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Seasonal Responses of Phytoplankton Productivity to Water-Quality Variations in a Coastal Karst Ecosystem of the Yucatan Peninsula

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Dzilam Lagoon (DL) is a shallow, semienclosed, coastal ecosystem located on the north coast of the Yucatan Peninsula. With 9.4 km^3 surface area, this system is influenced by groundwater (GD) supply and inorganic nutrients drained from the nearby mangrove. DL is highly preserved and provides a unique site to address the seasonal responses of phytoplankton production to environmental variability in a karstic and pristine scenario. Twelve monthly sampling trips were undertaken during Sep. 1998–Aug. 1999 to record in situ physicochemical parameters and collect water for inorganic nutrients, chlorophyll *a* (Chl *a*), and phytoplankton production at seven stations plus one GD. Highest Chl *a* concentrations were determined at the innermost points of the lagoon, whereas primary production peaked at brackish zones. The average net primary production in DL (80 g C m^{-3} yr^{-1}) is lower than that reported for other coastal lagoons of the Yucatan Peninsula. Differences in the physical setting and disturbance extent between DL and those ecosystems are discussed as the context underlying their distinct production levels.

Coastal lagoons (CL) are commonly enriched with materials and energy from neighboring systems. CL are therefore highly connected systems whose remarkable production is dependent on efficient mechanisms to preserve and recycle nutrients, as well as organic material (Kjerfve and Magill, 1989).

CL may be either net autotrophic or net heterotrophic, depending on the season (Reyes and Merino, 1991). Their metabolism is significantly associated with biogeochemical processes operating within the sediments and mediated by heterotrophic bacteria (Smith and Atkinson, 1994). Despite the marked seasonality of benthic respiration in Ria Lagartos Lagoon, at the eastern edge of the Yucatan, it entails a net nitrogen and phosphate sink condition along the yearly cycle (Valdes and Real, 2004). In contrast, Dzilam Lagoon (DL) exhibits distinct patterns for nitrogen species, acting as a sink for nitrate, while it is a net source for reduced nitrogen species (Medina-Gómez and Herrera-Silveira, 2003). The outcome of the dynamics between the external delivery of organic material and local processing adds variability to the nutrient status within DL, thus altering the primary production of this system (Medina-Gómez and Herrera-Silveira, 2006).

Groundwater (GD) discharge (occurring through fissures on the karst substrate) represents a conspicuous physiographic feature along the Yucatan coast of Mexico (Herrera-Silveira et al., 2004), influencing hydrographic patterns and nutrient availability (Carruthers et al., 2005), and primary productivity (Medina-Gómez and Herrera-Silveira, 2006). Local forcing in the Yucatan drives the phytoplankton community, defining patterns of production along the northern coast (Alvarez-Gongora and Herrera-Silveira, 2006). The DL, located in a zone strongly influenced by GD flow, experiences seasonal changes in phytoplankton structure that is dominated by diatoms, and more inconspicuously cryptomonads and dinoflagellates (Herrera-Silveira et al., 1999). It has also been argued that the nearshore phytoplankton community of Dzilam is altered by hydrodynamic factors such as advection and turbulence, in addition to the GD forcing (Alvarez-Gongora and Herrera-Silveira, 2006).

Despite small-size mats of benthic microalgae having been reported floating across the lagoon, particularly during dry season, the widespread distribution of submerged aquatic vegetation over DL sediments (cover equal to 85%; Medina-Gómez and Herrera-Silveira, 2006) suggests that the contribution of phytomicrobenthos to the primary production in the system is relatively small.

The limited water exchange with the sea may pose critical requirements to coastal lagoons as organic matter accumulated within the system may result in low oxygen concentration. The oxygen advected through the seaward boundary is usually negligible in coastal lagoons forced by microtidal regimes, as in the Yucatan Peninsula (Valdes-Lozano et al., 2006). Thus, the importance of alternative oxygen sources in maintaining healthy oxygen levels, including the photosynthetically produced O_2 and aeration due to wind-driven turbulence, is great.
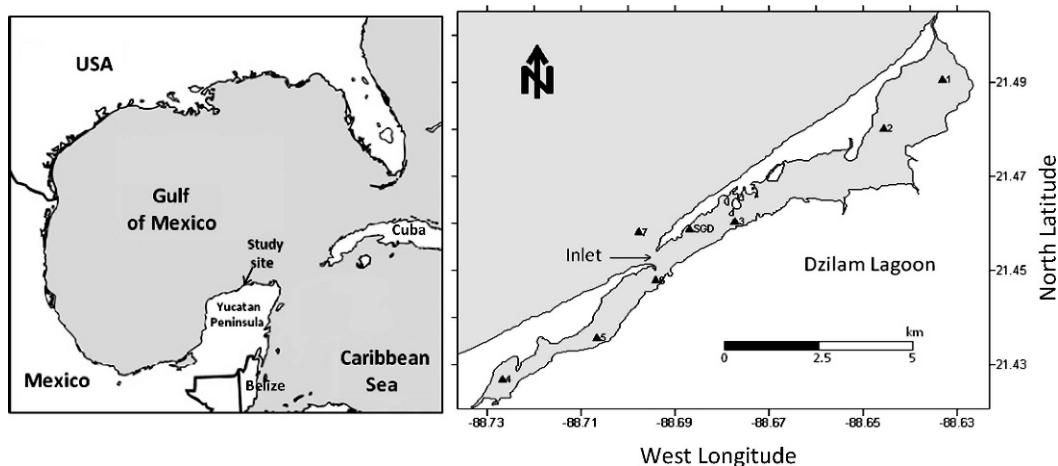
Fig. 1.   Map of the study site: seven sampling stations, plus one submerged groundwater discharge (SGD). Coordinates are in decimal degrees.

