ARTICLE

Annual cycle of phytoplankton with emphasis on potentially harmful species in oyster beds of Términos Lagoon, southeastern Gulf of Mexico

Ciclo anual del fitoplancton con énfasis en las especies potencialmente nocivas en bancos ostrícolas de la laguna de Términos, sureste del Golfo de México

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Resumen.- Para definir la composición de la comunidad fitoplanctónica con énfasis en las especies nocivas en los bancos ostrícolas de la laguna de Términos, SE del Golfo de México, 6 sitios de muestreo fueron monitoreados mensualmente desde agosto 2012 a septiembre 2013. Se midió la temperatura del agua, salinidad, potencial de hidrógeno, saturación de oxígeno, nutrientes inorgánicos y la abundancia de fitoplancton. La temperatura y la salinidad se caracterizaron por diferencias estacionales marcadas. Los valores de pH y saturación de oxígeno sugirieron un predominio de la actividad fotosintética. La comunidad fitoplanctónica se caracterizó por el predominio de nanoflagelados y diatomeas. La abundancia de fitoplancton y su variación estacional presentaron los valores mínimos (10^3 células L^{-1}) durante la época de secas (febrero-mayo) y valores altos (10^6 células L^{-1}) durante la temporada de lluvias (junio-septiembre). Otra característica importante de la comunidad fitoplanctónica fue la presencia de especies de dinoflagelados nocivos: *Akashiwo sanguinea*, *Karenia* cf. *mikimotoi*, *Pyrodinium bahamense* var. *bahamense*, *Prorocentrum mexicanum* y *P. minimum*. Las cianobacterias *Anabaena* y *Cylindrospermopsis cuspis* alcanzaron abundancias de 1.9×10^6 y 1.3×10^6 células L^{-1}, respectivamente. Los géneros *Alexandrium* y *Pseudo-nitzschia* estuvieron presentes, pero los taxones no fueron identificados a nivel de especie. En conclusión, la comunidad fitoplanctónica se somete a cambios en la composición de especies y en la estructura de la comunidad durante cada temporada climática, en respuesta a la variación ambiental, que permite el desarrollo de la comunidad fitoplanctónica de acuerdo a las condiciones imperantes.

Palabras clave: Cambios estacionales, cianobacterias, diatomeas, dinoflagelados, lagunas costeras

Abstract.- To define the composition of the phytoplankton community, with an emphasis on harmful species, 6 stations were monitored monthly in the oyster beds of Términos Lagoon, SE Gulf of Mexico, from August 2012 to September 2013. Water temperature, salinity, hydrogen potential, oxygen saturation, inorganic nutrients and abundance of phytoplankton were determined. Temperature and salinity were characterized by marked seasonal differences. The pH values and the oxygen saturation suggest a predominance of photosynthetic activity. The phytoplankton community was characterized by the dominance of nanoflagellates and diatoms. The abundance and seasonal variation of phytoplankton showed minimum values (10^3 cells L^{-1}) during the dry season (February-May) and high values (10^6 cells L^{-1}) during the rainy season (June-September). Another significant feature of the phytoplankton community was the presence of the harmful dinoflagellate species *Akashiwo sanguinea*, *Karenia* cf. *mikimotoi*, *Pyrodinium bahamense* var. *bahamense*, *Prorocentrum mexicanum* and *P. minimum*. The cyanobacteria *Anabaena* and *Cylindrospermopsis cuspis* reached abundance of 1.9×10^6 and 1.3×10^6 cells L^{-1}, respectively. The genera *Alexandrium* and *Pseudo-nitzschia* were present, but the taxa were not identified to the species level. In conclusion, the phytoplankton community undergoes changes in both species composition and structure of the community during each climatic season, in response to environmental variation, which allows the development of the phytoplankton community according to the conditions.

Key words: Seasonal changes, cyanobacteria, diatoms, dinoflagellates, coastal lagoons

Introduction

The worldwide increase in the occurrence and impact of harmful algal bloom (HABs) events (Anderson *et al.* 2002) has frequently been attributed to, either directly or indirectly, enhanced cultural eutrophication (Glibert *et al.* 2005, 2006; GEOHAB 2006, Kudela *et al.* 2008). Over the past decade, concern has grown over the possible role of toxic or other harmful algae in the increasing number of aquatic animals' health problems detected in several economic activities, such as aquaculture, fisheries and coastal tourism (Hallegraeff 2002, Smayda 2002, Hallegraeff *et al.* 2003, Landsberg *et al.* 2006, Núñez-Vázquez *et al.* 2011, Phlips & Badylak 2012). In Mexico, a recent review of the current status of HABs documents an increase in the number of records and reports of harmful algal species (Band-Schmidt *et al.* 2011).

Términos Lagoon is one of the key ecosystems in the southern Gulf of Mexico and has been the focus of both national and international attention because of its ecological and economic importance and because of the potential impact on this ecosystem exerted by human activities such as urban development, agricultural, oil and gas activities, overfishing, dredging, deforestation and scarcity of freshwater (Yáñez-Arancibia & Day 2005).

Términos Lagoon is characterized by high primary productivity and it is considered the most important breeding ground for several shrimp and finfish species (García-Ríos *et al.* 2013); extensive oyster reefs are located near the mouths of rivers flowing into the lagoon, mainly in the areas of brackish water along the fluvial Pom-Atasta-lagoon system (Fig. 1). This fluvial-lagoon system is connected with Términos Lagoon and it is a storage area; along with freshwater, the fluvial system transports sediment, organic matter, nutrients and organisms to the to the lagoon (Rojas-Galavíz *et al.* 1990, Bach *et al.* 2005, Muciño-Márquez *et al.* 2014).

