

Marine biotoxins and harmful algal blooms in Mexico's Pacific littoral

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Introduction

Figure 39 summarizes the locations of harmful algal bloom (HABs) events registered in Mexico during the last 25 years (Ochoa 2002). Despite our efforts, this reflects only part of the actual HAB episodes that occurred along the Mexican coastline in this period.

The map was prepared using information collected from over 100 reports of various Mexican researchers describing their observations. These reports are found in different media, sometimes difficult to access (Table 20). Yet, one very

important conclusion of the information is that only in a handful of cases has the nature of the toxins, the causative organisms, and/or the implicated ecological and socioeconomic impacts been studied in detail. In these records, very little information is provided about the conditions that triggered the sudden proliferation of noxious microalgal blooms along the Mexican coast. Analyzing the data displayed in Figure 39 and listed in Table 20 together, it can be observed that various reports correspond to the same location. This does not imply that a given “red tide” event was repeatedly reported, rather that such a location was hit several times within the studied period.

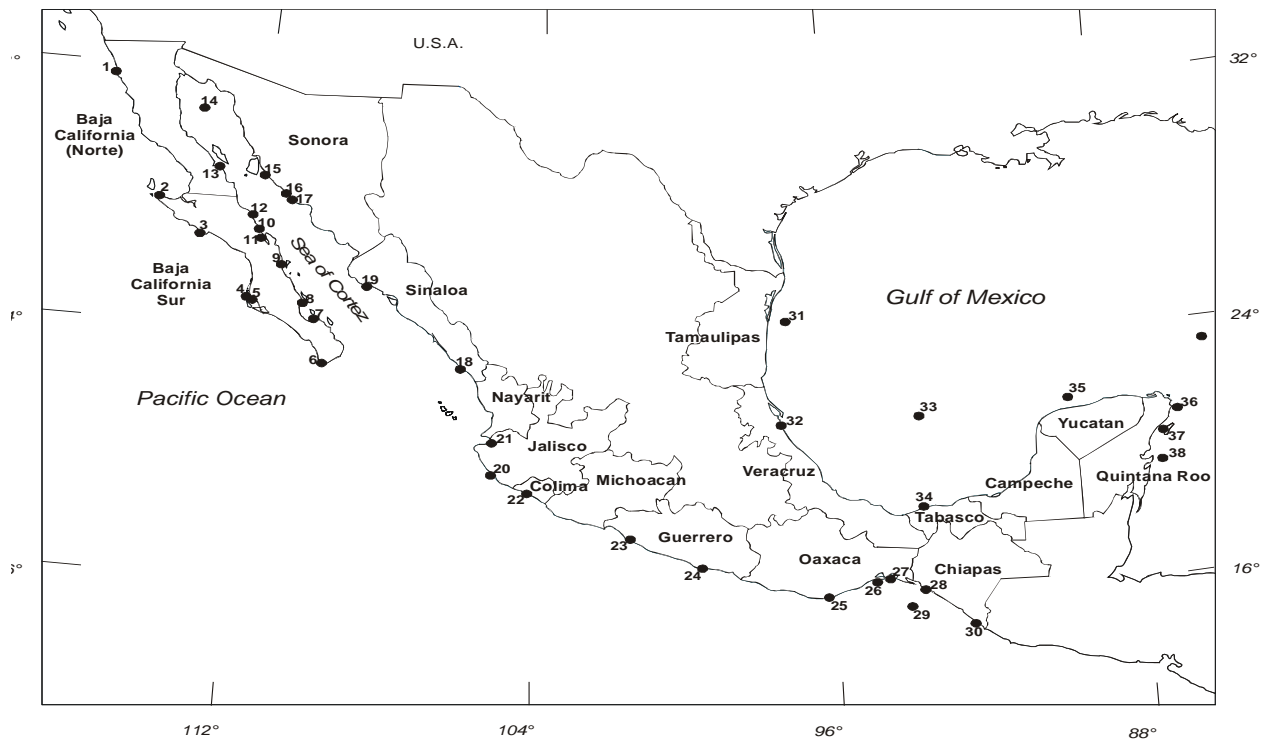


Fig. 39 Locations of the Mexican littoral affected by “red tides” in recent years.