This paper focuses in evaluating the intra-annual patterns of phytoplankton production and biomass in response to the seasonal variation and spatial heterogeneity in a karstic, undisturbed, tropical coastal lagoon lacking fluvial inputs, but influenced by submerged GD discharges. The specific questions we asked are: What is the spatial and temporal variability of phytoplankton production? Which are the key factors controlling this variability? Is there a seasonal shift in the trophic status of DL between autotrophy and heterotrophy?

MATERIALS AND METHODS

Study area.—DL lies within 61,000 ha of a protected reserve north of the Yucatan Peninsula, SE Mexico. It is a shallow ecosystem (1.1 m average depth), 13 km long, with a maximum width of 1.6 km and 9.4 km^2 of surface extension. The lagoon's main axis is parallel to the coast and separated from the ocean by a biogenic sandbar (i.e., constituted by skeletal remains and shells of marine organisms such as gastropods, corals, and calcareous algae). DL is connected with the Gulf of Mexico through a permanent inlet in the middle of the system, while an ephemeral narrow entrance can appear at the easternmost portion of the lagoon during the fall and summer (Fig. 1). This shallow lagoon harbors abundant waterfowl all year, but especially in early summer. Tides are mixed: diurnal spring tides with a maximum range of 1 m, and semidiurnal neap tides with a small range (< 0.20 m) propagating as a standing wave (Merino and Otero, 1991).

The almost complete absence of confining beds above limestone in the Yucatan Peninsula determines a high hydraulic conductivity in the karstic substrate (Back and Hanshaw, 1970). This geohydrological trait leads to high infiltration of the rainfall through subsurface layers, and eventually, full recharging of the aquifer during rainy seasons. Because of this enhanced permeability and proclivity to dissolution of the calcium carbonate, the Yucatan Peninsula is practically lacking of surface streams; instead, a significant amount of GD input to the Yucatan coastal zone operates via fissures on the aquifer, either through inland sinkholes (i.e., cenotes) or submerged groundwater discharges (SGD; Fig. 1) with a strong seasonal pattern (Pope et al., 2001).

Even though GD supply occurs during the whole year in the Yucatan CL (Young et al., 2008), a noticeable spatial and temporal heterogeneity is observed on the volume discharged (Beddows et al., 2007). This could be somehow related to the characteristic disproportion on the annual precipitation across the Yucatan Peninsula (Valdes et al., 2005) and the spatial distribution of underground conduit systems, responsible for 99.7% of the GD flow (Worthington 2002).

Beddows (2004) found evidence in the eastern Yucatan Peninsula of slightly higher cumulative freshwater outflow in a nearshore submarine spring during wet season than during dry season, as well as high-frequency variability of this discharge due to tidal forcing of the aquifer head: peak outflow velocity during neap tide and minimum outflow velocity on spring tide. Those high- and low-frequency signals are overlapped
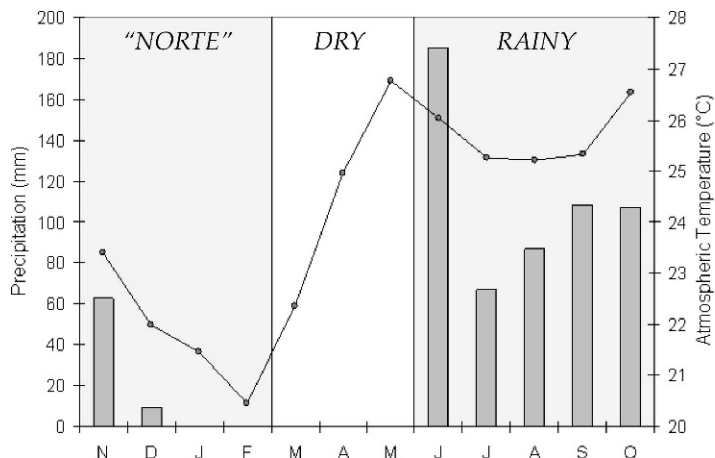
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Fig. 2.   Precipitation (bars) and atmospheric temperature (lines) in ''Dzilam the Bravo'' town located 22 km from Dzilam Lagoon for the period of the current study (data provided courtesy of the Servicio Meteorológico Nacional).

with the seasonal fluctuation. Despite the details of the discharge hydrodynamics on the northern Yucatan coast being still largely unknown, it is reasonable to consider that similar controls on its freshwater circulation to that reported for the eastern coast are operating here.

This geohydrological setting may have ecological implications for the Yucatan coast, as karstic aquifers provide routes for surface sources of nutrients to penetrate deeply into the aquifer and move rapidly through it, making them susceptible to contamination from agricultural discharges and waste disposal systems (Fitts, 2002). Furthermore, the Dzilam Protected Area is situated at the eastern edge of a semicircle-shaped zone of privileged GD discharge named as ''ring of cenotes,'' featured by a high hydraulic gradient at both arms of such region (Perry et al., 1995).

The complex interactions of such geomorphologic, physiographic, oceanographic, and climatologic mechanisms drive the hydrographic heterogeneity of DL by defining zones of similar characteristics (which might not be necessarily adjacent one each other) in terms of the magnitudes and rates of change of salt and nutrients [hydrological affinity zones (HAZ); Medina-Gómez and Herrera-Silveira, 2003]. There are 3 HAZ in DL: the innermost portions of the system, east and west HAZ, depicting high water residence times (τ) during dry season and low salinities in rainy season; and the central HAZ, a marine-influenced section showing both short τ and reduced inorganic nutrient concentrations.

The climate of the Yucatan Peninsula encompasses three seasons outlined by variations on the precipitation–evaporation balance rather than changes in the atmospheric temperature: dry; rainy; and ''norte'' seasons. During dry season, scarce precipitation (0 to 30 mm mo^{-1}) and high temperatures ($36°C$ to $38°C$) are recorded. Rainy season is characterized by maximum precipitation (220 mm mo^{-1}) and temperatures ($38°C$), as well as hurricane passage usually during late rainfall period, featuring high pluvial precipitation (350 mm mo^{-1}) and strong winds, up to 250 km/hr. Norte season is influenced by northerly cold fronts of polar air associated with high-pressure systems, low temperatures ($23°C$ mean temperature), and marginal precipitation (40 mm mo^{-1}; Fig. 2).

