

Species composition and seasonal changes in macroalgal blooms in lagoons along the southeastern Gulf of California

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Abstract

Species composition and seasonal changes in macroalgal blooms in six coastal lagoons highly impacted by human activities were tracked for the three seasons between May 2004 and April 2005. Though temperatures were lower during the cold season than during the dry and rainy seasons and some locations showed variations in salinity during the rainy season, nutrient concentrations showed no defined pattern and varied according to season and location. A total of 10 seaweed species and the cyanobacterium *Microcoleus lyngbyaceus* had biomasses >1 g m⁻² dry weight, but only four species represented $>1\%$ of the annual biomass. During the dry season, *Spyridia filamentosa* had the highest biomass (57.5 g m⁻²). During the rainy season, *Gracilaria vermiculophylla* was the most conspicuous and abundant species (64.0–291.0 g m⁻²) and during the cold season, *Caulerpa sertularioides* had the highest biomass (180.1 g m⁻²). Abundances of these species were higher than previously reported for this region. Correlation analyses showed a positive correlation between total phosphorus and the biomass of *G. vermiculophylla*, suggesting that this nutrient might be limiting its growth. *C. sertularioides* abundance had a positive correlation with N:P ratios, suggesting that high concentrations of nitrogen relative to low phosphorus levels favor its growth. These analyses revealed that nutrient concentrations are most likely to affect macroalgal growth, but temperature and salinity also play a role. This information may be useful for monitoring future blooms and determining changes over time.

Keywords: abundance; biomass; coastal lagoons; Gulf of California; macroalgal blooms; nutrients.

Introduction

Macroalgae are natural components of shallow-water marine and transitional soft-sediment communities (Abbott and Hollenberg 1976). Their growth is related to seasonal changes in light, temperature, salinity and nutrients (Fong and Zedler 1993, Pedersen and Borum 1996, Kentula and DeWitt 2003). Dense mats of macroalgae are increasing in abundance and frequency in coastal waters around the world as a result of anthropogenic nutrient enrichment (Valiela et al. 1997, Bricker et al. 2003, Lapointe et al. 2005). Macroalgal blooms in temperate, relatively nutrient-rich waters (those with concentrations of dissolved inorganic nitrogen greater than a few μM) are characterized by extraordinary growth and biomass dominance by a relatively small group of taxa (Valiela et al. 1997), often ephemeral green species (Lotze and Schramm 2000) and sometimes red algae of the genus *Gracilaria* (McGlathery 2001).

To examine macroalgal blooms, we studied several coastal lagoons along the east coast of the Gulf of California. The Gulf of California is a semi-enclosed sea on the Pacific coast of Mexico and one of the most biologically diverse marine areas in the world. The coastline of the gulf contains 40 lagoons. These coastal lagoons have a great variety of habitats, including mangroves, salt marshes, intertidal pools, freshwater inner lagoons, and brackish and seawater systems (Páez-Osuna et al. 2003). They are natural systems of great ecological concern, because they are highly productive and are resilient to large environmental fluctuations (Costanzo et al. 2001).

In previous studies of coastal areas in naturally nutrient-enriched pristine zones of the northwestern Gulf of California, *Ulva* spp. biomass peaks of 266 g m⁻² (dry weight, DW) were described by Pacheco-Ruiz et al. (2002). Biomass of this taxon ranges from 35.1 to 53.7 g m⁻² (DW) in La Paz Bay on the Gulf, where there is anthropogenic impact from tourist activities (Águila-Ramírez et al. 2005). In the same region, the green species *Ulva lactuca* was characteristic of the area with the highest human impact (shrimp farms) in a coastal lagoon in Sinaloa, with a biomass peak of 66.8 g m⁻² (DW) during the dry season. This species was later replaced by *Gracilaria sjoestedtii* Kylin (240.0 g m⁻² DW) during the rainy season (Ochoa-Izaguirre 1999). Nutrient concentrations reported at this site were higher than those expected for coastal lagoons [14.2 μM total nitrogen (TN) and 1.1 μM dissolved phosphorus (DP) during the dry season and 10.6 μM TN and 2.7 μM DP during the rainy season]. These concentrations and the N:P ratios (12.6 and 3.8 during dry and rainy seasons, respectively) suggested

that nutrients were not limiting factors for the development of macroalgae in the area (Ochoa-Izaguirre et al. 2002). Here, we describe seasonal species composition of macroalgal blooms and their biomasses from six lagoons along the Sinaloa coast of the Gulf of California, and document important environmental conditions associated with each season and location.

