



The State of Knowledge of Harmful Algal Blooms of *Margalefidinium polykrikoides* (a.k.a. *Cochlodinium polykrikoides*) in Latin America

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The marine dinoflagellate *Margalefidinium polykrikoides* is a harmful species that has affected aquaculture, fisheries and tourism activities. It produces reactive oxygen species (ROS) as well as hemolytic and neurotoxic-like substances that have been associated with mass mortalities of marine organisms. It has a tropical and subtropical distribution that has mainly affected Asia and North America. The economic impacts for aquaculture industries have been estimated to be up to US\$140M. In Latin America, no economic estimates have been performed. Harmful algal blooms by *M. polykrikoides* are more frequent in Mexico and Central America. Proliferations of this dinoflagellate are associated with winds, upwelling, convergence areas, local convection of seawater, and eutrophication of coastal areas by nitrogen and phosphorus compounds from rainwater runoff, as well as agricultural and aquaculture activities, into coastal waters. Eco-physiological and toxicological studies have provided detailed descriptions of the growth of algal strains from these regions and the harmful effects on fish and shrimp, as well as the role the production of ROS and polyunsaturated fatty acids in their toxicity. It is also possible that *M. polykrikoides* has an ecological role in the regulation of blooms of other harmful algae. In this contribution, we review the records of harmful algal blooms of *M. polykrikoides* in Latin America and the research that has been conducted with this species.

Keywords: dinoflagellates, *Margalefidinium polykrikoides*, *Cochlodinium polykrikoides*, HAB, Latin America

INTRODUCTION

Global Harmful Algal Blooms of *M. polykrikoides*

Margalefidinium polykrikoides (= *Cochlodinium polykrikoides*) is a photosynthetic and mixotrophic marine dinoflagellate that forms cysts. It forms harmful algal blooms (HABs), causing economic losses in fish farming areas (US\$140M in world wide; Dorantes-Aranda, 2012) mainly in Asia (Kim, 1998; Kim et al., 1999; Zhong and Gobler, 2009). *M. polykrikoides* was first identified in

Phosphorescent Bay, Puerto Rico by Margalef (1961), and since then *Margalefidinium* blooms have been reported across Asia, Europe and North America. In the last three decades, *Margalefidinium* HABs have impacted coastal regions of Australia, Canada, China, Croatia, India, Iran, Italy, Japan, Korea, Malaysia, Oman, Philippines, Russia, Saudi Arabia, United Arab Emirates, and the United States (Kudela and Gobler, 2012). The largest bloom recorded occurred in the Arabian Gulf from August to October 2008 affecting 1,200 km of coastline, killing wild, and farmed fish as well as damaging coral reefs (Richlen et al., 2010). A wide variety of harmful substances have been reported for this species (Figure 1), including reactive oxygen species (ROS) (superoxide anion, hydrogen peroxide, hydroxyl radical), hemolytic and neurotoxic-like substances, hemagglutinins, and free polyunsaturated fatty acids (Onoue and Nozawa, 1989; Hallegraeff, 1992; Lee, 1996; Landsberg, 2002; Jeong et al., 2004; Dorantes-Aranda et al., 2009, 2010). The genus *Cochlodinium* was established in the late nineteenth century with the identification of *C. strangulatum* (Schütt, 1895), and the first record of this genus in the Gulf of California occurred in 1942 (Osorio-Tafall, 1943). Recently, *C. polykrikoides* was re-assigned to the new genus *Margalefidinium* and renamed as *M. polykrikoides* (Gómez et al., 2017). In North America, HABs of *M. polykrikoides* have been observed in Canada and the US with impacts on fish and shellfish industries (Whyte et al., 2001; Gobler et al., 2008, 2012; Tomas and Smayda, 2008; Mulholland et al., 2009; Zhong and Gobler, 2009; Griffith et al., 2019). The damage by a *M. polykrikoides* bloom in Canada was estimated in a loss of US\$2M in 1999 (Whyte et al., 2001). In Latin America (LA) there are no estimates of the economic losses caused by this dinoflagellate. The purpose of this work is to review the HABs of *M. polykrikoides* and the impacts they have caused in LA by country.

MEXICO

Gulf of California

M. polykrikoides was first observed in Bahía de Mazatlán, Sinaloa, in spring of 1979 proliferating together with *Gymnodinium catenatum*. It was suggested that *M. polykrikoides* HABs are commonly formed in Bahía de Mazatlán during winter and early spring coinciding with the upwelling of cold waters in the region (Morey-Gaines, 1982; Cortés-Altamirano, 1987). From September to October 2000, *M. polykrikoides* was present during 22 days causing a notable odor and fish mortalities (Cortés-Altamirano and Gómez-Aguirre, 2001; Cortés-Altamirano et al., 2002; Table 1). Fish kills were also reported in 2003 and 2012 (Cortés-Altamirano et al., 2019). A record of HABs in Bahía de Mazatlán between 1979 and 2014 by Cortés-Altamirano et al. (2019) revealed that this species forms blooms during summer and fall when El Niño exerts its inhibitory effect. This dinoflagellate has also been reported forming blooms in shrimp farming ponds and coastal lagoons of Sinaloa with adverse effects such as fish, oysters and octopus mortality, as well as skin hyperpigmentation in swimmers (Alonso-Rodríguez et al.,

2004, 2008). Despite the occurrence of mortalities, the economic impacts of these blooms have not been determined.