Because of the spatial and temporal variability of precipitation (including the interannual component) introduced earlier, the aggregation of months into seasons is not straightforward, but for practical purposes of the current study the seasons will comprise the following months: norte season (Nov., Dec., Jan., and Feb.); dry season (March to May); rainy season (June to Oct.) (Fig. 2).

Sampling and laboratory techniques.—Twelve monthly samplings were undertaken in DL from Sep. 1998 to Aug. 1999 to collect data from eight stations: six within the system, one adjacent to the mouth of the lagoon (station 7), and one station placed in a SGD (Fig. 1). All field sampling was achieved between 0800 and 1100 h local time, during high tide to ensure suitable navigation conditions through this shallow lagoon. Abiotic and biotic data were concurrently collected at mid-depth in the water column (around 0.50 m and 1.0 m for the

within-lagoon and outlet stations, respectively) since no stratification was recorded during field sampling. This mid-depth consistently corresponded to 0.5 Secchi depth.

Water samples for nutrients and chlorophyll *a* (Chl *a*) were collected at all seven stations plus the SGD (except for Chl *a*), coupled with physical–chemical parameters (temperature, salinity, oxygen) recorded in situ using a YSI-85 multiparameter probe and irradiance measured with a LICOR LI-1000 spherical sensor. The conductivity measurements were compensated using a reference temperature of 25°C and default temperature coefficient of 1.91%. The YSI-85 probe was also routinely calibrated preceding each sampling station using the oxygen saturation percentage as reference.

Water samples were analyzed in the laboratory for ammonium (phenolhypochlorite method; Solórzano and Sharp, 1980), nitrite (sulfanilamide in an acid solution), nitrate (determined as nitrite prior reduction in a Cd-Cu column), soluble reactive phosphorous (SRP; mixing agents technique), and soluble reactive silica (SRSi; molybdenum-blue method) according to Strickland and Parsons (1972). In addition, 140 ml of the water samples were filtered using 0.45-μm membrane Millipore filters for Chl *a* determination; filters were further treated with 90% acetone to extract the pigments. The quantification of pigments was carried out spectrophotometrically using a Milton-Roy Spectronic Genesys-II spectrophotometer, under the method and equations provided by Jeffry and Humphrey (1975). Nutrients and chlorophyll determinations were performed using true duplicates (i.e., taken from separate bottles) of water collected at each sampling station.

The measurements of phytoplankton production were carried out by incubating triplicates of three sets of bottles: initial, clear, and dark (Vollenweider, 1974) during 4 hr under in situ conditions (i.e., submerged at 0.5 Secchi depth into the water column to avoid photoinhibition constraints). Incubations were performed between 1100 and 1500 h. This experimental design was pursued to minimize the shortcomings of the incubation technique, particularly those derived from the fast phytoplankton responses to short-term variability in the coastal zone (e.g., tidal forcing, meteorological processes). Additionally, to control the effects of a varied time delay ($\approx$ 3 hr) between the first water sample (station 4) and the last sample (station 1), clear and dark bottles were held submerged into a container filled with water from the lagoon to preserve near-initial conditions before the incubation. The water-filling the container was

manually recirculated every 20 min until start of the incubation.

For the measurements of dissolved oxygen concentration, a temperature-compensated YSI-59 oximeter calibrated against the Winkler technique and set with a 4.5 VDC stirring motor was used. Accuracy on the oxygen determinations was improved by using triplicates for each sampling station, along with performing short incubation times. Besides, this strategy allows controlling of phytoplankton dynamics in terms of its ecological interactions on the water column (i.e., respiration measured within the bottles might include not only that of the autotrophic algae, but also bacteria and zooplankton).

Hourly rates of aquatic primary production were converted into daily rates by multiplying by 8.6 to account for low light levels at morning and dusk (Randall and Day, 1987; Flores-Verdugo et al., 1988), whereas hourly respiration rates were multiplied by 24. The oxygen conversion into carbon amounts was achieved using the quotients 0.310 and 0.375 for production and respiration, respectively (Strickland and Parsons, 1972).

Statistical analysis.—Box-and-whisker plots were used to depict the variability of Chl *a*, net phytoplankton production, respiration, production/respiration ratio (P/R), and light extinction coefficient among sampling stations. These plots encompassed the three climatic seasons to portray the variability of every sampling station along the period of study.

Since data were generally not normally distributed, median values of physical–chemical parameters (Table 1), inorganic nutrient concentrations (Table 2), and phytoplankton variables (Table 3) are reported for DL.

Light extinction coefficient (K_d) was calculated according to the Lambert–Beer law:

$$K_d = \ln \frac{(I_0/I_z)}{z}$$

where I_0 is the incident (surface) light intensity, I_z is the light intensity at depth z, and K_d is the light attenuation coefficient (m^{-1}) (McPherson and Miller, 1987).

RESULTS

Water quality variables.—Temperatures and turbidity (K_d) were high in rainy season (31.5°C and 3.45 m^{-1}), with the latter parameter peaking at the shallowest zones of the lagoon, while showing relatively better transparency conditions nearby the inlet. Temperature depict-

TABLE 1. Seasonal medians of water quality in Dzilam Lagoon, Yucatan. The months gathered into seasons are as follows: norte = Jan., Feb., Nov., and Dec.; dry = March, April, and May; rainy = June, July, Aug., Sep., and Oct.

