



Pyrodinium bahamense One the Most Significant Harmful Dinoflagellate in Mexico

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Pyrodinium bahamense produces saxitoxins and can cause paralytic shellfish poisoning (PSP). This species has caused more human illnesses and fatalities than any other toxic dinoflagellate in Mexico. The distribution of dinoflagellate cysts with their vegetative stage is broad, mainly along Mexican Pacific coasts from the central Gulf of California to Chiapas, as well as in the southern Gulf of Mexico and the Mexican Caribbean Sea on the Atlantic coast. *In vitro* germination of living cysts from the southern Gulf of California occurs under thermophilic (20–35°C) and euryhaline (20–35 ups) conditions. Blooms occurred typically during summer rainy season (June through September), inside of restricted shallow lagoons surrounded by mangrove forests. The data obtained so far on *P. bahamense* spatial and population variability in Mexican Pacific and the Gulf of Mexico, suggest a seasonal and latitudinal pattern. Also, in these regions, the abundance, seasonality, and species distribution tend to decrease from tropical to subtropical areas. The local strain toxicity has only been corroborated in one isolate from the southern Gulf of California, which exhibited a high saxitoxin concentration of 95 pg STX eq cell⁻¹. PSP outbreaks linked with *P. bahamense* in the Gulf of Tehuantepec from 1989 to 2007, caused at least ~200 human cases, with 15 fatalities. This mini-review ends with a viewpoint of management and research strategies to better understand the factors that play essential roles in the bloom dynamics and toxicity of this species.

Keywords: *Pyrodinium bahamense*, Mexico, harmful blooms, saxitoxins, PSP

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INTRODUCTION

Pyrodinium bahamense Plate is a tropical/subtropical euryhaline dinoflagellate that produces saxitoxins and can cause paralytic shellfish poisoning (PSP). This species has caused more human illnesses and fatalities than any other paralytic shellfish toxin (PST) producing dinoflagellate, with a spate of toxic blooms in the Indo-Pacific and the Pacific coast of Central America (Usup et al., 2012). *Pyrodinium bahamense*, along with toxic *Gymnodinium catenatum* Graham, have caused direct adverse consequences for human health, aquaculture industries, tourism, and ecosystem functions in Mexican coastal waters (Hernández-Becerril et al., 2007; García-Mendoza et al., 2016). *Pyrodinium bahamense* has particular importance since it has caused a significant impact on human health, mainly in southern Mexican Pacific. The effect of harmful algae could be increasing and expand as a consequence of increasing local marine eutrophication (Heisler et al., 2008) and ocean climate change (Hallegraeff, 2010).

Globally *P. bahamense* is mainly distributed in tropical areas of both hemispheres. The vegetative stage has been reported into three regions, the Caribbean Sea and Central America, Persian Gulf and the Red Sea, and the western Pacific; while cyst stage distribution is broader, primarily in tropical to subtropical coastal areas from both the Atlantic and Pacific regions, and the Caribbean Sea (Usup et al., 2012). *Pyrodinium bahamense*, is one of the most critical harmful algal bloom (HABs) organisms in South Asian coastal waters (Mertens et al., 2015).

Pyrodinium bahamense is characterized by a high bioluminescence (Seliger et al., 1971), a heterothallic sexual cycle (Wall and Dale, 1969), and a simple toxins profile (dc-STX, STX, neoSTX, B1 and B2) (Usup et al., 2012). In 1980, the species taxonomic status was raised to variety, based on morphological variations in the motile stage, the capability of PSP toxin production, and the geographic distribution (Steidinger et al., 1980). However, based on morphologic and phylogenetic analysis of specimens (motile and cyst stages) from 13 coastal areas of various tropical and subtropical waters, Mertens et al. (2015) demonstrated that there is no consistent criterion to separate unequivocally both varieties based only in morphology. Additionally, Mertens et al. (2015) revealed within the *Pyrodinium* clade, both Indo-Pacific and Atlantic-Caribbean ribotypes, suggesting that *P. bahamense* is a species complex.