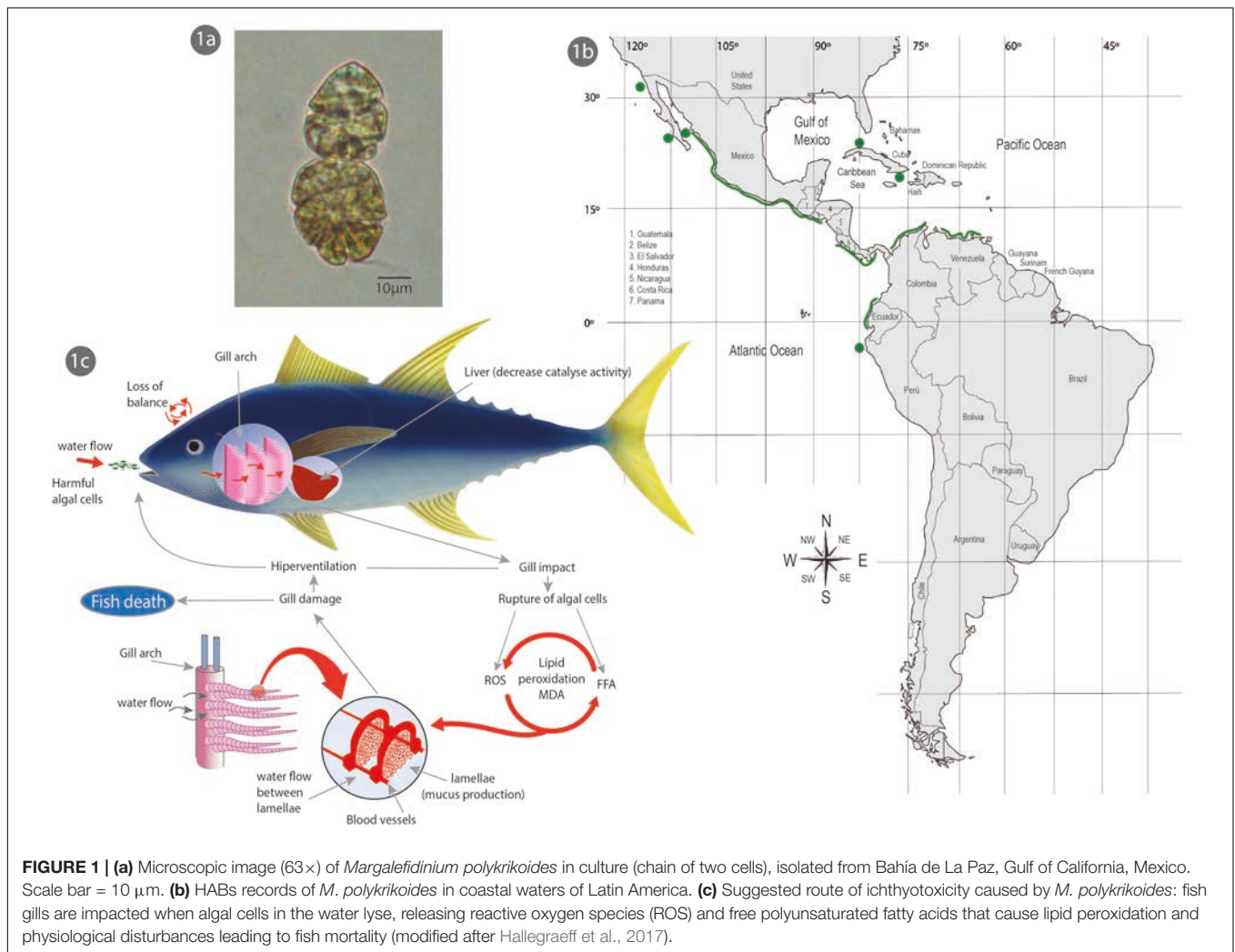
An outbreak of this dinoflagellate was reported for the first time in Bahía de La Paz, in the southern part of the Gulf of California, in September 2000 (Gárate-Lizárraga et al., 2000). Chlorophyll *a* concentrations ranged from 2.7 to 56.8 mg L⁻¹. Gárate-Lizárraga et al. (2004) described another bloom in this bay in November 2000. The bloom emerged after 2 days of heavy rain and wind coinciding with an increase in nutrient concentrations (Table 1). Another bloom occurred in September–November 2001, which extended outside the bay probably a result of Hurricane Juliette; mortalities of 166 fish (76 adults and 90 sub-adults fish) were observed in ponds, including the species *Lutjanus peru* (*n* = 102), *Pomadasys macracanthus* (*n* = 60), and *L. argentiventris* (*n* = 4), with abundant cells of *M. polykrikoides* observed in the gills (Núñez-Vázquez et al., 2003; Gárate-Lizárraga et al., 2004; Figure 2). Muciño-Márquez (2010) also reported *M. polykrikoides* near tuna pens in Bahía de la Paz in September 2006, however, no adverse effects were reported.

