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A review on marine benthic dinoflagellates in Mexico

Una revisión sobre dinoflagelados bentónicos marinos en México

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ABSTRACT

Background: Mexican studies on marine benthic dinoflagellates (MBD) began in 1942 from the offshore region of Oaxaca, based on water column samples. Subsequently, in ten Mexican maritime states, both epibenthos and plankton samples have been collected, species have been cultured, and field and laboratory studies have been carried out. **Goals:** The objective of this contribution is to review the studies on MBD in Mexican waters for current status and future risk assessment. **Methods:** Available literature on MBD from Mexico published from 1942 to 2022 was analyzed. **Results:** A review of the studies on MBD is presented herein, subdivided into four sections: (1) taxonomic diversity (morphological and molecular), (2) benthic phycotoxin vectors and toxigenicity, (3) toxicity and (4) species interactions. A map of the location of field populations of MBD and a reference list of taxonomic and ecological studies on MBD in Mexico is provided. A taxonomic list of *ca*. 60 species, mainly of *Prorocentrum*, followed in number by *Amphidinium, Gambierdiscus, Ostreopsis*, *Coolia*, and *Sinophysis* is presented. This list is accompanied by scanning electron microscopic images of 15 species. Knowledge of the toxigenicity of MBD is scarce, hence a reference table of known toxigenic species in Mexico and their respective associated syndromes is included. **Conclusions:** Studies on MBD in Mexico have slowly increased, probably due to the availability of a greater number of cultured strains, as well as to more extensive international collaborations. Confirmed links between benthic harmful algal bloom species and events associated with the etiology of toxic syndromes are rarely known in Mexico.

Keywords: benthic dinoflagellates, Dinoflagellata, epibenthos, microphytobenthos, phycotoxins

RESUMEN

Antecedentes: Los estudios sobre dinoflagelados bentónicos marinos (DBM) en México comenzaron en 1942 en la región oceánica de Oaxaca, basados en muestras de la columna de agua. En diez estados costeros mexicanos se han recolectado muestras de epibentos y plancton, se han cultivado especies, y se han realizado estudios de campo y de laboratorio. **Objetivos:** Revisar el estado actual de los estudios sobre DBM en aguas mexicanas para evaluar los riegos posibles en un futuro. **Métodos:** Se analizó la literatura disponible sobre DBM en México, publicada desde 1942 hasta 2022. **Resultados:** Se presenta una revisión de los estudios sobre DBM subdividida en cuatro secciones: (1) diversidad taxonómica (morfológica y molecular), (2) toxigenicidad y vectores de ficotoxinas de origen bentónico, (3) toxicidad y (4) interacciones entre especies. Se presenta un mapa de la ubicación de las poblaciones estudiadas de DBM y una lista de estudios taxonómicos y ecológicos sobre DBM en México. Se proporciona una lista de *ca*. 60 especies, principalmente de *Prorocentrum*, seguidas en cantidad por los géneros *Amphidinium*, *Gambierdiscus*, *Ostreopsis, Coolia* y *Sinophysis*. Esta lista está acompañada de imágenes de microscopía electrónica de barrido de 15 especies. Se ha añadido una tabla de referencia sobre especies toxigénicas reportadas y los respectivos síndromes asociados a estas. **Conclusiones:** Los estudios sobre DBM en México se han incrementado lentamente, probablemente debido a un mayor número de cepas en cultivo y por colaboración internacional. Los vínculos confirmados entre especies asociadas con florecimientos algales nocivos bentónicos y la etiología de los síndromes tóxicos son aún escasos en México.

Palabras clave: dinoflagelados bentónicos, Dinoflagellata, epibentos, ficotoxinas, microfitobentos

INTRODUCTION

On a global scale, benthic dinoflagellates have been much less studied than their planktonic counterparts, perhaps because they tend to form much less dramatic blooms, and their role in marine food webs is more cryptic. Nevertheless, over the past two decades, in particular, many benthic dinoflagellate species have attracted increasing attention as the causative agents of benthic harmful algal blooms (BHABs) and related syndromes, such as ciguatera fish poisoning (CFP) and diarrhetic shellfish poisoning (DSP) in human consumers of seafood (Heredia-Tapia *et al.*, 2002). Other BHAB species have recently emerged as the cause of acute respiratory distress in humans due to the release of toxic aerosols created by wind and wave action in coastal ecosystems (Blanfuné *et al.*, 2015). Although the mooted arguments for a general global increase in the number and frequency of HAB events were not sustained in the recent analysis of global databases (Hallegraeff *et al.*, 2021), the evidence indicates that the impacts on human populations and marine ecosystems have increased substantially. A similar pattern is apparent concerning BHAB events – almost all of which are generated by benthic dinoflagellates – but the associated databases are much less comprehensive than for planktonic blooms.

A recent review on toxigenic marine benthic dinoflagellates in Latin America (Durán-Riveroll *et al.*, 2019a) is essentially a status report focusing on key BHAB species, mainly of the genera *Amphidinium* Clap. et J. Lachm., *Coolia* Meunier, *Fukuyoa* Gómez, Lopes et Lin, *Gambierdiscus* Adachi et Fukuyo, *Ostreopsis* Schmidt and *Prorocentrum* Ehrenb. The geographical coverage in that review comprises the eastern Pacific, Caribbean Sea, Gulf of Mexico, Atlantic coastal waters of Latin America, and part of the southeastern coast of the USA, and thus includes all the relevant coasts of Mexico. A national review on HABs in Mexico (Durán-Riveroll *et al.*, 2019b) in the context of coastal contamination and climate change considers mainly planktonic species but also includes information on benthic dinoflagellates in the Mexican Caribbean. The last International Conference on Harmful Algae held online in October 2021 in La Paz, Mexico (ICHA, 2021), featured recent HAB studies. Special sessions opened avenues for future research directions on BHAB dinoflagellate community studies, *e.g.*, published abstracts on the section Ciguatera and Benthic HABs (ICHA, 2021). Some BHAB research from Mexico has been summarized in short papers on diversity (Durán-Riveroll *et al.*, 2022) and microbiome associations with bacteria (Martínez-Mercado *et al.*, 2022) in the conference proceedings (Band-Schmidt & Rodríguez-Gómez, 2022).

In fact, the only dinoflagellate species confirmed to form high-magnitude benthic blooms with potentially harmful consequences (*i.e.*, BHABs) in Mexico are *Prorocentrum rhathymum* A. R. Loebl., Sherley et R. J. Schmidt (Gárate-Lizárraga & Martínez-López, 1997; Gárate-Lizárraga & Muñetón-Gómez, 2008), *P. lima* (Ehrenb.) F. Stein (Heredia-Tapia *et al.*, 2002), *Blixaea quinquecornis* (T. H. Abé) Gottschling (Gárate-Lizárraga *et al.*, 2006; Gárate-Lizárraga & Muñetón-Gómez, 2008; Okolodkov *et al.*, 2016), and *Amphidinium* cf. *carterae* (Gárate-Lizárraga, 2012, 2020; Gárate-Lizárraga *et al.*, 2019).

Linkages of other known toxigenic benthic dinoflagellates (*e.g.*, *Gambierdiscus* and *Fukuyoa* species) to toxin syndromes such as CFP in Mexico are plausible but remain circumstantial. Parrilla-Cerrillo *et al.* (1993) reported an outbreak (200 cases) of CFP in Baja California Sur in 1984 due to consumption of snapper (*Lutjanus*) species. From 1992-1995, more fish poisoning events were registered at different locations in Baja California Sur, suggesting the presence of ciguatoxins (CTXs) in carnivorous sea bass (Serranidae) and snapper (Lutjanidae) fish (Ochoa *et al.*, 1997). In May 1993, another event of apparent ciguatoxicity in Mexico occurred, and it was based on the consumption of fish caught at Alijos Rocks, 300 miles offshore of Bahía Magdalena in Baja California Sur (Lechuga-Devéze & Sierra-Beltrán, 1995); although the toxin identification remains uncertain, the symptoms were characteristic of CFP in the affected fishermen. From 1993-1996, human poisoning events with similar symptoms also occurred at two locations in the Bahía de La Paz area including Isla El Pardito, after consumption of liver of the same fish families. In these cases, the presence of CTX1 was indicated by chromatography analysis but not structurally confirmed (Núñez-Vázquez *et al.*, 1998). Based on data from the Secretariat of Health of Mexico and scientific articles, during a 29-year period (1984-2013), 464 human poisoning cases caused by consumption of carnivorous fish were recorded from the genera *Lutjanus,* the groupers *Epinephelus* and *Mycteroperca* in the Pacific, and *Lutjanus* and the barracuda *Sphyraena* in the Caribbean (Núñez-Vázquez *et al.*, 2000). Most reports were from the states of Baja California Sur (52%), Quintana Roo (35%) and Yucatán (10%) and of Mexican tourists poisoned by eating fish in Cuba (3%). Although collectively ascribed to benthic dinoflagellates considered the precursors of ciguatera from the genera *Amphidinium* Clap. et J. Lachm., *Coolia* Meunier*, Fukuyoa, Gambierdiscus, Ostreopsis* Schmidt*,* and *Prorocentrum,* there is no conclusive evidence of particular dinoflagellate species linked to these specific events.

This review updates the current knowledge of benthic dinoflagellates in Mexican waters based on integrated field and laboratory studies interpreted in an ecological context. Laboratory experimental studies on cultured benthic dinoflagellate isolates and from live freshly collected field specimens from Mexico have been initiated only since around the turn of the 21st century. The focus herein is on unresolved taxonomic and nomenclatural issues, species diversity, biogeographical distribution and toxigenicity, with special emphasis on allelopathic species interactions. For the first time, this comprehensive approach allows a better understanding of the role of dinoflagellates in benthic communities and their functional interactions during BHAB events in marine ecosystems in Mexico. This review provides a more detailed integration of BHAB events and associated species, but with an exclusive focus on Mexico, and adds a missing dimension of knowledge on non-harmful dinoflagellate species.

DISCUSSION

Morphological diversity. More than 190 species of benthic dinoflagellates belonging to 45 genera had been described by 2014, primarily based on morphological criteria (Hoppenrath *et al.*, 2014), but the list is being constantly revised and extended by new morphological observations and molecular taxonomic data. Morphological traits of unarmored benthic dinoflagellate cells can be difficult to discriminate among closely related species due to extreme phenotypic plasticity in shape and surface microstructure. This plasticity results from “the ability of an organism to change morphology in response to stimuli or inputs from the environment” (West-Eberhard, 2008), and in some cases is presumably adaptive. In comparison, for armored, but dinoflagellate cells, the overall shape tends to be more constrained, but identification is complicated by phenotypic plasticity in thecal plate tabulation and variation in superficial features such as pore patterns and surface microstructure. When taxonomists lack experience with a particular taxon, alternative designations can be given to the same species because some benthic taxa have thecal tabulations difficult to interpret (Hoppenrath *et al*., 2014).

Most published information on the morphological diversity of marine benthic dinoflagellates in Mexico has been based on light microscopy (LM) or scanning electron microscopy (SEM). Numerous morphological studies on field or cultured material are derived from specimens collected from the coastal waters of Quintana Roo, Yucatán, Campeche, Veracruz, Baja California Sur, Baja California, Chiapas, Oaxaca, Guerrero, Colima (Revillagigedo Archipelago), Michoacán and Nayarit (Isla Isabel) (Fig. 1, Table 1). The inter-seasonal or annual dynamics of epibenthic/epiphytic dinoflagellate assemblages and their relationships with some physicochemical variables have been studied in some coastal localities (Okolodkov *et al*., 2007, 2014; Aguilar-Trujillo *et al*., 2014, 2017; Martínez-Cruz *et al*., 2015; Irola-Sansores *et al*., 2018). To our knowledge, no studies on the direct influence of physicochemical factors on dinoflagellate morphology have been conducted in Mexico. Individual species or entire epibenthic assemblages were considered in the above cited studies, and in some cases, the epiphytic assemblages were comprehensively described. In comparison, however, sand-dwelling species inhabiting Mexican waters have been neglected and deserve more attention.

Dinoflagellate reviews have highlighted the importance of life-history transitions in HAB dynamics (*e.g.*, Bravo & Figueroa, 2013), but reports of confirmed sexual cysts of benthic dinoflagellate species remain scarce on a global scale. There are publications on resting (sexual) cysts of planktonic dinoflagellate species collected from the benthic environment in the Mexican Pacific (cited below) that are outside the scope of this review. Studies of dinoflagellate cysts (presumably, hypnozygotes) of planktonic species of the Gonyaulacales, Peridiniales and Gymnodiniales dominate the literature from Mexico (Martínez-Hernández & Hernández-Campos, 1991; Peña-Manjarrez *et al*., 2001, 2005, 2009; Morquecho & Lechuga-Devéze, 2003, 2004; Kielt, 2006; Pospelova *et al*., 2008; Vásquez-Bedoya *et al*., 2008; Morquecho *et al*., 2009; Limoges *et al*., 2010, 2013; Helenes *et al*., 2020; Gu *et al*., 2021), whereas the resting cysts and life history transitions of benthic species are poorly known. As noteworthy exceptions, from the benthic community, cysts of *Amphidinium* cf. *carterae* Hulburt have been recorded in shallow coastal lagoons (Gárate-Lizárraga, 2012, 2020; Gárate-Lizárraga *et al*., 2019) and those of *A. thermaeum* Dolapsakis et Economou-Amilli in laboratory cultures isolated from Bahía de La Paz (Herrera-Herrera, 2022).

Figure 1. Location of the origin of marine benthic dinoflagellates and related studies reported in Mexico (1942-2022). Mexican states, including islands where field sampling was performed, and benthic dinoflagellates were found, are shaded light gray. Only geographic names mentioned in the text are given.

Table 1. Locations of taxonomic, biogeographical and ecological field studies on marine benthic dinoflagellates in Mexico (1942-2022). Abbreviations of Mexican states: BCS – Baja California Sur, Chis – Chiapas, Col – Colima, Gro – Guerrero, Mich – Michoacán, Nay – Nayarit, Oax – Oaxaca, QR – Quintana Roo, Sin – Sinaloa, Ver – Veracruz, Yuc – Yucatán. VRS – Veracruz Reef System. Note that although all the studies referenced are on species and assemblages considered primarily benthic, specimens are frequently dislodged or resuspended and may be found in the water column.

Region	Localities	Substrate/Compartment	Object of study	References
Caribbean Sea	Eastern Yucatán, QR	Macroalgae, sediments	Dinoflagellate assemblage	Almazán-Becerril, 2000
	Eastern Yucatán, QR	Macroalgae, sediments, water column	*Gambierdiscus, Fukuyoa yasumotoi*	Hernández-Becerril & Almazán-Becerril, 2004
	NE and eastern Yucatán, QR	Macroalgae	Dinoflagellate assemblage	Almazán-Becerril *et al*., 2015
	Puerto Morelos, Isla Contoy, QR	Macroalgae	*Gambierdiscus*	Almazán-Becerril *et al*., 2016a
	Eastern Yucatán, QR	Macroalgae	*Coolia, Ostreopsis*	Almazán-Becerril *et al*., 2016b
	Puerto Morelos, Isla Contoy, QR	Macroalgae	Dinoflagellate assemblage	Irola-Sansores *et al*., 2018
	Puerto Morelos, Isla Contoy, QR	Macroalga (*Dictyota*)	*Ostreopsis*	Méndez-Torres, 2019
	Puerto Morelos, QR	Macroalgae, seagrass (*Thalassia testudinum*)	*Prorocentrum lima* species complex	Tarazona-Janampa *et al*., 2020
	Puerto Morelos, QR	Macroalgae, seagrass (*T. testudinum)*	*Prorocentrum lima* and *P. hoffmannianum* species complexes, *P. rhathymum*	Cembella *et al*., 2021
Gulf of Mexico	VRS, Ver	Macroalgae, seagrasses, sediments	Dinoflagellate assemblage	Okolodkov *et al*., 2007, 2016
	Northern Yucatán, Yuc	Macroalgae, seagrasses	*Gambierdiscus*	Okolodkov *et al*., 2009
	Northern Yucatán, Yuc	Macroalgae, seagrasses, sediments, sponges	Dinoflagellate assemblage	Aguilar-Trujillo *et al*., 2014
	Northern Yucatán, Yuc	Macroalgae, seagrasses	Dinoflagellate assemblage	Okolodkov *et al*., 2014
	Dzilam, Yuc	Seagrass (*T. testudinum*)	Dinoflagellate assemblage	Martínez-Cruz *et al*., 2015
	Northern Yucatán, Yuc	Macroalgae, seagrasses, sediments, sponges	Dinoflagellate assemblage	Aguilar-Trujillo *et al*., 2014
	VRS, Ver	Macroalgae, seagrass (*T. testudinum*)	*Prorocentrum lima* species complex	Tarazona-Janampa *et al*., 2020
	VRS, Ver	Macroalgae, seagrass (*T. testudinum*)	*Prorocentrum lima* and *P. hoffmannianum* species complexes	Cembella *et al*., 2021

Region	Localities	Substrate/Compartment	Object of study	References
Pacific Ocean	Salina Cruz, Oax	Water column	*Prorocentrum rhathymum* (reported as *P. mexicanum*)	Osorio-Tafall, 1942
	Bahía de La Paz, BCS	Water column	*Prorocentrum rhathymum* (reported as *P. mexicanum*)	Gárate-Lizárraga & Martínez-López, 1997
	Bahía de La Paz, BCS	Water column	*Prorocentrum lima*	Heredia-Tapia *et al.*, 2002
	Bahía de La Paz, BCS	Water column	*Prorocentrum rhathymum*	Cortés-Altamirano & Sierra-Beltrán, 2003
	Isla Isabel, Nay	Water column	*Ostreopsis siamensis*	Cortés-Lara *et al.*, 2005
	Bahía de La Paz, BCS	Water column	*Blixaea quinquecornis*	Gárate-Lizárraga *et al.*, 2006
	Coastal lagoons, Sin	Water column	*Prorocentrum rhathymum, Blixaea quinquecornis*	Alonso-Rodríguez *et al.*, 2008
	Bahía de La Paz, BCS	Water column	*Blixaea quinquecornis*	Gárate-Lizárraga & Muñetón-Gómez, 2008
	Isla Isabel, Nay	Water column	*Ostreopsis siamensis*	Cortés-Altamirano *et al.*, 2011
	Bahía de La Paz, BCS	Water column	*Amphidinium carterae*	Gárate-Lizárraga, 2012, 2020
	Lázaro Cárdenas, Mich	Water column	*Vulcanodinium rugosum*	Hernández-Becerril *et al.*, 2013
	Coastal waters, Chis	Water column	*Prorocentrum*	Maciel-Baltazar, 2015
	Bahía de La Paz, BCS	Water column	*Prorocentrum*	Muciño-Márquez *et al.*, 2015
	Bahía de La Paz, BCS	Water column, macroalgae	*Coolia, Ostreopsis, Prorocentrum*	Morquecho-Escamilla *et al.*, 2016
	La Piedra Tlacoyunque Beach, Gro	Water column	*Ostreopsis ovata*	Gallegos-Mendiola *et al.*, 2017
	Revillagigedo Archipielago, Col	Water column	*Ostreopsis lenticularis*	Gárate-Lizárraga *et al.*, 2018
	Bahía de La Paz, BCS	Macroalgae	*Amphidinium, Coolia, Ostreopsis, Prorocentrum*	Sepúlveda-Villarraga, 2017
	Bahía de La Paz, BCS	Water column	*Amphidinium* cf. *carterae, Coolia, Gambierdiscus, Ostreopsis, Prorocentrum*	Gárate-Lizárraga *et al.*, 2019
	Bahía de La Paz, BCS	Macroalgae, seagrass (*T. testudinum*)	*Prorocentrum lima* and *P. hoffmannianum* species complexes	Cembella *et al.*, 2021
	Central Mexican Pacific	Water column	*Prorocentrum rhathymum* (reported as *P. mexicanum*)	Hernández-Becerril *et al.*, 2021
	Bahía de La Paz, BCS	Water column	*Prorocentrum*	Villa-Arce, 2021
	Bahía de La Paz, BCS	Water column	*Coolia malayensis*	Ramos-Santiago *et al.*, 2022
	Bahía de La Paz, BCS	Water column	*Coolia malayensis, Amphidinium thermaeum*	Herrera-Herrera, 2022
	Bahía de La Paz, BCS	Macroalgae	*Coolia*	Morquecho *et al.*, 2022

The distinctive morphological features of vegetative cells of dinoflagellates may be reflected in the overall morphology and/or thecal paratabulation (armored species) of their respective cyst forms, but this is rarely the case. In Mexican waters, many undescribed cyst forms may belong to known species, but the life-history relationships remain undefined.