There are few studies of the phytoplankton community of fluvial-lagoon systems adjacent to Términos Lagoon. Barreiro-Güemes & Aguirre-León (1999) conducted a study on the spatial-temporal distribution of phytoplankton biomass, reporting an average chlorophyll *a* concentration of 19.86 mg m^{-3}. Suárez-Caabro & Gómez-Aguirre (1965) and Gómez-Aguirre (1974) reported the genera *Coscinodiscus* Ehrenb., *Biddulphia* S.F. Gray, *Chaetoceros* Ehrenb., *Rhizosolenia* Brightw., *Nitzschia* Hassall, *Ceratium* Schrank and *Protoperidinium* Bergh as the main taxonomic groups in Boca Atasta and Boca Chica. Muciño-Márquez *et al.* (2014) presented the results of a two-day survey in Pom-Atasta and Palizada del Este, in February 2011, recorded that *Cylindrotheca closterium* was the most abundant species in both systems, with an abundance of 5.3×10^4 cells L^{-1}. Furthermore, in the course of an annual investigation, conducted from July 2012 to May 2013, Poot-Delgado *et al.* (2013) reported that phytoplankton abundance and seasonal variation showed minimum values (10^3 cells L^{-1}) during the rainy season (July-October) and high values (10^6 cells L^{-1}) during the windy season (November-February). Additionally, the presence of the harmful dinoflagellate species *Pyrodinium bahamense* var. *bahamense*, *Prorocentrum hoffmanianum*, *P. mexicanum* y *P. minimum* was noted.

In the present study, unlike in all previous ones performed in Términos Lagoon, we followed seasonal changes in species composition, with an emphasis on major taxonomic groups and potentially harmful species, based on the analysis of monthly samples taken from August 2012 to September 2013. The purpose of this study was to characterize the phytoplankton community and to determine the physical-chemical factors that favor the presence of harmful species throughout an annual cycle.

Material and methods

The present study was conducted in the areas of extraction of bivalve molluscs in the Lagoon of San Carlos and Puerto Rico subsystem in Términos Lagoon (Fig. 1a), located 30 km west of Ciudad del Carmen, state of Campeche (18°33-38'N, 92°01'-14'W). The area is characterized by 3 meteorological seasons: dry from February to May, rainy from June to September and windy from October to January (Yáñez-Arancibia & Day 1988, Ramos-Miranda *et al.* 2006). Monthly sampling was performed in 6 oyster banks (2-m depth), from August 2012 to September 2013 (Fig. 1b).

At each site, surface seawater samples were collected with a plastic bottle; an aliquot of 100 ml was used to analyze cell abundances for phytoplankton taxa (Lindahl 1986). Samples were fixed *in situ* with an alkaline solution of iodine (Utermöhl 1958) and subsequently preserved by adding 4% neutralized formalin (Throndsen 1978). Additionally, circular horizontal tows were performed for 5 min with a conical hand net, 20 μm mesh size, at each sampling site. The collected material was placed in glass vials and fixed using the same procedure as for the quantitative analysis to identify the phytoplankton taxa. *In situ* temperature (°C), salinity, pH and oxygen saturation
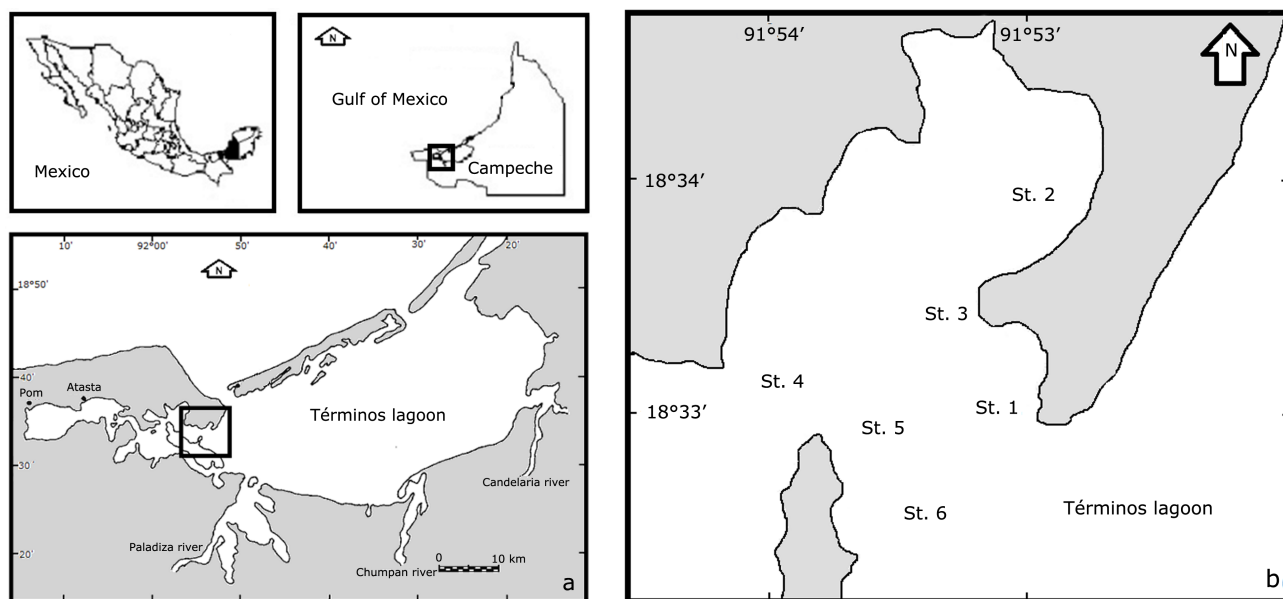
Figure 1. a) Study area and b) location of sampling stations / a) Zona de estudio y b) localización de las estaciones de muestreo

(%) were measured on-board using a HANNA Multiparameter probe, model HI9828, with sensor model HI769828 and a HACH Multiparameter probe, model HQ40d (HANNA Instruments Inc., Woonsocket, Rhode Island, USA). Orthophosphate (P-PO$_4^{3-}$), ammonium (N-NH$_4^+$), nitrite (N-NO$_2^-$), nitrate (N-NO$_3^-$) and silicate (Si-SiO$_2^{4-}$) analyses were performed following Strickland & Parsons (1972).