López-Cortés et al. (2014) followed the development of a bloom of *M. polykrikoides* in Bahía de La Paz from the beginning (September) to its decay (October) in 2012. This event reached a maximum cell density of 8.6 × 10⁶ cell L⁻¹, with a chlorophyll *a* content of 121.2 mg m⁻³ and peridinin of 40.2 mg m⁻³, coinciding with a N:P (nitrogen:phosphorus) ratio of 2:3. This event was associated with NNE winds and rain, which may have contributed to the enrichment of nutrients in the water column; the direction of the wind changed to the SE, and its intensity decreased to <1.3 m s⁻¹, which was when the bloom appeared. No mortality of marine organisms were observed during this period. According to Gárate-Lizárraga (2013) and López-Cortés et al. (2014), recurrent blooms of *M. polykrikoides* in this bay are associated with the mixing of the water column and upwelling of deep waters.

Mexican Pacific

The first record of *M. polykrikoides* was recorded in Bahía de Manzanillo, Colima in 2000 (López, 2000; Morales-Blake et al., 2001). Another extensive bloom by *Margalefidinium* sp. was reported during late winter and early spring of 1999, where the paralytic toxin producing dinoflagellate *G. catenatum* was also found. However, no impacts in wildlife were reported (Morales-Blake et al., 2000). Another event was recorded in this bay between March and May in 2007, involving again several HAB species such as *Akashiwo sanguinea*, *Karenia mikimotoi*, *G. catenatum* as well as *M. polykrikoides*. This event was associated with upwelling of deep waters (González-Chan et al., 2007).

The most extensive bloom by *M. polykrikoides* (1.1 × 10⁶–3.0 × 10⁶ cell L⁻¹) reported in Mexico lasted 12 weeks (September to November 2000), affecting 63 km of coastline in Bahía de Banderas. This event impacted tourism activities in Puerto Vallarta and Nuevo Vallarta in the states of Jalisco and Nayarit, respectively (Cortés-Lara et al., 2004). Another *M. polykrikoides* bloom was reported in the area the following year (Cortés-Lara, 2002). Cortés-Lara (2002) mentioned that the phenomenon remained for 5 months in Puerto Vallarta causing



mortality of eels, octopuses, and 13 species of fish, including flounders, sardines, snappers and puffers. Gómez-Villarreal et al. (2008) monitored HABs in Bahía Banderas using satellite images during 2000 and 2001 (Figure 2). High chlorophyll *a* levels were associated with blooms of *M. polykrikoides* during the summer-fall season, which were more intense in 2000 than in 2001, with a range in cell abundances from 7×10^3 to 1.2×10^6 cell L^{-1} in 2000, and an average cell abundance of 1×10^6 cell L^{-1} in 2001.

Gárate-Lizárraga and Muñetón-Gómez (2008) reported mortalities of farmed tuna in Bahía Magdalena, B.C.S associated with *M. polykrikoides* and reported that this dinoflagellate is distributed from Ensenada, B.C. to the coasts of Oaxaca. Gárate-Lizárraga et al. (2009) also reported HAB events of *M. polykrikoides* and *G. catenatum* in Bahía de Acapulco. Both species were recorded from December 2005 to December 2007. The abundance of *M. polykrikoides* ranged from 39×10^3 cell L^{-1} in January 2008 to $8,228 \times 10^3$ cell L^{-1} in December 2005, within a thermal range of 25–29°C; however, no mortalities of marine organisms were observed. Maciel-Baltazar and Hernández-Becerril (2013) reported this species in 2009 for the first time in the Gulf of Tehuantepec.

Recently, Fimbres-Martínez et al. (2018), Fimbres-Martínez (2019) described the presence of *Margalefidinium* sp. and raphidophytes of the genera *Chattonella*, *Heterosigma* and *Fibrocapsa* in Bahía de Todos Santos, in the northern Pacific of Mexico, which were the suspected cause of mortalities of farmed tuna (*Thunnus thynnus*) in this region (García-Mendoza et al., 2018).