	Season	Sample sizes (n)	Temperature (°C)	Salinity (psu)	Oxygen saturation (%)	K_d (m^{-1})
Lagoon	Norte	24	27.6	25.4	94	1.55
	Dry	18	31.5	36.4	119	1.86
	Rainy	30	32.1	17.8	53	3.59
Outlet[a]	Norte	4	26.3	35.5	102	0.87
	Dry	3	26.9	38.2	93	3.00
	Rainy	5	31.1	35.7	95	1.93
Groundwater	Norte	4	26.0	2.1	1	
	Dry	3	26.2	1.9	2	
	Rainy	5	26.5	3.5	2	

[a] Data collected on station 7 (see Fig. 1).

TABLE 2. Seasonal medians of inorganic nutrients in Dzilam Lagoon, Yucatan. The months gathered into seasons are as follows: norte = Jan., Feb., Nov., and Dec.; dry = March, April, and May; rainy = June, July, Aug., Sep., and Oct.

	Season	Sample size (n)	NO_3^- (µM)	NO_2^- (µM)	NH_4^+ (µM)	SRP[b] (µM)	SRSi[b] (µM)
Lagoon	Norte	24	3.23	0.17	3.78	0.03	52.10
	Dry	18	4.67	0.11	0.94	0.10	18.30
	Rainy	30	1.48	0.19	2.74	0.05	145.63
Outlet[a]	Norte	4	2.25	0.20	4.30	0.02	9.70
	Dry	3	4.06	0.03	0.49	0.10	3.30
	Rainy	5	1.49	0.17	0.92	0.05	5.20
Groundwater	Norte	4	74.57	0.25	2.66	0.06	154.01
	Dry	3	102.40	1.33	0.99	0.04	35.17
	Rainy	5	88.77	0.74	1.92	0.10	121.88

[a] Data collected on station 7 (see Fig. 1).
[b] SRP, soluble reactive phosphorus; SRSi, soluble reactive silica.

ed an abrupt gradient during rainfalls, with increasing values from the inlet toward the inner portions of the system (Fig. 3). The lowest oxygen saturation percentage was recorded in between early and late rainy seasons. Norte season was characterized by low temperatures in the water column. Light extinction coefficients showed consistently high values at the shallowest innermost branches of DL and a maximum K_d recorded in the rainy season (Table 1).

The salinity distribution showed a clear influence of the SGD during the whole year, but it was more significant in late rainy season at the western edge of the system. Hyperhaline [> 50 practical salinity units (psu)] conditions occurred at the eastern part of DL during dry season (Fig. 3). Peak oxygen saturation was

TABLE 3. Seasonal medians of phytoplankton productivity in Dzilam Lagoon, Yucatan. The months gathered into seasons are as follows: norte = Jan., Feb., Nov., and Dec.; dry = March, April, and May; rainy = June, July, Aug., Sep., and Oct.

	Season	Sample size (n)	Chlorophyll a (mg m^{-3})	Net production (P) (mg C m^{-3} d^{-1})	Respiration (R) (mg C m^{-3} d^{-1})	P/R ratio
Lagoon	Norte	24	2.32	134	186	0.62
	Dry	18	2.43	203	216	0.94
	Rainy	30	3.91	123	226	0.85
Outlet[a]	Norte	4	1.64	124	133	1.02
	Dry	3	2.22	122	128	0.87
	Rainy	5	0.85	65	81	0.81

[a] Data collected on station 7 (see Fig. 1).
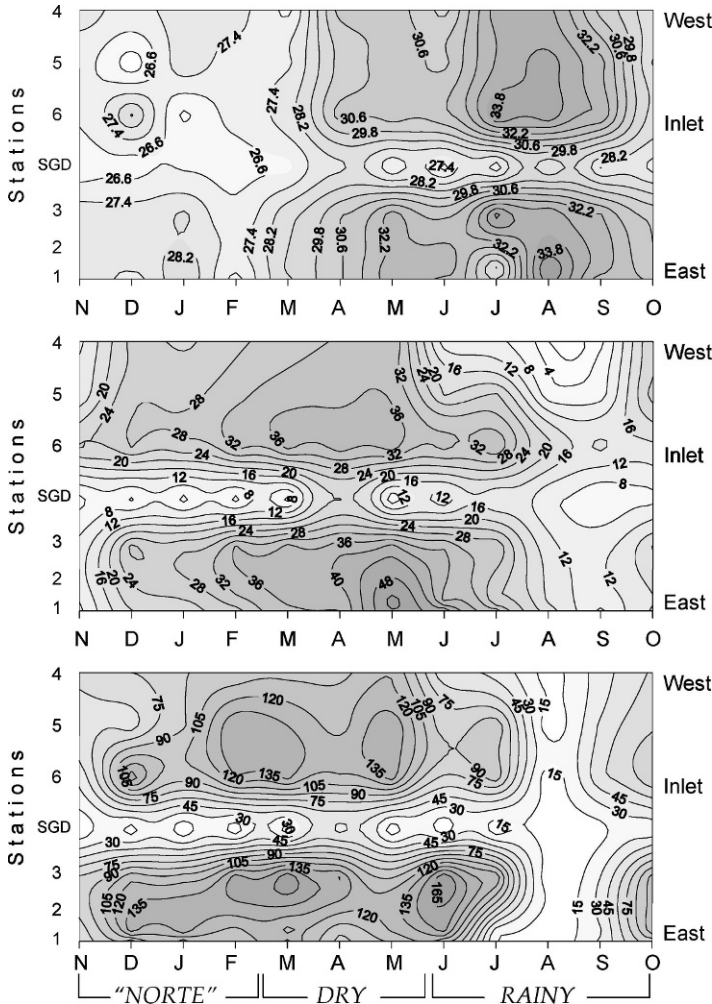
Fig. 3. Seasonal and spatial variation of physical–chemical parameters in Dzilam Lagoon (top panel) temperature (°C), (middle panel) salinity (psu), and (bottom panel) oxygen saturation (%).

observed on the shallowest zones of the lagoon during norte and dry seasons, particularly at the eastern branch of the system, whereas in rainy season, the oxygen saturation percentage was relatively lower and more homogenous than in the rest of the year (Fig. 3).