In general, vegetative cells of benthic dinoflagellates often tend to be more dorso-ventrally compressed compared to planktonic forms, probably due to their natural habitats on surfaces of macroalgal thalli, on seagrass leaves, or between sand grains. Presumably, this is an adaptive strategy to optimize substrate attachment and deal with turbulence and hydrodynamic flow in more stationary habitats. In any case, diagnostic morphological features more or less easily visible in planktonic species are often less obvious in benthic species. For example, in planktonic species within the Peridiniales and Gonyaulacales, these features are usually the sulcal platelets that are rarely suitable for identifying benthic dinoflagellate species.

Prorocentrum is the richest genus in benthic samples in terms of the number of species among all benthic dinoflagellate genera: of more than 80 *Prorocentrum* species, at least 29 are benthic (Hoppenrath *et al.*, 2014). In this genus, the platelets of the periflagellar area are of great importance in distinguishing among species, whereas for the identification of planktonic species, the cell shape (in fact, the valve outline) is usually sufficient. In Mexican coastal waters, the most common *Prorocentrum* species, preliminarily identified as *P. lima* and *P. hoffmannianum* M.A. Faust, turned out to be species complexes that are not fully resolved from morphological criteria on a global basis (Cembella *et al.*, 2021).

The validity of *Prorocentrum rhathymum* has caused endless discussion among researchers ever since the publication of the original description of *P. mexicanum* by Osorio-Tafall (1942) (Cortés-Altamirano & Sierra-Beltrán, 2003; Litaker *et al.*, 2011; Gómez *et al.*, 2017; for further references, see Cembella *et al.*, 2021). Cortés-Altamirano & Sierra-Beltrán (2003) later separated these species. *Prorocentrum emarginatum* Fukuyo and *P. sculptile* M. A. Faust are both relatively common but never dominant in epiphytic dinoflagellate assemblages of the Gulf of Mexico; these species are difficult to distinguish, and it remains unclear whether or not they are synonymous.

After the publication of new molecular and toxigenicity data on *Gambierdiscus*, it became apparent that the earlier reports of the most notorious BHAB species *G. toxicus* Adachi et Fukuyo from the Greater Caribbean are most likely misidentifications; true *G. toxicus* has been found only in the Pacific (Litaker *et al.*, 2010). *Coolia monotis* Meunier, earlier reported as a cosmopolitan species (Steidinger & Tangen, 1996), has also turned out in later studies to comprise a species complex. Various strains assigned to *C. monotis* were later reassigned to *C. malayensis* Leaw, Lim et Usup*, C. santacroce* Karafas, Tomas et York, and *C. palmyrensis* Karafas, Tomas et York, based on molecular data and subtle morphological differences (Karafas *et al.*, 2015). Momigliano *et al.* (2013) suggested that *C. monotis* is geographically restricted to the Mediterranean Sea and the eastern Atlantic, representing the original European clade.

About 60 benthic dinoflagellate species from 18 genera have been identified in Mexican waters (Table 2; number of species indicated in parentheses): *Amphidiniella* Horiguchi (1), *Amphidiniopsis* Wołoszyńska (1), *Amphidinium* (6), *Ankistrodinium* M. Hoppenrath, Shauna Murray, Sparmann et Leander (1), *Blixaea* Gottschling (1), *Bysmatrum* M.A. Faust et Steidinger (3), *Cabra* Shauna Murray et Patterson *emend*. Chomérat, Couté et Nézan (2), *Coolia* (5), *Durinskia* S. Carty et E.R. Cox (1), *Fukuyoa* (1), *Gambierdiscus* (6), *Gymnodinium* F. Stein (1), *Ostreopsis* (6), (?)*Pileidinium* Tamura et Horiguchi (1), *Plagiodinium* M.A. Faust et Balech (1), *Prorocentrum* (14), *Sinophysis* Nie et Wang (5), *Thecadinium* Kof. et Skogsb. (1), (?)*Togula* Flø Jørgensen, Shauna Murray et Daugbjerg (1), and *Vulcanodinium* Nézan et Chomérat (1). Critical taxonomy and identification of species in field samples and establishment of new benthic dinoflagellate species are challenging without molecular confirmation, and therefore identifications based only on morphology should be considered tentative (Leaw *et al.*, 2016).

Molecular diversity. In Mexico, studies on the molecular taxonomy of benthic dinoflagellates began less than 15 years ago when sequences of LSU and SSU rDNA subunits were obtained from *Gambierdiscus* isolate CM515 from Cancún by Donald R. Tindall, from Southern Illinois University, Illinois, USA (cited in Richlen *et al.*, 2008). The *Gambierdiscus* species, however, was not identified. Sequencing of the D8-D10 domain of the LSU rDNA of the same strain later identified it as *G. carolinianus* Litaker, Vandersea, M. A. Faust, Kibler, W. C. Holland et P. A. Tester (Litaker *et al.,* 2010), but a GenBank accession number for the sequences was not provided. Fourteen LSU and SSU rDNA sequences of *Prorocentrum* species, including three planktonic and the questionably benthic species, *P. rhathymum* from the Pacific coast of Mexico were also published around this time (Cohen-Fernández *et al.*, 2010). Herrera-Sepúlveda *et al.* (2013) applied a capillary electrophoresis DNA fingerprint technique (CE-SSCP) to rDNA fragments as an alternative rapid identification of harmful dinoflagellates. After application to 10 species, including *P. rhathymum* and *P. minimum* (Pavill.) J. Schill., they concluded that this method could serve as an element of an early warning system for HABs in coastal waters of Baja California Sur. Unfortunately, this method has not been systematically applied and validated for benthic dinoflagellates in Mexico.

Within the last five years, several molecular studies and publications have focused on benthic dinoflagellates from Mexico. Based on morphology and LSU rDNA sequences, Sepúlveda-Villarraga (2017) analyzed strains of *Ostreopsis*, *Coolia*, *Amphidinium* and *Prorocentrum*, identifying *C. malayensis*, *O. lenticularis* and *P. rhathymum*; once again, however, these sequences are not available for comparison in the GenBank database. Méndez-Torres (2019) identified three species by morphological characters (*O. lenticularis*, *O. heptagona* and *O.* cf. *siamensis*) from Isla Contoy and Puerto Morelos, Quintana Roo; only the morphological identification of *O. lenticularis* was corroborated by partial sequences of internal transcribed spacers (ITS) of the rRNA gene operon. Ramos-Santiago *et al.* (2022) carried out both morphological and molecular identification of two isolates of *Coolia* from Bahía de La Paz, Baja California Sur. Morphological descriptions and partial sequences of LSU rDNA agreed; both strains (OM177218 and OM177219) were identified as *C. malayensis*, previously considered a synonym to *C. monotis* (Hoppenrath *et al.*, 2014). Based on the phylogenetic analysis of D1-D2 LSU rDNA sequences and morphological differences in thecal structure, *C. malayensis* has since been shown to be an independent species, forming a separate lineage within the genus *Coolia* (Ho & Nguyen, 2014; Leaw *et al.*, 2016). These results agree with a morphological and molecular study performed by Morquecho *et al.* (2022), who isolated 16 strains of *Coolia* from Bahía de La Paz and identified

14 of these with partial sequences of D1-D2 rDNA. Four strains belonged within the *C. canariensis* M. A. Faust complex; eight strains in the *C. malayensis* clade; one strain aligned with *C. palmyrensis*, and one strain belonged to *C. tropicalis* M. A. Faust. Comparative analysis of sequences of the ITS1/5.8S/ITS2 region of nine strains identified three as *C. malayensis*, one as *C. palmyrensis*, four belonging to the *C. canariensis* complex, and one as *C. tropicalis*. The authors of this study proposed a review and reclassification of *Coolia* strain CMPV-1, previously identified as *C. monotis*; the new sequences indicate that this strain may belong to *C. canariensis*.

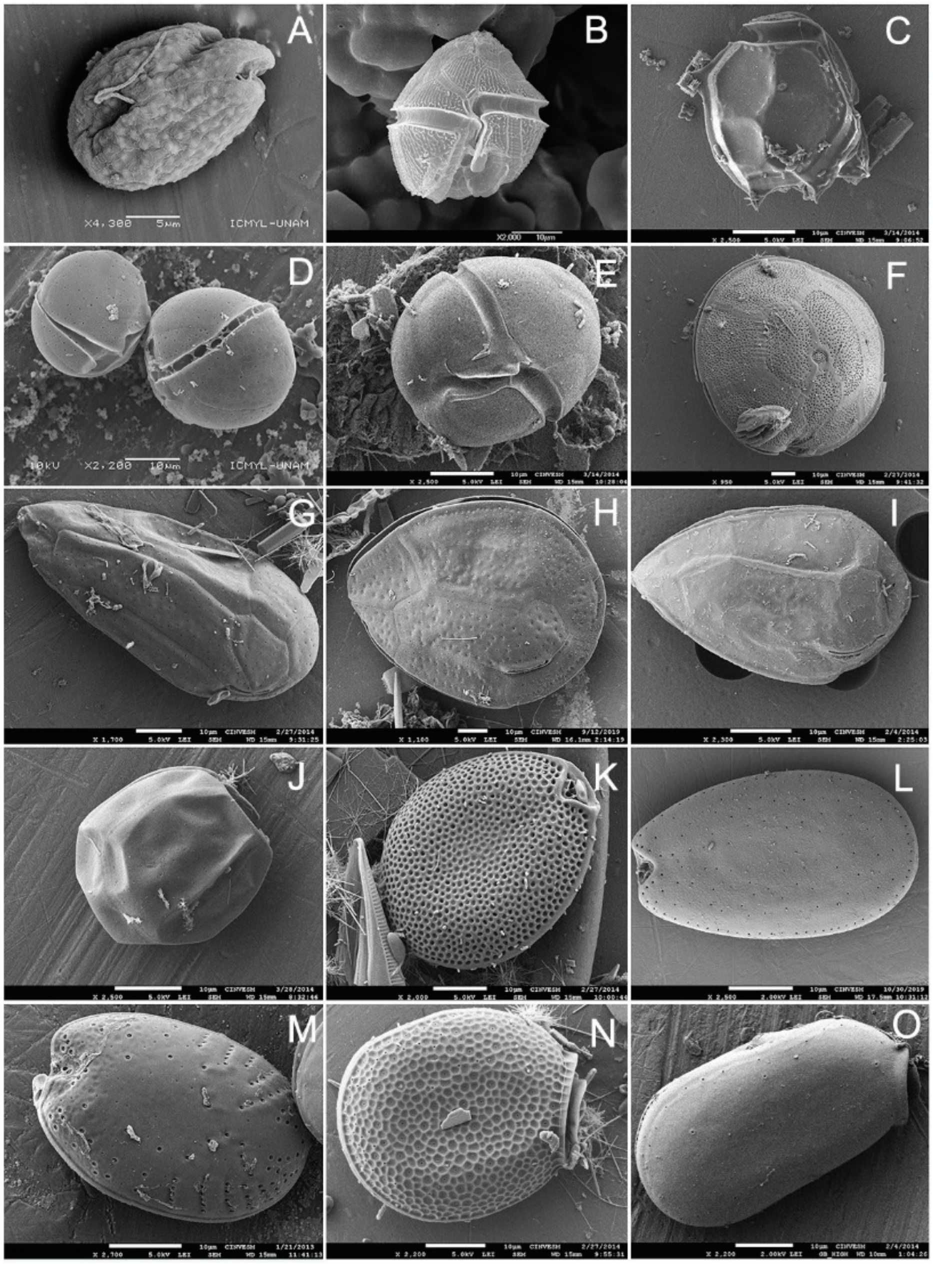

Figure 2. Marine benthic dinoflagellates from Mexican coastal waters: A – *Amphidinium theodorei* (Bahía de la Paz); B – *Bysmatrum caponii* (Veracruz Reef System (VRS), Veracruz); C – *Cabra* cf. *aremonica* (northern Yucatán); D – *Coolia malayensis* (Veracruz); E – *Durinskia* sp. (northern Yucatán); F – *Gambierdiscus caribaeus* (northern Yucatán); G – *Ostreopsis heptagona* (VRS, Veracruz); H – *Ostreopsis lenticularis* (Isla Pérez, Arrecife Alacranes); I – *Ostreopsis* cf. *ovata* (northern Yucatán); J – *Plagiodinium belizeanum* (northern Yucatán); K – *Prorocentrum hoffmannianum* (northern Yucatán); L – *Prorocentrum lima* (Isla Pérez, Arrecife Alacranes); M – *Prorocentrum rhathymum* (northern Yucatán); N – *Prorocentrum microcephala* (northern Yucatán); O – *Prorocentrum stenosoma* (northern Yucatán). Images A and D were taken with a JEOL JSM-6360LV SEM (ICMyL-UNAM); B was taken with a JEOL JCM-5310LV (Facultad de Ciencias – UNAM); C and E-O were taken with a JEOL JSM 7600F (CINVESTAV-IPN, Unidad Mérida). Scale bar: 5 µm in A, 10 µm in B-O.

Table 2. List of benthic marine dinoflagellate species found in Mexico (1942-2022). Abbreviations of Mexican states: BCS – Baja California Sur, Chis – Chiapas, Col – Colima, Gro – Guerrero, Mich – Michoacán, Nay – Nayarit, Oax – Oaxaca, QR – Quintana Roo, Sin – Sinaloa, Ver – Veracruz, Yuc – Yucatán.

Species	Mexican states	References
Amphidiniella sp.	BCS	Gárate-Lizárraga et al., 2019
Amphidiniopsis *hirsuta* (Balech) J. D. Dodge (= *Thecadinium hirsutum* Balech)	BCS	Gárate-Lizárraga et al., 2019
Amphidiniopsis sp.	Ver	Okolodkov et al., 2007
Amphidinium cf. *carterae* Hulburt (= *A. klebsii* Carter)	BCS, Ver, Yuc	Núñez-Vázquez, 2005; Okolodkov et al., 2007, 2014, 2016; Gárate-Lizárraga, 2012, 2020; Hernández-Castro, 2017; Aguilar-Trujillo et al., 2014, 2017; Almazán-Becerril et al., 2015; Martínez-Cruz et al., 2015 (*A. carterae*); Sepúlveda-Villarraga, 2017; Gárate-Lizárraga et al., 2019; Mejía-Camacho, 2020 (*A. carterae*)
A. klebsii Kof. et Swezy	BCS	Núñez-Vázquez, 2005
A. massartii Biecheler	BCS	Mejía-Camacho, 2020
A. operculatum Clap. et J. Lachm.	BCS, Ver	Núñez-Vázquez, 2005; Mejía-Camacho, 2020; Mejía-Camacho et al., 2021
A. theodorei Tomas et Karafas	BCS	Mejía-Camacho, 2020
A. thermaeum Dolapsakis et Economou-Amilli	BCS	Herrera-Herrera, 2022
Amphidinium sp.	Yuc, QR	Aguilar-Trujillo et al., 2014, 2017; Irola-Sansores et al., 2018; Herrera-Herrera, 2022
Ankistrodinium *semilunatum* (Herdman) Hoppenrath, Shauna Murray, Sparmann et Leander (= *Amphidinium semilunatum* Herdman)	BCS,	Gárate-Lizárraga et al., 2019
Blixaea *quinquecornis* (T. H. Abé) Gottschling (= *Peridinium quinquecorne* T. H. Abé; *P. quadridentatum* (F. Stein) Gert Hansen)	BCS, Ver	Gárate-Lizárraga et al., 2006 (as *P. quinquecorne*), 2016a, b (as *P. quadridentatum*); Gárate-Lizárraga & Muñetón-Gómez, 2008 (as *P. quinquecorne*); Okolodkov *et al.*, 2016 (as *P. quadridentatum*); Rodríguez-Gómez *et al.*, 2021 (as *P. quadridentatum*)
Bysmatrum *gregarium* (E. H. Lombard et B. Capon) T. Horiguchi et Hoppenrath *(= B. caponii* M. A. Faust et Steidinger, nom. illeg.)	Ver, Yuc	Okolodkov et al., 2007 (as *Bysmatrum* sp.), 2014, 2016; Aguilar-Trujillo et al., 2014, 2017; Martínez-Cruz *et al.*, 2015; Irola-Sansores et al., 2018 (as *Bysmatrum*)
B. granulosum Ten-Hage, Quod, Turque et Couté	QR	Almazán-Becerril et al., 2015
B. subsalsum (Ostenf.) M. A. Faust et Steidinger (= *Peridinium subsalsum* Ostenf.; *Scrippsiella subsalsa* (Ostenf.) Steidinger et Balech)	QR	Almazán-Becerril et al., 2015
Cabra cf. *aremonica* Chomérat, Couté et Nézan	Yuc	Aguilar-Trujillo et al., 2014, 2017; Okolodkov *et al.*, 2014; Martínez-Cruz *et al.*, 2015
C. matta Shauna Murray et Patterson	Col, Ver	Okolodkov et al., 2007; Aguilar-Trujillo *et al.*, 2017 (as *Cabra* cf. *matta*); Gárate-Lizárraga & González-Armas, 2017
Coolia *areolata* Ten-Hage, Turquet, Quod et Couté	QR	Almazán-Becerril et al., 2016b; Irola-Sansores et al., 2018
C. cf. *canariensis* S. Fraga	BCS	Morquecho *et al.*, 2022
C. malayensis Leaw, Lim et Usup	BCS	Hernández-Castro, 2017; Sepúlveda-Villarraga, 2017; Gárate-Lizárraga et al., 2019 (as *Coolia* cf. *malayensis*), Durán-Riveroll *et al.*, 2022; Herrera-Herrera, 2022; Morquecho *et al.*, 2022; Ramos-Santiago *et al.*, 2022
**C. monotis* Meunier	BCS, Ver, Yuc	Okolodkov & Gárate-Lizárraga, 2006; Okolodkov et al., 2007, 2014; Morquecho *et al.*, 2016; Almazán-Becerril et al., 2016b (as *C.* cf. *monotis*); Hernández-Castro, 2017; Gárate-Lizárraga et al., 2019 Morquecho et al., 2022
C. palmyrensis Karafas, Tomas et York	BCS	