According to Balech (1985), *P. bahamense* cells are polyhedral and irregularly rounded, with strong crests along the sutures and tend to be compressed when they are in chains. Most cells have a well-developed left antapical spine and a smaller right spine that is an extension of the sulcal list (Figure 1A). The theca has a granular surface and numerous trichocyst pores, there is a pore in the 4' apical plate, and the apical pore complex consists of a comma-shaped granular closing plate and 9–14 pores. Cysts are spherical, of chorate type, with ~152 oblate tubular processes of variable length and randomly arranged (Figures 1D,E). The colorless wall is bi-layered, with a scabrate outer surface and a smooth inner surface. In living cysts, the yellow-green cytoplasm encloses a red accumulation body (Figure 1D) and numerous starch grains (Morquecho et al., 2014). Vegetative stage is easy to identify with basic microscopy equipment, and it could hardly be confused with other species. By contrast, due to its similarity with the cysts of other dinoflagellates, the resting stage may be confused with other species.

Blooms of *P. bahamense* are generally aperiodic and unpredictable (Usup et al., 2012); nevertheless, on a large temporal scale, there is some evidence that significant blooms overlap with peaks of El Niño and La Niña cycles (Maclean, 1989; Usup and Azanza, 1998; Philips et al., 2006). Even though, no relationship has been established between blooms and these cycles, the enhanced delivery of nutrients into the coastal waters could be a factor (Usup et al., 2012). Despite species seasonality that vary with local physiography, hydrography, and climate (Usup et al., 2012), blooms are more predictable at a smaller and local scale (Azanza and Taylor, 2001). Critical elements such as environmental factors, specifically removal of top-down predators and a change from eutrophic to oligotrophic conditions, likely promote the dominance and toxicity of *P. bahamense* in Florida (Walsh et al., 2011).

In this mini-review, the most significant information about *Pyrodinium bahamense* in Mexico since 1942 to date is summarized and analyzed. Aspects such as vegetative and cyst stage distribution, Mexican strains physiology and toxicology, as well as ecology and bloom dynamics, toxicity, human illnesses, and other significant impacts are discussed. Also, research priorities will be proposed to support the establishment of the guidelines for a transnational scientific approach, which is needed to coordinate and advance the understanding and management of HABs in coastal areas of Latin America.

METHODOLOGY USED IN MEXICO TO STUDY AND MONITOR TO *Pyrodinium bahamense*

In Mexico, *P. bahamense* studies focus on the vegetative stage taxonomy, occurrence, and distribution, as well as HABs recordings. Research on ecology, bloom dynamics, toxicology, and genetic characterization is minimal. Until now short-term studies have been undertaken, and there is no permanent scientific monitoring.