The SGD was a significant NO_3^- and SRSi source to the lagoon, as high concentrations were observed at this point discharge (i.e., middle section of the lagoon) during the year (Table 2). Both nitrate and silicate depicted clear discrepancies relative to their spatial patterns (Figs. 4 and 5) as peak SRSi concentrations (260 µM) were observed at the innermost sections of DL, particularly late rainy season. During late rainy season the ammonium showed a gradient of high concentrations on sites located between the extremes of the system

and the inlet zone (i.e., intermediate water residence time). These high NH_4^+ values were propagated during nortes and maximum ammonium concentrations occurred in late norte season (Fig. 4). Also, low NH_4^+ concentrations were recorded in dry season throughout the lagoon. On the other hand, NO_2^- peaked during April and July in the SGD, whereas nitrate did the same during May and along the entire rainy season. Moreover, high nitrite concentrations were observed during rainy season at the eastern section (Fig. 4). Finally, the SRP depicted low concentrations throughout the lagoon, except for dry season and early rainfalls, when peak values were determined at both extremes of the system, particularly in the eastern zone, as well as in the SGD, which showed the maximum SRP concentration (1.83 µM) during Aug. (Fig. 5).
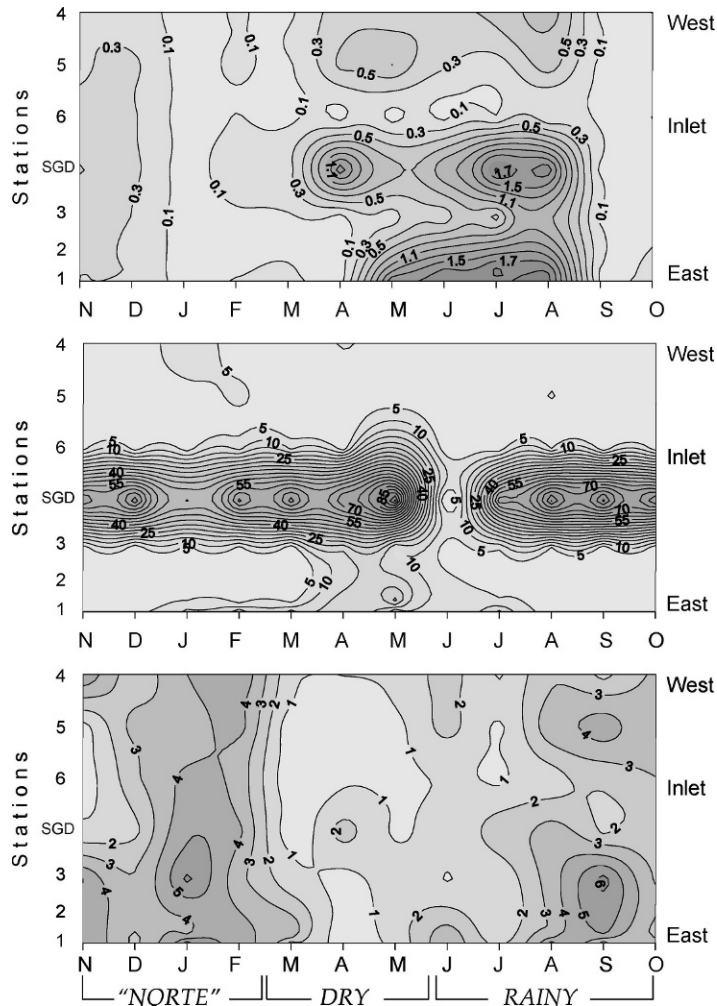
Fig. 4. Seasonal and spatial variation of inorganic nutrients in Dzilam Lagoon: nitrite (top panel), nitrate (middle panel), and ammonium (bottom panel). Units are given in micromoles per liter.

Chl a.—The highest Chl *a* median was recorded in rainfalls (3.91 mg m^{-3}) and the lowest during nortes (2.32 mg m^{-3}). During this latter season, a fairly spatially homogeneous Chl *a* distribution was evident, as opposed to rainfalls, when large variability was observed among stations, with a general pattern of peak concentrations at the innermost sections of the lagoon and decreasing values in the middle zone adjacent to the inlet and in the SGD (Fig. 6).

Net production.—The highest net phytoplankton production in DL was recorded during dry season (203 mg C m^{-3} d^{-1}), whereas the maximum production rate at the outlet station (124 mg C m^{-3} d^{-1}) was observed in norte season. Stations 2 and 4 yielded high production rates during dry period (382 and 315 mg C m^{-3} d^{-1}, respectively), with station 3 defining the higher variability [coefficient of variation (C.V.) = 92%]. The highest phytoplankton production in nortes was equal to 223 mg C m^{-3} d^{-1} concerning station 3, and the larger variability corresponded to station 6 (C.V.= 119%). In rainy season, phytoplankton production was both lower (median equal to 123 mg C m^{-3} d^{-1}) and less varying than that recorded during the rest of the year; peak production rate was observed at station 1, with a median of 220 mg C m^{-3} d^{-1} and C.V. equal to 53% (Fig. 6).