Species	Mexican states	References
C. tropicalis M.A. Faust	BCS, QR	Almazán-Becerril et al., 2015 (as *C.* cf. *tropicalis*); Morquecho *et al.*, 2022
Coolia sp.	Yuc, QR	Gárate-Lizárraga *et al.*, 2016a; Martínez-Cruz *et al.*, 2015; Aguilar-Trujillo *et al.*, 2017; Irola-Sansores et al., 2018
Durinskia *capensis* Pienaar, H. Sakai et T. Horiguchi	BCS, Yuc	Martínez-Cruz *et al.*, 2015; Okolodkov *et al.*, 2016; Gárate-Lizárraga et al., 2019
Fukuyoa *yasumotoi* (M. J. Holmes) F. Gómez, D. X. Qiu, R. M. Lopes et Senjie Lin (= *Gambierdiscus yasumotoi* M. J. Holmes)	Ver	Hernández-Becerril & Almazán-Becerril, 2004 (as *G. yasumotoi*); Okolodkov et al., 2007 (as (?)*G. yasumotoi*)
Gambierdiscus *belizeanus* M. A. Faust	QR	Hernández-Becerril & Almazán-Becerril, 2004
G. caribaeus Vandersea, Litaker, M. A. Faust, Kibler, Holland et Tester	Yuc, QR	Litaker et al., 2010; Aguilar-Trujillo et al., 2014, 2017; Okolodkov *et al.*, 2014
G. carolinianus Litaker, Vandersea, M. A. Faust, Kibler, Holland et Tester	QR	Litaker et al., 2010; Almazán-Becerril et al., 2015 (as *G.* cf. *carolinianus*); Núñez-Vázquez et al., 2019
G. carpenteri Kibler, Litaker, M. A. Faust, Holland, Vandersea et Tester	QR	Litaker et al., 2010
G. excentricus S. Fraga	BCS	Gárate-Lizárraga et al., 2019
G. toxicus Adachi et Fukuyo	BCS, Nay, Col, Ver, Yuc, QR	*Hernández-Becerril & Almazán-Becerril, 2004; Okolodkov & Gárate-Lizárraga, 2006; Okolodkov et al., 2007 (as *G.* cf. *toxicus*), 2009; Cortés-Altamirano, 2012; Gárate-Lizárraga, 2013; Gárate-Lizárraga *et al.*, 2007, 2019
Gambierdiscus spp.	BCS, QR	Okolodkov & Gárate-Lizárraga, 2006; Gárate-Lizárraga *et al.*, 2016a; Irola-Sansores et al., 2018
Gymnodinium *venator* Flø Jørgensen et Shauna Murray	BCS	Gárate-Lizárraga et al., 2019
Ostreopsis cf. *belizeana* M.A. Faust	QR	Almazán-Becerril et al., 2016b (as O. cf. *belizeanus*)
O. heptagona Norris, Bomber et Balech	QR, Ver, Yuc	Okolodkov et al., 2007, 2014, 2016; Aguilar-Trujillo et al., 2014, 2017; Almazán-Becerril et al., 2015, 2016b; Irola-Sansores et al., 2018; Méndez-Torres, 2019; Núñez-Vázquez et al., 2019
O. lenticularis Fukuyo	BCS, Col, QR	Okolodkov & Gárate-Lizárraga, 2006; Gárate-Lizárraga *et al.*, 2018, 2019; Sepúlveda-Villarraga, 2017 (*O.* cf. *lenticularis*); Méndez-Torres, 2019
O. cf. *marina* M. A. Faust	QR	Almazán-Becerril *et al.*, 2016b (as *O. marinus*); Irola-Sansores et al., 2018
O. cf. *ovata* Fukuyo	BCS, Gro	Núñez-Vázquez, 2005; Cortés-Altamirano *et al.*, 2011 (*O. ovata*); Morquecho-Escamilla *et al.*, 2016; Gallegos-Mendiola *et al.*, 2017
O. siamensis Schmidt	Nay, QR	Cortés-Lara *et al.*, 2005; Esqueda-Lara & Hernández-Becerril, 2010; Cortés-Altamirano *et al.*, 2011; Almazán-Becerril et al., 2015, 2016; Méndez-Torres, 2019 (as *O.* cf. *siamensis*); Núñez-Vázquez et al., 2019
Ostreopsis sp.		Núñez-Vázquez, 2005
(?)**Pileidinium sp.	Yuc	Okolodkov *et al.*, 2014
Plagiodinium *belizeanum* M. A. Faust et Balech	Yuc, QR	Okolodkov & Gárate-Lizárraga, 2006; Aguilar-Trujillo et al., 2014, 2017; Okolodkov *et al.*, 2014; Almazán-Becerril et al., 2015
Prorocentrum *arenarium* M. A. Faust	QR	Almazán-Becerril et al., 2015
P. caribbaeum M. A. Faust	BCS, QR	Almazán-Becerril et al., 2015; Gárate-Lizárraga et al., 2019
P. concavum Fukuyo	Chis, Ver, Yuc	Núñez-Vázquez, 2005; Okolodkov et al., 2007, 2014; Gárate-Lizárraga & Muñetón-Gómez, 2008; Aguilar-Trujillo *et al.*, 2014 (as *P.* cf. *concavum*), 2017 (as *P.* cf. *concavum*); Almazán-Becerril et al., 2015; Maciel-Baltazar, 2015; Martínez-Cruz *et al.*, 2015; Morquecho-Escamilla *et al.*, 2016; Gárate-Lizárraga et al., 2019

Species	Mexican states	References
P. emarginatum Fukuyo	BCS, QR	Núñez-Vázquez, 2005; Almazán-Becerril et al., 2015; Muciño-Márquez et al., 2015; Irola-Sansores et al., 2018; Gárate-Lizárraga et al., 2019
P. foraminosum M. A. Faust	Yuc	Aguilar-Trujillo *et al.*, 2014 (as *P.* cf. *foraminosum*), 2017 (as *P.* cf. *foraminosum*); Okolodkov *et al.*, 2014; Martínez-Cruz *et al.*, 2015
P. fukuyoi Shauna Murray et Nagahama	QR	Almazán-Becerril et al., 2015
P. hoffmannianum M. A. Faust (= *P. belizeanum* M. A. Faust)	BCS, Chis, Yuc, QR	Okolodkov & Gárate-Lizárraga, 2006; Gárate-Lizárraga et al., 2007 (as *P. belizeanum*); Aguilar-Trujillo et al., 2014, 2017 (also as *P.* cf. *belizeanum*); Okolodkov *et al.*, 2014, 2017; Almazán-Becerril et al., 2015 (also as *P. belizeanum*); Maciel-Baltazar, 2015 (as *P. belizeanum*); Martínez-Cruz et al., 2015; Morquecho-Escamilla et al., 2016; Irola-Sansores et al., 2018 (also as *P. belizeanum*); Núñez-Vázquez et al., 2019; Gárate-Lizárraga et al., 2019; Cembella et al., 2021 (as *Prorocentrum hoffmannianum* species complex)
P. cf. *leve* M. A. Faust, Kibler, Vandersea, Tester et Litaker	QR	Irola-Sansores et al., 2018 (as *P.* cf. *levis*)
P. lima (Ehrenb.) F. Stein (= *Cryptomonas lima* Ehrenb.)	BCS, Ver, Yuc, QR	Heredia-Tapia *et al.*, 2002; Gárate-Lizárraga et al., 2007, 2019; Okolodkov et al., 2007, 2014; Gárate-Lizárraga & Muñetón-Gómez, 2008; Aguilar-Trujillo et al., 2014, 2017; Almazán-Becerril et al., 2015; Muciño-Márquez et al., 2015; Okolodkov *et al.*, 2016; Martínez-Cruz *et al.*, 2015; Irola-Sansores et al., 2018; Gárate-Lizárraga et al., 2019; Tarazona-Janampa *et al.*, 2020; Cembella et al., 2021 (as *Prorocentrum lima* species complex)
P. maculosum M. A. Faust	QR	Almazán-Becerril et al., 2015; Morquecho-Escamilla et al., 2016
P. panamense D. Grzebyk, Y. Sako et B. Berland	Col	Gárate-Lizárraga & González-Armas, 2017
P. rhathymum A.R. Loebl., Sherley et R.J. Schmidt	BCS, Oax, Chis, Yuc, QR	Osorio-Tafall, 1942 (as *P. mexicanum*); Gárate-Lizárraga & Martínez-López 1997; Cortés-Altamirano & Sierra-Beltrán, 2003; Gárate-Lizárraga & Muñetón-Gómez, 2008; Herrera-Sepúlveda *et al.*, 2013; Aguilar-Trujillo et al., 2014, 2017; Okolodkov *et al.*, 2014; Almazán-Becerril et al., 2015; Maciel-Baltazar, 2015; Martínez-Cruz *et al.*, 2015; Muciño-Márquez et al., 2015; Irola-Sansores et al., 2018; Sepúlveda-Villarraga, 2017 (as *P.* cf. *rhathymum*); Cembella *et al.*, 2021; Hernández-Becerril *et al.*, 2021 (as *P. mexicanum*)
P. sculptile M.A. Faust	Yuc	Aguilar-Trujillo et al., 2014, 2017; Okolodkov et al., 2014; Martínez-Cruz *et al.*, 2015; Morquecho-Escamilla et al., 2016
P. cf. *sipadanensis* Mohammad-Noor, Daugbjerg et Moestrup	Yuc	Aguilar-Trujillo et al., 2014, 2017; Okolodkov et al., 2014; Martínez-Cruz *et al.*, 2015
Sinophysis *canaliculata* Quod, Ten-Hage, Turquet, Mascarell et Couté	BCS, Col, Oax, QR	Okolodkov & Gárate-Lizárraga, 2006; Almazán-Becerril et al., 2015; Gárate-Lizárraga & González-Armas, 2017; Gárate-Lizárraga-Lizárraga *et al.*, 2019; Okolodkov (pers. obs.)
S. ebriola (Herdman) Balech	Ver, Yuc	Okolodkov et al., 2007, 2014, 2016; Aguilar-Trujillo *et al.*, 2017; Martínez-Cruz *et al.*, 2015
S. microcephala Nie et Wang	Ver, Yuc	Okolodkov et al., 2007, 2014; Aguilar-Trujillo et al., 2014, 2017; Almazán-Becerril et al., 2015; Martínez-Cruz *et al.*, 2015
S. stenosoma Hoppenrath	Ver, Yuc	Okolodkov et al., 2007, 2014, 2016; Martínez-Cruz *et al.*, 2015; Aguilar-Trujillo *et al.*, 2017
S. cf. *vespertilio* Chomérat	BCS	Gárate-Lizárraga et al., 2019
Sinophysis sp.	Yuc	Aguilar-Trujillo et al., 2014, 2017; Irola-Sansores et al., 2018 (as *Sinophysis*)
Thecadinium sp.	BCS	Gárate-Lizárraga, 2012
(?)*Togula*** sp.	Yuc	Okolodkov et al., 2014; Martínez-Cruz *et al.*, 2015; Aguilar-Trujillo *et al.*, 2017
Vulcanodinium *rugosum* Nézan et Chomérat	BCS, Mich	Hernández-Becerril *et al.*, 2013; Morquecho-Escamilla (pers. comm.)

* - misidentification; ** - tentative identification.

The first sequence data for genus *Amphidinium* from Mexico was provided from the study to determine the toxigenicity and cytotoxic effects of *A. operculatum* in culture (Mejía-Camacho *et al.,* 2021). The identification of *Amphidinium* strain AA60 as *A. operculatum* was confirmed by SEM and sequencing of the LSU and ITS regions of rDNA. Comparative sequences of *A. massartii*, *A. carterae* and *A. operculatum* from Mexico are also available in the GenBank database (https://www.ncbi.nlm.nih.gov/nucleotide/; Table 3).

A study on phylogeography and diversity of the *Prorocentrum lima* and *P. hoffmannianum* species complexes, including *P. mexicanum/P. rhathymum*, was published by Cembella *et al.* (2021). In this work, 69 strains were identified to species, based on morphology and selected sequences that included the LSU, SSU and ITS regions of rDNA, with complementary base-pair analysis of secondary structures. These sequences are available in GenBank, and details of the taxonomic and phylogenetic analysis are provided in the Supplementary materials of the paper (Cembella *et al.*, 2021).

As of November 2022, 702 DNA/RNA gene sequences of dinoflagellates from Mexico are archived in GenBank. Only about 10% correspond to epibenthic dinoflagellates, including 68 sequences of LSU, SSU and ITS regions of rDNA, and one sequence of cytochrome b. As shown in Table 3, with GenBank accession numbers when available, most benthic dinoflagellate gene sequences (42) belong to *Prorocentrum,* and of these the majority (29) correspond to *P. lima.* Other benthic genera are less well represented - 4 sequences belong to *Amphidinium*, whereas 24 correspond to *Coolia.*

Benthic phycotoxin vectors and toxigenicity. Most studies on benthic dinoflagellates in Mexico have been directed towards species known or suspected to be responsible for BHABs on a global scale and which are common in Latin America (Durán-Riveroll *et al.*, 2019a). Phycotoxins have drawn attention worldwide because of their adverse effects on public health, marine faunal mortalities and economic losses. Toxic events occur through the accumulation of phycotoxins in seafood species via direct or indirect consumption of toxigenic microalgae (mainly dinoflagellates). Within vector species, phycotoxins are often bio-converted into more potent compounds and thereby transferred to higher trophic levels (Núñez-Vázquez *et al.*, 2019). Phycotoxin transfer through the food web to seafood consumed by humans is responsible for many cases of seafood poisoning, such as CFP linked to benthic dinoflagellates around the globe in tropical and subtropical regions (FAO, 2004).

For Mexico in particular, the paucity of reports of BHABs does not necessarily signify the absence of confirmed poisoning incidents or respiratory distress caused by such blooms. Significant economic losses in aquaculture facilities have occurred due to HABs of dinoflagellates, particularly on the northern Pacific coasts (Alonso-Rodríguez & Páez-Osuna, 2003; Orellana-Cepeda *et al.*, 2004; Gárate-Lizárraga *et al.*, 2007).

Many studies have been conducted worldwide to determine which species act as the origin and vectors of phycotoxins in seafood for human food consumption (for references, see Deeds *et al.*, 2008). Mexican researchers have been mainly concerned with the effects of toxic dinoflagellates on diverse marine species in an effort to understand the physiological responses and toxin transfer mechanisms, especially in species of commercial interest. Confirmed links between particular BHAB species and toxic events associated with the etiology of toxic syndromes such as CFP are rare in Mexico.

There remains a substantial gap in knowledge on the toxigenicity of benthic dinoflagellates from Mexico, including which species produce toxins that impact human health and whether or not toxigenicity is limited to particular genetic strains or geographical populations of the species or is conditional upon prevailing environmental or substrate habitat types. Benthic dinoflagellates reported from Mexico include numerous species known to synthesize a wide array of phycotoxins and structurally related natural bioactive compounds. In most cases, such as the confirmation of CTX3C-bioactivity in *Gambierdiscus caribaeus* Vandersea, Litaker, M. A. Faust, Kibler, Holland et Tester from Cancún, Mexico (Litaker *et al.*, 2017), the potent ciguatoxic response in the mouse neuroreceptor-binding assay CBA-N2a has not been accompanied by chemical structural analysis. Structural confirmation of toxin composition among clonal isolates of most toxigenic benthic dinoflagellate species is usually unavailable or remains unpublished to date (Table 4). There is even less information on the chemodiversity of natural benthic populations in Mexico.

Toxigenic BHAB species commonly co-occur and occasionally in high cell abundance in natural epibenthic dinoflagellate assemblages. In Mexican coastal waters, these assemblages most commonly include *Amphidinium*, *Coolia*, *Fukuyoa, Gambierdiscus*, and *Prorocentrum* species. It has been previously assumed that these species may collectively and synergistically contribute to the CFP syndrome (Wu *et al.*, 2020). In most CFP cases in Mexico, there are circumstantial inferences towards *Gambierdiscus/Fukuyoa* based on what is known about the global toxigenicity of BHAB species and the etiology of toxin syndromes from other regions, but the culprit species are rarely determined.

Knowledge of the toxigenicity of benthic dinoflagellate species in Mexico is scarce, and research has begun only within the last few years (Durán-Riveroll *et al.*, 2019a). Lately, some studies related to toxigenicity and toxicity of benthic dinoflagellates from the Mexican coasts have been presented at local or national conferences (*e.g.*, SOMEFAN, October 2022). Other studies have been published but remain as gray literature, primarily as conference abstracts (*e.g.*, ICHA, 2021), brief proceedings (*e.g.*, Band-Schmidt & Rodríguez-Gómez, 2022), and summaries, or are archived only in graduate theses within academic libraries and are not easily accessible.

Members of the genera *Gambierdiscus* and *Fukuyoa* are known producers of large polyether ciguatoxins (CTX) and maitotoxins (MTX) associated with CFP, particularly in tropical and subtropical ecosystems of the continental shelf, islands and archipelagos of the Pacific Ocean, eastern Atlantic margins and the Greater Caribbean (Fleming *et al.*, 1998; FAO, 2004; Loeffler *et al.*, 2021). Species of these genera are commonly reported in Mexico (Table 2), mainly from the Caribbean Sea, but knowledge of their specific toxigenicity is generally lacking (note general absence from Table 4).

According to Almazán-Becerril *et al.* (2021), from 1997 to 2017, at least 28 CFP events were registered, with 262 cases mainly in Cozumel and Isla Mujeres, Quintana Roo. To avoid these poisoning incidents, the consumption of potentially ciguateric fish, such as barracuda (*Sphyraena barracuda* Edwards), has been banned in the Mexican Caribbean area. Recently, ciguatoxicity has been also detected in waters of the states of Campeche, Yucatán and Quintana Roo along the coast of the Yucatán Peninsula (Barón-Campis *et al.*, 2014; Ley-Martínez *et al.*, 2014; Ley-Martínez, 2016, 2018; Poot-Delgado *et al.*, 2022). Carnivorous fish from the families Carangidae, Carcharhinidae, Centropomidae, Haemulidae, Labridae, Lutjanidae, Sciaenidae, Scorpaenidae, Serranidae, Sphyraenidae and Sphyrnidae were studied; ciguatoxicity was reported for Campeche for the first time (Ley-Martínez, 2018).

Table 3. Strains of dinoflagellates species from Mexican waters and their gene sequence accession numbers available in the GenBank database (https://www.ncbi.nlm.nih.gov/nucleotide/). Abbreviations of Mexican states: BCS – Baja California Sur, Camp – Campeche, Gro – Guerrero, Mich – Michoacán, QR – Quintana Roo, Ver – Veracruz.