Also, considering the proportion of detected events, it would seem that the Pacific coast had more HAB events than the Gulf of Mexico and the Caribbean together. However, this may be just a result of more research activity in the Pacific region than in the rest of Mexico. In other words, we lack evidence to support the idea that the Mexican Pacific shoreline is more susceptible to HAB episodes than the rest of the Mexican littoral.

It is also interesting to note in Table 20 that at least 39 different dinoflagellate and diatom species have been associated with “red tides” in the Mexican littoral. Of these, some are known to produce toxins (Table 21) and can provoke human seafood poisoning through various vectors (Table 22). Following, some examples are discussed.

Amnesic shellfish poisoning (ASP) in Mexico

HAB events in the Pacific coastline of Mexico have been studied at CIBNOR for the last 12 years. During this period, not only toxins, but also causative organisms in different events have been identified.

The most notorious events involved high mortality of fish, sea birds, and sea mammals, provoked by domoic acid, the toxin responsible for ASP (Ochoa *et al.* 1996, 1997a; Sierra-Beltrán *et al.* 1997). Such events occurred at the tip of the Baja California Peninsula and in the upper Gulf of California in the winter of 1996, and again in 1997. We were able to identify the causative organisms as members of the *Pseudo-nitzschia* genus, and in one case, as *P. australis* (Ochoa *et al.* 1997a). Because previous records indicate its presence in the Gulf of California (Cortés-Altamirano *et al.* 1996), and because of its ability to proliferate under certain oceanographic conditions such as “El Niño” and “La Niña” (Sierra-Beltrán *et al.* 1999), *P. australis* is a suitable candidate for ASP-monitoring in Mexico. In fact, time series analysis have shown that a cooling trend of the water in the upper Gulf of California during the period 1993-1997 (Beier 1997) could have played an important role in ASP outbreaks in this region.

Ciguatera toxin (CTX) and diarrhetic shellfish poisoning (DSP) in Mexico

DSP has not been acknowledged in Mexico by health authorities, although a high incidence of undiagnosed, non-infectious, seafood-related diarrhea events are found in the epidemiological records of the Health Ministry (Ochoa *et al.* 1998a). The presence of toxic species causing DSP (such as *Dinophysis* spp. and *Prorocentrum* spp.) has been well established along much of the Mexican littoral. Therefore, this coastline should be considered a DSP risk area. Incidents where fishermen have been poisoned after eating fish belonging to the Serranidae and Lutjanidae families, at Rocas Alijos (Lechuga and Sierra-Beltrán 1995), and Isla El Pardito (Heredia-Tapia *et al.* 2002), have been linked to “ciguatera,” rather than to DSP events. Therefore, further work is necessary to clarify which toxins are affecting the Pacific marine resources. If CTX at Rocas Alijos is confirmed, this will present a new record for a northerly latitude at which the risk of such fish poisoning occurs. On the other hand, if this event and the one reported at El Pardito Island is considered a DSP case, then we can declare that DSP is indeed impacting Mexico’s coastal population. As proof, the dinoflagellate *Prorocentrum lima*, associated elsewhere with CTX and DSP cases, was isolated from Isla El Pardito (Heredia-Tapia *et al.* 2002). This isolate has been shown to be smaller, different in toxin composition (at least two components remain to be identified), distinct in toxin profile (dinophysin toxin: okadaic acid ratio is 2:1), and is more toxic than related species. All these properties point to adaptations to local environmental conditions that reinforce the idea of geographic toxic variability within the same species.

Paralytic shellfish poisoning (PSP) in Mexico

PSP is also present along the Pacific littoral of Mexico (Sierra-Beltrán *et al.* 1996; Ochoa *et al.* 1998b). In Mexico, all cases of hospitalization and human casualties recorded after consuming oysters, mussels, or clams, were PSP-related. Either *Gymnodinium catenatum* or *Pyrodinium*

Table 20 “Red tide” forming microalgae in the Mexican littoral.