Respiration.—The highest median respiration in the lagoon was recorded during rainy season (226 mg C m^{-3} d^{-1}) and the maximum for the outlet station corresponded to norte period
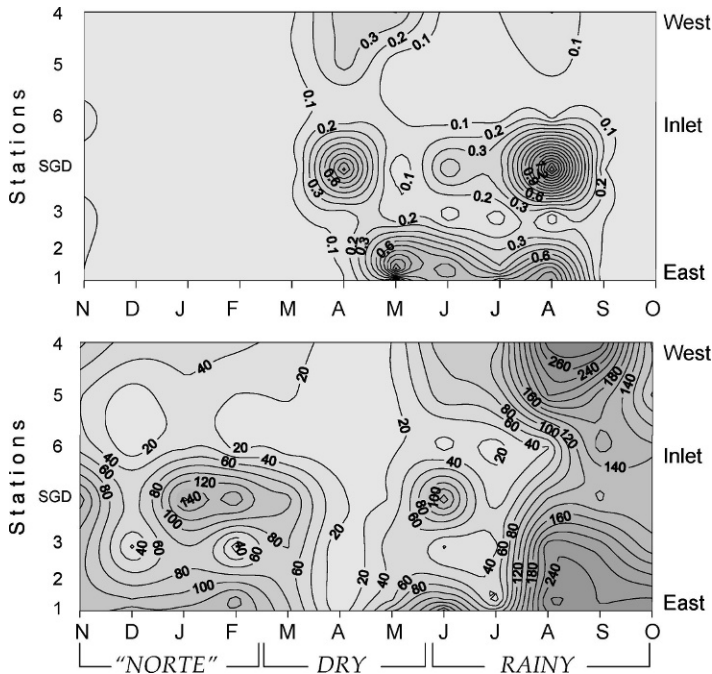
Fig. 5. Seasonal and spatial variation of phosphorus (upper panel) and silicate (lower panel) in Dzilam Lagoon. Units are given in micromoles per liter.

(133 mg C m^{-3} d^{-1}). Lowest median respiration in the system corresponded to this latter season as well (186 mg C m^{-3} d^{-1}). The peak median respiration in dry season occurred at station 4 (313 mg C m^{-3} d^{-1}), whereas the highest variability was attained by station 1 (C.V.= 70%) (Fig. 6).

Phytoplankton production and respiration ratio.— The lowest phytoplankton P/R ratio corresponded to norte season (0.62), whereas the median ratio calculated in dry season was close to balance between production and respiration (0.94). Despite the high phytoplankton primary production observed in dry season, a slightly heterotrophic condition was still observed in DL (Table 3). The variability of the P/R ratio during dry season was relatively homogenous across the lagoon, with the innermost stations showing generally higher values than the middle zone (Fig. 7). The same condition was observed during norte season, which showed not only peak P/R ratios, but substantially more variable P/R ratios (Fig. 7). Station 4, in the western edge of the lagoon (Fig. 1), consistently showed a P/R ratio above 1 throughout the year (Fig. 7). It is important though, to note the large variability characterizing the data, particularly at station 4.

DISCUSSION

The seasonal changes characterizing the north coast of the Yucatan Peninsula dictated the variability of phytoplankton production in DL, which depicted as well a marked spatial heterogeneity tied to the hydrographic gradients prevailing across the system. It is well documented that GD (both inland and SGD) constitutes a significant source of nitrate and silicate to the coastal environment of the northern Yucatan Peninsula (Herrera-Silveira, 1994). In the current study, however, these nutrients exhibited different distribution patterns within DL, defined by peak NO$_3^-$ concentrations associated with the SGD located proximate to the inlet, whereas SRSi recorded a more complex spatial behavior, portraying maximum values at the innermost portions of the lagoon, in addition to those observed at the SGD (Figs. 4, 5).

The spatial pattern shown by the SRSi in DL, particularly during late rainy season, may be the result of seasonal trends in the GD intruding into the surface water through bedrock fissures at inland springs (cenotes). The hydrographic properties alteration induced in this water mass is a function of its residence time within the mangrove forest (e.g., hydroperiod) before it is advected to the lagoon. This adjacent ecosystem is connected to DL through small waterways and
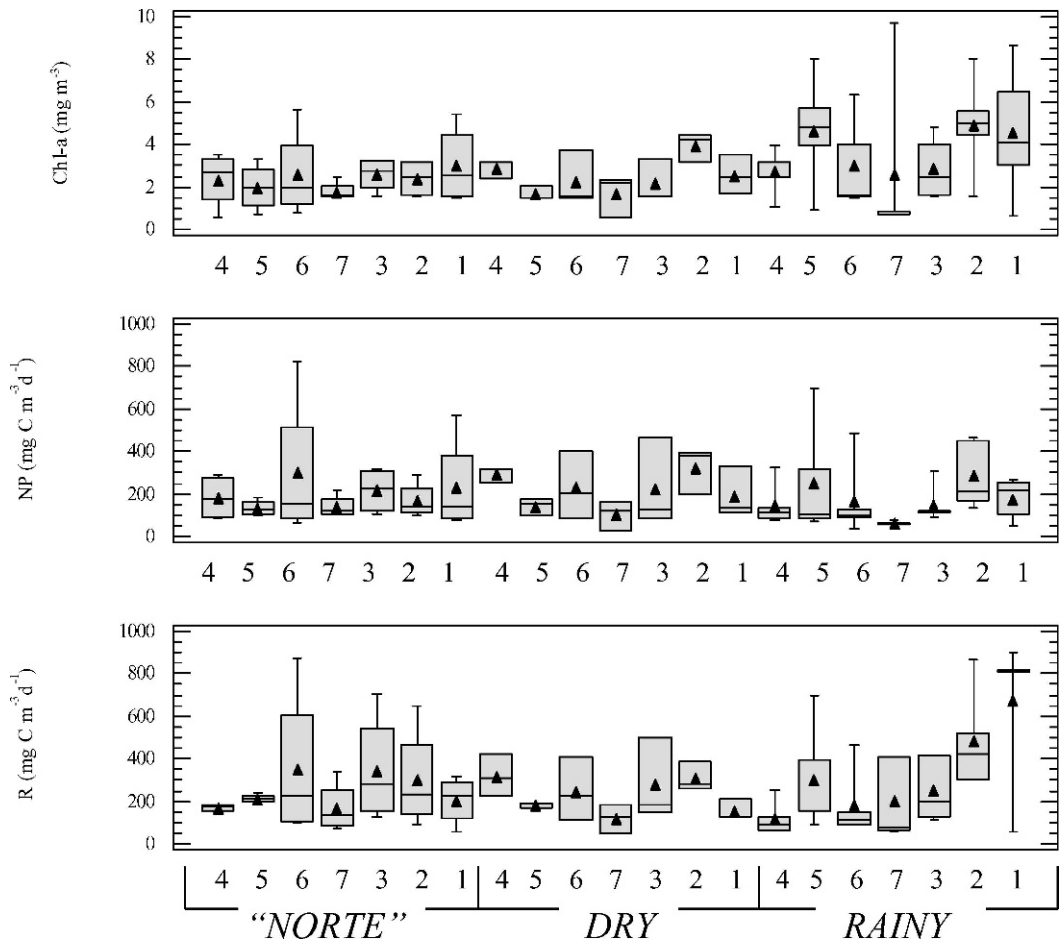
Fig. 6. Seasonal variability of chlorophyll *a* (upper), net phytoplankton production (middle), and respiration (lower) in Dzilam Lagoon. Mean values are depicted by filled triangles and medians are the horizontal lines bisecting the boxes. Sampling stations are arranged from west (left) to east (right), and climatic seasons shown along *x*-axis on the lower panel.