Species	Strain	Locality	Coordinates	LSU	SSU	LSU D7	SSU/ITS/LSU	Cyt b	ITS1/5.8S /ITS2	Authors
***Amphidinium** carterae*	AA105	Ver	19°11'56.02"N, 96°04'5.00"W	MT325892						Duran-Riveroll, pers. comm.
A. massartii	AA112	Camp		MT325893						
A. operculatum	AA60	Ver	19°11’54”N, 96º4’0.7"W	MT325891						
A. theodorei	AA38	BCS	24°19’23.89”N, 110°19’44.45”W	MT325890						
***Coolia** malayensis*	CMBAPAZ-1	BCS	24°31’00”N, 110°64’00”W	OM177218						Ramos-Santiago *et al.*, 2022
	S/i72	BCS	24°31’00”N, 110°64’00”W	OM177219						
	CAPV-1	BCS	24°19’08”N, 110°19’16”W	MW865385						Morquecho *et al.,* 2022
	CAPV-2	BCS	24°19’24”N, 110°19’44”W	MW865386					ON943078	
	CAPV-3	BCS	24°08’25”N, 110°21’08”W	MW865387						
	CAPV-4	BCS	24°08’25”N, 110°21’08”W	MW865388						
	CAPV-5	BCS	24°08’25”N, 110°21’08”W	MW865389					ON943079	
	CAJV-1	BCS	24°52’31”N, 110°33’27”W	MW865390					ON943077	
	CAJV-2	BCS	24°52’31”N, 110°33’27”W	MW865391						
	CAJV-3	BCS	24°52’31”N, 110°33’27”W	MW865392						
C. palmyrensis	CLJV-1	BCS	24°52’31”N, 110°33’27”W	MW865393					ON943084	
C. tropicalis	CLJV-2	BCS	24°52’31”N, 110°33’27”W	MW865396					ON943085	
C. cf. *canariensis*	CMPV-1	BCS	24°17’12”N, 110°20’31”W						ON943083	
	CCJV-1	BCS	24°52’31”N, 110°33’27”W	MW865382					ON943080	
	CCJV-2	BCS	24°52’31”N, 110°33’27”W	MW865383					ON943081	
	CCJV-3	BCS	24°52’31”N, 110°33’27”W	MW865384					ON943082	
***Prorocentrum** hoffmannianum*	PA85	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308610			Cembella *et al.* 2021
	PA89	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308612			
	PA91	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308614			
	PA71	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310162			
P. lima	PL6	BCS		JQ616836			JQ616837	KJ410755	JQ616837	Herrera-Sepúlveda *et al.*, 2013 cited Cembella *et al.*, 2021
	PRL1	BCS	23°35’N, 110º49.6’W	EF517252	EF517266					Cohen-Fernández *et al.*, 2010
	PA61	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308608			Cembella *et al.,* 2021

Species	Strain	Loca-lity	Coordinates	LSU	SSU	LSU D7	SSU/ITS/LSU	Cyt b	ITS1/5.8S/ITS2	Authors
	PA97	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310171			
	PA95	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310170			
	PA84	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310169			
	PA83	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310168			
	PA82	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310167			
	PA80	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310166			
	PA8	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310165			
	PA78	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310164			
	PA77	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310163			
	PA66	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310161			
	PA63	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310160			
	PA62	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310159			
	PA72	Ver	19°11’54.10”N, 96°4’0.7”W				MZ310158			
	PA49	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308617			
	PA72	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308616			
	PA94	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308615			
	PA49	BCS	24°09’30.00”N, 110°19’12.1”W				MZ310157			
	PA46	BCS	24°09’30.00”N, 110°19’12.1”W				MZ310156			
	PA17	BCS	24°09’30.00”N, 110°19’12.1”W				MZ310155			
	PA90	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308613			
	PA86	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308611			
	PA48	BCS	24°09’30.00”N, 110°19’12.1”W				MZ308607			
	PA104	Ver	19°11’54.10”N, 96°4’0.7”W				MZ308606			
P. mexicanum	24A	Gro	16°48’58”N, 99°53’59”W	EF517259	EF517271					Cohen-Fernández *et al.*, 2010
	31L	Mich	17°56’17”N, 102°11’6”W		EF517272					
	91L	Mich	17°56’17”N, 102°11’6”W	EF517258	EF517273					
	PCMX	BCS		EF517260	EF517275					
P. rhathymum	PXPV-1	BCS		JQ616822		JQ616832				Herrera-Sepúlveda *et al.*, 2013
	PA20	QR	20°50’48.55”N, 86°52’30.53”W							Cembella *et al.*, 2021

Núñez-Vázquez *et al*. (2019) reported a study on commercial carnivorous fish from Campeche in the southern Gulf of Mexico, including seven fish species: barracuda (*S. barracuda*)*,* crevalle jack (*Caranx hippos* (L.)*,* hogfish (*Lachnolaimus maximus* (Walbaum)*,* bonnethead (*Sphyrna tiburo* (L.)*,* common snook (*Centropomus undecimalis* (Bloch)*,* lane snapper (*Lutjanus synagris* (L.) and the scrawled cowfish (*Acanthostracion quadricornis* (L.). The mouse bioassay (MBA) for lipophilic toxins, the official method in Mexico for ciguatoxicity, the brine shrimp *Artemia* (Crustacea: Anostraca: Artemiidae) bioassay, and the neuroreceptor binding assay (RBA) have all been applied in Mexico to determine ciguatoxicity, which was detected in 13 of 23 fish samples tested by MBA and RBA. The Mexican regulatory limit for CTX-related toxicity is 2.5 MU (mouse units) 100 g^{-1} of tissue (Norma Oficial Mexicana NOM-242-SSA1-2009; DOF, 2009). This first report of ciguatoxicity in Campeche (Núñez-Vázquez *et al*., 2019) yielded more than 10 MU 100 g^{-1}, primarily from samples of fish viscera.

The lionfish *Pterois volitans* (L.) is an invasive species posing an ecological problem in the Caribbean and the Gulf of Mexico. Official management programs have included sponsored eradication, fishing tournaments, and gastronomic exhibitions to encourage fishing and consumption. However, lionfish have been proven to be a CTX-retaining species. Ley-Martínez (2016) reported CTX in lionfish for the first time in Mexican waters, specifically in the Mexican Caribbean. Almazán-Becerril *et al.* (2021) analyzed lionfish and barracuda from Isla Contoy, Puerto Morelos and Isla Cozumel, in the north of Quintana Roo (Fig. 1). They found 68% of the lionfish positive for ciguatoxicity in muscle tissue, with >50% of the lionfish and 57% of the barracuda containing sublethal ciguatoxicity levels. There was an apparent latitudinal gradient for the ciguatoxicity levels, with more positive samples from the north (Isla Contoy).

Data on CFP events are considered underestimated in Mexico, partly because of the reluctance or inability of victims to report them (Dickey & Plakas, 2010). In many cases, the CFP victims do not report to medical services. True CFP cases are often mistaken as common “food poisoning” from bacterial causes and mistreated with antibiotics (McKee *et al*., 2001). Furthermore, a large proportion of the putative CFP cases reported in Almazán-Becerril *et al.* (2021) were from among national and international tourists, for whom follow-up diagnoses, treatment, and medical reports cannot be confirmed.

Several *Coolia* species produce bioactive polyether metabolites (Holmes *et al*., 1995; Rhodes *et al*., 2010; Karafas *et al*., 2015), but putative cooliatoxins have not been fully structurally characterized (Junqueira de Azevedo Tibiriçá *et al*., 2020). Some of the proposed “cooliatoxins” have proven to be toxic to mice, human cell lines *in vitro*, and some crustaceans, such as *Artemia* Leach (Rhodes *et al*., 2010; Karafas *et al*., 2015; Leung *et al.,* 2017), but toxicity has been registered only for a few strains of *Coolia*. Several authors have reported that *C. malayensis*, *C. palmyrensis, C. santacroce* and *C. tropicalis* M. A. Faust strains may also produce yessotoxin (YTX) analogs, whereas other strains of the same species were found to be non-toxic (Wakeman *et al*., 2015; Phua *et al*., 2021). *Coolia* species occur occasionally in high cell abundance in epibenthic dinoflagellate assemblages in Mexico, commonly together with potentially toxigenic members of *Gambierdiscus*, *Fukuyoa, Amphidinium* and *Prorocentrum.* Still, there are no confirmed reports of *Coolia* involved in BHAB events in Mexico. No information is available on their specific toxicity or toxin composition. However, there is one report on *C. malayensis* and *C. monotis* from Mexican coastal waters with proven toxicity against *Artemia salina* L. nauplii and against several cancer cell lines (García Santos Reyes, 2022).

Species of the genus *Ostreopsis* produce palytoxins (PLTXs), which are amongst the most potent non-peptide toxins (Ramos & Vasconcelos, 2010; Ajani *et al*., 2017). Accumulation of these toxins and their derivatives by fish and mollusks has been reported from *Ostreopsis* blooms in Europe (Munday, 2008). The species *O. ovata* Fukuyo is most widely known as responsible for causing respiratory distress from aerosol inhalation during blooms, particularly in the Mediterranean Sea and southern European waters (Ciminiello *et al*., 2006). In Mexico, a few reports on this species have been published (Cortés-Altamirano *et al*., 2011; Gallegos-Mendiola *et al*., 2017), but with little information on toxigenicity or human health risks. *Ostreopsis siamensis* has been found in the southern part of the Gulf of California (Cortés-Lara *et al*., 2005), and *O. heptagona* in the Veracruz Reef System in the southern Gulf of Mexico (Okolodkov *et al*., 2007), but neither toxicity nor human or marine fauna poisonings have been associated with the genus.

Members of the genus *Amphidinium* have been recognized as producers of bioactive compounds for more than three decades (Yasumoto *et al*., 1987). No toxic events have been definitively linked to *Amphidinium* blooms and their confirmed toxins to date in Mexico. This is in spite of the fact that *A. carterae* and *A. operculatum* occur frequently in Mexico, and both species are known to produce ichthyotoxic compounds (Kobayashi & Tsuda, 2004; Kobayashi & Kubota, 2007; Murray *et al*., 2015). *Amphidinium* blooms have been linked to rare fish kills globally, and at least four species (*A. carterae, A. gibossum, A. massartii,* and *A. operculatum*) have been reported as ichthyotoxic (Murray *et al*., 2012, 2015; Pagliara & Caroppo, 2012). Ichthyotoxicity of *Amphidinium* species is likely due to the production of amphidinols (AM) (Wellkamp *et al*., 2020), hairpin-shaped polyketides forming different subgroups with the same core unit. Preliminary analysis of a few *Amphidinium* isolates from Mexico - three isolates from Baja California Sur (AA39, AA40) and the Veracruz Reef System (AA60), did not detect any AM derivatives by advanced mass spectrometry techniques (Wellkamp *et al*., 2020). A more comprehensive recent survey of multiple isolates from the Gulf of California (La Paz, Baja California Sur), Gulf of Mexico (Veracruz Reef System, Veracruz and Laguna de Términos, Campeche), southern Mexican Pacific (Isla de La Roqueta, Acapulco, Guerrero), and the northern Mexican Pacific (San Quintín, Baja California) from *A. eilatiensis* J. J. Lee*, A. massartii, A. operculatum,* and *A. theodorei* revealed a high diversity of AM analogs. These AM derivatives include the known AM02, 04, 05, 06, 07, 09, 11, 14, 15, and 17, as well as four recently described by Wellkamp *et al.* (2020), and three new variants. This study showed that the *A. eilatiensis* strains from the northern Pacific coast of Mexico produced a higher diversity of AMs and total quantities per cell than any previously analyzed strains (Durán-Riveroll, pers. comm.). The non-AM-producing *Amphidinium* isolates (AA39, AA40, and AA60) have shown significant cytotoxic activities against cancer cell lines (Mejía-Camacho, 2020; Mejía-Camacho *et al*., 2021), meaning that this bioactivity could be expressed by unknown metabolites other than AMs.

On a global scale, species of *Prorocentrum* are widely known as the proximal source of polyketide toxins associated with DSP, primarily okadaic acid (OA) and various related dinophysistoxin (DTX) derivatives (Durán-Riveroll *et al*., 2019a). Collectively, these are referred to as diarrhetic shellfish toxins (DSTs), although the potency and relative toxicity of many of these analogs have not been confirmed. *Prorocentrum* species that produce DSTs are almost exclusively (epi)benthic forms, but they can occasionally be found as members of the tychoplankton via spontaneous detachment or through disturbance of their benthic habitat, *e.g.*, by winds, currents, and other mechanical agitation. In fact, there are no confirmed cases of any truly planktonic *Prorocentrum* known to produce DSTs.

Epibenthic *Prorocentrum* are common throughout the tropical and subtropical coastal waters of Latin America (Durán-Riveroll *et al*., 2019a), but toxigenicity has only been confirmed for a few populations from cultured isolates from Mexico (Cembella *et al*., 2021). *Prorocentrum lima* from Isla El Pardito, Baja California Sur, was suspected as a possible cause of poisoning of five local fishermen after consumption of the liver of the Colorado snapper (*Lutjanus colorado* Jordan et Gilbert (Eupercaria: Lutjanidae) and the sawtail grouper (*Mycteroperca prionura* Rosenblatt et Zahuranec (Perciformes: Serranidae). Indeed, a cultured *P. lima* isolate from this event was found to produce DSTs and was toxigenic in bioassays (Heredia-Tapia *et al.,* 2002). The symptoms of the poisoned fisherman, however, were more similar to those of CFP, lasted a few days, and involved diarrhea, numbness, vomiting, weakness, pruritus, desquamation, hyperesthesia, lip and tongue paralyses, and in one case, convulsions – not classic symptoms of DSP. Benthic species other than *P. lima* were likely involved in this event because *Prorocentrum* species are not known to produce CTXs. No further effort has been made to isolate epibenthic dinoflagellates from this site to confirm a relationship to fish poisoning events.

DST toxigenicity among epibenthic *Prorocentrum* species has been intensively investigated among multiple cultured isolates from various locations in Mexico, including the Gulf of California, the Caribbean Sea and the Gulf of Mexico (Tarazona-Janampa *et al.,* 2020; Cembella *et al*., 2021). The application of advanced liquid chromatography coupled with tandem mass spectrometry (LC-MS/MS) (Krock *et al*., 2008; Nielsen *et al*., 2013) permitted the resolution of the DST compositional profile and cell quota of 67 isolates from Mexico – the largest chemodiversity analysis of polyketide-derived toxins from a benthic dinoflagellate genus (Cembella *et al*., 2021). All *P. lima* and *P. hoffmannianum* (except one) isolates were toxigenic, but the total cell DST content was not apparently well linked at the species level. The species complexes defined by morphological and molecular criteria to separate *P. lima* from *P. hoffmannianum sensu lato* could be distinguished by the relative composition of some analogs (OA, OA-D8, DTX1, DTX1a and DTX1a-D8), including two new undescribed DTX isomers. In any case, toxin composition exhibited no clear associations with substrate type or geographical origin, in spite of some clear affiliations within geographical populations.

Toxicity and species interactions. The functional role and allelochemical effects of BHAB species in chemical defense responses and competitive species interactions are still poorly understood.

There are a few experimental studies on strains of epibenthic dinoflagellates from Mexico. Most have focused on *Prorocentrum* that may be associated with the production of DSTs, and hence pose a potential (but unconfirmed) risk of DSP from shellfish consumption (Table 5). In fact, the first known culture of a benthic dinoflagellate from Mexican coastal waters was a strain of *P. lima* established from Isla El Pardito, Baja California Sur, after the poisoning of five local fishermen by consumption of fish liver from the area.

After the isolation of the aforementioned first strain of *P. lima*, many studies have been conducted to determine toxic responses of exposure in several vertebrate and invertebrate species. Heredia-Tapia *et al.* (2002) confirmed the toxicity and toxigenicity of *P. lima* by bioassays with adults of the brine shrimp *Artemia franciscana* Kellogg and by MBA of lipophilic toxins of lipophilic toxins. When exposed to a *P. lima* cell density of 2 x 10^3 cells mL^{-1}, the crustaceans died within 2 h. The MBA showed typical symptoms for DSP toxins in mice (diarrhea, hind limb paralysis, dyspnea, respiratory failure), followed by death after 1 h after i.p. administration of a more concentrated cell extract (3.35 x 10^4 cells mL^{-1}). The possible occurrence of DSTs in the cell extract was indicated by thin-layer chromatography (TLC), and the presence of OA and DTX1 were later confirmed by LC-MS.

Antioxidant enzymes have been used to evaluate oxidative stress induced by toxic microalgae in crustaceans and bivalve mollusks (Oyaneder-Terrazas *et al*., 2022; Tchivelekete *et al*., 2022). Campa-Córdova *et al.* (2009) compared the changes in superoxide dismutase (SOD) activity in the hepatopancreas and muscle of juveniles of the white leg shrimp, *Litopenaeus vannamei* (Boone) (Crustacea: Decapoda: Penaeidae) and in the giant lion-paw scallop, *Nodipecten subnodosus* G. B. Sowerby I (Bivalvia: Ostreoida: Pectinidae), after exposure to different cell densities of *P. lima*. The results indicated the activation of antioxidant defenses, especially in the hepatopancreas, with higher levels of SOD in shrimp than in scallops. A cell concentrate of 500 cells mL^{-1} of *P. lima* was enough to trigger SOD activity in both species, indicating that oxidative stress is induced by application of *P. lima* extracts, but the specific toxin content is unknown.

The Pacific oyster, *Magallana gigas* (Thunberg) (= *Crassostrea gigas* (Thunberg) (Bivalvia: Ostreoida: Ostreidae), a species of high commercial interest in Mexico, was introduced from Japan in 1973 (Arizpe, 1996). Since then, it has become distributed in many coastal areas of Mexico (Paniagua-Chávez & Acosta-Ruiz, 1995; Arizpe, 1996; Cáceres-Martínez *et al*., 1998, García-Rico *et al*., 2001). Among other suspension-feeding bivalves, this species is widely known to accumulate DSTs (Mafra *et al*., 2015; Karlson *et al*., 2021), although primarily from pelagic blooms of *Dinophysis* spp. Contamination of bivalve mollusks with DSTs occurs only rarely from epibenthic *Prorocentrum* (Lawrence *et al*., 2000; Gayoso *et al*., 2002). Romero-Geraldo & Hernández-Saavedra (2014) determined the effect of *P. lima* strain PRL-1 isolated from Isla El Pardito on stress response genes in *M. gigas*. Gene expression of glutamine synthetase (GS), glutathione S-transferase (GST), heat shock protein 70 (HSP70) and 90 (HSP90), Cu/Zn SOD and melanogenic peroxidase (POX) were assayed by semi-quantitative reverse-transcription polymerase chain reaction (RT-PCR). In general, an increased expression was observed at all *P. lima* cell densities tested, as a rapid response to exposure (from 0 to 3 h), whereas lower expression levels than the control were observed after 6 h exposure. The most noticeable differences in the expression levels of the analyzed genes were observed in juvenile oysters at 14 days of exposure, suggesting that the *P. lima* cell densities affect oyster metabolism irreversibly under sub-chronic exposure. Oysters are thus considered highly susceptible to the presence and persistence of BHABs of *P. lima*. The expression of the key genes involved in the first line of defense is significantly affected, making juvenile oysters vulnerable to the cumulative impact of multiple stressors (environmental, chemical, or biological). The authors (Romero-Geraldo & Hernández-Saavedra, 2014) conclude that this explains the mass mortalities observed in oyster farms, particularly in newly sown oyster seed of 3-5 mm length in the field.

Table 4. Benthic marine dinoflagellates found in Mexico and considered as BHAB species associated with toxigenicity and/or toxic syndromes (as acknowledged in the IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae (Lundholm *et al.*, 2009 onwards; https://www.marinespecies.org/hab) or known to cause other harmful events on a global basis. Known specific toxins and potentially harmful bioactive metabolites of uncertain toxicity and bioassay activity are included only when confirmed in benthic dinoflagellate species from Mexico (cited from Murray *et al.*, 2012; Hernández-Becerril *et al.*, 2013; Hoppenrath *et al.*, 2014; Litaker *et al.*, 2017; Cembella *et al.*, 2021; Mejía-Camacho *et al.*, 2021; Durán-Riveroll *et al.*, 2022). Toxin acronym codes: OA = okadaic acid; OA-D8 = okadaic acid diol-ester; DTX1: dinophysistoxin 1; DTX1-D8 = dinophysistoxin 1 diol-ester; DTX1a = undescribed isomer of DTX1; DTX1a-D8: undescribed isomer of DTX1a-D8; UNK = unknown, unpublished, or unconfirmed. Abbreviations of Mexican states: BCS – Baja California Sur, Chis – Chiapas, Col – Colima, Gro – Guerrero, Mich – Michoacán, Nay – Nayarit, Oax – Oaxaca, QR – Quintana Roo, Sin – Sinaloa, Ver – Veracruz, Yuc – Yucatán.