Species	Location	Reference
<i>Alexandrium catenella</i>	Baja California Sur: Concepción Bay.	Gárate-Lizárraga, 1996; Herrera-Silveira, 1999; Lechuga-Deveze <i>et al.</i> , 2000.
<i>Alexandrium monilatum</i> (= <i>Gonyaulax monilata</i>)	Sinaloa: Mazatlán Bay.	Cortés-Altamirano and Núñez-Pastén, 1992.
<i>Ceratium sp</i>	Jalisco: Banderas Bay Oaxaca: Laguna Superior.	Cortés-Altamirano <i>et al.</i> , 1996.
<i>Ceratium dens</i>	Baja California.	Blasco, 1977.
<i>Ceratium furca</i>	Baja California: Ensenada Baja California Sur: Concepción Bay Sinaloa: Mazatlán Bay Colima: Manzanillo Tabasco: Del Carmen Lagoon.	Blasco, 1977; Cortés-Altamirano <i>et al.</i> , 1995, 1996; Herrera-Silveira, 1999; Lechuga-Deveze <i>et al.</i> , 2000; Orellana-Cepeda <i>et al.</i> , 1993.
<i>Ceratium fusus</i>	Baja California Sur: Concepción Bay	Lechuga-Deveze <i>et al.</i> , 2000.
<i>Ceratium tripos var. ponticum</i>	Baja California Sur: Concepción Bay Sinaloa: Mazatlán Bay.	Cortés-Altamirano <i>et al.</i> , 1995; Herrera-Silveira, 1999; Lechuga-Deveze <i>et al.</i> , 2000;
<i>Chatonella sp.</i>	Baja California Sur: Cabo San Lucas.	Herrera-Silveira, 1999.
<i>Cochlodinium catenatum</i>	Baja California: Ensenada	Orellana-Cepeda <i>et al.</i> , 1993.
<i>Dinophysis acuminata</i>	Baja California: Ensenada	Orellana-Cepeda <i>et al.</i> , 1993.
<i>Dynophysis caudate</i>	Baja California Sur: Concepción Bay.	Morquecho-Escamilla <i>et al.</i> , 1997; Lechuga-Deveze <i>et al.</i> , 2000.
<i>Gambierdiscus toxicus</i>	Baja California Sur: Rocas Alijos (?), El Pardito Gulf of California(?) Quintana Roo: Isla Mujeres, Cozumel.	Cortés-Altamirano, <i>et al.</i> , 1966; Herrera-Silveira, 1999; Heredia-Tapia <i>et al.</i> , 2002.
<i>Gonyaulax sp.</i>	Sonora: Bacochibampo Sinaloa: Mazatlán, Nayarit.	Cortés-Altamirano <i>et al.</i> , 1995; Herrera-Silveira, 1999.
<i>Gonyaulax catenella</i>	Oaxaca: Salina-Cruz Huatulco.	Saldate-Castañeda <i>et al.</i> , 1991.
<i>Gonaulax digitale</i>	Baja California.	Blasco 1977.
<i>Gonyaulax polyedra</i>	Baja California: San Hipólito Baja California Sur.	Blasco. 1977; Cortés-Altamirano <i>et al.</i> , 1996; Gárate-Lizárraga, 1996; Orellana-Cepeda <i>et al.</i> , 1993.
<i>Gonyaulax polygramma</i>	Baja California: Los Angeles Bay Gulf of California.	Cortés-Altamirano <i>et al.</i> , 1996; Herrera-Silveira, 1999.
<i>Gonyalax triacantha</i>	Sinaloa: Mazatlán.	Cortés- Altamirano <i>et al.</i> , 1995; Herrera-Silveira, 1999.
<i>Gonyaulax verior</i>	Baja California Sur: Concepción Bay.	Morquecho-Escamilla <i>et al.</i> , 1997.
<i>Gymnodonium catenatum</i>	Sonora: Bacochibampo, Guaymas Sinaloa: Mazatlán Baja California Sur: Concepción Gulf of California Oaxaca: Salina-Cruz Huatulco	Cortés-Altamirano <i>et al.</i> , 1995, 1996; Gárate-Lizárraga, 1996; Herrera-Silveira, 1999; Saldate-Castañeda <i>et al.</i> , 1991.
<i>Gymnodinium breve</i> = <i>Ptychodiscus brevis</i>	Veracruz	Cortés-Altamirano <i>et al.</i> , 1996.
<i>Gymnodinium peridinium</i>	Guerrero: Acapulco, Puerto Marquéz	Cortés-Altamirano <i>et al.</i> , 1996.
<i>Gymnodinium sanguineum</i>	Baja California: San Hipólito Baja California Sur: Tortugas Bay, Magdalena Bay, Concepción Bay	Cortés-Altamirano <i>et al.</i> , 1996; Gárate-Lizárraga, 1996; Herrera-Silveira, 1999; Orellana-Cepeda <i>et al.</i> , 1993.