Identification and quantification of phytoplankton cells were performed according to the Utermöhl technique (Utermöhl 1958), taking 10 cm^3 of a sample and using inverted microscope Carl Zeiss Axio Observer.A1 equipped with phase contrast objectives (10x/0.25 Ph1 ADL and LD 20x/0.30 Ph1). Nanoflagellates (< 20 µm), due to their small size, were not identified to species level, nor were autotrophic and heterotrophic nanoflagellates distinguished. Abundance values were expressed as cells L^{-1}. Observation and identification of phytoplankton species were performed on fixed samples with a Motic compound microscope equipped with planachromatic objectives 4x/0.10, 10x/0.25, 20x/0.40, 40x/0.65 and 100x/ 1.25, using specialized taxonomic literature.

The hypothesis of differences among months and among sampling stations was tested by analysis of variance, and Tukey TSD (Truly Significant Difference) was applied with a significance level of 0.05 (Daniel 1993).

The normality of the recorded data was assessed by the Kolmogorov-Smirnov test and homoscedasticity with the Bartlett's test (Garson 2012). The calculation routine was performed with Statgraphics Centurion XV program, version 18.2.06.

To determine the main environmental factors affecting the distribution patterns of phytoplankton groups of species in the oyster banks, canonical correspondence analysis (CCA) was performed using a matrix of environmental factors and abundances of species (Ter Braak 1986). Data were transformed to Log $_{10}$ (data + 1) before analysis, because 1) data did not follow a normal distribution, and 2) a large difference in magnitude between the values of biological and physical-chemical data occurred. The significance of the axes of the CCA was tested using a Monte Carlo analysis with 199 permutations. The calculation routine was performed using the CANOCO program, version 201.4.56.

RESULTS

TEMPERATURE, SALINITY, OXYGEN SATURATION AND pH

Temperature in the study area showed a range of temporal variability of ± 3°C. Minimum average values (26.8-27.3°C) were recorded during the windy season and maximum average values (29.7-30.6°C) during the rainy season

(Table 1). Salinity minimum average values were measured in the windy season (6.1-8.7), and maximum average values during the dry season, with a range of 17.4-19.5 (Table 1). For the pH, minimum mean values were observed during the dry and rainy seasons (7.1-7.6), while the maximum mean was registered during the windy season, with a range of 7.9-8.4 (Table 1). Minimum average oxygen saturation values were recorded in the rainy season (88.4-96.3%), while maximum average values (106.2-118.2%) were observed in the dry season (Table 1). All the variables mentioned above showed significant differences among seasons ($P < 0.05$).

NUTRIENTS

Variations in the concentrations of the inorganic nutrients were relatively wide as shown in Table 1. Average concentrations of nitrite ($N-NO_2^-$) and nitrate ($N-NO_3^-$) were low throughout the study compared to ammonium. However, nitrite concentrations showed maximum values, ranging 0.30-3.40 $\mu mol\ L^{-1}$ in the rainy season (Table 1). Nitrate concentrations showed maximum values, ranging from 1.31 to 3.42 $\mu mol\ L^{-1}$ in the rainy season and minimum values (0.54-1.28 $\mu mol\ L^{-1}$) in the dry season (Table 1). Ammonium ($N-NH_4^+$) concentrations were observed in the dry season (1.62-2.05 $\mu mol\ L^{-1}$), while maximum (2.80-3.64

$\mu mol\ L^{-1}$) were observed in the windy season (Table 1). Orthophosphate ($P-PO_4^{3-}$) concentrations showed minimum average values (0.14-0.60 $\mu mol\ L^{-1}$) during the rainy season, while maximum average values (0.73-1.52 $\mu mol\ L^{-1}$) were registered during the dry season (Table 1). Silicate ($Si-SiO_2^{4+}$) levels showed maximum mean values (9.05-35.91 $\mu mol\ L^{-1}$) in the windy season, while minimum mean values (6.48-18.81 $\mu mol\ L^{-1}$) were measured in the dry season (Table 1). All the variables mentioned above showed significant differences between seasons ($P < 0.05$).

COMMUNITY COMPOSITION OF PHYTOPLANKTON

In total, 114 species were identified, of which 52 (46%) were diatoms, 34 (30%) dinoflagellates, 14 (12%) cyanobacteria, 10 (8%) nanoflagellates and 4 (4%) silicoflagellates. The total average phytoplankton abundance was $2.4x10^5$ cells L^{-1}, with a minimum value of $1.4x10^5$ cells L^{-1} and a maximum of $8.6x10^6$ cells L^{-1}. Nanoflagellates (5 to 19 μm in size) were the most abundant taxa. Nanoflagellates varied slightly in abundance, decreasing in the dry season and increasing in the rainy season. Diatoms, cyanobacteria and dinoflagellates were observed as minor components (Fig. 2).