Experimental Studies

During the last decade, efforts have been directed toward the isolation of strains from Bahía de La Paz to study their ecology and toxicology. Growth rates calculated for these strains varied between 0.11 and 0.39 div day^{-1} with maximum biomasses of 7.1 ± 0.5 and $9.4\text{--}11.0 \times 10^6$ cell L^{-1} using modified GSe and GSe media (Dorantes-Aranda et al., 2009, 2010; Zumaya-Higuera, 2017). Some authors have suggested that *M. polykrikoides* is an invasive species that has been transported by seawater currents and ship ballast water (Sierra-Beltrán et al., 2001; Cortés-Altamirano et al., 2006; Meave del Castillo, 2014; Páez-Osuna et al., 2017). However, the sequences of strains isolated from Bahía de La

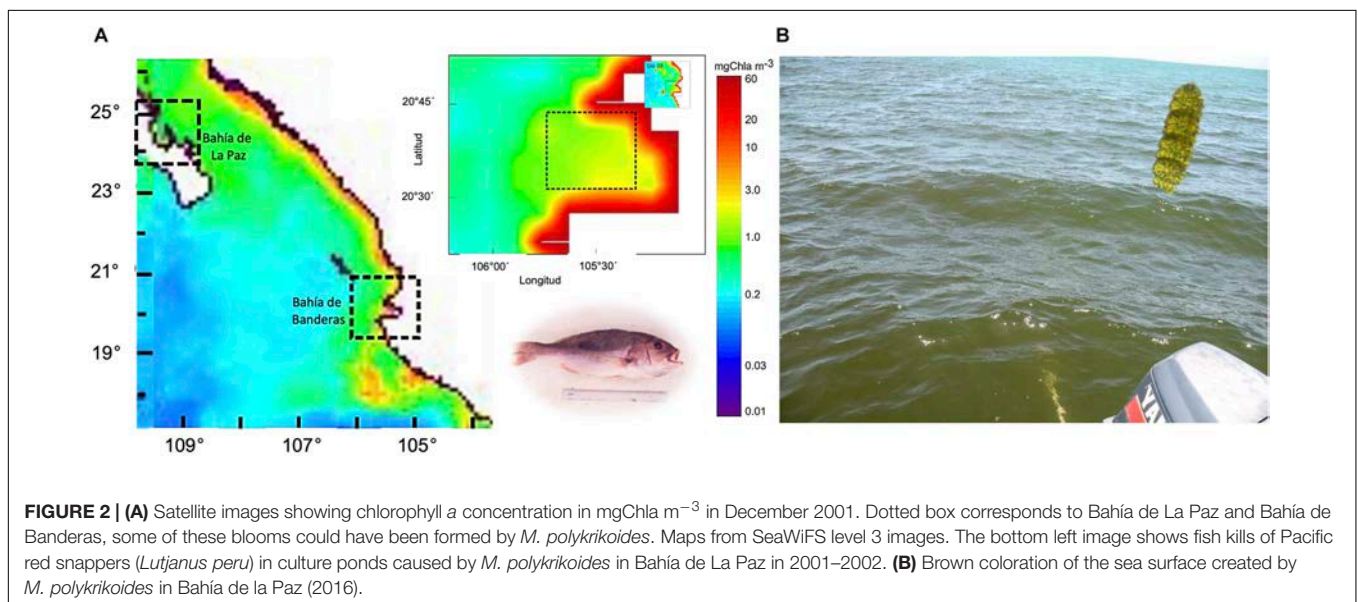
TABLE 1 | Events of harmful algal blooms by the ichthyotoxic dinoflagellate *Margalefidinium polykrikoides* in Latin America.