surface streams proliferating at its eastern and western branches (Fig. 1); the thick tannin plume observed in rainy season suggests that these channels may drain a significant water volume during this period.

This complex process may lower the nitrate concentration both by root uptake or loss through soil respiration, whereas the silicate maintains a more conservative condition until it reaches the lagoon, thus depicting relatively higher concentrations than nitrate at the inner sections of the system. Indeed, phytoplankton cells are more abundant in DL during rainfalls (4.8×10^7 cells/liter) than in droughts (3.1×10^7 cells/liter), with a marked dominance of Bacillariophyta during the former season (Herrera-Silveira et al., 1999). This seasonal increase of diatoms in the lagoon may be explained by the

high silicate concentrations distributed across the entire system during rainy period (Fig. 5).

The Dzilam reserve comprises a vast array of vegetation–geohydrological features known as "Petenes," which are islands of vegetation associated with the nutrient-enriched freshwater input supplied by springs. The high biomass and diversity attained by such tropical vegetation patches contrasts with the coastal landscape, dominated by the mangrove and deciduous forest communities. The amount of organic matter in shallow coastal ecosystems is a controlling factor of the microbial reduction of nitrate, or denitrification, and further loss to the atmosphere or transfer to other metabolic pathways within the system (Boynton et al., 1995). Thus, the overall low nitrate concentrations observed across the lagoon in rainfalls may
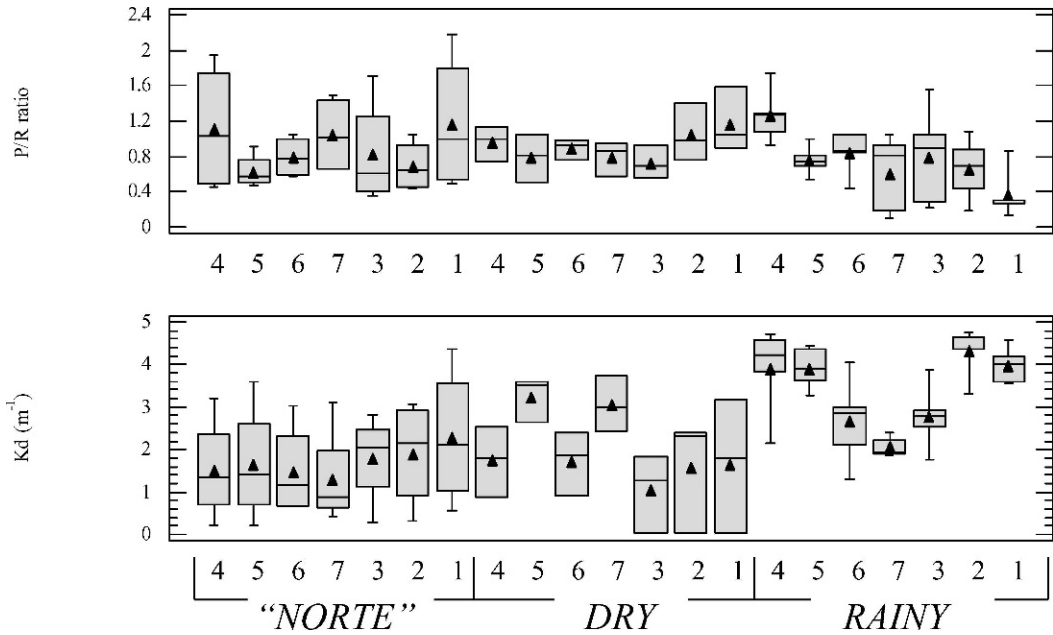
Fig. 7. Seasonal and spatial variation of production/respiration ratio (upper panel) and light extinction coefficient (lower panel) in Dzilam Lagoon. Mean values are depicted by filled triangles and medians are the horizontals line bisecting the boxes. Sampling stations are arranged from west (left) to east (right), and climatic seasons shown along *x*-axis on the lower panel.

be partially explained by the organic material loaded to the system after profuse precipitation in the zone.

However, with the current data on water-column nutrients we can at best speculate about the nitrogen metabolism dynamics and the implications of any alteration in the nutrient status in DL. When we consider that denitrification controls an important fraction of the biologically available nitrogen in shallow, semi-enclosed ecosystems (Koch et al., 1992), as well as entails a buffer complex against their eutrophication (Valiela et al., 1992), the previous knowledge gap emphasizes the relevance of addressing the rates and magnitude characterizing this biogeochemical process (i.e., denitrification) in DL under a management and conservation perspective.