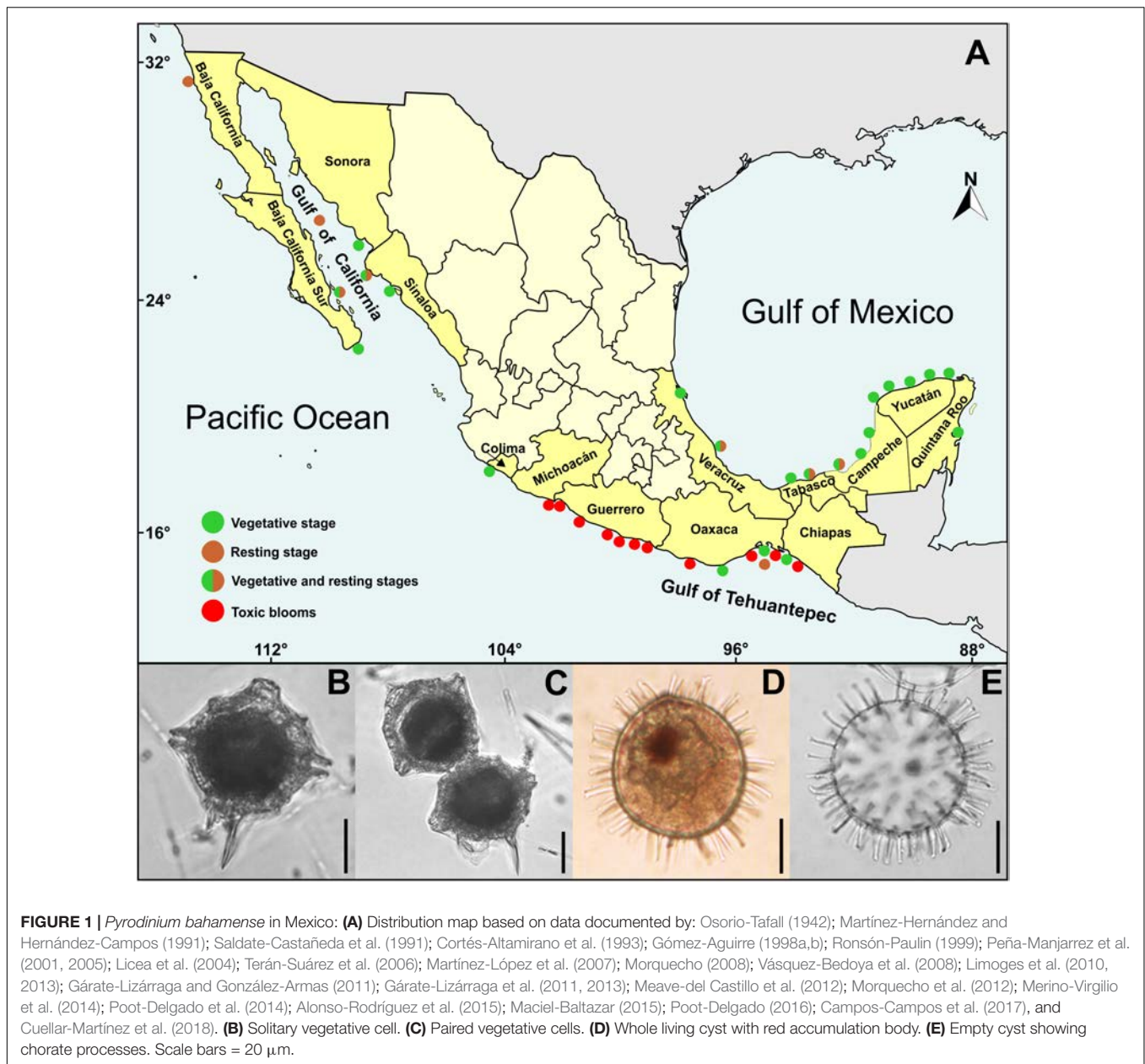
Basic methodologies such as water samplers (quantitative analysis), plankton nets (20 μ m, qualitative analysis), as well as, segmented tubes are applied to obtain marine phytoplankton sample collection at the superficial level or along the water column. For sample preservation, both Lugol and neutralized formalin are used (Thronsen, 1978), and in few cases, the combination of these fixatives is considered to preserve samples for long periods. For quantitative analysis, light microscopy is used to estimate the cell density by the Utermöhl (Hasle, 1978) or Sedgewick-Rafter (Guillard, 1978) methods.

Concerning ambient variables, the record of *in situ* hydrological variables such as temperature and salinity are the most common, while nutrients rarely are considered. Basic water quality sonde or CTD is the regular multiparameter equipment to record these variables. Nutrients analysis is carried out with standard chemical analytical methods (Strickland and Parsons, 1972).

Research on *P. bahamense* cysts is mainly developed with palynological procedures (de Vernal et al., 2010). Marine sediments are collected with gravitational corers or boxes, and scuba dive is also used to collect surface sediments or corers by hand. Biological procedures to clean and concentrate cysts (Matsuoka and Fukuyo, 2000) has been used for identification, quantification, germination assays, and strains establishment.

The identification of species is carried out by different techniques such as light and scanning electron microscopy, which allows the morphological and theca arrangement observations. It is worth noting that although Mertens et al. (2015) showed that there was no basis for distinction of two species varieties of *P. bahamense*, some researchers still accept this taxonomic status.

For research purposes, shellfish toxicity is determined by standard mouse bioassay (AOAC, 1995), and high-performance liquid chromatography (HPLC-FD with pre-column oxidation) (AOAC, 2005; Lawrence et al., 2005). For food safety, health authorities use the standard AOAC mouse bioassay



(AOAC, 1995) and fast track probes (Scotia Rapid Tests) to estimate PSP toxins concentration in shellfish monthly. Phytoplankton samples are collected weekly and abundances $\geq 5 \times 10^3$ cells L^{-1} of *P. bahamense* are considered a potential indicator of toxins accumulation in shellfish¹.