| Country and region | Date | Number of cells (cell L ⁻¹) | Temperature (°C) | Impact | References |
|---|-----------------------------|--|-------------------------|---|--|
| Mexico | | | | | |
| Bahía de Mazatlán | April 1985 | 5.0 × 10 ⁵ | ~20.0 | Mortality of fish, crustaceans and annelids | Cortés-Altamirano, 1987 |
| | September–October 2000 | 8.9 × 10 ⁵ to 3.4 × 10 ⁶ | No data | Fish mortality | Cortés-Altamirano and Gómez-Aguirre, 2001 |
| | 2003 and 2012 | No data | No data | Fish kill | Cortés-Altamirano et al., 2019 |
| Bahía de Manzanillo | March, April, and May 1999 | No data | 23.0–25.0 | Foam accumulation | Morales-Blake et al., 2000 |
| | March–April 2000 | 3.2 × 10 ⁶ | 21.2–25.5/34.5–34.6 | No data | Morales-Blake et al., 2001 |
| Puerto de Manzanillo | March–May 2007 | 4.0 × 10 ³ | 24.8–32.6 | No data | González-Chan et al., 2007 |
| Bahía de Banderas | October–November 2001 | 3.0 × 10 ⁶ to 1.1 × 10 ⁶ | No data | Fish mortality. Skin irritation, excess of nasal mucosa, eyes, and dermatitis in humans | Cortés-Lara, 2002 |
| | July–December 2000 | 10.8 × 10 ⁶ | 25.0–32.0/33–35 | Fish mortality. Impact in tourist activities | Cortés-Lara et al., 2004 |
| | 2000–2001 | 7.0 × 10 ³ –1.2 × 10 ⁶ 1.0 × 10 ⁶ | No data | No data | Gómez-Villarreal et al., 2008 |
| Ensenada de La Paz, Bahía de La Paz | 15–28 September 2000 | 3.6 × 10 ⁵ to 7.0 × 10 ⁶ | 29.0–321.50 | Fish mortality | Gárate-Lizárraga et al., 2000; Núñez-Vázquez et al., 2003; Gárate-Lizárraga et al., 2004 |
| Ensenada de La Paz, Bahía de La Paz | September 2000 | 3.6 × 10 ⁵ to 7.0 × 10 ⁶ | 20.0–32.5 | Fish mortality | Gárate-Lizárraga et al., 2004 |
| Bahía de La Paz | April–June 2006, April 2007 | 3.6 × 10 ⁵ to 8.0 × 10 ⁹ | 20.0–26.0 and 29.0–31.0 | Fish mortality | Gárate-Lizárraga and Muñetón-Gómez, 2008 |
| Bahía de La Paz | August 16–17, 2012 | 0.073–1.4 × 10 ⁶ | 29.0–30.0 | No impact | Gárate-Lizárraga, 2013 |
| Ensenada de La Paz, Bahía de La Paz | September–November 2012 | 6.2 × 10 ⁵ –8.6 × 10 ⁶ | 30.3–31.3/35.2–36.8 | No impact | López-Cortés et al., 2014 |
| Bahía de Acapulco | March 1999–October 2008 | 0.7–7.8 × 10 ⁴ to 8.2 × 10 ⁶ | 25.0–29.0 | No impact | Gárate-Lizárraga et al., 2009 |
| Cuba | | | | | |
| Bahía de Santiago | April–May 2005 | No data | No data | Mortality of juvenile wild fishes | Gómez et al., 2007 |
| Channels of Marine Hemingway in Havana | September 2015 | 1.8 × 10 ⁶ to 7.5 × 10 ⁵ | | No Impact | |
| Guatemala | | | | | |
| Guatemala Coast | May 28, 2004 | 9.6 × 10 ⁵ | 30.3–32.7 | Fish mortality | Carrillo-Ovalle et al., 2007 |
| | January 8–29 2007 | 6.9 × 10 ⁶ | 28.0 | Fish mortality | |
| El Salvador | | | | | |
| Punta Roca and Puerto de Punta Libertad | March 2012 | 2.1 × 10 ⁸ | 28.5–34.8 | Fish mortality, putrid odors, headache to tourists and local people | Espinoza et al., 2013 |
| La Libertad | October 2013 | No data | No data | Massive sea turtle mortality | Amaya et al., 2014 |
| Costa Rica | | | | | |
| Gulf of Nicoya | February–March 1979 | 80.0 × 10 ⁶ | 28.0/32.2 | Co-occurring with other toxic species, damage to human health, such as... | Hargraves and Víquez, 1981 |

(Continued)

TABLE 1 | Continued

| Country and region | Date | Number of cells (cell L ⁻¹) | Temperature (°C) | Impact | References |
|------------------------------|--------------------------------|---|----------------------|--|---|
| Gulf of Nicoya | June–November 1986 | 2.2 × 10 ⁶ | 26.0–31.0 | Mortality of fish and coral | Guzmán et al., 1990; Viquez and Hargraves, 1995 |
| Isla Caño | July 12, 1985 | 8.3 × 10 ⁵ | | | |
| Pacific Coast | November 2000–December 2001 | 14.4 × 10 ⁶ | No data | Co-occurring with others toxic species, impact fisherman's economy | Valverde, 2002 |
| Pacific Coast | May 2002 | 1.2 × 10 ⁵ | No data | Fish mortality | Vargas-Montero and Freer, 2004 |
| Pacific coast | January 2003–June 2004 | 1.7 × 10 ⁸ | No data | Fish mortality | Vargas-Montero et al., 2006 |
| Pacific coast | April 2004 | 3.8 × 10 ⁸ | No data | Fish mortality, foam formation on the beach | Vargas-Montero et al., 2008 |
| Gulf of Nicoya | January 2008–December 2010 | 11.7 × 10 ⁶ | 26.6–28.7/27.9–31.4 | Unpleasant odor, sickness and vomiting in children | Calvo et al., 2016 |
| Colombia | | | | | |
| Caribe, Bahía de Santa María | October 2010 and November 2011 | 5.0 × 10 ⁶ | 29.0–31.0/~20.0–33.0 | No impact | Malagón and Perdomo, 2013 |
| | 2010–2017 | No data | No data | No impact | Cuellar-Martínez et al., 2018 |
| Ecuador | | | | | |
| Puerto bolívar | February 1992 | 5.2 × 10 ⁶ | No data | No data | Torres-Zambrano, 2000 |
| Estero salado | 1993 | | | | |
| Guayas river | June 1999 | | | | |
| Peru | | | | | |
| Bahía de Sechura | February 2010, May 2014 | 9.6 × 10 ⁵ | 17.1–23.3/32.8 | No data | Orozco et al., 2017 |