Materials and methods

Sampling locations

This study covered six lagoons on the Sinaloa coast of the southeastern Gulf of California (Figure 1). A summary of the main characteristics of each lagoon and their watersheds, including human activity, is shown in Table 1. Each lagoon along the coast was surveyed where access permitted, in order to select sampling locations. Deep water was checked for macroalgae by means of free diving when needed. No macroalgal blooms were found far from shore or in deep water. Macroalgal blooms

were defined as an area longer than 50 m parallel to the shore conspicuously covered with beds of benthic macroalgae. A total of 10 sampling locations was selected (Table 1). To check for seasonal distributional patterns, each location was sampled once during each of three seasons: the nominal dry season from May to June 2004, the nominal rainy season from August to October 2004, and the nominal cold season from February to April 2005. Rainy seasons are based on well-defined periods of rainfall (Flores-Verdugo et al. 1993). Dry and rainy seasons are defined by monthly average air temperatures between 27°C and 30°C, and cold seasons by temperatures between 22°C and 26°C (CNA 2005).

Biotic parameters

To obtain macroalgal biomass for each bloom, replicate transects were laid out perpendicular to the coast according to the length of each bloom mat, with one transect at each end and the other in the middle of the bloom. In total, there were three transects through each bloom in each season of the year. Six equidistant points

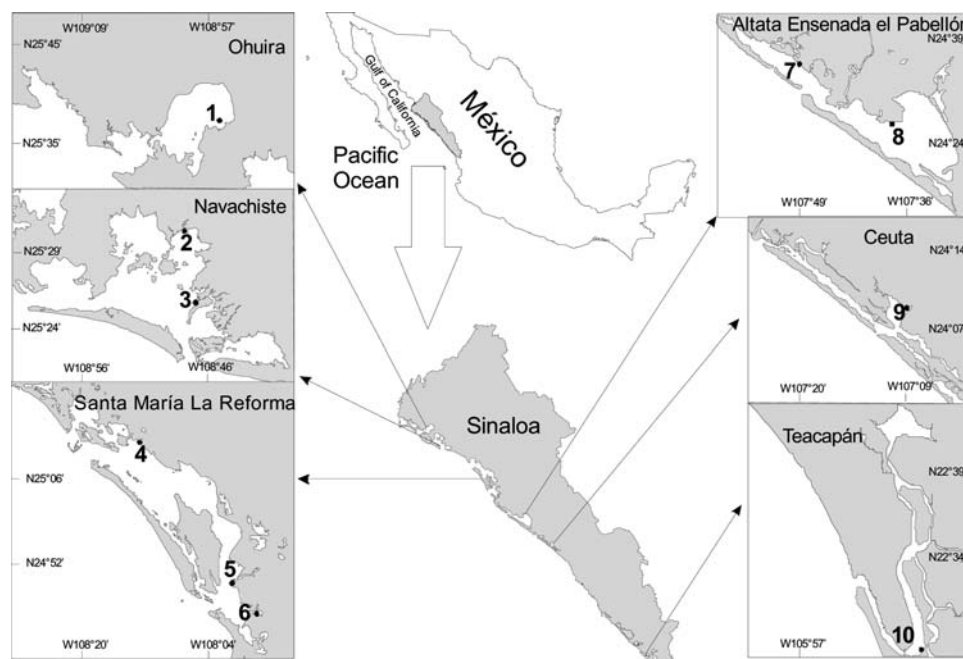


Figure 1 Sampling locations in Sinaloa where macroalgal blooms were found in 2004.

Table 1 Location, area, depth (range) and activities in coastal lagoons in the southeastern region of the Gulf of California.

Lagoon	Location	Area (ha)	Depth (m)	Activities
Ohuira	25°32'–25°36' N, 108°50'–109°15' W	29.772	2–4	Fisheries, agriculture, shrimp farming, industry, urban sewage from Los Mochis
Navachiste	25°22'–25°35' N, 109°05'–108°45' W	28.075	1–4	Fisheries, shrimp farming, agriculture
Sta. María La Reforma	25°20'–24°40' N, 107°27'–108°00' W	51.172	1–7	Fisheries, shrimp farming, agriculture
Altata Ensenada El Pabellón	24°18'–24°40' N, 107°27'–108°00' W	30.949	1–5	Fisheries, shrimp farming, urban sewage, agriculture Culiacán River discharge runoff
Ceuta	24°00'–24°15' N, 107°05'–107°27' W	6.737	0.5–2	Fisheries, shrimp farming, agriculture, rural communities
Teacapán	22°40'–22°25' N, 105°35'–105°47' W	5.506	1–7	Fisheries, shrimp farming, agriculture, rural communities

were defined for each transect, with end points at the shoreline and at the far edge of the bloom. At each point, macroalgae were collected from four, non-overlapping, randomly placed quadrants (0.25 m²) for a total sample area of 18 m² for each bloom (a stratified random sampling design). Samples were washed in the field with water from the lagoon and the species were separated by hand. Only species with biomasses >1 g m⁻² (designated “important” species hereafter) were weighed with a digital balance (± 0.5 g) and considered for analyses of species composition and seasonal changes. A sample of each species was fixed with 4% formaldehyde-seawater solution for further determination at species level in the laboratory. Three reference works were used to identify species (Abbott and Hollenberg 1976, Wynne 1986, Ochoa-Izaguirre et al. 2007). For each “important” species, a duplicate subsample (30 g wet weight) was taken to estimate dry biomass (g m⁻² DW). This DW was used for all subsequent analyses of species biomass. Subsamples were oven-dried at 60°C to constant weight (Downing and Anderson 1985).