Species	Location	Reference
<i>Gymnodinium splendens</i>	Sinaloa: Mazatlán Jalisco: Chametla	Cortés-Altamirano <i>et al.</i> , 1996; Herrera-Silveira, 1999.
<i>Gymnodinium tripos</i> var. <i>ponctic.</i>	Sinaloa: Mazatlán	Cortés-Altamirano <i>et al.</i> , 1996.
<i>Mesidinium rubrum</i>	Sinaloa: Mazatlán Gulf of California Baja California Sur: La Paz Bay Oaxaca: Barra de San, Francisco, Zicatella Bay, Puerto Escondido, Tonalá	Alonso-Rodríguez <i>et al.</i> , 1999; Cortés-Altamirano <i>et al.</i> , 1995, 1996; Gárate-Lizárraga, 1996; Herrera-Silveira, 1999.
<i>Nitzschia</i> spp	Guerrero: Zihuatanejo.	Cortés-Altamirano <i>et al.</i> , 1996.
<i>Nitzschia pungens</i>	Baja California: Ensenada Bay.	Orellana-Cepeda <i>et al.</i> , 1993.
<i>Noctiluca scintillans</i>	Baja California: Ensenada Sonora: Bacochibampo Baja California Sur: Mulegé, Loreto, Concepción Bay Jalisco: Banderas Bay Oaxaca: Salina Cruz	Cortés-Altamirano <i>et al.</i> , 1995, 1996; Gárate-Lizárraga, 1996; Herrera-Silveira, 1999; Morquecho-Escamilla <i>et al.</i> , 1997; Orellana-Cepeda <i>et al.</i> , 1993;
<i>Oscillatoria erythraea</i>	Baja California Sur: La Paz, Concepción Bay Sinaloa: Mazatlán	Cortés-Altamirano <i>et al.</i> , 1995; Gárate-Lizárraga, 1996; Herrera-Silveira, 1999; Morquecho-Escamilla <i>et al.</i> , 1997;.
<i>Proboscia alata</i>	Baja California Sur: Magdalena Bay	Gárate-Lizárraga and Siqueiros-Beltrones, 1998.
<i>Prorocentrum</i> spp.	Sonora: Bachohibampo, Baja California Sur Jalisco: Chametla Oaxaca: Laguna Superior	Cortés-Altamirano <i>et al.</i> , 1995, 1996; Gárate-Lizárraga, 1996.
<i>Prorocentrum dentatum</i>	Sonora: Bacochibampo	Cortés-Altamirano <i>et al.</i> , 1995.
<i>Prorocentrum micans</i>	Baja California: San Hipólito Baja California Sur: Concepción Bay	Blasco, 1977; Herrera-Silveira, 1999; Lechuga-Devéze <i>et al.</i> , 2000; Orellana-Cepeda <i>et al.</i> , 1993.
<i>Prorocentrum minimum</i>	Sinaloa: Mazatlán Bay	Cortés-Altamirano <i>et al.</i> , 1996; Lechuga-Devéze <i>et al.</i> , 2000.
<i>Prorocentrum compressum</i>	Baja California Sur: Concepción Bay	Lechuga-Devéze <i>et al.</i> , 2000.
<i>Prorocentrum lima</i>	Baja California Sur: Isla El Pardito	Heredia-Tapia <i>et al.</i> , 2002.
<i>Prorocentrum mexicanum</i>	Baja California Sur: Concepción Bay	Lechuga-Devéze <i>et al.</i> , 2000; Morquecho-Escamilla <i>et al.</i> , 1997;
<i>Pseudonitzschia</i> sp.	Baja California Sur: Cabo San Lucas, Loreto	Herrera-Silveira, 1999; Sierra-Beltrán <i>et al.</i> , 1997.
<i>Ptychodiscus brevis</i>	Tamaulipas-Veracruz, Gulf of México, Yucatán	Cortés - Altamirano <i>et al.</i> , 1996; Herrera-Silveira, 1999.
<i>Pyrodinium bahamense</i> var. <i>bahamense</i>	Veracruz: Tamiahua Lagoon Gulf of México Mexican Caribbean	Cortés -Altamirano <i>et al.</i> , 1996; Gómez-Aguirre and Licea, 1998; Herrera - Silveira, 1999.
<i>Pyrodinium bahamense</i> var. <i>compressum</i>	Guerrero: Acapulco Oaxaca: Salina Cruz, Huatulco Chiapas: Puerto Madero	Cortés -Altamirano <i>et al.</i> , 1996; Herrera-Silveira, 1999; Ramírez- Camarena <i>et al.</i> , 1996; Sotomayor -Navarro and Domínguez-Cuellar, 1993.
<i>Scriptsiella trochoidea</i>	Baja California: Ensenada Sinaloa: Mazatlán Bay	Alonso-Rodríguez <i>et al.</i> , 1999; Cortés - Altamirano <i>et al.</i> , 1995; Orellana - Cepeda <i>et al.</i> , 1993.
<i>Skeletonema costatum</i>	Sinaloa: Mazatlán Bay	Herrera-Silveira, 1999.
<i>Stephanopyxis palmeriana</i>	Sonora: Kino Bay Gulf of California	Molina <i>et al.</i> , 1996.