Table 1. Summarized statistics (for a meteorological season) of environmental variables and nutrients from 6 sampling sites in the oyster beds of Términos Lagoon, Campeche, Mexico, in 2012-2013 (mean, range and standard deviation) / Resumen estadístico por estación climática de los variables ambientales y nutrientes en 6 sitios de muestreo en los bancos ostrícolas de la laguna de Términos, Campeche, México, en 2012-2013 (media, rango y desviación estándar)

Season	Environmental variables				Nutrients ($\mu mol\ L^{-1}$)				
	T°C	Salinity	pH	D.O (%)	Nitrite	Nitrate	Ammonia	Phosphate	Silicate
Rainy	30.2	13.2	7.6	93.2	0.97	2.20	2.10	0.30	38.21
	29.7-30.6	11.6-14.3	7.4-7.8	88.4-96.3	0.30-3.40	1.31-3.42	1.15-3.79	0.14-0.60	29.50-51.52
	±0.37	±0.15	±0.15	±2.82	±1.26	±0.83	±1.12	±0.18	±8.65
Windy	27.0	7.4	8.2	104.6	0.58	1.09	3.16	0.38	22.22
	26.8-27.3	6.1-8.7	7.9-8.4	98.9-111.8	0.04-3.39	0.47-2.26	2.80-3.64	0.20-0.63	9.05-35.91
	±0.19	±1.12	±0.18	±4.73	±1.24	±0.70	±0.31	±0.17	±10.00
Dry	28.0	18.4	7.1	112.2	0.17	0.78	1.80	1.05	11.61
	27.8-28.4	17.4-19.5	6.9-7.3	106.2-118.2	0.07-0.35	0.54-1.28	1.62-2.05	0.73-1.52	6.48-18.81
	±0.25	±0.13	±0.13	±5.03	±0.09	±0.28	±0.19	±0.30	±5.14
SD ÷ season	F= 260.1*	F= 225.1*	F= 64.8*	F= 44.5*	F= 53.3*	F= 11.9*	F= 6.5*	F= 15.2*	F= 8.5*

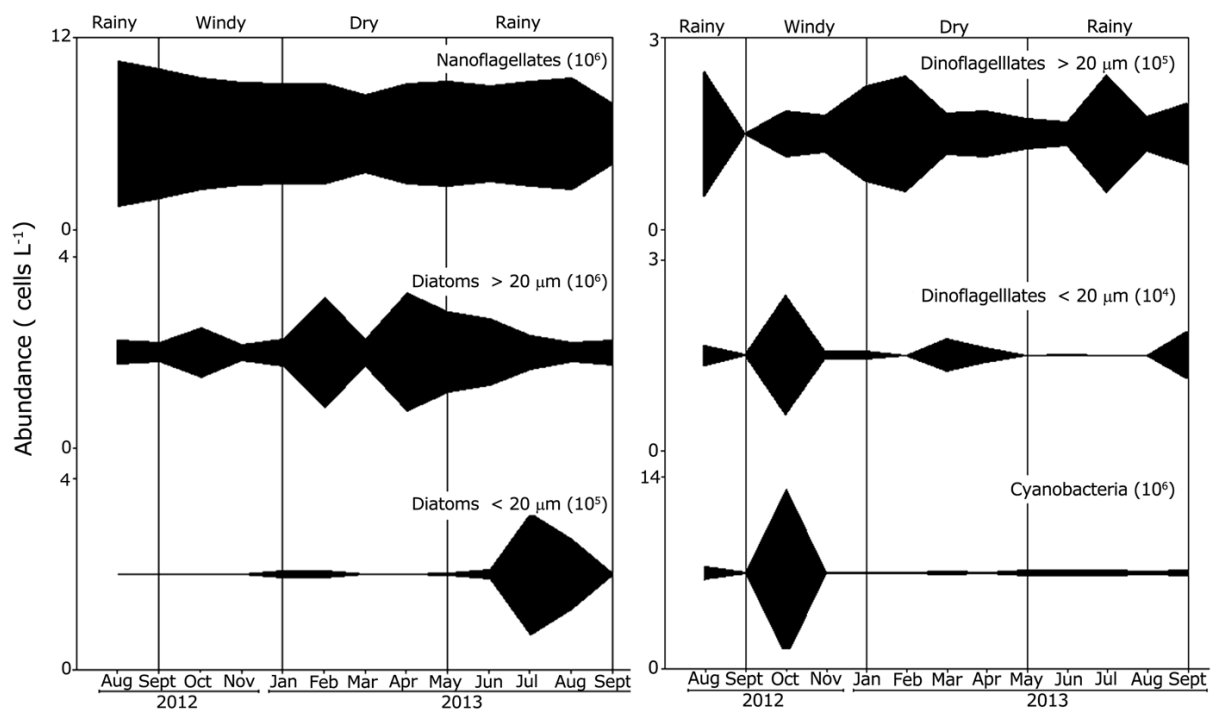*Significant differences SD ($P < 0.05$, ANOVA nonparametric one-way) between the seasons

Figure 2. Temporal variation of abundances of major phytoplankton groups in the oyster beds of Términos Lagoon, Campeche, Mexico, in 2012-2013 / Variación temporal de la abundancia de los principales grupos taxonómicos del fitoplancton en los bancos ostrícolas de la laguna de Términos, Campeche, México, en 2012-2013

The highest abundances of diatoms > 20 µm were observed in the dry season; abundances declined in the rainy season. Diatoms < 20 µm were markedly present in the rainy season (Fig. 2). The genus *Pseudo-nitzschia* reached abundances of 1.7×10^5 to 5.0×10^5 cells L^{-1} and was present throughout the study period, with an average abundance of 3.3×10^5 cells L^{-1} in the windy and dry seasons (Table 2, Fig. 3b). *Cylindrotheca closterium* showed high abundances of 1.2×10^6 and 3.5×10^5 cells L^{-1} during the rainy and windy seasons, respectively, being a species of rapid growth (Table 2, Fig. 3a). *Thalassiosira* sp. showed a maximum abundance of 1.5×10^6 cells L^{-1} during the rainy season, while *Rhizosolenia setigera* and *Skeletonema costatum* showed maximum abundances of 1.4×10^4 and 8.0×10^5 cells L^{-1} during the windy season, respectively (Table 2).