Species	Mexican states	Type of toxin/bioactive	Effect/syndrome	Specific toxins/ bioactives
Amphidinium Clap. et J. Lachm.		Polyketides: long chain (*e.g.*, amphidinols) and macrolides (*e.g.*, amphidinolides)	Cytotoxic, anti-mycotic, anti-cell proliferation, ichthyotoxic	
Amphidinium cf. *carterae*	BCS, Ver, Yuc			UNK
Amphidinium klebsii	BCS			UNK
A. massartii	BCS			UNK
A. operculatum	BCS, Ver			UNK
A. theodorei	BCS			UNK
A. thermaeum	BCS			UNK
Coolia Meunier		Polyketides: polyether "cooliatoxins" not structurally well characterized; some related to yessotoxins (YTX) and gambierone analogs	Cell extracts toxic to mice, by interperitoneal (i.p.) injection; human cell lines *in vitro*; and crustaceans (*e.g.*, brine shrimp) in bioassays	
Coolia areolata	QR			UNK
C. malayensis	BCS			UNK
**C. monotis*	BCS, Ver, Yuc			UNK
C. cf. *tropicalis*	QR			UNK
Coolia sp.	Yuc, QR			UNK
Fukuyoa Gómez, Qiu, Lopes et Lin		Polyketides: large cyclic ladder-frame polyethers – ciguatoxins (CTX) and maitotoxins (MTX), and gambierol analogs, gambierones and gambieric acid	Ciguatera fish poisoning (CFP); membrane depolarization of voltage-gated Na^+ channels cause symptoms	
Fukuyoa yasumotoi	Ver			UNK
Gambierdiscus Adachi et Fukuyo		Polyketides: large cyclic ladder-frame polyethers - CTX and MTX, and gambierol analogs, gambierones and gambieric acid	CFP; membrane depolarization of voltage-gated Na^+ channels cause symptoms	
Gambierdiscus belizeanus	QR			UNK
G. caribaeus	Yuc, QR			CTX3C-bioactivity in CBA-N2a assay

Species	Mexican states	Type of toxin/bioactive	Effect/syndrome	Specific toxins/ bioactives
G. carolinianus	QR			UNK
G. carpenteri	QR			UNK
G. excentricus	BCS			UNK
G. toxicus	BCS, Nay, Col, *Ver, *Yuc, *QR			CTX-1**
Gambierdiscus spp.	BCS, QR			UNK
Ostreopsis Schmidt		Polyketides: long-chain polyether palytoxins (PLTX) and ovatoxin analogs, ostreocins, ostreotoxins and mascarenotoxins	Na^+/K^+ ion channel disruptor; potent vasoconstrictor in mammals; respiratory distress in aerosol form; nonspecific human poisoning from ingestion of fish or crabs	
Ostreopsis cf. *belizeana*	QR			UNK
O. heptagona	QR, Ver, Yuc			UNK
O. lenticularis	BCS, Col, QR			UNK
O. cf. *marina*	QR			UNK
O. cf. *ovata*	BCS, Gro			UNK
O. siamensis	Nay, QR			UNK
Ostreopsis sp.				UNK
Prorocentrum Ehrenb.		Polyketides: linear-polyethers (*e.g.*, okadaic acid and dinophysistoxins); cyclic imine macrolides (*e.g.*, prorocentrolides, hoffmannniolide); borbotoxins and PLTX analogs	Diarrhetic shellfish poisoning (DSP), inhibitors of protein-phosphatase PP1A, PP2A; tumor-promotion; fast-acting toxicity (FAT) in mice i.p. injection of cyclic imine macrolides; PLTX-like effects on nicotinic acetylcholine receptors	
Prorocentrum arenarium	QR			UNK
P. caribbaeum	BCS, QR			UNK
P. concavum	Chis, Ver, Yuc			UNK
P. emarginatum	BCS, QR			UNK
P. foraminosum	Yuc			UNK
P. fukuyoi	QR			UNK
P. hoffmannianum	BCS, Chis, Yuc, QR			OA, OA-D8, DTX1, DTX1-D8, DTX1a,
P. cf. *leve*	QR			UNK

Species	Mexican states	Type of toxin/bioactive	Effect/syndrome	Specific toxins/ bioactives
	BCS, Ver, Yuc, QR			OA, OA-D8, DTX1, DTX1-D8, DTX1a, DTX1a-D8
P. maculosum	QR			UNK
P. panamense	Col			UNK
P. rhathymum	BCS, Oax, Chis, Yuc, QR			UNK
P. sculptile	Yuc			UNK
P. cf. *sipadanensis*	Yuc			UNK
Vulcanodinium Nézan et Chomérat		Polyketides: cyclic imines, *i.e.*, pinnatoxins (PnTx) and portimines		
Vulcanodinium rugosum	Mich, BCS		Contact dermatitis by swimming in blooms; fast-acting toxicity (FAT) in rodents i.p. injection; inductor of cell apoptosis; neurological effects in high i.p. and oral doses in mammals	UNK

* - misidentification; ** - tentative identification.

To further understand the acute and sub-chronic exposure effects of *P. lima* cells on *Magallana gigas* juveniles (3-5 mm)*,* Romero-Geraldo *et al.* (2014) followed the effects of *P. lima* on oysters by analyzing the expression levels of three genes involved in cell cycle regulation and one gene involved in the immune response. The analyses by PCR and real-time quantitative PCR (qPCR), detected changes in expression patterns with exposure time and *P. lima* cell concentration. The highest expression levels (fold above baseline) were found in oysters fed 3 x 10^3 cells mL^{-1} at 168 h for the cycle regulator *p21* protein (9-fold), chromatin assembly factor 1 *p55* subunit (8-fold), elongation factor 2 (2-fold) and lipopolysaccharide/b-1,3 glucan-binding protein (13-fold). Additionally, the transcript level of all the genes decreased in oysters fed with 30 x 10^3 cells mL^{-1} of the planktonic *P. micans* Ehrenb. after 72 h, and was lowest for the chromatin assembly factor 1 *p55* subunit (0.9-fold below baseline). In *M. gigas,* whole-cell ingestion of *P. lima* caused a clear mRNA modulation expression of the genes involved in cell cycle regulation and the immune system. Acute exposure caused an alteration of the transcript levels of all the studied genes, indicating an immediate or early stress response. Sub-chronic exposure generated a higher expression level in all the genes, causing a significant impact that could be related to DNA damage and control loss of the cell cycle. This genomic instability might lead to diseases, severe pathologies, or death in oysters. The increased Cg-LGBP expression level shows an activation of the innate immune system as the first line of defense in *M. gigas* against *P. lima* cells (or their DSTs and other bioactives), suggesting it was recognized by the oyster as a pathogenic agent. The authors conclude that overexpression of the genes could be related to DNA damage, disturbances in the cell cycle continuity, and was probably a genotoxic effect, as well as an activator of the innate immune system as the first line of defense.

Continuing this line of research, Romero-Geraldo *et al.* (2016) reported the results of *M. gigas* exposed to *P. lima* cells to determine behavioral changes, histopathological alterations, and changes in expression patterns of the genes involved in the cell cycle (*p21, cafp55, p53*), cytoskeleton (*tub, act*) and the inflammatory process (*casp1*). The results demonstrated that *P. lima* under a realistic BHAB cell density of 3 x 10^3 cells mL^{-1} affected the feeding behavior of *M. gigas*, causing hemocyte accumulation and infiltration, structural loss of the digestive gland epithelium tubules, and inducing tissue-specific gene expression pattern modifications. These changes were found at the transcript level in a set of time-dependent tested genes (*p53*, *cafp55*, *ef2*, *act*, *tub* and *casp1*), suggesting the presence of *P. lima* in the digestive gland of *M. gigas* might trigger an inflammatory tissue process and cytoskeleton disruption. The authors also pointed out that a disruption of the hyperphosphorylation process generated by the presence of the OA by *P. lima* cells probably resulted in eliminating some cell cycle control points, which compromised the tissue process, disturbed the cell cycle and cytoskeleton and represented a risk to oyster integrity. The presence of DSTs in *P. lima* cells decreased the clearance rate, induced structural loss, significantly decreased the tubule area of the digestive gland and up-regulated the expression of all genes.

Following the same research theme, García-Lagunas *et al.* (2019) compared the effect of the paralytic shellfish toxin-producing (PST) planktonic dinoflagellate, *Gymnodinium catenatum* H. W. Graham, and the DST-producer, *P. lima*, on the differential expression of the immune response genes in *M. gigas* spat. Again, the consumption of toxic dinoflagellates by the oyster spat caused changes at the expression level of the genes involved in the immune response. Combined diets of both dinoflagellates generated changes in the feeding behavior of oysters, with a greater preference for feeding on *G. catenatum.* Expression levels of lipopolysaccharide (LPS)-binding protein 1,3-glucan were higher in oysters exposed to both dinoflagellates, which was probably related to an activation of the oyster immediate immune response during the first 24 h. Protein 44 interferon-induced gene expression level was repressed in treatments with the highest dinoflagellate concentration and overexpressed in the diet with equal dinoflagellate concentration. Interaction protein-Toll and immunoglobulin gene transcript levels reached the highest values on day 7 in oysters exposed to combined diets. The results indicated that the immune defense appeared activated in oyster spat as a response to DSTs versus PSTs (or other bioactives) and/or extracellular compounds produced by the dinoflagellates.

These experiments demonstrate the high susceptibility of the immune defense of three common invertebrate species from the Gulf of California - the shrimp *Litopenaeus vannamei*, the giant lion-paw scallop *Nodipecten subnodosus* and the oyster *Magallana gigas* – when exposed to low cell abundances of *P. lima.* Exposure likely makes them susceptible to other biological stressors and contributes to mortalities observed in aquaculture facilities. Unfortunately, these studies have been performed only with one epibenthic dinoflagellate species. As the number of available benthic dinoflagellate strains with different toxin profiles increases, such experimental studies can be better targeted to address the effects of benthic dinoflagellates on the physiology of diverse marine fauna, including key seafood species.

Several studies have demonstrated strong interactions between marine bacteria and epibenthic dinoflagellates (Sakami *et al.*, 1999; Wang *et al.*, 2018). The extension of these close bacterial interactions with the phycosphere are still being elucidated. Tarazona-Janampa *et al.* (2020) studied the effect of culturable associated bacteria on the growth and toxigenicity of nine strains of the *P. lima* species complex from Isla Verde (Veracruz Reef System), Veracruz, and Puerto Morelos, Quintana Roo. Twenty-one bacterial genera belonging to Proteobacteria, Actinobacteria and Bacteroidetes were identified by amplifying the 16S rRNA gene marker from clonal *Prorocentrum* cultures, with gamma-Proteobacteria comprising the dominant class. A positive correlation was found among the bacterial genera associated with two *Prorocentrum* clones and the esterified toxin analog DTX1a-D8, but there was no apparent correlation between the other dinoflagellate clones and their associated bacteria with the other five detected DSTs. Additionally, there was no significant correlation between *Prorocentrum* cell volume, growth rate, bacterial cell counts, or cellular toxin concentration over the entire time-series culture cycle.

These results provided little confirmatory evidence that extracellular bacteria played a critical role in the regulation of DSP toxin production in *Prorocentrum* or modulation of their growth under non-nutrient limited conditions in culture. Nevertheless, the percentage of culturable bacteria is low compared to the total number of species found in the environment (Joint *et al.*, 2001); an approach considering non-culturable bacteria found in the natural environment and associated with BHAB species will give us a further understanding of this interaction.

Ramos-Santiago *et al.* (2022) determined the effects of the extracts from the brown macroalga *Dictyota dichotoma* (Hudson) J. V. Lamour. (Phaeophyceae: Dictyotales: Dictyotaceae) on the growth of two strains of *C. malayensis* isolated from Bahía de La Paz, BCS, southern Gulf of California. Both isolates were cultured in GSe medium with and without macroalgal extracts: 1) GSe medium, 2) GSe plus a crude extract of *D. dichotoma*, 3) GSe plus the carbohydrate fraction of *D. dichotoma*, and 4) GSe with the addition of the non-precipitable fraction of *D. dichotoma*. The results indicated that the different fractions of *D. dichotoma* neither favor nor limit the growth *of C. malayensis*.

A biotechnological approach based on physiological changes in *Amphidinium carterae* is currently underway to explore the potential for biofuel production (Mendoza-Flores *et al.*, 2022). A strain of *A. carterae* isolated from a bloom in Bahía Todos Santos, Ensenada, Baja California, was exposed to five irradiance levels (50, 100, 150, 200 and 250 µmol photons m^{-2} s^{-1}), and the effect on the growth rate, photosynthesis and the content in protein, carbohydrate, lipid and pigment was determined. The highest cell concentration was found in the cultures grown at 150 µmol photons m^{-2} s^{-1} (130×10^3 cells mL^{-1}), and the lowest value at 50 µmol photons m^{-2} s^{-1} (49×10^3 cells mL^{-1}). Cultures maintained under the lowest irradiance had the highest cell yield by organic and inorganic dry weight. The protein and carbohydrate content changed significantly with the irradiance level, with the highest values (1600 and 560 pg $cell^{-1}$, respectively) at 200 µmol photon m^{-2} s^{-1}. The lipid content was modified by the effect of irradiance, with the highest values (6920 pg $cell^{-1}$) at the lowest irradiance. As a general trend, the highest irradiances increased the photosynthetic rates. These findings demonstrate that although the strain of *A. carterae* can grow well at higher irradiances (100 to 250 µmol photons m^{-2} s^{-1}), a significant increase in the lipid content occurred at low irradiances. The authors suggest that this increase makes this species a candidate for use in biodiesel or ethanol production.

Concluding remarks and future perspectives. Due to negative impacts of benthic dinoflagellates causing BHABs in marine ecosystems with major consequences on human health and socioeconomic activities, studies on taxonomy, species diversity, allelochemical and toxic interactions and ecodynamics have increased during recent years in Mexico. The primary focus on a handful of key BHAB species has been necessary because of resource and personnel limitations, but has led to a relative neglect of cryptic, rare and non-BHAB taxa – hence a likely underestimate of diversity of benthic dinoflagellates in Mexican waters. In most cases, taxonomic studies have simply corroborated original descriptions based on morphological traits and strengthened local knowledge for accurate species identification (Cortés-Altamirano & Sierra-Beltrán, 2003; Hernández-Becerril & Almazán-Becerril, 2004; Almazán-Becerril *et al.*, 2015, 2016a, b). A few more profound taxonomic investigations have indeed contributed to reclassification of genera or species within newly created genera or to resolving species complexes (Tarazona-Janampa *et al.*, 2020; Cembella *et al.*, 2021). In Mexico, the need for and importance of reinforcing the identification of toxigenic species with molecular genetic data to minimize health risks has been previously emphasized by Núñez-Vázquez *et al.* (2019). The point is worth repeating herein because studies focused on molecular taxonomy of these BHAB dinoflagellates remain scarce, in particular for biogeographical investigations integrating morphological and molecular descriptors with toxin phenotype and composition (*e.g.*, Cembella *et al.*, 2021). This review presents limited molecular genetic information available for toxigenic species of the genera *Amphidinium, Coolia*, *Gambierdiscus*, *Ostreopsis* and *Prorocentrum*. However, there are no molecular data available for populations of *Fukuyoa*, *Vulcanodinium* and other BHAB genera found in Mexico, highlighting a window of opportunity to confirm or reject previous identifications based only on morphological criteria, as well as to corroborate the presence of cryptic species and to discard misidentifications of species with high

Table 5. A record of experimental studies on epibenthic dinoflagellates in Mexico. BC – Baja California; BCS – Baja California Sur; QR – Quintana Roo.

Authors	Year	Type of research	Species	Origin of strain
Heredia-Tapia *et al.*	2002	Toxicity tests with *Artemia franciscana*, mouse bioassays, toxin profile, growth data	*Prorocentrum lima*	El Pardito, BCS
Campa-Córdoba *et al.*	2009	SOD and toxicity on *Litopenaeus vannamei* and *Nodipecten subnodosus*	*P. lima*	El Pardito, BCS
Cohen-Fernández *et al.*	2010	LSU rDNA and SSU rDNA sequences	*P. lima* and other planktonic *Prorocentrum* species	El Pardito, BCS
Romero-Geraldo & Hernández-Saavedra	2014	Gene expression in *Magallana gigas*	*P. lima*	El Pardito, BCS
Romero-Geraldo *et al.*	2014	Gene expression related to cell cycle regulations and immune response in *M. gigas*	*P. lima*	El Pardito, BCS
Romero-Geraldo *et al.*	2016	Histological and gene expression effects on digestive gland of *M. gigas*	*P. lima*	El Pardito, BCS
Durán-Riveroll *et al.*	2019a	Review of the studies of benthic dinoflagellates in Latin America		
García-Lagunas *et al.*	2019	Immune response of *M. gigas*	*P. lima*	El Pardito, BCS
Pelayo-Zárate	2019	Associated culturable bacteria and DSP toxins	*P. lima*	Isla Verde, Ver, and Pto. Morelos, QR
Tarazona-Janampa *et al.*	2020	Associated bacteria, effect of growth and toxigenicity	*P. lima*	9 isolates from Isla Verde, Ver. and Pto. Morelos, QR
Cembella *et al.*	2021	Chemodiversity analyses of polyketide derived toxins, toxin profiles, sequences, morphology	*P. lima, P. hoffmannianum*	67 isolates from the Gulf of California, Gulf of Mexico, and Caribbean coasts
Villa-Arce	2021	Growth characteristics	*Prorocentrum*	Four isolates from Bahía de La Paz
Mejía-Camacho *et al.*	2021	Toxicity and cytotoxicity	*Amphidinium operculatum*	Veracruz Reef System, Ver.
Mendoza-Flores *et al.*	2022	Physiological changes when exposed at five irradiance levels	*Amphidinium carterae*	One strain from Bahia Todos Santos, BC
Ramos-Santiago *et al.*	2022	Impact of extracts of the macroalga *Dictyota dichotoma* (Phaeophyceae) on its growth	*Coolia malayensis*	2 isolates from Bahía de La Paz
Herrera-Herrera	2022	Allelopathy	*Coolia malayensis* and *Amphidinium thermaeum*	Isolates from Bahía de La Paz
Martínez-Mercado *et al.*	2022	Bacterial communities in cultures	*Prorocentrum lima*	Isolates from Bahía de La Paz and the Veracruz Reef System

morphological similarities within a group. The latter problem has occurred frequently with species such as *Ostreopsis ovata*, *O. siamensis*, *O. fattorussoi* Accoroni, Romagnoli et Totti and *O. rhodesiae* Verma, Hoppenrath et Shauna Murray that are difficult to distinguish only by light microscopy (Carnicer *et al.*, 2020). In a broader context, application of ecogenomics technology – *e.g.*, a DNA approach – will allow for genotyping *in situ* natural populations of benthic dinoflagellates for exploring their diversity, cryptic speciation and their functional role in marine ecosystems in Mexican waters.

Ecosystem level studies on benthic dinoflagellates with molecular tools have barely scratched the surface to date. As for habitats for epibenthic dinoflagellates, the few studies done in Mexico have focused on macroalgae and seagrasses. Other natural solid substrates, such as rocks, corals (both alive and dead) and other invertebrates, vertebrate species, mangrove roots, sediments (*e.g.*, sandy or silty) and anthropogenic artificial substrates have not been paid much attention hitherto.