Table 21 Potentially harmful microalgae present in the Pacific littoral of Mexico.

Group	Species	Reference
Dinoflagellate		
	<i>Amphidinium carterae</i> Hulburt	Licea <i>et al.</i> , 1995
	<i>Ceratium fusus</i> (Ehrenberg) Dujardin var. <i>fuscus</i>	Hernández-Becerril, 1989
	<i>Cochlodinium polykrikoides</i> Margalef ?	Morales-Blake, Cavazos Guerra y Hernández-Becerril, 2001
	<i>Dinophysis fortii</i> Pavillard	Hernández-Becerril, 1988
	<i>Dinophysis mitra</i> (Schütt) Abé	Hernández-Becerril, 1988
	<i>Dinophysis rotundata</i> Claparede et Lachmann	Hernández-Becerril, 1988
	<i>Dinophysis tripos</i> Gourret	Hernández-Becerril, 1988
	<i>Lingulodinium polyedrum</i> (Stein) Dodge (<i>Gonyaulax polyedra</i> Stein)	Hernández-Becerril, 1988
Haptophytes		
	<i>Phaeocystis pouchetii</i> (Hariot) Lagerheim	Hernández-Becerril <i>et al.</i> , (unpublished)
Bacillariophytes (Diatoms)		
	<i>Cerataulina pelagica</i> (Cleve) Hendeby	Hernández-Becerril, 1987
	<i>Chaetoceros concavicornis</i> Mangin	Hernández-Becerril, 1996
	<i>Chaetoceros convolutus</i> Castracane	Hernández-Becerril, 1996
	<i>Coscinodiscus centralis</i> Ehrenberg	Hernández-Becerril, 2000
	<i>Coscinodiscus concinnus</i> Smith	Hernández-Becerril, 2000
	<i>Coscinodiscus walesii</i> Gran et Angst	Hernández-Becerril, 2000
	<i>Pseudo-nitzschia delicatissima</i> (Cleve) Heiden in Heiden et Kolbe	Cortés Altamirano & Hernández-Becerril, 1998
	<i>Pseudo-nitzschia pseudodelicatissima</i> (Hasle) Hasle	Cortés Altamirano & Hernández-Becerril, 1998
	<i>Thalassiosira diporocyclus</i> Hasle	Cortés Altamirano & Hernández-Becerril, 1998
	<i>Thalassiosira mala</i> Takano	Hernández-Becerril & Tapia Peña, 1995
	<i>Thalassiosira minuscula</i> Krasske	Hernández-Becerril & Tapia Peña, 1995
	<i>Thalassiosira subtilis</i> (Ostenfeld) Gran	Hernández-Becerril & Tapia Peña, 1995
Raphidophytes		
	<i>Heterosigma akashiwo</i> (Hada) Hada ex Hara et Chihara	Hernández-Becerril & Bravo Sierra
Cyanophytes		
	<i>Trichodesmium erythraeum</i> Ehrenberg	Cortés-Altamirano y Hernández-Becerril, 1998
	<i>Trichodesmium hildebrandtii</i> Gomont	Cortés-Altamirano y Hernández-Becerril, 1998
	<i>Trichodesmium thiebautii</i> Gomont ex Gomont	Cortés-Altamirano y Hernández-Becerril, 1998