Dinoflagellates > 20 µm showed total abundances one order of magnitude lower (10^5 cells L^{-1}) than that of diatoms in both the rainy (July-August) and dry seasons (February-May). During the windy season (September-January) the lowest cell abundances were observed. The highest abundance of dinoflagellates < 20 µm (up to 10^4 cells L^{-1}) was observed in the windy season (January-February),

showing two small peaks in the dry and rainy seasons (Fig. 2). Among dinoflagellates, *Prorocentrum minimum* showed its maximum abundance in the windy season with a value of 6.9×10^4 cells L^{-1} (Table 2, Fig. 3i). *Prorocentrum mexicanum* abundances averaged 2.0×10^4 cells L^{-1} in the windy season with a maximum of 4.0×10^4 cells L^{-1} in the rainy seasons (Table 2, Fig. 3j). *Peridinium quinquecorne* was found in the rainy season with an abundance of 2.1×10^5 cells L^{-1} and varied in abundance throughout the dry and windy seasons (Table 2, Fig. 3h). The genus *Alexandrium* Halim that includes toxic representatives showed maximum abundances of 1.6×10^4 cells L^{-1} in the windy season, and 1.1×10^4 cells L^{-1} in the dry season, with an average value of 1.0×10^4 cells L^{-1} (Table 2, Fig. 3d). The Gymnodiniales gen. spp., including *Akashiwo sanguinea* showed higher abundances of 6.0×10^4 cells L^{-1} in the windy season; however, *A. sanguinea* was also observed in the rainy and dry seasons with a maximum abundance of 3.7×10^4 and 4.9×10^4 cells L^{-1}, respectively (Table 2, Fig. 3e). *Gymnodinium* cf. *catenatum* showed high abundances of 9.5×10^4 cells L^{-1} in the rainy season and was also present in the windy and dry seasons, with values of 5.0×10^3 and 3.9×10^4 cells L^{-1}, respectively (Table 2, Fig. 3f). As an

Table 2. List of potentially harmful species (HAB) observed from 6 sampling sites in the oyster beds of Términos Lagoon, Campeche, Mexico, in 2012-2013. The taxonomic group (Tax Group) is indicated: diatoms (DIA), dinoflagellates (DIN), and cyanobacteria (CYA) / Lista de especies potencialmente nocivas (FAN) observadas en 6 sitios de muestreo en los bancos ostrícolas de la laguna de Términos, Campeche, México, en 2012-2013. Grupo taxonómico (Grupo Taxonómico) se indica: dinoflagelados (DIN), diatomeas (DIA) y cianobacterias (CYA)

Species	Tax Group	Rainy	Windy	Dry
		Maximum abundances (cells L^{-1})		
Human potentially toxic species[1]				
Paralytic Shellfish Poisoning (PSP)				
Alexandrium sp.	DIN	11,000	16,000	5,000
Gymnodinium cf. *catenatum* Graham	DIN	95,000	39,000	5,000
Pyrodinium bahamense Plate var. *bahamense*	DIN	6,000	3,000	3,000
Amnesic Shellfish Poisoning (ASP)				
Pseudo-nitzschia spp.	DIA	178,000	329,000	500,000
Neurotoxic (NTX, mouse assay)[2]				
Prorocentrum hoffmannianum Faust	DIN	2,000		
Prorocentrum minimum (Pavillard) J. Schiller	DIN	30,000	69,000	26,000
Microcystin LR and lipopolysaccharide (LPS)[3]				
Merismopedia sp.	CYA	33,000	106,000	-
Oscillatoria sp.	CYA	83,000	258,000	195,000
Microcystin, anatoxin-a, anatoxin-a (S), saxitoxin and lipopolysaccharide (LPS)[3]				
Anabaena sp.	CYA	1,941,000	36,000	485,000
Microcystin LR cylindrospermopsin, saxitoxin, neusaxitoxin and neosaxitoxin[3]				
Cylindrospermopsis cuspis Komárek et Kling	CYA	-	13,248,000	-
Potentially fish-killing species[4]				
Karenia cf. *mikimotoi* (Miyake & Kominami ex Oda) G. Hansen & Ø.Moestrup	DIN	1,000	-	9,000
Prorocentrum mexicanum B. F. Osorio	DIN	40,000	20,000	32,000
Skeletonema costatum (Grev.) Cleve	DIA	-	80,000	35,000
Thalassiosira sp.	DIA	1,591,000	-	15,000
Potentially bloom-forming species[5]				
Akashiwo sanguinea (K.Hirasaka) G.Hansen & Ø.Moestrup	DIN	37,000	60,000	49,000
Cylindrotheca closterium Ehrenberg.	DIA	1,241,000	356,000	1,689,000
Peridinium quinquecorne T. H. Abé	DIN	210,000	1,000	-
Rhizosolenia setigera Brightw.	DIA	9,000	14,000	11,000