GEOGRAPHIC DISTRIBUTION

The first report of *P. bahamense* on Chiapas coast, in southern Mexican Pacific (Figure 1A), came from Osorio-Tafall (1942). At that time, it was believed that the species had a distribution

restricted to the Bahamas; however, at present, the vegetative stage (Figures 1B,C) is distributed in almost all coastal margin of Gulf of Mexico, Caribbean Sea, Gulf of California, and Mexican Pacific (Figure 1A). Cysts (Figures 1D,E) have been reported in limited areas, both Mexican Pacific as in the Gulf of Mexico (Figure 1A). However, it is highly probable that its distribution is as broad as that of vegetative cells, considering that *P. bahamense* cysts have been found in the central Gulf of California (Martínez-Hernández and Hernández-Campos, 1991), and in Baja California northern limit (Peña-Manjarrez et al., 2001, 2005) (Figure 1A). Despite these findings, a limited distribution of *P. bahamense* cysts has been reported (Martínez-Hernández and Hernández-Campos, 1991), restricted only to Guaymas basin phosphorite sediments, where it was

¹<https://www.gob.mx/cofepris/acciones-y-programas/marea-roja-76038>

TABLE 1 | *Pyrodinium bahamense* blooms associated with human PSP outbreaks and wildlife mortalities in Mexican Pacific.

Localities	Month/year	<i>In situ</i> maximum dinoflagellate abundance (cells L ⁻¹)	Shellfish toxicity (μg STX eq kg ⁻¹)	Impacts	Reference
Oaxaca and Chiapas	12/1989	1.7 × 10 ⁶	8,110 (<i>Crassostrea iridescens</i>) 5,420 (<i>Choromytilus palliopunctatus</i>)	99 human intoxications 3 fatalities	Saldade-Castañeda et al., 1991; Cortés-Altamirano et al., 1993
Oaxaca (Huatulco)	12/1990 to 01/1991	ND	ND	6 human fatalities	Cortés-Altamirano et al., 1995
Oaxaca	11/2001	1.14 × 10 ⁶	14,560 (<i>Mytella arciformis</i>)	17 human intoxications 3 fatalities	Gárate-Lizárraga et al., 2008
Oaxaca (La Colorada and La Ventosa)	06/2010 to 02/2011	ND	ND	23 human intoxications	COFEPRIS, 2018
Guerrero	07–08/2010	ND	ND	16 human intoxications	COFEPRIS, 2018
Guerrero (Costa Grande)	12//2010	410 × 10 ³	1,460–5,360 (rock oyster) 25,410 (unidentified clam)	12 human intoxications by ingesting raw and cooked clam	Gárate-Lizárraga et al., 2011
Guerrero (Bahía de Acapulco)	07/2010 to 01/2011	773.5 × 10 ³	1,000–20,920	Precautionary closure of fisheries and seafood consumption	Gárate-Lizárraga et al., 2012; Meave-del Castillo et al., 2012
Guerrero (Costa Chica)	06–12/2010	194 × 10 ³	460–7,890 (rock oyster) 520–4,410 (farmed rocky oysters)	Precautionary closure of fisheries and seafood consumption	Gárate-Lizárraga et al., 2013
Oaxaca (Santiago Astata and Puerto Escondido)	06/2009 to 06/2010	32 × 10 ³	Toxins concentration exceeded the permissible limit (<i>Striostrea prismatica</i>)	Precautionary closure of fisheries and seafood consumption	Alonso-Rodríguez et al., 2015
Guerrero (Bahía de Acapulco, Costa Chica, and Costa Grande)	01–02/2016	ND	ND	Precautionary closure of fisheries and seafood consumption Mortality of turtles	COFEPRIS, 2018
Oaxaca (seven coastal municipalities)	02–03/2016	ND	ND	Precautionary closure of fisheries and seafood consumption Mortality of turtles and some cetaceans	COFEPRIS, 2018

ND, not documented.

the dominant morphotype (34%). This distribution is likely attributed to the scarcity of the vegetative stage along the Gulf of California, whereas its presence in the phosphorite, could indicate the influence of slightly hypersaline and tropical warmer water masses. To date, it has been demonstrated that cysts have a broader distribution in southern Gulf of California, primarily in restricted coastal lagoons, where it is the dominant morphotype (33–86%) (Morquecho et al., 2012; Cuellar-Martínez, 2018; Cuellar-Martínez et al., 2018).