In a previous review of data published from 1940 to 2011 on the status of HAB studies in Mexico (Band-Schmidt *et al.*, 2011), it was pointed out that most research was conducted during short-term research programs based on sampling from limited local field sites and focused on few selected HAB-forming species. The authors also commented that many research topics had not been adequately addressed: allelopathy, cyst and life-history studies, advective transport of species and blooms, effect of climate change on HABs, socioeconomic analyses and mitigation strategies, among others. Even a decade later these comments remain equally valid for Mexico. In the recent past most attention has focused on the classic phycotoxins affecting human health and marine ecosystem functioning, while relatively neglecting the fact that many benthic dinoflagellates produce bioactive natural products with allelochemical effects on species interactions. In particular, the polyketide-derived polyether metabolites with uncharacterized functional roles (Durán-Riveroll *et al.*, 2019a) warrant closer scrutiny. Several of these compounds are under investigation in Mexico for biotechnological potential as anticancer or cell division inhibitors and as future therapeutants.

The claim of inadequate studies on HABs for the above topics remains valid on a global basis – not just for Mexico, where in fact the skills, knowledge, and infrastructure to address these issues have improved dramatically in recent years. Global research initiatives on benthic dinoflagellate blooms (BHABs), initiated more than a decade ago via international coordinating programs, such as GEOHAB (Global Ecology and Oceanography of Harmful Algal Blooms; since 2001) and its successor GlobalHAB (Global Harmful Algal Blooms; 2016-2025) of IOC-SCOR UNESCO, have yielded a more clearly defined perspective on the natural phenomena and the causative mechanisms and impacts. Nevertheless, science and monitoring in Mexico has not kept pace with other major regions faced with acute BHAB events (*e.g.*, South Pacific, Caribbean Sea, Mediterranean Sea, including islands and archipelagos). In the near future, Mexico may experience even more cases of human intoxication, ecosystem disruption and crisis events (*e.g.*, of ciguatera), caused by climate change or direct anthropogenic effects on marine ecosystems. The BHAB problem is not in crisis state in Mexico, cases are few, sporadic and widely dispersed, but the current status of scientific knowledge is clearly inadequate to describe and explain the extent of the phenomena, much less to predict and design appropriate monitoring and mitigation strategies in collaboration with the seafood industry and public health agencies. A comprehensive BHAB strategy will require more than fine-tuning morphotaxonomy for accurate identification of benthic dinoflagellates and describing new species and toxins.

From the present review it is evident that studies on epibenthic dinoflagellates in Mexico have begun to emerge more frequently in recent years. Hitherto, most studies on BHAB species and their effects have been crude investigations based on acute mortalities and toxicities of seafood species, *e.g.*, on the effect of *P. lima* on shrimps and bivalves. There is ongoing work with international partners and collaborators that will lead to a greater understanding of these important epibenthic assemblages in the country. There are now several species banks including live strains of benthic dinoflagellates isolated from diverse coastal regions of Mexico available for laboratory research. Collaborations with international colleagues and global research initiatives with access to advanced technology platforms support the required studies on toxicity, allelopathy, ecological interactions, effects on mariculture species, biosynthesis of metabolites and biotechnological potential that remain to be addressed for benthic dinoflagellates in Mexico.

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REFERENCES

Aguilar-Trujillo, A.C., Y.B. Okolodkov, J.A. Herrera-Silveira, F. del C. Merino-Virgilio & C. Galicia-García. 2017. Taxocoenosis of epibenthic dinoflagellates in the coastal waters of the northern Yucatán Peninsula before and after the harmful algal bloom event in 2011–2012. *Marine Pollution Bulletin* 119: 396-406. http://dx.doi.org/10.1016/j.marpolbul.2017.02.074

Aguilar-Trujillo, A.C., Y.B. Okolodkov, F. del C., Merino-Virgilio, I. Osorio-Moreno & J.A. Herrera-Silveira. 2014. Variación espacial de dinoflagelados bentónicos/epifíticos en aguas costeras del norte de Yucatán (agosto de 2011). *In*: Botello, A.V., J. Rendón-von Osten, J.A. Benítez & G. Gold-Bouchot (Eds.). *Golfo de México. Contami-*

nación, impacto ambiental, diagnóstico y tendencias. 3a ed. UAC, UNAM-ICMYL, CINVESTAV-Unidad Mérida, Mérida, Yucatán, México, pp. 147-160.

Ajani, P., D.T. Harwood & S.A. Murray. 2017. Recent trends in marine phycotoxins from Australian coastal waters. *Marine Drugs* 15(2)**:** 33. DOI: 10.3390/md15020033

Almazán-Becerril, A. 2000. Estudio taxonómico de dinoflagelados tóxicos y potencialmente tóxicos en el Caribe Mexicano. Tesis de Maestría. Facultad de Ciencias, UNAM. 52 p., 17 lám.

Almazán-Becerril, A. S., Escobar-Morales, G. Rosiles-González & F. Valadez. 2015. Benthic epiphytic dinoflagellates from the northern portion of the Mesoamerican Reef System. *Botanica Marina* 58: 115-128. DOI: 10.1515/bot-2014-0093

Almazán-Becerril, A., B. Delgado-Pech, E. Núñez-Vázquez, M. Escalante-Abusto, E.D. Irola-Sansores, A.T. Arredondo-Chávez, J.C. Peniche-Pérez, A. Caballero- Vázquez, D.A. Uitzil-Castañeda, J. Méndez Torres, G. Reséndiz Colorado & M. García Rivas. 2021. Presencia de ciguatoxinas en la especie invasora pez león (*Pterois volitans*) y en otros peces arrecifales en dos áreas naturales protegidas de Quintana Roo: Arrecife de Puerto Morelos e Isla Contoy. Project ID: SNIB-MQ001-MQ0011912F_SIB2020.03.26-ND. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Ciudad de México, México. https://www.gbif.org/dataset/1a903bc5-bedf-4414-809c-7439843dc336

Almazán-Becerril, A., E.D. Irola-Sansores & S. Escobar-Morales. 2016a. El género *Gambierdiscus* de Quintana Roo, México. *In*: García-Mendoza, E., S.I. Quijano-Scheggia, A. Olivos-Ortiz & E.J. Núñez-Vázquez (Eds.). *Florecimientos algales nocivos en México*. CICESE, Ensenada, Baja California, México, pp. 366-377.

Almazán-Becerril, A., S. Escobar-Morales, E.D. Irola-Sansores & B. Delgado-Pech. 2016b. Morfología y taxonomía de los géneros *Ostreopsis* y *Coolia* en el Caribe Mexicano *In*: García-Mendoza, E., S.I. Quijano-Scheggia, A. Olivos-Ortiz & E.J. Núñez-Vázquez (Eds.). *Florecimientos algales nocivos en México*. CICESE, Ensenada, Baja California, México, pp. 378-393.

Alonso-Rodríguez, R., D.U., Hernández-Becerril & I. Gárate-Lizárraga. 2008. *Catálogo de microalgas de las lagunas costeras de Sinaloa*. F. Páez-Osuna (Ed.). Serie Lagunas Costeras de Sinaloa. Núm. 4. UNAM, ICML, CODESIN, CESASIN, SEMARNAT, CONACYT, Sinaloa, México. 208 p.

Alonso-Rodríguez, R. & E. Páez-Osuna. 2003. Nutrients, phytoplankton and harmful algal blooms in shrimp ponds: a review with special reference to the situation in the Gulf of California. *Aquaculture* 219: 317-336. DOI: 10.1016/S0044-8486(02)00509-4

Arizpe, Ó. 1966. Secondary production, growth and survival of the Pacific oyster *Crassostrea gigas* (Thunberg) in tropical waters, Bahía de La Paz, Mexico. *Journal of Shellfish Research* 15: 601-607.

Band-Schmidt C.J., J.J. Bustillos-Guzmán, D.J. López-Cortés, E. Núñez-Vázquez & F.E. Hernández-Sandoval. 2011. El estado actual del estudio de florecimientos algales nocivos en México. *Hidrobiológica* 21(3): 381-413. http://www.redalyc.org/articulo.oa?id=578214830016

Band-Schmidt, C.J. & C.F. Rodríguez-Gómez (Eds.). 2022. *Proceedings of the 19th International Conference on Harmful Algae, October 10-15, 2021*. International Society for the Study of Harmful Algal Blooms, La Paz, B.C.S., Mexico. 365 p.

Barón-Campis, S.A., Y.B. Okolodkov, G.V. Ríos-Lara, N. Vázquez-Gómez, V. Rubio-Sánchez, G. Arce-Rocha, W.A. González-López & E.J. Núñez-Vázquez. 2014. Dinoflagelados nocivos y ciguatoxinas en la costa norte de Yucatán: un riesgo para el futuro desarrollo de la maricultura. *In*: Resúmenes del XXI Congreso Nacional de Ciencia y Tecnología del Mar, Isla Cozumel, Quintana Roo, México, 8 al 11 de octubre de 2014. [7 p.].

Blanfuné, A., C.F. Boudouresque, H. Grossel & T. Thibaut. 2015. Distribution and abundance of *Ostreopsis* spp. and associated species (Dinophyceae) in the northwestern Mediterranean: the region and the macroalgal substrate matter. *Environmental Science and Pollution Research* 22(16): 12332-12346.

Bravo, I. & R.I. Figueroa. 2013. Towards an ecological understanding of dinoflagellate cyst functions microorganisms 2013, 1, 1-x manuscripts; DOI: 10.3390/microorganisms10x000x

Cáceres-Martínez, J., P.M. De Oca & R. Vásquez-Yeomans. 1998. *Polydora* sp. infestation and health of the Pacific oyster *Crassostrea gigas* cultured in Baja California, NW Mexico. *Journal of Shellfish Research* 17: 259-264.

Campa-Córdova, A.I., E.J. Núñez-Vázquez, A. Luna-González, M.J. Romero-Geraldo & F. Ascencio. 2009. Superoxide dismutase activity in juvenile *Litopenaeus vannamei* and *Nodipecten subnodosus* exposed to the toxic dinoflagellate *Prorocentrum lima*. *Comparative Biochemistry and Physiology, Part C: Toxicology & Pharmacology* 149(3): 317-322. DOI: 10.1016/j.cbpc.2008.08.006

Carnicer, O., Y.B. Okolodkov, M. Garcia-Altares, I. Keith, K.B. Andree, J. Diogène & M.F. Tejedor. 2020. *Ostreopsis* cf. *ovata* and *Ostreopsis lenticularis* (Dinophyceae: Gonyaulacales) in the Galapagos Marine Reserve. *Scientia Marina* 84(3): 1-16. DOI: 10.3989/scimar.05035.08A

Cembella, A.D., L.M. Durán-Riveroll, U.I. Tarazona-Janampa, Y.B. Okolodkov, R. García-Sandoval, B. Krock, C. Hörstmann & U. John. 2021. Phylogeography and diversity among populations of the toxigenic benthic dinoflagellate *Prorocentrum* from coastal reef systems in Mexico. *Frontiers in Marine Science* 8: article 716669. DOI: 10.3389/fmars.2021.716669

Ciminiello, P., C. Dell'Aversano, E. Fattorusso, M. Forino, S.G. Magno, L. Tartaglione, C. Grillo & N. Melchiorre. 2006. The Genoa 2005 outbreak. Determination of putative palytoxin in Mediterranean *Ostreopsis ovata* by a new liquid chromatography mass spectrometry method. *Analytical Chemistry* 78(17): 6153-6159. DOI: 10.1021/ac060250j

Cohen-Fernández, E.J., F.F. Pedroche, M.R. Palacios, S. Álvarez-Hernández & E. Meave del Castillo. 2010. Molecular phylogeny of *Prorocentrum* (Dinoflagellata) from the Pacific coast of Mexico based on the parsimony analysis of fragments of LSUrDNA and SSUrDNA. *International Journal of Plant Physiology and Biochemistry* 2(3): 29-37. http://www.academicjournals.org/ijppb

Cortés-Altamirano, R. 2012. Two new localities for *Gambierdiscus toxicus* in the Mexican Pacific. *Harmful Algae News* 45: 10-11.

Cortés-Altamirano, R. & A.P. Sierra-Beltrán. 2003. Morphology and taxonomy of *Prorocentrum mexicanum* and reinstatement of *Prorocentrum rhathymum* (Dinophyceae). *Journal of Phycology* 39: 221-225. https://doi.org/10.1046/j.1529-8817.2003.01112.x

Cortés-Altamirano, R., A. Sierra-Beltrán & M. Cortés-Lara. 2011. Ultraestructura de *Ostreopsis siamensis* y *O. ovata* (Dinophyceae): referencia especial a la placa 2´, el poro apical (Po) y poros tecales. *In:* XIV Congresso Latino-Americano de Ciências do Mar – XIV COLACMAR, Baneário Camboriú (SC / Brasil), 30 de outubro a 04 de novembro de 2011. [3 p.]

Cortés-Lara, M.C., R. Cortés-Altamirano, A. Sierra-Beltrán & A. Reyes-Juárez. 2005. *Ostreopsis siamensis* (Dinophyceae), a new tychoplanktonic record from Isabel Island National Park, Pacific Mexico. *Harmful Algal News* 28: 4-5.

Deeds, J.R., J.H., Landsberg, S.M. Etheridge, G.C. Picther & A.W. Longan. 2008. Non-traditional vectors for paralytic shellfish poisoning. *Marine Drugs* 6: 308-348. DOI: 10.3390/md20080015

Dickey, R.W. & S.M. Plakas. 2010. Ciguatera: a public health perspective. *Toxicon* 56(2): 123-136. DOI: 10.1016/j.toxicon.2009.09.008

DOF (Diario Oficial de la Federación). 2009. Norma Oficial Mexicana NOM-242-SSA1-2009. Secretaría de Salud, Ciudad de México, México. https://www.dof.gob.mx/normasOficiales/4295/salud2a/salud2a.htm

Durán-Riveroll, L.D., A.D. Cembella & Y.B. Okolodkov. 2019a. A review on the biodiversity and biogeography of toxigenic benthic marine dinoflagellates of the coasts of Latin America. *Frontiers in Marine Science* 6:148.11.012. DOI: 10.3389/fmars.2019.00148

Durán-Riveroll, L.M., C.J. Band-Schmidt, Y.B. Okolodkov & A. Almazán-Becerril. 2019b. Florecimientos algales nocivos en las costas de México: estado actual y perspectivas. *In*: Botello A.V., S. Villanueva & J. Gutiérrez (Eds.). *Costas y mares mexicanos: contaminación, impactos, vulnerabilidad y cambio climático*. UNAM, UAC, México, D.F., México, pp. 277-312. DOI: 10.26359/epomex.0419

Durán-Riveroll, L.M., A.D. Cembella & Y.B. Okolodkov. 2022. Diversity, biogeography, and chemically mediated interactions of toxigenic benthic marine dinoflagellates from Mexican coastal waters. *In*: Band-Schmidt, C.J. & C.F. Rodríguez-Gómez (Eds.). *Proceedings of the 19th International Conference on Harmful Algae, October 10-15, 2021, International Society for the Study of Harmful Algal Blooms, La Paz, B.C.S., Mexico,* p. 132-137.

Esqueda-Lara, K. & D.U. Hernández-Becerril. 2010. *Dinoflagelados microplanctónicos marinos del Pacífico central de México (Isla Isabel, Nayarit y costas de Jalisco y Colima).* Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, México. 254 p.

FAO. 2004. Marine biotoxins. FAO Food and Nutrition paper 80. Food and Agriculture Organization of the United Nations, Rome, Italy. xii+278 p. https://www.fao.org/publications/card/en/c/9261a330-3477-5896-b66c-20f68d261f55/

Fleming, L.E., D.G. Baden, J.A. Bean, R. Weisman & D.G. Blythe. 1998. Seafood toxin diseases: issues in epidemiology and community outreach. *In*: Reguera, B., J. Blanco, M.L. Fernández & T. Wyatt (Eds.). *Harmful Algae*. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, pp. 245-248.

Gallegos-Mendiola, V., B. Pérez-Cruz, J.A. Díaz-Ortiz, D.E. Morán-Vega, R. Huante-Catalán & I. Gárate-Lizárraga. 2017. Ocurrencia *de Ostreopsis ovata* en la playa Piedra de Tlalcoyunque en la región Costa Grande, Guerrero, México. *In: 4o Congreso Nacional de la Sociedad Mexicana para el Estudio de los Florecimientos Algales Nocivos A.C. y 2a Reunión de la Asociación Latinoamericana para el Estudio de Algas Nocivas*. Cancún, Quintana Roo, México, p. 96.

Gárate-Lizárraga, I. 2012. Proliferation of *Amphidinium carterae* (Gymnodiniales: Gymnodiniaceae) in Bahía de La Paz, Gulf of California. *CICIMAR Oceánides* 27: 1-13. http://dx.doi.org/10.37543/oceanides.v27i2.115

Gárate-Lizárraga, I. 2013. Bloom of *Cochlodinium polykrikoides* (Dinophyceae: Gymnodiniales) in Bahía de La Paz, Gulf of California. *Marine Pollution Bulletin* 67: 217-222. DOI: 10.1016/j.marpolbul.2012.11.031

Gárate-Lizárraga, I. 2020. Dinoflagelados atecados y su importancia como causantes de florecimientos en la Bahía de La Paz, Golfo de California. *In:* Riosmena-Rodríguez, R., J.M. López-Vivas, E.A. Gómez-Gallardo-Unzueta, G. Cruz-Piñón & A. Romo-Piñera (Eds.). *La Bahía de La Paz, biodiversidad, procesos ecológicos y sociales*. Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México, pp.197-242.

Gárate-Lizárraga, I., C.J. Band-Schmidt, G. Verdugo-Díaz, M.S. Muñetón-Gómez & E. Félix-Pico. 2007. Dinoflagelados (Dinophyceae) del sistema lagunar Magdalena-Almejas. *In*: Funes-Rodríguez, R., J., Gómez-Gutiérrez & R. Palomares-García (Eds.). *Estudios ecológicos en Bahía Magdalena*. Gobierno del Estado de B.C.S., Secretaría de Turismo de B.C.S., Fondo para la Protección de los Recursos Marinos de B.C.S., Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur, México, pp. 145-174.

Gárate-Lizárraga, I. & R. González-Armas. 2017. First record of the dinoflagellate *Prorocentrum panamense* (Prorocentrales, Dinophyceae) in the Mexican Pacific from the Archipiélago de Revillagigedo. *CICIMAR Oceánides* 32(1): 63-66. DOI: 10.37543/oceanides.v32i1.197

Gárate-Lizárraga, I., R. González-Armas & Y.B. Okolodkov. 2018. Occurrence of *Ostreopsis lenticualris* (Dinophyceae: Gonyaulacales) from the Archipiélago de Revillagigedo, Mexican Pacific. *Marine Pollution Bulletin* 128: 390-395. DOI: 10.1016/j.marpolbul.2018.01.020

Gárate-Lizárraga, I., Y.B. Okolodkov & R. Cortés-Altamirano. 2016a. Microalgas formadoras de florecimientos algales en el Golfo de California. *In:* García-Mendoza, E., S.I. Quijano-Scheggia, A. Olivos-Ortiz & E.J. Núñez-Vázquez (Eds.). *Florecimientos Algales Nocivos en México*. CICESE, Ensenada, México, pp. 130-145.

Gárate-Lizárraga I., G. Verdugo-Díaz & Y. Okolodkov. 2016b. Florecimientos algales nocivos en la costa occidental de Baja California Sur *In*: García-Mendoza, E., S.I. Quijano-Scheggia, A. Olivos-Ortiz & E.J. Núñez-Vázquez (Eds.). Florecimientos Algales Nocivos en México. CICESE, Ensenada, México, pp. 44-59.

