
- Villalobos, A., Suárez-Cabroo, J., Gómez, S., et al. 1966. Considerations on the hydrography and productivity of Alvarado Lagoon, Veracruz, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute*, 19: 75-85.

- Yingling, N., Kelly, T.B., Shropshire, T.A., et al. 2022. Taxon-specific phytoplankton growth, nutrient utilization and light limitation in the oligotrophic Gulf of Mexico. *Journal of Plankton Research*, 44: 656-676. doi: 10.1093/plankt/fbab028
- Zamudio, M.E., Licea, S. & Luna, R. 2013. Relative abundance and distribution of unarmoured dinoflagellate species in the southern Gulf of Mexico (2005-2010). *Biological and Geological Perspectives of Dinoflagellates*, 5: 233-238.
- Zernova, V.V. 1969. The horizontal distribution of phytoplankton in the Gulf of Mexico. *Oceanology*, 9: 695-706.
- Zernova, V.V. 1970. About planktonic algae of the Gulf of Mexico and the Caribbean Sea. *Oceanological Studies*, 20: 69-104.
- Zernova, V.V. & Krylov, V.V. 1974. Species of unicellular algae new to the Gulf of Mexico and the Caribbean Sea. *Soviet-Cuban Fishery Research (VNIRO-CIP)*, 4: 132-134.
- Zhao, Y. & Quigg, A. 2014. Nutrient limitation in northern Gulf of Mexico (NGOM): Phytoplankton communities and photosynthesis respond to nutrient pulse. *Plos One*, 9: e88732. doi: 10.1371/journal.pone.0088732

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