[1]Known species that are potentially toxic: PSP, DSP, ASP, NTX (IOC 2002)

[2]Responsible for mouse mortality via a water-soluble toxin. However, there are no data indicating impacts to human consumers (Grzebyk *et al.* 1997)

[3]Known species that are potentially toxic: Microcystin LR, lipopolysaccharide (LPS), microcystin, anatoxin-a, anatoxin-a (S), saxitoxin, cylindrospermopsin, neusaxitoxin and neosaxitoxin (UNESCO 2009)

[4]Those species that are known or suspected to cause fish losses in mariculture (Anderson *et al.* 2001)

[5]Those species that are known to produce blooms elsewhere (Anderson *et al.* 2001) or that occasionally reached abundances exceeding 10^6 cells L^{-1} in our samples
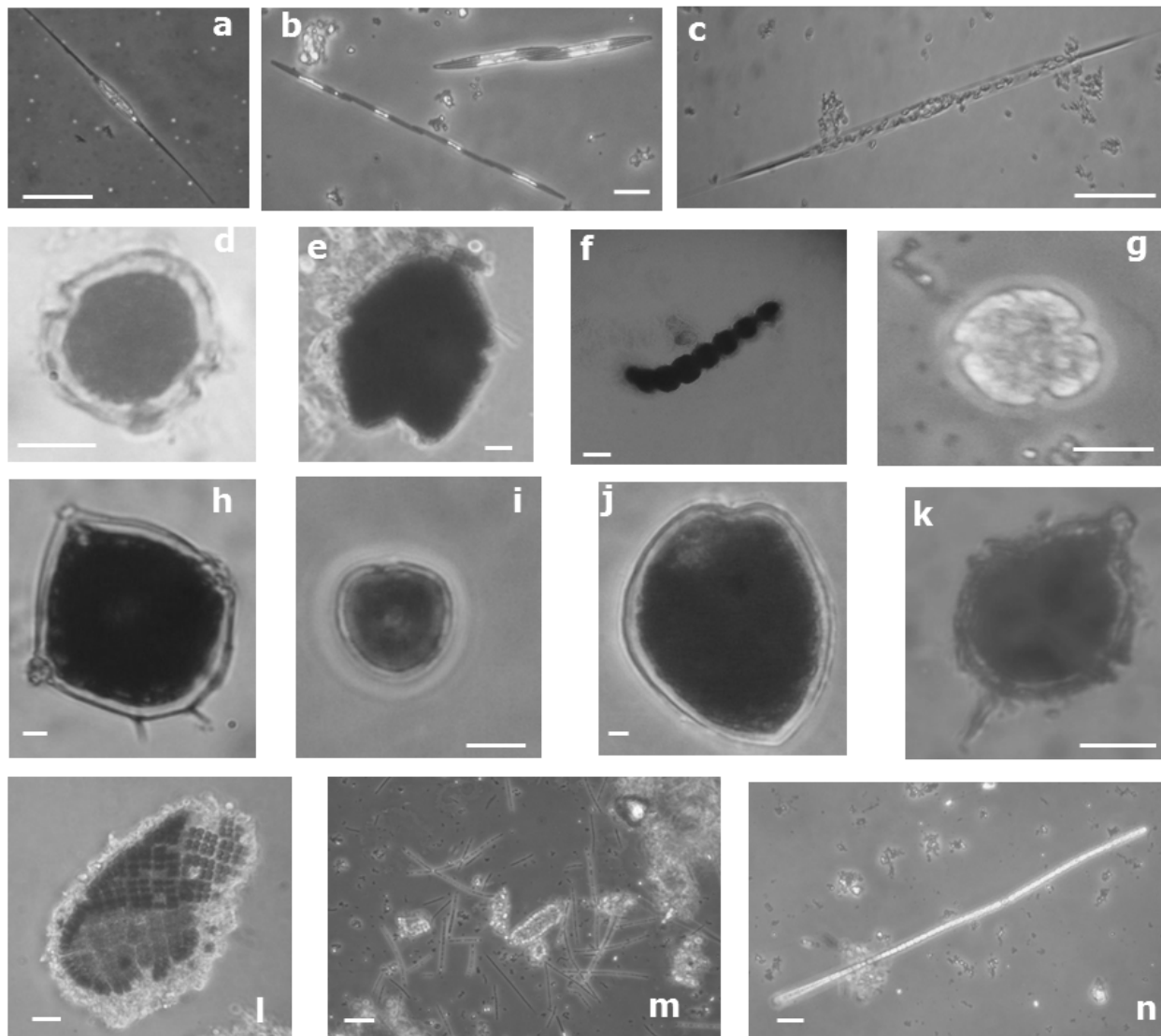
Figure 3. Photomicrographs of potentially harmful diatoms, dinoflagellates and cyanobacteria in oyster beds of Términos Lagoon, Campeche, Mexico (bright-field optics): a) *Cylindrotheca closterium*, **b)** *Pseudo-nitzschia* cf. *americana* and *P.* cf. *seriata*, **c)** *Rhizosolenia setigera*, **d)** *Alexandrium* **sp.**, **e)** *Akashiwo sanguinea*, **f)** *Gymnodinium* cf. *catenatum*, **g)** *Karenia* cf. *mikimotoi*, **h)** *Peridinium quinquecorne*, **i)** *Prorocentrum minimum*, **j)** *Prorocentrum mexicanum*, **k)** *Pyrodinium bahamense* **var.** *bahamense*, **l)** *Merismopedia* **sp., m)** *Cylindrospermopsis cuspis*, **n)** *Anabaena* **sp. Scale bar= 10 μm /** Microfotografías de diatomeas, dinoflagelados y cianobacterias potencialmente nocivos en los bancos ostrícolas de la laguna de Términos, Campeche, México (óptica de campo claro): a) *Cylindrotheca closterium*, b) *Pseudo-nitzschia* cf. *americana* and *P.* cf. *seriata*, c) *Rhizosolenia setigera*, d) *Alexandrium* sp., e) *Akashiwo sanguinea*, f) *Gymnodinium* cf. *catenatum*, g) *Karenia* cf. *mikimotoi*, h) *Peridinium quinquecorne*, i) *Prorocentrum minimum*, j) *Prorocentrum mexicanum*, k) *Pyrodinium bahamense* var. *bahamense*, l) *Merismopedia* sp., m) *Cylindrospermopsis cuspis*, n) *Anabaena* sp. Escala de la barra= 10 μm