Gárate-Lizárraga, I., R. González-Armas, G. Verdugo-Díaz, Y.B. Okolodkov, B. Pérez-Cruz & J.A. Díaz-Ortiz. 2019. Seasonality of the dinoflagellate *Amphidinium* cf. *carterae* (Dinophyceae: Amphidiniales) in Bahía de

La Paz, Gulf of California. *Marine Pollution Bulletin* 146: 532-541. DOI: 10.1016/j.marpolbul.2019.06.073

Gárate-Lizárraga, I. & A. Martínez-López. 1997. Primer registro de una marea roja de *Prorocentrum mexicanum* (Prorocentraceae) en el Golfo de California. *Revista de Biología Tropical* 45:1263.

Gárate-Lizárraga, I. & M.S. Muñetón-Gómez. 2008. Bloom of *Peridinium quinquecorne* Abé in la Ensenada de la Paz, Gulf of California (July 2003). *Acta Botanica Mexicana* 83: 33-47.

Gárate-Lizárraga, I., M.S. Muñetón-Gómez & V. Maldonado-López. 2006. Florecimiento del dinoflagelado *Gonyaulax polygramma* frente a la isla Espíritu Santo, Golfo de California, México. *Revista de Investigaciones Marinas*, 27: 31-39. https://www.researchgate.net/publication/253645728_Florecimiento_del_dinoflagelado_Gonyaulax_polygramma_frente_a_la_Isla_Espiritu_Santo_Golfo_de_California_Octubre_2004

García-Lagunas, N., R., Romero-Geraldo, A.K., Kao-Godínez & N.Y. Hernández-Saavedra. 2019. Differential expression of immune response genes in Pacific oyster, *Crassostrea gigas* spat, fed with dinoflagellates *Gymnodinium catenatum* and *Prorocentrum lima*. *Latin American Journal of Aquatic Research* 47(4), 699-705. http://dx.doi.org/10.3856/vol47-issue4-fulltext-12

García-Rico, L., R.E., Ramos-Ruiz & J. Vivian-Jiménez. 2001. Determination of total metals in cultivated oysters (*Crassostrea gigas*) from the Northwest Coast of Mexico by microwave digestion and atomic absorption spectrometry. *Journal of AOAC International* 84: 1909–1913. https://doi.org/10.1093/jaoac/84.6.1909

García Santos Reyes, P.G. 2022. Identificación de dinoflagelados bentónicos del género *Coolia* de costas mexicanas y caracterización de los efectos citotóxicos de sus extractos sobre *Artemia salina* y células tumorales humanas. Informe de servicio social para obtener el título de Licenciada en Biología. Universidad Simón Bolívar, Ciudad de México, México.

Gayoso, A.M., S. Dover, S. Morton, M. Busman, P. Moeller, V.K. Fulco & L. Maranda. 2002. Diarrhetic shellfish poisoning associated with *Prorocentrum lima* (Dinophyceae) in Patagonian Gulfs (Argentina). *Journal of Shellfish Research* 21(2): 461–463. https://www.researchgate.net/publication/269097077_Diarrhetic_shellfish_poisoning_associated_with_Prorocentrum_lima_Dinophyceae_in_Patagonian_Gulfs_Argentina

Gómez, F., D. Qui & S. Lin. 2017. The synonymy of the toxic dinoflagellates *Prorocentrum mexicanum* and *P. rhathymum* and the description of *P. steidingerae* sp. nov. (Prorocentrales, Dinophyceae). *Journal of Eukaryotic Microbiology* 64: 668-677. DOI: 10.1111/jeu.12403

Gu, H., K. Huo, B. Krock, G. Bilien, V. Pospelova, Z. Li, C. Carbonell-Moore, L. Morquecho, Ž. Ninčević & K.N. Mertens. 2021. Cyst-theca relationships of *Spiniferites bentorii*, *S. hyperacanthus*, *S. ramosus*, *S. scabratus* and molecular phylogenetics of *Spiniferites* and *Tectatodinium* (Gonyaulacales, Dinophyceae). *Phycologia* 60(4): 332-353. DOI: 10.1080/00318884.2021.1930796

Hallegraeff, G., D.M. Anderson, C. Belin, M.J. Dechraoui Bottein, E. Bresnan, M. Chinain, H. Enevoldsen, M. Iwataki, B. Karlson, C.H. McKenzie, I. Sunesen, G.C. Pitcher, P. Provoost, A. Richardson, L. Schweibold, P.A. Tester, V.L. Trainer, A.T. Yñiguez & A. Zingone. 2021. Perceived global increase in algal blooms is attributable to intensified monitoring and emerging bloom impacts. *Communications Earth & Environment* 2:117. https://doi.org/10.1038/s43247-021-00178-8

Helenes, J., A.L. Carreño & R.Y. Marcos-Girón. 2020. Miocene-Pliocene biochronology of the Obregón Basin and it's bearing on the evolution of the Proto-Gulf of California. *Journal of South American Earth Sciences* 104:102758. DOI: 10.1016/j.jsames.2020.102758

Heredia-Tapia, A.B., O. Arredondo-Vega, E.J. Núñez-Vázquez, T. Yasumoto, M. Yasuda & J.L. Ochoa. 2002. Isolation of *Prorocentrum lima* (Syn. *Exuviaella lima*) and diarrhetic shellfish poisoning (DSP) risk assessment in the Gulf of California, Mexico. *Toxicon* 40: 1121-1127. DOI: 10.1016/s0041-0101(02)00111-3

Hernández-Becerril, D.U. & A. Almazán-Becerril. 2004. Especies de dinoflagelados del género *Gambierdiscus* (Dinophyceae) del Mar Caribe mexicano. *Revista de Biología Tropical* 52 (Suppl. 1): 77–87. https://www.scielo.sa.cr/scielo.php?script=sci_arttext&pid=S0034-77442004000500011

Hernández-Becerril, D.U. S.A. Barón-Campis, J.G.A. Ceballos-Corona, R. Alonso-Rodríguez, K.M. Rincones-Reyes, R.T. Becerra-Reynoso & G. Arce-Rocha. 2021. *Catálogo del fitoplancton del Pacifico central mexicano, Cruceros "MareaR" (2009-2019). B/O "El Puma"*. Universidad Nacional Autónoma de México, Ciudad de México, México. 254 p.

Hernández-Becerril, D.U., M.C. Rodríguez-Palacio & C. Lozano-Ramírez. 2013. Morphology and life stages of the potentially pinnatoxin-producing thecate dinoflagellate *Vulcanodinium rugosum* from the tropical Mexican Pacific. *Botanica Marina* 56(5-6): 535-540. DOI: 10.1515/bot-2013-0079

Hernández-Castro, J.E. 2017. Dinoflagelados y toxinas lipofílicas en bancos naturales de bivalvos al sur de la Bahía de La Paz, B.C.S., México. Tesis de Maestría. Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur, México. 90 p.

Herrera-Herrera, N.V. 2022. *Interacciones alelopáticas de dinoflagelados epibentónicos de los géneros Amphidinium y Coolia en condiciones de cultivo*. Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur, México. vii+160 p.

Herrera-Sepúlveda, A., N.Y. Hernandez-Saavedra, L.K. Medlin & N. West. 2013. Capillary electrophoresis fingerprint technique (CE-SSCP): an alternative tool for the monitoring activities of HAB species in Baja California Sur Costal. *Environmental Science and Pollution Research* 20(10): 6863-6871. DOI: 10.1007/s11356-012-1033-7

Ho, T.V. & L.N. Nguyen. 2014. Morphology and distribution of the three epiphytic dinoflagellate species *Coolia monotis, C. tropicalis*, and *C. canariensis* (Ostreopsidaceae, Gonyaulacales, Dinophyceae) from Vietnamese coastal waters. *Oceanic Science Journal* 49(3): 211-221. DOI: 10.1007/s12601-014-0021-x

Holmes, M.J., R.J. Lewis, A. Jones & A.W. Hoy. 1995. Cooliatoxin, the first toxin from *Coolia monotis* (Dinophyceae). *Natural Toxins* 3(5)**:** 355-362. DOI: 10.1002/nt.2620030506

Hoppenrath, M., S.A. Murray, N. Chomérat & T. Horiguchi. 2014. *Marine benthic dinoflagellates – unveiling their worldwide biodiversity*.

Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Stuttgart, Germany. 276 p.

ICHA 2021 Abstract Book. 2021. 19th International Conference on Harmful Algae. October 10-15, 2021, La Paz, Baja California Sur, Mexico. 448 p. https://issha.org/wp-content/uploads/2022/01/ICHA2021_Abstracts-10-oct.pdf

Irola-Sansores, E.D., B. Delgado-Pech, E. García-Mendoza, E.J. Núñez-Vázquez, A. Olivos-Ortiz & A. Almazán-Becerril. 2018. Population dynamics of benthic-epiphytic dinoflagellates on two macroalgae from coral reef systems of the northern Mexican Caribbean. *Frontiers Marine Science* 5:487. DOI: 10.3389/fmars.2018.00487

Joint, I., M. Mühling & J. Querellou. 2010. Culturing marine bacteria - an essential prerequisite for biodiscovery. *Microbial Biotechnology* 3: 564-575. DOI: 10.1111/j.1751-7915.2010.00188.x

Junqueira de Azevedo Tibiriçá, C.E., M. Sibat, L.F. Fernandes, G. Bilien, N. Chomérat, P. Hess & L.L. Mafra Jr. 2020. Diversity and toxicity of the genus *Coolia* Meunier in Brazil, and detection of 44-methyl gambierone in *Coolia tropicalis*.

Toxins 12(5):327. https://doi.org/10.3390/toxins12050327 Karafas, S., R. York & C. Tomas. 2015. Morphological and genetic analysis of the *Coolia monotis* species complex with the introduction of two new species, *Coolia santacroce* sp. nov. and *Coolia palmyrensis* sp. nov. (Dinophyceae). *Harmful Algae* 46: 18-33. DOI: 10.1016/j.hal.2015.05.002

Karlson, B., P. Andersen, L. Arneborg, A. Cembella, W. Eikrem, U. John, J.J. West, K. Klemm, J. Kobos, S. Lehtinen, N. Lundholm, H. Mazur-Marzec, L. Naustvoll, M. Poelman, P. Provoost, M. De Rijcke & S. Suikkanen. 2021. Harmful algal blooms and their effects in coastal seas of Northern Europe. *Harmful Algae* 102:101989. https://doi.org/10.1016/j.hal.2021.101989

Kielt, J.-F. 2006. Distribution des assemblages palynologiques et microfaunistiques le long des côtes Ouest mexicaines. Memoire présenté comme exigence partielle de la Maîtrise en Sciences de la Terre. Université du Québec à Montréal, Montréal, Québec, Canada. ix+83 p.

Kobayashi, J. & T. Kubota. 2007. Bioactive macrolides and polyketides from marine dinoflagellates of the genus *Amphidinium*. *Journal of Natural Products* 70: 451-460. DOI: 10.1021/np0605844

Kobayashi, J. & M. Tsuda. 2004. Amphidinolides, bioactive macrolides from symbiotic marine dinoflagellates. *Natural Product Reports* 21: 77-93.

Krock, B., U. Tillmann, U. John & A. Cembella. 2008. LC-MS-MS aboard ship: tandem mass spectrometry in the search for phycotoxins and novel toxigenic plankton from the North Sea. *Analytical and Bioanalytical Chemistry* 392: 797-803. DOI: 10.1007/s00216-008-2221-7

Lawrence, J.E., J. Grant, M.A. Quilliam, A.G. Bauder & A.D. Cembella. 2000. Colonization and growth on the toxic dinoflagellate *Prorocentrum lima* and associated fouling macroalgae on mussels in suspended culture. *Marine Ecology Progress Series* 201: 147-154. https://www.int-res.com/articles/meps2000/201/m201p147.pdf

Leaw, C.P., T. Hii-Tan, H. Chang-Lim, S. Tung-Teng, H. Lin-Yong, K.F. Smith, L. Rhodes, M. Wolf, W.C. Holland, M.W. Vandersea, R.W. Litaker, P.A. Tester, H. Gu, G. Usup & P. Teen-Lim. 2016. New scenario for speciation in the benthic dinoflagellate genus *Coolia* (Dinophyceae). *Harmful Algae* 55: 137-149. DOI: 10.1016/j.hal.2016.02.010

Lechuga-Devéze, C.H. & A.P. Sierra-Beltrán. 1995. Documented case of ciguatera on the Mexican Pacific coast. *Natural Toxins* 3(6): 415-418. DOI: 10.1002/nt.2620030603

Leung, P.T., M. Yan, K.F. Yiu, V. Lam, J.C. Ip, M.W.Y., C. Chen, T. Wai & P.K.S. Lam. 2017. Molecular phylogeny and toxicity of harmful benthic dinoflagellates *Coolia* (Ostreopsidaceae, Dinophyceae) in a subtropical marine ecosystem: the first record from Hong Kong. *Marine Pollution Bulletin* 124(2): 878-889. DOI: 10.1016/j.marpolbul.2017.01.017

Ley-Martínez, T.-C. 2016. Bioprospección de toxinas tipo ciguatoxinas en peces carnívoros del Caribe mexicano y aguas adyacentes. Tesis de Licenciatura. La Paz, Baja California Sur, México. xvi+74 p.

Ley-Martínez, T.-C. 2018. Identificación y cuantificación de ciguatoxinas en peces carnívoros de la Península de Yucatán. Tesis de Maestría. La Paz, Baja California Sur, México. xviii+135 p.

Ley-Martínez, T.-C., E.J. Núñez-Vázquez, A. Almazán-Becerril, S. Barón-Campis, C. Ramírez-Camarena, J. A. Caballero-Vázquez & E.F. Balart. 2014. Bioprospección de toxinas tipo ciguatoxinas en peces carnívoros del Caribe mexicano y aguas adyacentes. *In*: XXI Congreso Nacional de Ciencia y Tecnología del Mar, Cozumel, Quintana Roo, México, 8-11 de octubre de 2014. [14 p.].

Limoges, A., J.-F. Kielt, T. Radi, A.C. Ruíz-Fernández & A. de Vernal. 2010. Dinoflagellate cyst distribution in surface sediments along the south-western Mexican coast (14.76º N to 24.75º N). *Marine Micropaleontology* 76(3-4): 104-123. https://doi.org/10.1016/j.marmicro.2010.06.003

Limoges, A., L. Londeix & A. de Vernal. 2013. Organic-walled dinoflagellate cyst distribution in the Gulf of Mexico. *Marine Micropaleontology* 102: 51-68. http://dx.doi.org/10.1016/j.marmicro.2013.06.002

Litaker, R.W., W. Holland, S.R. Kibler, M.W. Vandersea, M.A. Faust & P.A. Tester. 2011. *Prorocentrum mexicanum* vs. *Prorocentrum rhathymum*: comparative taxonomy, ecology and toxicology. *Journal of Phycology* 47: S69. DOI: 10.1046/j.1529-8817.2003.01112.x

Litaker, R.W., M.W. Vandersea, M.A. Faust, S.R. Kibler, M. Chinain & M.J. Holmes. 2009. Taxonomy of *Gambierdiscus* including four new species, *Gambierdiscus caribaeus*, *Gambierdiscus carolinianus*, *Gambierdiscus carpenteri* and *Gambierdiscus ruetzleri* (Gonyaulacales, Dinophyceae). *Phycologia* 48: 344-390. DOI: 10.3390/md16010007

Litaker, R.W., M.W. Vandersea, M.A. Faust, S.R. Kibler, A.W. Nau, W.C. Holland, M. Chinain, M.J., Holmes & P.A. Tester. 2010. Global distribution of ciguatera causing dinoflagellates in the genus *Gambierdiscus*. *Toxicon* 56: 711-730. DOI: 10.1016/j.toxicon.2010.05.017

Litaker, R.W., W.C. Holland, D.R. Hardison, F. Pisapia, P. Hess, S.R. Kibler & P.A. Tester. 2017. Ciguatoxicity of *Gambierdiscus* and *Fukuyoa* species from the Caribbean and Gulf of Mexico. *PLoS One* 12:e0185776. DOI:10.1371/journal.pone

Loeffler, C.R., L. Tartaglione, M. Friedemann, A. Spielmeyer, O. Kappenstein & D. Bodi. 2021. Ciguatera mini review: 21st century environmental challenges and the interdisciplinary research efforts rising to meet them. *International Journal of Environmental Research and Public Health* 18(6):3027. DOI: 10.3390/ijerph18063027

Lundholm, N., C. Churro, S. Fraga, M. Hoppenrath, M. Iwataki, J. Larsen, K. Mertens, Ø. Moestrup & A. Zingone (Eds.). 2009 onwards. IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae. https://www.marinespecies.org/hab. DOI: 10.14284/362

Maciel-Baltazar, E. 2015. Dinoflagelados (Dinoflagellata) tóxicos de la costa de Chiapas, México, Pacífico centro oriental. *Cuadernos de Investigación UNED* 7(1): 39-48. http://www.redalyc.org/articulo.oa?id=515651508005

Mafra Jr., L.L., T. Ribas, T.P. Pereira Alves, Oliveira Proença, M.A. Schramm, H. Uchida & T. Suzuki. 2015. Differential okadaic acid accumulation and detoxification by oysters and mussels during natural and simulated *Dinophysis* blooms. *Fisheries Science* 81: 749-762. DOI: 10.1007/s12562-015-0882-7

Martínez-Hernández, E. & E. Hernández-Campos. 1991. Distribución de quistes de dinoflagelados y acritarcas en sedimentos holocénicos del Golfo de California. *Paleontología Mexicana* 57: 1-120, lám. 1-6.

Martínez-Cruz, M. E., Y.B. Okolodkov, A.C. Aguilar-Trujillo & J.A. Herrera-Silveira. 2015. Epiphytic dinoflagellates on the seagrass *Thalassia testudinum* at Dzilam, southeastern Gulf of Mexico. *Cymbella* 1: 2-9.

Martínez-Mercado, M., C.E. Galindo-Sánchez, E. Sánchez-Castrejón, A. Saavedra-Flores, A.D. Cembella & L.M. Durán-Riveroll. 2022. Comparison of bacterial communities among geographically distinct populations of the benthic dinoflagellate *Prorocentrum lima*. *In*: Band-Schmidt, C.J. & C.F. Rodríguez-Gómez (Eds.). *Proceedings of the 19th International Conference on Harmful Algae, October 10-15, 2021*. International Society for the Study of Harmful Algal Blooms, La Paz, B.C.S., Mexico, p. 93-98.

McKee, D.B., L.E. Fleming, R. Tamer, R. Weisman & D. Blythe. 2001. Physician diagnosis and reporting of ciguatera fish poisoning in an endemic area. *In*: Hallegraeff, G., S.I. Blackburn, C.J. Bolch & R. Lewis. *Proceedings of the Ninth International Conference on Harmful Algal Blooms, Hobart, Australia, 7-11 February 2000*. Intergovernmental Oceanographic Commission of UNESCO, Paris, France, pp. 451-453.

Mejía-Camacho, A.L. 2020. Caracterización morfológica y molecular de dinoflagelados del género *Amphidinium* de costas mexicanas y su actividad citotóxica. Informe final del proyecto, Licenciatura en Biología Molecular. Universidad Autónoma Metropolitana, Unidad Cuajimalpa, Ciudad de México, México. 42 p.