Nitrate also was in relatively high concentrations at the eastern lagoon in early rainy season (Fig. 4), which may have been associated with the presence of a population of aquatic birds during rainfalls. The physical resuspension and bioturbation enhances the oxygen penetration deeper into the sediments and may stimulate the microbiological oxidation of ammonium to nitrate, or nitrification, as long as it occurs under aerobic conditions and is highly dependent on the supply of dissolved oxygen within the first few millimeters of sediment. The

waterfowl inhabiting this section of the lagoon could carry out the oxygen irrigation within the substrate and favor not only high nitrate concentrations, but also the release of nitrite and phosphate from the bottom, as observed at the eastern lagoon (Fig. 4).

The eastern branch of DL exhibits a long and narrow channel connecting the system with the ocean through an ephemeral inlet (Fig. 1), the flow of which is regulated by several hydrodynamic and meteorological processes such as precipitation, northerly winds, and tides. Hence, the entrance was opened late rainy (Sep. and Oct. samplings) and norte seasons (Jan. and Feb. samplings), whereas it remained closed for the entire dry season campaign. This is expected to drive a well-flushed condition, at least intermittently, during such periods in the easternmost lagoon, yielding an increased marine influence in the lagoon during norte season, and oppositely directed from the system to the nearshore after exceptionally high rainfall.

The increasing salinity toward the end of norte season and progressively brackish conditions observed along late rainfalls, combined with the prominent hyperhaline environment depicted during the entire dry season, lead us to infer that the characteristic water turnover rates at this inner portion of the lagoon are significantly controlled by the opening of this ephemeral

connection with the adjacent ocean. The dynamics of this exchange with the sea might partially regulate the renewing of the water within the lagoon and result in variations of nutrient availability, which may in turn imply relevant consequences for the trophic state in DL (Herrera-Silveira et al., 2002).

The diurnal tidal regime of the northern Yucatan coast, although of small amplitude, may contribute in determining the relative importance of the autotrophic–heterotrophic pathways to process the materials supplied from neighboring systems to DL, as a function of the periodic signal alternating spring and neap tides. This hydrodynamic forcing may alter, within tidal frequencies, the relationship of production–respiration maxima between phytoplankton and heterotrophic bacteria (Morales-Zamorano et al., 1991) and potentially shift to the dominance of the trophic chain via dissolved organic carbon instead of phytoplankton during such tidal events.

Accordingly, during norte and rainy seasons with the eastern inlet opened, the marine influence turns the lagoon into a heterotrophic system, as established by the P/R ratio estimated for those seasons (Table 3), whereas in dry season, when the circulation was limited by the temporary closure of this entrance, the high phytoplankton production ought to be developed upon the mineralization of organic matter favored by the high salinity and temperature co-occurring during this period (Fig. 3).

Moreover, the inconspicuous phytoplankton productivity observed during rainy season (Fig. 6; Table 3) may be a consequence of the phytoplankton cells carried away from the system owing to the significant freshwater drained in this period, and perhaps the transient dominance of the incoming bacteria resulting from mixing with the sea, to the expenses of the enriched material (e.g., dissolved organic matter) delivered to the lagoon through surface streams.

The annual phytoplankton production in DL ($80 \text{ g C m}^{-3} \text{ yr}^{-1}$) was inferior to that estimated in Celestun Lagoon, another karstic coastal lagoon of Yucatan ($125 \text{ g C m}^{-3} \text{ yr}^{-1}$; Herrera-Silveira, 1994). It was also substantially lower than the production recorded in Terminos Lagoon, a two-inlet coastal lagoon located in the western Yucatan coast ($219 \text{ g C m}^{-3} \text{ yr}^{-1}$; Stevenson et al., 1988), and El Verde Lagoon on the Pacific coast of Mexico ($522 \text{ g C m}^{-3} \text{ yr}^{-1}$; Flores-Verdugo et al., 1988).

As opposed to DL, Celestun Lagoon exhibits only one inlet at the southern portion of the system, with no ephemeral connections with the

sea, and is influenced by a luxuriant mangrove forest, including fringe and riverine-like mangrove systems (Herrera-Silveira, 1995). This physical–biological environment in Celestun may engage a more efficient setting to preserve longer the material delivered from neighboring systems and thereby take full advantage of this input by transferring it into higher production pathways within the system.

The other two ecosystems, one in the Gulf of Mexico and the other in the Mexican Pacific, exhibit some level of human impact, and thus, their relative higher primary production rate and reduced variability along the year might be ecological manifestations of such disturbances. The preceding assumption is based upon the finding that the natural state in coastal lagoons is supported by attributes such as hydrographic heterogeneity, numerous physical–chemical gradients, and habitat diversity (Kjerfve, 1994). Accordingly, a more prominent fluctuation of the primary production in DL would be expected given its pristine condition, than that exhibited by affected systems.

Finally, the importance of regulating the land use on the coastal zone of karst regions such as the Yucatan is recognized, since anthropogenic activities undertaken several kilometers inland may exert a significant impact over its coastal ecosystems, owing to the high connectivity through the extensive GD network featuring the Yucatan platform.

This study provides strong evidence of the deep influence that the GD discharges determine on the variability of the phytoplankton production in DL. The importance of monitoring the water quality drained to the coastal zone via GD inputs is also stressed. This strategy will provide an appropriate framework for preventing further deterioration of this vulnerable coastal region.

CONCLUSIONS

The phytoplankton showed maximum production during dry season as a result of intense autochthonous nutrient input through organic matter mineralization and limited water circulation, and lowest in rainy season due to turbulence and advection of phytoplankton cells away from the system.

Peak production was defined at the zones with intermediate salinity between marine and freshwater, particularly at the east portion of the lagoon where an ephemeral inlet controls the water turnover time.

The DL depicted a slight heterotrophic status in terms of the phytoplankton production for

the whole period of the study, with a more substantial heterotrophic condition in norte season and close to trophic balance between autotrophy and heterotrophy during dry season.

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