Paz were identical to that of American and Malaysian strains (Zumaya-Higuera, 2017).

Núñez-Vázquez et al. (2003) observed that fish juveniles of *Mugil* sp. died when exposed to *M. polykrikoides* at a cell abundance of 4.1 × 10⁶ cell L⁻¹. However, cell extracts showed

no toxicity by mouse bioassay and did not have adverse effects on juvenile shrimp *Litopenaeus vannamei*. However, Pérez-Morales et al. (2017) reported 100% mortality of *L. vannamei* zoea larvae after exposing them for 120 h to cells of *M. polykrikoides* (3.0 × 10⁶ cell L⁻¹). Dorantes-Aranda et al. (2010), also observed

100% mortality of the spotted rose snapper *Lutjanus guttatus* after exposure to $\geq 3.0 \times 10^6$ cell L^{-1} of *M. polykrikoides*. Fish showed loss of balance, breathing difficulty, oxidative stress in gill lamellae and liver, abnormal production of mucus and asphyxiation, suggesting that the production of ROS by the dinoflagellate caused oxidative damage that led to their death. In a complimentary study, the same authors observed that extracts from 5.2×10^6 *M. polykrikoides* cell L^{-1} and 27.0×10^6 cell L^{-1} caused 50% hemolysis in *L. guttatus* and human erythrocytes, respectively. The authors also reported hexadecaenoic (16:0), docosahexaenoic (22:6n3), and octadecapentanoic (18:5n3) as the most abundant fatty acids (Dorantes-Aranda et al., 2009). The latter fatty acid has also been found in other nocive microalgae showing fish cell toxicity, suggesting that it plays a key role in the ichthyotoxicity caused by microalgae (Dorantes-Aranda et al., 2009; Mooney et al., 2011). The possible ichthyotoxic pathway of *M. polykrikoides* is shown in **Figure 1c**, as suggested by Hallegraeff et al. (2017).

Allelopathy of *M. polykrikoides* has been demonstrated by exposing cells and filtrates of *M. polykrikoides* to live cells of *G. catenatum*. *M. polykrikoides* caused cell damage to *G. catenatum*, such as detachment of the membrane, deformation, prominent nuclei, loss of flagella, and lysis, suggesting that *M. polykrikoides* could inhibit or regulate the growth of *G. catenatum* in the natural environment (Zumaya-Higuera, 2017).

Caribbean and Central America

Cuba

M. polykrikoides proliferated in Bahía de Santiago in April and May 2005 covering an area of 0.8 km². The HAB was short (4 days), however, it caused mortality of wild juvenile fish (*Mujil curema*, *Opisthonema oglinum*, *Acanthurus chirurgus*, *Haemulon* spp.) and crabs (*Callinectes sapidus*). During the bloom, cysts and high cell concentrations were recorded (**Table 1**; Gómez et al., 2007). Another bloom occurred in the channels of the Marina Hemingway in Havana in September 2015. A cell concentration of 1.8×10^6 cell L^{-1} was reported, and the bloom declined after 2 days of torrential rain, decreasing to 7.5×10^5 cell L^{-1} . No impact on wildlife was reported (Delgado et al., 2016).

Guatemala to Nicaragua

A HAB of *M. catenatum* was recorded for the first time in Guatemala in 2004, which lasted 32 days and occurred from May to June. Toward the end of the bloom, on the 23rd of June, samples for species identification and cell density were obtained that contained 9.6×10^5 cell L^{-1} which explained the abnormal values of chlorophyll *a* (> 30 mg m^{-3}) observed in satellite images (Carrillo-Ovalle et al., 2007). High chlorophyll *a* levels (10 – 39 mg m^{-3}) were also found off the coast of Honduras, El Salvador and the Gulf of Fonseca (gulf shared between El Salvador, Honduras and Nicaragua). Rain contributed to high nutrient concentrations (**Table 1**), and the water temperature was 30.3°C. A second event was recorded in January 2007 with a higher cell concentration (6.9×10^6 cell L^{-1}). This bloom occurred at a lower temperature (28°C) during the influence of coastal water

upwelling. Wild fish mortalities were observed during both events (Carrillo-Ovalle et al., 2007).