Mejía-Camacho, A.L., L.M. Durán-Riveroll & A.D. Cembella. 2021. Toxicity bioassay and cytotoxic effects of the benthic marine dinoflagellate *Amphidinium operculatum*. *Journal of Xenobioics* 11: 33-45. DOI: 10.3390/jox11020003

Méndez-Torres, J. 2019. Diversidad y toxicidad del género *Ostreopsis* Schmidt, 1902 (Dinophyceae) en la zona norte del Caribe Mexicano. Tesis de Maestría. Centro de Investigación Científica de Yucatán A.C., Cancún, Quintana Roo, México. 107 p.

Mendoza-Flores, A., C.E. Galindo-Sánchez & M.P. Sánchez-Saavedra. 2022. Effects of the light irradiance on the growth and lipids content of *Amphidinium carterae* (Dinophyceae) for biofuels production. *Bio-Energy Research* [9 p.], DOI:10.1007/s12155-022-10455-9

Momigliano, P., L. Sparrow, D. Blair & K. Heimann. 2013. The diversity of *Coolia* spp. (Dinophyceae Ostreopsidaceae) in the central Great Barrier Reef Region. *PLoS ONE* 8(10):e79278. DOI: 10.1371/journal.pone.0079278

Morquecho, L. & C.H. Lechuga-Devéze. 2003. Dinoflagellate cysts in recent sediments from Bahía de Concepción, Gulf of Mexico. *Botanica Marina* 46: 132-141. DOI: 10.1515/BOT.2003.014

Morquecho, L. & C.H. Lechuga-Devéze. 2004. Seasonal occurrence of planktonic dinoflagellates and cyst production in relationship to environmental variables in subtropical Bahía Concepción, Gulf of California. *Botanica Marina* 47: 313-322. DOI: 10.1515/BOT.2004.037

Morquecho, L., D.T. Góngora-González & Y.B. Okolodkov. 2009. Cyst-theca relationships of Gonyaulacales and Peridiniales (Dinophyceae) from Bahía Concepción, Gulf of California. *Acta Botanica Mexicana* 88: 9-29. https://www.scielo.org.mx/pdf/abm/n88/n88a2.pdf

Morquecho, L., I. Gárate-Lizárraga & H. Gu. 2022. Morphological and molecular characterization of the genus *Coolia* (Dinophyceae) from Bahía de La Paz, southwest Gulf of California. *Algae* 37(3): 185-204. DOI: 10.4490/algae.2022.37.9.2

Morquecho-Escamilla, L., A. Reyes-Salinas & Y.B. Okolodkov. 2016. *Illustrated taxonomic guide of the Marine Dinoflagellate Collection (CODIMAR)/Guía taxonómica ilustrada de la Colección de Dinoflagelados Marinos (CODIMAR)*. Centro de Investigaciones Biológicas del Noreste, S.C. (CIBNOR), La Paz, Baja California Sur, México. 147 p.

Muciño-Márquez, R.E., I. Gárate-Lizárraga & D.J. López-Cortés. 2015. Variación estacional del género *Prorocentrum* (Dinophyceae) en dos granjas atuneras en la Bahía de La Paz, México. *Acta Biológica Colombiana* 20(1): 195-206. DOI:10.15446/abc.v20n1.42442

Munday, R. 2008. Occurrence and toxicology of palytoxins. *In*: Botana, L.M. (Ed.). *Seafood and freshwater toxins: Pharmacology, physiology, and detection*. 2nd ed. CRC Press, Boca Raton, FL, USA, pp. 693-713.

Murray, S., T. Garby, M. Hoppenrath & B. Neilan. 2012. Genetic diversity, morphological uniformity and polyketide production in dinoflagellates (*Amphidinium*, Dinoflagellata). PLoS ONE 7(6): 1-14:e38253. DOI: 10.1371/journal.pone.0038253

Murray, S.A., G.S., Kohli, H. Farrell, Z.B., Spiers, A.R., Place, J.J., Dorantes-Aranda, & J. Ruszczyk. 2015. A fish kill associated with a bloom of *Amphidinium carterae* in a coastal lagoon in Sydney, Australia. *Harmful Algae* 49: 19-28. DOI: 10.1016/j.hal.2015.08.003

Nielsen, L.T., B. Krock & P.J. Hansen. 2013. Production and excretion of okadaic acid, pectenotoxin-2 and a novel dinophysistoxin from the DSP-causing marine dinoflagellate *Dinophysis acuta* – Effects of light, food availability and growth phase. *Harmful Algae* 23: 34-45. DOI: 10.1016/j.hal.2012.12.004

Núñez-Vázquez, E.J. 2005. Biotoxinas marinas en peces comestibles de Baja California Sur: origen, identificación y cuantificación. Tesis de Licenciatura. Universidad Autónoma de Baja California Sur, La Paz, México. 109 p.

Núñez-Vázquez E.J., A. Almazán-Becerril, A. Heredia-Tapia, D.U. Hernández-Becerril, L. Troccoli-Ghinaglia, B.O. Arredondo-Vega, J.A. Herrera-Silveira, J.L. Vázquez-Castellanos & J.L. Ochoa. 2000. Incidencia del envenenamiento por ciguatera en México. *In*: 4a Reunión de Expertos en Envenenamiento por Animales Ponzoñosos. Cuernavaca, Morelos, México.

Núñez-Vázquez, E.J., A. Almazán-Becerril, D.J. López-Cortés, A. Heredia-Tapia, F.E. Hernández-Sandoval, C.J. Band-Schmidt, J.J. Bustillos-Guzmán, I. Gárate-Lizárraga, E. García-Mendoza, C.A. Salinas-Zavala & A. Cordero-Tapia. 2019. Ciguatera in Mexico (1984-2013). *Marine Drugs* 17(1):13. DOI: 10.3390/md17010013

Núñez-Vázquez, E.J., A.P. Sierra-Beltrán, A.A. Cruz-Villacorta & J.L. Ochoa. 1998. Ciguatoxinas on serranidae and lutjanidae fish of Baja California Sur, Mexico. *In*: 12th World Congress on Animal, Plant and Microbial Toxins, Abstracts from Symposia, Cuernavaca, México, 21-26 September 1997, p. 1224.

Ochoa, J.L., A. Sánchez-Paz, A. Cruz-Villacorta, E. Núñez-Vázquez & A. Sierra-Beltrán. 1997. Toxic events in the northwest Pacific coastline of Mexico during 1992-1995: origin and impact. *Hydrobiologia* 352: 195-200. https://www.researchgate.net/publication/226929522_Toxic_events_in_the_Northwest_Pacific_coastline_of_Mexico_during_1992-1995_origin_and_impact

Okolodkov, Y.B., G. Campos-Bautista, I. Gárate-Lizárraga, J.A.G. González-González, M. Hoppenrath & V. Arenas. 2007. Seasonal changes of benthic and epiphytic dinoflagellates in the Veracruz reef zone, Gulf of Mexico. *Aquatic Microbial Ecology* 47: 223-237. DOI: 10.3354/ame047223

Okolodkov, Y.B. & I. Gárate-Lizárraga. 2006. An annotated checklist of dinoflagellates (Dinophyceae) from the Mexican Pacific. *Acta Botanica Mexicana* 74: 1-154. http://www.redalyc.org/articulo.oa?id=5740740

Okolodkov, Y.B., F. del C. Merino-Virgilio, J.A. Herrera-Silveira, S. Espinosa-Matías & M.R. Parsons. 2009. *Gambierdiscus toxicus* in the southeastern Gulf of Mexico. *Harmful Algal News*, 40: 12-14.

Okolodkov Y.B., F. del C. Merino-Virgilio, J.A. Aké-Castillo, A.C. Aguilar-Trujillo, S. Espinosa-Matías & J.A. Herrera-Silveira. 2014. Seasonal changes in epiphytic dinoflagellate assemblages near the northern coast of Yucatán Peninsula, Gulf of Mexico. *Acta Botanica Mexicana* 107: 121-151. http://www.redalyc.org/articulo.oa?id=57430483008

Okolodkov, Y.B., G. Campos-Bautista & I. Gárate-Lizárraga. 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

Orellana-Cepeda, E., C. Granados-Machuca & J. Serrano-Esquer. 2004. *Ceratium furca*: one possible cause of mass mortality of cultured blue-fin tuna at Baja California, Mexico. *In:* Steidinger, K.A., J.H. Landsberg, C.R. Tomas & G.A. Vargo (Eds.). *Harmful Algae 2002. Xth International Conference*. Florida Fish and Wildlife Conservation Commission, Florida Institute of Oceanography, and Intergovernmental Oceanographic Commission of UNESCO. St. Pete Beach, Florida, USA. pp. 514-516.

Osorio-Tafall, B.F. 1942. Notas sobre algunos dinoflagelados planctónicos marinos de México, con descripción de nuevas especies. *Anales Escuela Nacional Ciencias Biológicas* 2: 435-450.

Oyaneder-Terrazas, J., D. Figueroa, O.F. Araneda & C. García. 2022. Saxitoxin group toxins accumulation induces antioxidant responses in tissues of *Mytilus chilensis*, *Ameghinomya antiqua*, and *Concholepas concholepas* during a bloom of *Alexandrium pacificum. Antioxidants* 11:392. DOI: 10.3390/antiox11020392

Pagliara, P. & C. Caroppo. 2012. Toxicity assessment of *Amphidinium carterae*, *Coolia* cfr. *monotis* and *Ostreopsis* cfr. *ovata* (Dinophyta) isolated from the northern Ionian Sea (Mediterranean Sea). *Toxicon* 60: 1203-1214. DOI: 10.1016/j.toxicon.2012.08.005

Paniagua-Chávez, C. & M. Acosta-Ruiz. 1995. Gonadal development of *Crassostrea gigas* in Bahía San Quintín, Baja California, Mexico. *Ciencias Marinas 21:* 225-242. DOI: 10.7773/cm.v21i2.986

Parrilla-Cerrillo, M.C., J.L. Vázquez, E.O. Saldate & L.M. Nava. 1993. Brotes de toxiinfecciones alimentarias de origen microbiano y parasitario. *Salud Pública de México* 35(5): 456-463. http://www.redalyc.org/articulo-oa?id=10635505

Pelayo-Zárate, M. del C. 2019. Relación entre las bacterias asociadas al dinoflagelado *Prorocentrum lima* y la producción de toxinas diarreicas. Tesis de Licenciatura. 2019. Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, México. 57 p.

Peña-Manjarrez, J.L. G. Gaxiola-Castro & J. Helenes-Escamilla. 2009. Environmental factors influencing the variability of *Lingulodinium polyedrum* and *Scrippsiella trochoidea* (Dinophyceae) cyst production. *Ciencias Marinas* 35(1): 1-14. https://www.redalyc.org/articulo.oa?id=48013192001

Peña-Manjarrez, J.L. G. Gaxiola-Castro, J. Helenes-Escamilla & E. Orellana-Cepeda. 2001. Cysts of *Lingulodinium polyedricum*, red tide producing organisms in the Todos Santos Bay (winter-spring, 2000). *Ciencias Marinas* 27(4): 543-558. DOI: 10.7773/cm.v27i4.501

Peña-Manjarrez, J.L., J. Helenes-Escamilla, G. Gaxiola-Castro & E. Orellana-Cepeda. 2005. Dinoflagellate cysts and bloom events at Todos Santos Bay, Baja California, México, 1999-2000. *Continental Shelf Resources* 25: 1375-1393. DOI: 10.1016/j.csr.2005.02.002

Phua, Y.H., M.C. Roy, S. Lemer, F. Husnik & K.C. Wakeman. 2021. Diversity and toxicity of Pacific strains of the benthic dinoflagellate *Coolia* (Dinophyceae), with a look at the *Coolia canariensis* species complex. *Harmful Algae* 109:102120. DOI: 10.1016/j.hal.2021.102120

Poot-Delgado, C.A., E.J. Núñez-Vázquez, L.A. Barra-González, J.I. López-Ruiz & W.E. Sosa-González. 2022. Presencia de toxinas tipo ciguatoxinas en peces comerciales del litoral de Campeche, golfo de México. *In*: Memorias del Séptimo Simposio RECORECOS, 20-24 de junio de 2022, Mérida, Yucatán, pp. 40-41.

Pospelova, V., A. de Vernal & T.F. Pedersen. 2008. Distribution of dinoflagellate cysts in surface sediments from the northeastern Pacific Ocean (43–25°N) in relation to sea-surface temperature, salinity, productivity and coastal upwelling. *Marine Micropaleontology* 68: 21-48. DOI: 10.1016/j.marmicro.2008.01.008

Ramos-Santiago, A.E., C.J. Band-Schmidt, I. Leyva-Valencia, M. Muñoz-Ochoa, Y.B. Okolodkov & I.S. Santiago-Morales. 2022. Análisis morfológico y molecular de *Coolia malayensis* (Dinophyceae) y efectos de extractos de la macroalga *Dictyota dichotoma* (Phaeophyceae) en su crecimiento. *CICIMAR Oceánides* 37(1-2): 1-20.

Ramos, V. & V. Vasconcelos, V. 2010. Palytoxin and analogs: biological and ecological effects. *Marine Drugs* 8**:** 2021-2037. DOI: 10.3390/md8072021

Richlen, M.L., S.L. Morton, P.H. Barber & P.S. Lobel. 2008. Phylogeography, morphological variation and taxonomy of the toxic dinoflagellate *Gambierdiscus toxicus* (Dinophyceae). *Harmful Algae* 7: 614-629. DOI: 10.1016/j.hal.2007.12.020

Rhodes, L.L., K.F. Smith, R. Munday, A.I. Selwood, P.S. Mcnabb, P.T. Holland & M.-Y. Bottein. 2010. Toxic dinoflagellates (Dinophyceae) from Rarotonga, Cook Islands. *Toxicon* 56**:** 751-758. DOI: 10.1016/j.toxicon.2009.05.017

Rodríguez-Gómez, C.F., G., Vázquez, C.A. Maya-Lastra, J.A., Aké-Castillo, C.J., Band-Schmidt, P., Moreno-Casasola & O. Rojas-Soto. 2021. Potential distribution of the dinoflagellate *Peridinium quadridentatum* and its blooms in continental shelves globally: an environmental and geographic approach. *Marine Biology* 168: 29. DOI: 10.1007/s00227-021-03825-y

Romero-Geraldo, R.J., N. García-Lagunas & N.Y. Hernández-Saavedra. 2014. Effects of *in vitro* exposure to diarrheic toxin producer *Prorocentrum lima* on gene expressions related to cell cycle regulation and immune response in *Crassostrea gigas. PLOS One* 9(5):e97181. DOI: 10.1371/journal.pone.0097181

Romero-Geraldo, R.J., N. García-Lagunas & N.Y. Hernández-Saavedra. 2016. *Crassostrea gigas* exposure to the dinoflagellate *Prorocentrum lima*: Histological and gene expression effects on the digestive gland. *Marine Environmental Research* 120: 93-102. DOI: 10.1016/j.marenvres.2016.07.011

Romero-Geraldo, R.J. & N.Y. Hernández-Saavedra. 2014. Stress gene expression in *Crassostrea gigas* (Thunberg, 1793) in response to experimental exposure to the toxic dinoflagellate *Prorocentrum lima* (Ehrenberg) Dodge, 1975. *Aquaculture Research* 45(9): 1512-1522. DOI: 10.1111/are.12100

Sakami, T., H. Nakahara, M. Chinain & Y. Ishida. 1999. Effects of epiphytic bacteria on the growth of the toxic dinoflagellate *Gambierdiscus toxicus* (Dinophyceae). *Journal of Experimental Marine Biology and Ecology* 233: 231-246. DOI: 10.1016/S0022-0981(98)00130-0

Sepúlveda-Villarraga, M. 2017. Dinoflagelados potencialmente tóxicos asociados a macroalgas en la Bahía de La Paz, B.C.S. Tesis de Maestría. Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN), La Paz, Baja California Sur, México. 69 p.

Sierra-Beltrán, A.P., A. Cruz, E. Núñez, L.M. Del Villar, J. Cerecero & J.L. Ochoa. 1998. An overview of the marine food poisoning in Mexico. *Toxicon* 36(11): 1493-1502. DOI: 10.1016/s0041-0101(98)00139-1

Steidinger, K.A. & K. Tangen. 1996. Dinoflagellates. *In*: Tomas, C. (Ed.). *Identifying marine phytoplankton*. Academic Press, Inc., San Diego, CA, USA, pp. 387-584.

Tarazona-Janampa, U.I., A.D. Cembella, M.C. Pajares S. Pelayo-Zárate, L.M. Márquez-Valdelamar, Y.B. Okolodkov, J. Tebben & B. Krock. 2020. Associated bacteria and their effects on growth and toxigenicity of the dinoflagellate *Prorocentrum lima* species complex from epibenthic substrates along Mexican coasts. *Frontiers in Marine Science* 7:569. DOI: 10.3389/fmars.2020.00569

Tchivelekete, G.M., M. Almarhoun, Y. Cao, X. Zhou, P.E. Martin & X. Shu. 2022. Evaluation of okadaic acid toxicity in human retinal cells and zebrafish retinas. *Toxicology* 473:153209. DOI: 10.1016/j.tox.2022.153209

Vásquez-Bedoya, L.F., T. Radi, A.C. Ruiz-Fernández, A. de Vernal, M.L. Machain-Castillo, J.F. Kielt & C. Hillaire-Marcel. 2008. Organic-walled dinoflagellate cysts and benthic foraminifera in coastal sediments of the last century from the Gulf of Tehuantepec, South Pacific Coast of Mexico. *Marine Micropaleontology* 68(1-2): 49-65. DOI: 10.1016/j.marmicro.2008.03.002

Villa-Arce, G.V. 2021. Curvas de crecimiento e identificación de cepas de dinoflagelados del género *Prorocentrum* (Dinophyceae) procedentes de la Bahía de La Paz, B.C.S. México. Tesis de Licenciatura. Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México. 67 p.

Wakeman, K.C., A. Yamaguchi, M.C. Roy & H. Jenke-Kodama. 2015. Morphology, phylogeny and novel chemical compounds from *Coolia malayensis* (Dinophyceae) from Okinawa, Japan. *Harmful Algae* 44: 8–19. https://doi.org/10.1016/j.hal.2015.02.009

Wang, B., M. Yao, J. Zhou, S. Tan, H. Jin, F. Zhang, Y.L. Mak, J. Wu, L. Lai Chan & Z. Cai. 2018. Growth and toxin production of *Gambierdiscus* spp. can be regulated by quorum-sensing bacteria. *Toxins* 10:257. DOI: 10.3390/toxins10070257

Wellkamp, M., F. García-Camacho, L.M. Durán-Riveroll, J. Tebben, U. Tillmann & B. Krock. 2020. LC-MS/MS method development for the discovery and identification of amphidinols produced by *Amphidinium*. *Marine Drugs* 18: 1-22. DOI: 10.3390/md18100497

West-Eberhard, M.J. 2008. Phenotypic plasticity. *In*: Jorgensen, S.E. & B.D. Fath (Eds.). *Encyclopedia of ecology*. Elsevier, Amsterdam, The Netherlands, pp. 1701-1707.

Wu, Z., H. Luo, L. Yu, W.H. Lee, L. Li, Y.L. Mak, S. Lin, & P.K. Lam. 2020. Characterizing ciguatoxin (CTX)-and Non-CTX-producing strains of *Gambierdiscus balechii* using comparative transcriptomics. *Science of the Total Environment* 717: 137184. DOI: 10.1016/j.scitotenv.2020.137184

Yasumoto, T., N. Seino, Y. Murakami & M. Murata. 1987. Toxins produced by benthic dinoflagellates. *The Biological Bulletin* 172: 128-131. https://www.researchgate.net/publication/237583627_Toxins_Produced_by_Benthic_Dinoflagellates