In Gulf of Tehuantepec, and Gulf of Mexico *P. bahamense* cysts are also one of most dominant morphotype. For the northern part of the Gulf of Tehuantepec, the dinoflagellate dominates in the upper productivity zone associated with seasonal upwelling (Vásquez-Bedoya et al., 2008). This gulf has an average and a maximum water depth of ~250 m and ~1,000 m, respectively (Vásquez-Bedoya et al., 2008). During boreal winter (December through April), a strong but intermittent wind blows across central America from the Gulf of Mexico and the Caribbean driving upwelling events (Antoine et al., 1996; Pennington et al., 2006). During these events, the average 0–100 m NO₃ concentration is very high at 18.3 μmol l⁻¹ (Pennington et al., 2006), and surface chlorophyll concentrations

reaching as high as 2 mg Chl m³ (Lluch-Cota et al., 1997; McClain et al., 2002). For the Gulf of Mexico, the annual temperature (approximately 25–28°C) is the most critical factor that controls nearshore cyst distribution and where *P. bahamense* achieve very high abundances, notably on the west Florida shelf and in the Mexican lagoons (Limoges et al., 2013).

ECOLOGY AND BLOOMS DYNAMICS

Pyrodinium bahamense usually blooms during the rainy summer (June through September), in restricted shallow lagoons surrounded by mangrove forests (Licea et al., 2004; Meave-del Castillo et al., 2012; Morquecho et al., 2012; Merino-Virgilio et al., 2014), with coastal underground drainage (Gómez-Aguirre, 1998b).

In the southern Gulf of Mexico, *P. bahamense* appears to have a continuous distribution and occurrence in a wide salinity range (3–38 ups) throughout the year, reaching densities of up to 1.5 × 10⁶ cells L⁻¹ Gómez-Aguirre (1998a). In contrast, in the southern Gulf of California, moderate (63–151 × 10³ cells L⁻¹), and short-term blooms are influenced by a short summer

rainy season (August–September), relatively high seawater temperature (25–32°C), typical salinity (31–36 ups), intense sunlight, and relatively high concentrations of ammonium (0.37–33.04 μM) and phosphates (0.68–2.87 μM); the last one, in turn, depending on rainfall and runoff and seems stronger on the eastern side of the gulf (Morquecho et al., 2012).

In southern Mexican Pacific and the Gulf of Tehuantepec, *P. bahamense* harmful blooms, with cell densities of up to 3×10^6 cells L^{-1} , have occurred from summer to winter (see **Table 1**) and have been associated with upwelling events (Cortés-Altamirano et al., 1993). The local winds “tehuanos”, and currents systems can move the dinoflagellate towards Mexico along the Central Pacific Coast through the Costa Rica Current Flow and Mexican Western Current (Vargas-Montero et al., 2008).

In Mexican coasts, *P. bahamense* has co-occurred with the diatom *Pseudo-nitzschia* spp. (Morquecho, 2008), and other dinoflagellates such as *Ceratium furca*, *C. dens*, *Dinophysis caudata*, *G. catenatum*, *Margalefidinium polykrikoides*, *Polykrikos* sp., *Prorocentrum lima*, *P. gracile*, *Protopeiridium oceanicum* and *P. pellucidum* (Terán-Suárez et al., 2006; Gárate-Lizárraga et al., 2011; Meave-del Castillo et al., 2012). Interactions or environmental factors that may promote these co-occurrence has not yet been clarified. However, a similar co-occurrence between *P. bahamense* and *Pseudo-nitzschia* species has also been reported in the Indian River Lagoon, Florida (Phlips et al., 2004).

MEXICAN STRAINS TOXICITY AND CYSTS GERMINATION CHARACTERISTICS

Ecophysiological studies with regional *P. bahamense* strains are insufficient in México, and so far, strains from Isla San José, Gulf of California have only been studied. To elucidate the toxicity of vegetative cells grown from cyst germination, Morquecho et al. (2014) analyzed nine strains through fluorescence high-performance liquid chromatography, and only one exhibited toxicity with high saxitoxin concentration (95 pg STX eq cell⁻¹). Additionally, morphological features and size of cysts agreed with previous descriptions, particularly morphotypes found in the subtropical North Atlantic. Cysts germination exhibit thermophilic (20–35°C with the peak between 25 and 30°C) and euryhaline characteristics (salinities from 20 to 35 ups). Also, the *in vitro* germination is improved in growth medium enriched with terrestrial soil extract and selenium.