important component of the phytoplankton community, the following potentially toxic dinoflagellates were present: *Akashiwo sanguinea*, *Karenia* cf. *mikimotoi*, *Pyrodinium bahamense* var. *bahamense*, *Prorocentrum mexicanum* and *P. minimum* (see Table 2).

Cyanobacterial abundance increased by orders of magnitude to 10^6 cells L^{-1} in the windy season (October) and small peaks were also observed in the dry and rainy seasons (Fig. 2). Among cyanobacteria, the genus *Anabaena* Bory de Saint-Vincent was present throughout the study period, with a maximum abundance of 1.9×10^6 cells L^{-1} and a minimum abundance of 3.6×10^4 cells L^{-1} (Table 2, Fig. 3n). *Merismopedia* sp. and *Oscillatoria* sp. showed high abundances of 1.0×10^5 and 2.5×10^5 cells L^{-1}, respectively, in the windy season (Table 2, Fig. 3l) During the windy season, a bloom of *Cylindrospermopsis cuspis* was recorded with 1.3×10^6 cells L^{-1}, and it lasted throughout the season with an abundance of up to 2.4×10^3 cells L^{-1} (Table 2, Fig. 3m).

RELATIONSHIP BETWEEN PHYSICAL-CHEMICAL PARAMETERS AND PHYTOPLANKTON

The effect of the set of physical-chemical variables on phytoplankton species composition was tested using canonical correspondence analysis (CCA). As indicated by the CCA, the response of the species to physical-chemical variables was primarily explained by the first three axes (67.1%; Table 3). The correlation between species and physical-chemical variables was low ($r \sim 0.5$), indicating an insignificant relationship between taxa and the physical-chemical variables used in the analysis. In the CCA, all canonical axes were not statistically significant ($P > 0.05$, Monte Carlo). This means that the community phytoplankton structure cannot be explained, at least, for the studied period, by the environmental parameters evaluated.

DISCUSSION

PHYSICAL-CHEMICAL VARIABLES

The water temperature variation observed during the study period is in accordance with the values reported by Robadue *et al.* (2004) and Yáñez-Arancibia & Day (2005) for Términos Lagoon during at least 50 years, which, in general, is characteristic of a subtropical marine environment. The registered salinity range, which varied depending on the season, was accentuated in the rainy season. According to Ramos-Miranda *et al.* (2006), this reflects the seasonal change in insolation. In turn, it results in greater evaporation and hence a higher concentration of salts in the months before the start of the rainy season. At this time, the high freshwater input by rainfall and/or water discharges would inundate the entire lagoon, inducing a marked salinity gradient (Hernández-Guevara *et al.* 2008), coinciding with that observed during the study period. The values of pH and oxygen saturation suggested the activity of primary producers in the water column, resulting in changes in water quality (especially in pH and dissolved oxygen) as reported by Martínez-López *et al.* (2006), Poot-Delgado (2006), Hakspiel-Segura (2009) and Escobedo-Urías (2010) for the lagoons of the northwestern Mexican Pacific. The

Table 3. Eigenvalues and percentage of total variance explained by temporal canonical correspondence analysis of the oyster beds of Términos Lagoon, Campeche, Mexico, in 2012-2013 / Eigenvalores y porcentaje de la varianza total explicada por el análisis de correspondencia canónica temporal de los bancos ostrícolas de la laguna de Términos, Campeche, México, en 2012-2013

Axes	Eigenvalue	Species-environment correlations	Cumulative percentage variance
1	0.025	0.476	29.8
2	0.017	0.523	50.5
3	0.014	0.431	67.1
4	0.011	0.399	79.9
Test of significance of first canonical axes		F-ratio= 2.025	P-value= 0.850
Test of significance of all canonical axes		F-ratio= 0.813	P-value= 0.916

average values observed for nitrite, nitrate and ammonium recorded in different seasons are well below the values reported by Contreras-Espinoza *et al.* (1996), Herrera-Silveira *et al.* (2002) and Ramos-Miranda *et al.* (2006) for the southern Gulf of Mexico; however, the same pattern of high values recorded in the rainy season, coupled with the proximity of river mouths with strong freshwater influence, can be seen (Yáñez-Arancibia & Day 2005, Ramos-Miranda *et al.* 2006). High values of orthophosphate and silicate are associated with the period of increased river discharge determined by circulation and biogeochemical processes (Botello & Mandelli 1975, Ramos-Miranda *et al.* 2006).

These are variables that are linked to the period of high river discharge by rainfall enriching the waters at the entrance by new nutrients and causing high turbidity and low salinity (Yáñez-Arancibia & Day 2005).

COMMUNITY COMPOSITION OF PHYTOPLANKTON

Being a body of shallow water, generally, no vertical stratification was found in the lagoon, so the wind and tidal currents probably keep the water well-mixed and allow a greater aeration of the water column (Magaña-Álvarez 2004).