Table 22 Seafood poisoning caused by marine biotoxins in Mexico.

Location	Edible organism (Common name)	Edible organism (Scientific name)	Toxin	Reference
Baja California Sur: Concepción Bay	White clam	<i>Diosinia ponderosa</i>	PSP	Sierra-Beltrán <i>et al.</i> , 1996.
Baja California Sur: Concepción Bay San Carlos Magdalena Bay	Catarina Clam	<i>Argopecten ventricosus</i>	PSP	Sierra-Beltrán <i>et al.</i> , 1996.
Baja California Sur: La Paz	Almeja Chocolate	<i>Megapitaria aurantiaca</i>	PSP	Sierra-Beltrán <i>et al.</i> , 1998.
Baja California Sur: Concepción Bay Santa Rosalía	Callo de hacha	<i>Pinna rugosa</i>	PSP	Sierra-Beltrán <i>et al.</i> , 1996.
Baja California Sur: Concepción Bay	Almeja voladora	<i>Pecten vogdesi</i>	PSP	Sierra-Beltrán <i>et al.</i> , 1996.
Gulf of Tehuantepec	Goose barnacle	<i>Pollicipes polinerus</i>	PSP	Sotomayor-Navarro and Domínguez- Cuellar, 1993.
Baja California Sur: Concepción Bay	Choros	<i>Modiolus capax</i>	PSP	Sierra-Beltrán <i>et al.</i> , 1996.
Chiapas Oaxaca Guerrero Gulf of Tehuantepec	Mejillón	<i>Choromytilus palliopuncyayus</i> and <i>Mytilus sp</i>	PSP	Saldade-Castañeda <i>al.</i> , 1991; Sotomayor-Navarro and Domínguez-Cuellar, 1993.
Baja California Sur: Concepción Bay	Ostión	<i>Crasostrea palmula</i>	PSP	Sierra-Beltrán <i>et al.</i> , 1996.
Campeche, Chiapas Guerrero, Oaxaca Quintana Roo, Tabasco Tamaulipas, Veracruz Yucatán	Ostión	<i>Crasostrea virginica</i>	PSP?	Saldade-Castañeda, <i>al.</i> , 1991; Gómez-Aguirre and Licea , 1998.
Guerrero: Acapulco Gulf of Tehuantepec Michoacán	Ostión	<i>Ostrea iridiscens</i>	PSP	Ramírez-Camarena <i>et al.</i> , 1996; Sotomayor-Navarro and Domínguez-Cuellar, 1993.
Quintana Roo	Barracuda fish	<i>Sphyraena sp.</i>	CTX	Cortés-Altamirano <i>et al.</i> , 1996; Sierra-Beltrán <i>et al.</i> , 1998.
Baja California Sur	Pargo, snapper and grouper fish	<i>Lutjanus sp.</i> <i>Seranidae sp.</i> <i>labridae sp.</i> <i>Mycteroperca prionura,</i> <i>Lutjanus colorado.</i>	CTX? Okadaic acid and DTX-1	Parrilla- Cerrillo <i>et al.</i> , 1993; Heredia-Tapia <i>et al.</i> , 2002.
Baja California Sur Gulf of California	Mackerel Sardine	<i>Scomber japonicus</i> <i>Sardinops sagax</i>	ASP ASP	Sierra-Beltrán <i>et al.</i> , 1997. Ochoa <i>et al.</i> , 1998; SEMARNAPROFEPA, 1997.
Gulf of California	Puffer fish, Bullseye puffer, lobeskin puffer, Guineafowl puffer, spined sharpnose puffer	<i>Sphoeroides annulatus,</i> <i>S. lobatus,</i> <i>Arothron melagris,</i> <i>Canthigaster punctatissima,</i> <i>Sphaeroides sp.</i>	TTX	Ochoa <i>et al.</i> , 1997; Nuñez- Vázquez <i>et al.</i> , 2000.