El Salvador

Espinoza et al. (2013), documented a bloom of *M. polykrikoides* off the coast of El Salvador in March 2012, with a maximum cell density of 2.1×10^8 cell L^{-1} . The bloom was 3 km wide and 13 km long, and mortality of benthic fish, bad odor and severe headaches in tourists and local residents were reported. The major tourist season in El Salvador is from March to April, however, no economic losses were estimated for this event. Mass sea turtle mortalities occurred in La Libertad in October 2013 (Amaya et al., 2014). PSP toxins were detected in turtle tissues as well as in oysters. Although the most abundant species during this event was *G. catenatum*, other species such as *P. bahamense*, *A. monilatum*, and *M. polykrikoides* were also reported. In July 2017 a mixed bloom caused by *M. polykrikoides* and *Scirpsiella trochoidea* affected several coastal areas of El Salvador (Ochoa-Arguello, 2017). During this event, a sanitary closure was applied.

Costa Rica and Panama

A bloom of *M. polykrikoides* reported as *M. catenatum* occurred in the Gulf of Nicoya, Costa Rica in February–March 1979 with a width of 200 m and length of 2–3 km. A strain was isolated from this event and growth rate of 0.3 div day^{-1} was estimated. The maximum abundance of cells during the event was 80.0×10^6 cell L^{-1} (Hargraves and Viquez, 1981; **Table 1**).

An annual monitoring program of harmful dinoflagellates was conducted in the middle and upper Gulf of Nicoya between January 1985 and March of 1986. HABs of *M. polykrikoides* were commonly observed in the lower gulf between June and October, mainly during the rainy season. The highest abundance of *M. polykrikoides* was 5.0×10^6 cell L^{-1} during this period (Viquez and Hargraves, 1995). Ramírez et al. (1989) suggested that the decline of anchovy eggs in the estuary of Punta Morales recorded was caused by a red tide near the estuary in August 1985 (**Table 1**).

In the second half of 1985, in Panama (Caño Island, Costa Rica, and Uva Island), mass mortalities of reef fish, invertebrates and corals were associated with a bloom of *M. catenatum* and *Gonyaulax monilata*. In Caño Island, a coral mortality up to 100% was observed between the surface and 3 m of depth. The species most affected were *Pocillopora elegans* and the zooxantella *Tubastrea coccinea*. Additionally, hundreds of fish of the family Scaridae, Balistidae, Acanthuridae, Pomacentridae, and Tetraodontidae; hermit crabs, brachyuran crabs and gastropods. In Uva Island, 13% mortality of *Pocillopora* spp. occurred. Mucus adhesion to polyps and interference with the expansion of polyps appeared to be the cause of coral mortality (Guzmán et al., 1990). Valverde (2002) reported a toxic bloom of *Pyrodinium bahamense* var. *compressum*, *G. catenatum*, and *M. polykrikoides*, on the Pacific Coast of Costa Rica from late November 2000 to December 2001 (**Table 1**). No impact was observed when the abundance of cells of *M. polykrikoides* reached 14.4×10^6 cell L^{-1} . Vargas-Montero and Freer (2004) reported a bloom in Puntarenas and Caldera beach in the Gulf of Nicoya in May 2002 (1.2×10^5 cell L^{-1}). This event

was dominated by *M. polykrikoides* and the cyanobacterium *Trichodesmium erythraeum*. Large fish died, and deformity of fish larvae was also observed.

M. polykrikoides bloomed again on the Pacific region of Costa Rica between January 2003 and June 2004. Cell abundance was 1.7×10^8 cell L⁻¹ (Table 1), and cysts were also observed in October 2003 (Vargas-Montero et al., 2006). The following bloom, in January 2004, covered an area of 50 km² and in April of the same year a high number of cells were also found (3.8×10^8 cell L⁻¹). During these events, corals died and fish mortalities of the families Carangidae, Lutjanidae, Muraenidae, Engraulidae, and the Solidae occurred (Vargas-Montero et al., 2006). *M. polykrikoides* commonly bloomed in this region with low abundance of other dinoflagellate species such as *Ceratium dens*, *Gonyaulax spinifera*, *Heterocapsa* sp., *Mesodinium rubrum*, *P. bahamense* var. *compressum* and the cyanobacterium *T. erythraeum*. Vargas-Montero et al. (2006, 2008) concluded that northeaster winds may be the most influential factor in the formation of HABs of *M. polykrikoides* in Costa Rica.