Contributing to changes in phytoplankton composition and abundance, nanoflagellates and diatoms < 20 µm presented their highest abundances, on the order of 10^6 cells L^{-1}, in the rainy season. These groups are likely to benefit from the high temperatures (30.2°C); the relatively low salinity of 13.2 was most likely linked to the period of increased river discharge by rainfall (Yáñez-Arancibia & Day 2005).

Phytoplankton responds quickly to environmental changes (Biswas *et al.* 2010). Thus, the highest abundances of diatoms > 20 µm were observed in the dry season characterized by relatively high salinities (17.4-19.5) and an average temperature of 28°C. Phytoplankton associations were characterized by the predominance of nanoflagellates and diatoms.

This situation was somewhat in contrast to data from the offshore region of the Bay of Campeche where the coccolithophores and nanoplanktonic diatoms numerically dominated the phytoplankton community in the dry season in April 2000 (Hernández-Becerril *et al.* 2008). In the tropical waters of the western Indian Ocean, the contribution of coccolithophores to total phytoplankton abundance is also important (Sá *et al.*

2013). In the present study, coccolithophores were observed only once in winter (1000 cells L^{-1}). They are known to prefer the nutrient-poor conditions and often thrive in areas where their competitors are starving (Weier 1999). Furthermore, in the southern Gulf of Mexico, including the offshore area in front of Términos Lagoon, maximum abundances of coccolithophores were observed in the subsurface (deeper than 10-30 m) layer (Hernández-Becerril *et al.* 2008). However, both studies in the offshore area and in the coastal lagoon, respectively, showed the importance of nanoplankton, at least in terms of cell abundance. This was also recently confirmed for the Gulf of California where phytoplankton abundance was dominated both temporally and spatially by nanoplankton (Verdugo-Díaz *et al.* 2012). Furthermore, the dominance of chlorophytes < 10 µm as one of the most abundant taxa among flagellates and in general in natural samples was also observed at Puerto Morelos in the Mexican Caribbean (Halac *et al.* 2013). Modern techniques such as HPLC pigment analysis applied recently to the studies of the taxonomic composition of tropical phytoplankton, apart from the groups mentioned above, also suggest the presence of at least some of the following taxonomic groups: *Prochlorococcus* sp., euglenophytes, prasinophytes, chrysophytes, prymnesiophytes and cryptophytes (Sá *et al.* 2013).

The presence of potentially harmful species reduces the percentage of oxygen saturation by an extraordinary increase in the number of phytoplankton cells, secondary metabolites and by the plugging of gills by highly silicified planktonic diatoms and silicoflagellates (Smayda 1997, Band-Schmidt *et al.* 2011). This can cause different responses in the life cycle of oysters: for example, *Alexandrium taylori* Balech produced mortality in larvae of *Crassostrea gigas* Thunberg in experimental exposure (Matsuyama *et al.* 2000).

The experimental exposure to toxic *Alexandrium tamarense* (Lebour) Balech produced mortalities in the bivalves *Crassostrea virginica*, *Ostrea edulis* Linnaeus (Lesser & Shumway 1993) and *Mytilus edulis* Linnaeus (Shumway & Cucci 1987). *Alexandrium minutum* Halim produced mortalities in juveniles and adults of *Mytilus edulis* and *M. galloprovincialis* Lamarck (Gainey & Shumway 1988).

Some phytoplankters have structural features that may adversely affect other marine species. They are characterized by having a silicic frustule that is not only very strong, but also often provided with projections,

spines or setae that can dig or tear the animal soft tissues. The frustules of *Chaetoceros convolutus* Castrac. and *C. concavicornis* Mangin possess setae or extensions that are covered with fine spinules that can damage gills of various fish species (Horner *et al.* 1990).

The CCA did not reveal an impact of nutrients on changes in the composition of the phytoplankton community. Along with the statistically insignificant correlation, our results demonstrate that the nutrients in general reflected the residence time of water in the lagoon, which in turn depends on the nature of the inputs that connect the lakes with the ocean (Pospelova *et al.* 2004). For Términos Lagoon, a nonlinear relationship between the concentration of nutrients and phytoplankton abundance was observed; this can be explained on the basis of the residence time of water in the lagoon. According to Yáñez-Arancibia & Day (2005), the residence time is one month during the rainy season, 22 days during the windy season and almost 7 months during the dry season, unlike Alvarado Lagoon in the state of Veracruz in the southern Gulf of Mexico, where the primary production is controlled by the temperature and salinity (De la Lanza-Espino & Lozano-Montes 1999). This difference was attributed to the residence time of the water, which is consistent with our suggestion.

This situation was observed by Varona-Cordero *et al.* (2010) for the coastal tropical lagoons Carretas-Pereyra and Chantuto-Panzacola in the southeastern Mexican Pacific, where the phytoplankton species composition during each season was dominated by different groups of species, which most likely allows the community to adapt to changes in resources and the physical-chemical environment.

Physical-chemical parameters such as temperature and salinity can determine the distribution or the occurrence of HABs, coupled with the availability of nutrients that regulate the growth rate, biomass and duration of bloom (Vargo 2009).

A possible link between nutrient enrichment of anthropogenic origin and increasing frequency of HAB events has not been rigorously tested, although there is growing evidence in favor of this from other parts of the world (Montresor & Smetacek 2002). As understanding of the factors governing the competitive ability of different phytoplankton species increases, greater comprehension of the dynamics of microalgal blooms in this region will be obtained.

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