bahamense var. *compressum* have been clearly identified as the causative organisms in all cases. It is interesting that *G. catenatum* has a maximum distribution from the upper Gulf of California to Acapulco, a range of about 13° of latitude (2200 km of coastline), while *P. bahamense* var. *compressum* has a maximum distribution from Costa Rica to Manzanillo, a range of about 8° of latitude (2200 km of coastline). Both species share a transition zone, between Manzanillo and Zihuatanejo, but do not appear to occur at the same time. The southern expansion of *G. catenatum* and the northern expansion of *P. bahamense* are responses to the influence and mixing of different coastal currents along the western Mexican coastline. It is noteworthy that the majority of *G. catenatum* outbreaks occur in Mazatlán Bay. This area may be considered as a “PSP-spreading center” from which cells are carried southward by the California Current. *P. bahamense* var. *compressum*, on the other hand, seems to originate from a center near Costa Rica and is carried northward by the Panama Current. The impact of ENSO events has a direct influence on the distribution of the two species, which is dictated by the mixing zone or front where the Panama Current encounters the California Current. A deeper study on the links between environmental changes and algal physiology may shed more light on the causes, distribution, and frequency of such noxious blooms.

Marine cyanotoxins in Mexico

The risk of harmful marine cyanobacteria blooms in aquaculture has been recognized during several incidents affecting the shrimp farms of northwestern Mexico in which blooms of *Schizothrix calcicola* were observed. To determine the noxious role of this organism, we ran several experiments and found that *S. calcicola* caused lesions in the gut of exposed post-larval white shrimp (*Litopenaeus vannamei*) interfering with food absorption. The exposed shrimp grew slower and were more prone to be attacked by infectious agents that could induce death (Pérez-Linares *et al.* 2002).

Other fish toxins in Mexico

In addition to suspected DSP and ciguatera cases, some fish poisoning events in Mexico are caused by tetrodotoxin (TTX) in various tissues of edible puffer fish (Tetrodontidae) species. TTX is not produced by harmful algal species but is included here for completeness. Fortunately, poisoning cases involving this toxin are less frequent in Mexico than in Japan. At least 5 edible species of puffer fish are found along the Pacific littoral of Mexico. About 700 tons are harvested every year, and yet only 18 casualties have been registered in the state of Baja California Sur in the past 30 years. Interestingly, the analysis of the various species (*Arothron meleagris*, *Spheroides annulatus*, *S. lispus*, *S. lobatus* and *Canthigaster punctatissima*) revealed that different tissues (mucus, muscle, liver, gonad, and intestine) possess distinct degrees of toxicity (Nuñez-Vázquez *et al.* 2000). In the case of *A. meleagris* and *S. lispus*, for example, the toxicity of the muscle is so high that its consumption should be avoided. The safest species in this family seems to be *Spheroides lobatus*, yet its mucus tested positive for toxin in the mouse bioassay. A conclusion of that work was a suggestion to the Fishery Department and Health Ministry to advise the population of the risk of eating pufferfish, which many consider a delicacy.

Relationship between “El Niño” and the pattern of incidence of HABs in Mexico

In the Gulf of California, there seems to be a positive relationship between occurrences of El Niño events and outbreaks of HAB (Ochoa and Lluch-Cota 2001). In other areas of Mexico, the opposite relationship is true. This is an important problem to approach, and additional attention should be paid to understand and isolate anthropogenic and natural mechanisms underlying HABs (Ochoa *et al.* 1998; Sierra-Beltrán *et al.* 1998).

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