TOXICITY AND IMPACTS

Pyrodinium bahamense has caused more human illnesses and fatalities than any other PST producing dinoflagellate in Mexico (**Table 1**). Southeast Mexican Pacific has been the most affected area, particularly the Gulf of Tehuantepec, as well as Guerrero and Michoacán (**Figure 1** and **Table 1**). From 1989 to 2007 shellfish toxicity reached concentrations above the permissible limits for human consumption (800 μg STX eq kg^{-1}), and consequently caused 200 human cases, with

15 fatalities (Hernández-Becerril et al., 2007). By comparison, *Gymnodinium catenatum* is another toxic species linked with PSP deaths in Mexico, from 1989 to 2015 has caused, in some localities of the Gulf of California, 37 human PSP cases and three fatalities (Mee et al., 1986; Cortés-Altamirano and Núñez-Pasten, 1992; Núñez-Vázquez et al., 2016).

According to the registry of Federal Commission for the Protection against Sanitary Risks (COFEPRIS, by its acronym in Spanish) of the 118 HABs that have been reported from 2004 to 2014 in Mexico, 12% were linked to *P. bahamense*. The entity most affected was Oaxaca, followed by Guerrero and Chiapas (COFEPRIS, 2018). *Pyrodinium bahamense* HABs also have been linked to endangered marine fauna (sea turtles and cetaceans) with ecologic importance, leading in some cases to mass mortalities (**Table 1**), and the establishment of precautionary closures (COFEPRIS, 2018).

DISCUSSION AND CONCLUSION

The data obtained so far on *P. bahamense* spatial and population variability in Mexican Pacific and the Gulf of Mexico, suggest a seasonal and latitudinal pattern. From tropical to subtropical regions, the abundance, seasonality, and species distribution, tends to decrease. For example, the dinoflagellate may develop persistent moderate and massive toxic blooms in Guerrero, Oaxaca, and Chiapas coastal margin (**Figure 1**), which is characterized by a large-scale hydrological and atmospheric influence (**Table 1**); while in the southern Gulf of California, moderate blooms are restricted to coastal lagoons inhabited by mangroves, and develop only during the summer and the short-term rainy period. However, comparative research is needed on both coasts of Mexico to define precisely the hydrologic and climatic variables that are triggering *P. bahamense* blooms.

Epidemiological numbers of outbreaks of food poisoning related to *P. bahamense*, reveal that this dinoflagellate is the major source of PSP in Mexico. Monitoring for food safety on the coasts of Mexico, with particular emphasis on aquaculture areas or the exploitation of marine products, requires essential adjustments to validate and strengthen the management and decision-making database. Permanent records of hydrological variables, climate signals, harmful species abundance, seasonal variation, impacts in human and environmental health, as well as economic activities are essential to implement early warnings and minimize impacts.

Frequency and intensity of HABs as well as, the variation in phytoplankton composition toward toxic species have increased throughout the world (Fu et al., 2012). Recent studies suggest that ocean acidification, combined with the limitation of nutrients, or temperature changes, might dramatically increase the toxicity of some harmful groups (Fu et al., 2012). Mexico and Latin America are not immune to this problem as was discussed in this mini-review. *Pyrodinium bahamense* and other toxic dinoflagellates are significantly impacting human and environmental health, as well as having significant impact on economic activities.

The United States of America, the European Union, and other countries such as Australia and New Zealand, have managed

significant advances to counteract the impact of harmful microalgae. However, the information that we currently have on blooms dynamics, and toxicological and autecological characteristics of harmful species inhabiting Mexico and Latin America is insufficient. This prevents, in the short term, the establishment of management plans to minimize HABs impacts as well as the advance of the understanding and prediction of them.

Short-term perspectives about scientific research and monitoring activities related with *P. bahamense* populations in Mexico and Central America may include:

- Design and implement an interdisciplinary, specific and permanent monitoring program that consider meroplanktonic characteristic of the species and ecosystems comparison.
- Select as target ecosystems the coastal lagoons with and without mangrove populations. Usup et al. (2012) have questioned the significance of the presence or absence of mangrove forests in the distribution pattern of *P. bahamense*. Also, they have highlighted the importance of carrying out comparative studies between the western Pacific and tropical Atlantic populations, to understand better the factors that play essential roles in the bloom dynamics and toxicity of the species.

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AUTHOR CONTRIBUTIONS

The author participated in all the activities of research: data collection, analyses, interpretation of the results, and manuscript writing.

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Conflict of Interest Statement: The author declares 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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