A total of 11 HABs of different species of dinoflagellates were reported in the Gulf of Nicoya from 2008 to 2010. Of these, eight were observed during the rainy season (May to November) and three during the dry season (December to April) (Calvo et al., 2016). Authors emphasize that the most impacting HAB occurred in September 2010, when 16 phytoplankton species were observed, with *M. polykrikoides* as the dominant species, occurring during a La Niña event. Heavy rain contributed to the enrichment of nutrients in the Gulf of Nicoya, as a result of runoff discharges of the rivers Tempisque and Grande de Tárcoles.

South America

Venezuela

Only one report exists on a bloom of *Margalefidinium* sp. on the coast of Sucre, Venezuela, which occurred in August 1977. Cells of *Margalefidinium* were found in the digestive tract of the mussel *Perna perna*. During this bloom, *Gonyaulax tamarensis* var. *excavate* (= *Alexandrium catenella*) and *Noctiluca miliaris* were also observed, and the presence of paralytic shellfish toxins were detected in mussels, which were associated with human intoxications (Reyes-Vásquez et al., 1979).

Colombia

A bloom of *M. polykrikoides* was recorded for the first time in Bahía de Santa María, in the Colombian Caribbean in October and November 2010. The maximum density was 5.0×10^6 cell L⁻¹, and the event covered an area of 6 km², however, no impact on fauna was observed (Malagón and Perdomo, 2013). The key factor for the proliferation was the contribution of terrestrial nutrients during the rainy season. This bloom coincided with SSE and SE winds during the day, and NNW and NW during the night. Cuellar-Martínez et al. (2018) reported two more blooms in the same bay between 2010 and 2017 with no harmful effects.

Ecuador

HABs are frequent in Ecuador, more commonly in the Gulf of Guayaquil. There have also been reports of blooms in the

southern part of the Santa Elena peninsula, Manglar alto, Manta, Cojimies and in the Galápagos Islands. One of the most frequent and abundant species is *Margalefidinium* sp., which bloomed in Puerto Bolívar (March 1992), Estero Salado (March 1993), and Guayas river in June 1999, reaching a maximum cell abundance in Guayas River of 5.2×10^6 cell L⁻¹ (Torres-Zambrano, 2000). The high frequency of HABs in the Gulf of Guayaquil is associated with poor water quality due to mangrove removal, ship traffic, shrimp farming, population increase, combined with El Niño events.

Peru

Individual blooms of *A. sanguinea*, *M. rubrum*, *Protoceratium minimum*, and *M. polykrikoides* occurred in Bahía de Pisco in February 2010 and May 2014. These events were associated with upwelling of deep waters, with a temperature range from 17.1 to 23.3°C. The bacteria *Vibrio alginolyticus*, *V. metschnikovich*, *V. vulnificus*, and *V. parahaemolyticus* were isolated during the bloom. A strain of *V. parahaemolyticus* was virulent and a public health event with diarrhetic symptoms was associated with the bacteria (Orozco et al., 2017).

CONCLUSION

The toxic dinoflagellate *M. polykrikoides* is wide spread in Latin American coastal waters. It has formed recurrent blooms that have been documented mainly in Mexico and Central American countries. *M. polykrikoides* has been able to proliferate in a wide temperature range (17–32°C), and has affected several marine organisms, including fish, crabs, corals, shrimp, eels, octopuses, and gastropods. Blooms of *M. polykrikoides* in Latin America have been associated with periods of heavy rain that cause an increase in nutrients in coastal waters due to runoff from rivers. Moreover, coastal upwellings associated with wind patterns, mixing of the water column and rain, all of which can create nutrient enrichment of surface waters, seem to favor proliferation and recurrence of this dinoflagellate. Although significant economic losses have been reported in other countries due to the negative impacts of *M. polykrikoides*, this information is still lacking in Latin America, possibly due to scarce socioeconomic studies. A continuous monitoring program is required to obtain information, during and after bloom occurrence. Also, data of cyst beds should be included to generate ecological information that can provide the opportunity to evaluate the potential impacts on fisheries and aquaculture. Especially to address the economic and social repercussions that HABs may have, given the recent experience of two continuous blooms created by *Pseudochattonella verruculosa* and *Alexandrium catenella* in Chile in 2016 that caused economic losses of US\$800M, creating unemployment and social riots triggered by protests (Mascareño et al., 2018). Mitigation approaches for HABs of this dinoflagellate are also a subject not yet investigated in Latin America. The higher amount of reports from Mexico might be because this country possesses a longer coastal area, as well as having a high number of experts on harmful algae, or simply because

M. polykrikoides has formed more blooms in the Mexican coastline than in other Latin America countries. The presence of *Margalefidinium* as well as other species of marine fish-killing microalgae in Latin America will require constant monitoring mainly in fish-growing areas to avoid severe economic impacts, such as the recent cases in Chile and Mexico (Clement et al., 2016; García-Mendoza et al., 2018; León-Muñoz et al., 2018; Mardones et al., 2019).

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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