To describe the occurrence of important species during the surveys, biomass was obtained on seasonal and annual bases for all locations using formulas modified from Cruz-Ayala et al. (1998):

$i=1$ to 10 sampling locations;

$j=1$ to s number of species;

$k=1$ to 3 sampling seasons;

$sb_j = mb_{ijk}$ [mb =mean biomass, sb =seasonal biomass];

$sb\% = \frac{sb_i}{sb_{js}} \times 100$ [$sb\%$ =relative seasonal abundance];

$Ab_{k=3} = \overline{X}mb_j$ [mb =mean biomass, Ab =annual biomass].

The mean biomass of each species (j) at each site (i) was expressed as g m⁻² of DW and plotted on a seasonal basis for each macroalgal bloom. For each season, biomass data were used to describe changes within and between macroalgal blooms.

Environmental parameters

Water samples were taken in the middle of the bloom and close to the edges during low and high tides. Temperature and salinity were determined in the field using a handheld multi-probe meter (YSI 556-Rickly Hydrological, YSI, Yellow Springs, USA) ($n=4$). A volume of water (200–600 ml) was filtered through a previously weighed nitrocellulose membrane (0.45 μ m) and the total suspended solids (TSS) were obtained by weight difference (APHA-AWWA-WPCF 1989). Additional water samples (2–6 replicates depending on the site location) were frozen and taken back to the laboratory for further determination of nutrients: dissolved inorganic nitrogen (DIN), TN, DP and total phosphorus (TP). Techniques used were those recommended by Strickland and Parsons (1972) and Grasshoff et al. (1983). Finally, the N:P ratio was obtained. A two-way analysis of variance model was used to determine significant differences in seawater temperature, salinity and nutrients using season (dry, rainy, cold) and sampling station (1–10) as independent variables. Normality (Kolmogorov-Smirnov test) and var-

iance homogeneity (Cochran's test) were tested. Means comparisons were carried out using Tukey's test only when there was a significant effect of the interaction ($p<0.05$) (Zar 1984).

Biotic vs. environmental parameters

Multiple linear regression analysis was used to identify whether any of the studied environmental parameters (temperature, salinity, TSS, DIN, TN, DP, and TP) explained variations in the biomass of each important species. Only results that were significant ($p<0.01$) are reported (Zar 1984). The relationships between environmental parameters and species biomass were analyzed by principal component analysis (PCA) (Sfriso and Marcomini 1997). The significance criterion for each component was the eigenvalue (>1). The greatest absolute values were selected from the correlation matrix. If there are two or more values in the same column, there is a correlation, if the signs are the same there is a direct relation, and if the signs are different, there is an inverse association (Ballesteros-Grijalva et al. 1996). All analyses were carried out using the program STATISTICA (StatSoft 1996).

Results

Environmental parameters

Mean seawater temperature, salinity and nutrients in the lagoons were affected by location (main effect: $p<0.05$), season (main effect: $p<0.05$) and by location in relation to the season (interaction: $p<0.05$). Overall, mean seawater temperatures during the cold season were lower than those during the dry and rainy seasons ($23.4\pm 0.3^\circ\text{C}$ vs. $30.3\pm 0.3^\circ\text{C}$ and $30.6\pm 0.3^\circ\text{C}$ for the cold, dry and rainy seasons, respectively; mean $\pm$ SE; Figure 2A). Temperature was higher at locations 2, 3 and 10 (see Figure 1 for location codes) during the dry and rainy seasons than at the rest of the locations (range between 31.6 and 32.3; Tukey's test, $p<0.05$). The pattern of seawater salinity among sampling locations was similar during the sampling period, with the lowest values at locations 9 and 10 during the rainy season (16.6 ± 1.4 and 22.8 ± 1.1 psu; Tukey's test, $p<0.05$) (Figure 2B). The mean TSS at location 2 (259.6 ± 81.1 mg l⁻¹) during the rainy season was significantly higher than during other seasons or at the other locations (Tukey's test, $p<0.05$), which had similar patterns and little variation (Figure 2C). Among nutrients, mean seawater N:P ratios were significantly higher at locations 1 and 3 during the cold season (>1000) and at 2 and 3 (>500) during the rainy season than at the rest of the locations during the entire sampling period (Tukey's test, $p<0.05$; Figure 2D). No evident pattern was observed in DIN concentrations. During the cold season, locations 2, 3 and 5 had concentrations double (36.2 ± 6.2 , 33.7 ± 1.1 and 51.0 ± 20.8 μM , respectively) those at the other locations during the dry and rainy seasons (Tukey's test, $p<0.05$; Figure 2E). The mean TN concentrations were variable and did not show a clear pattern. The mean TN concentration at location 3 during the cold season (129.8 ± 21.6 μM) was double that of

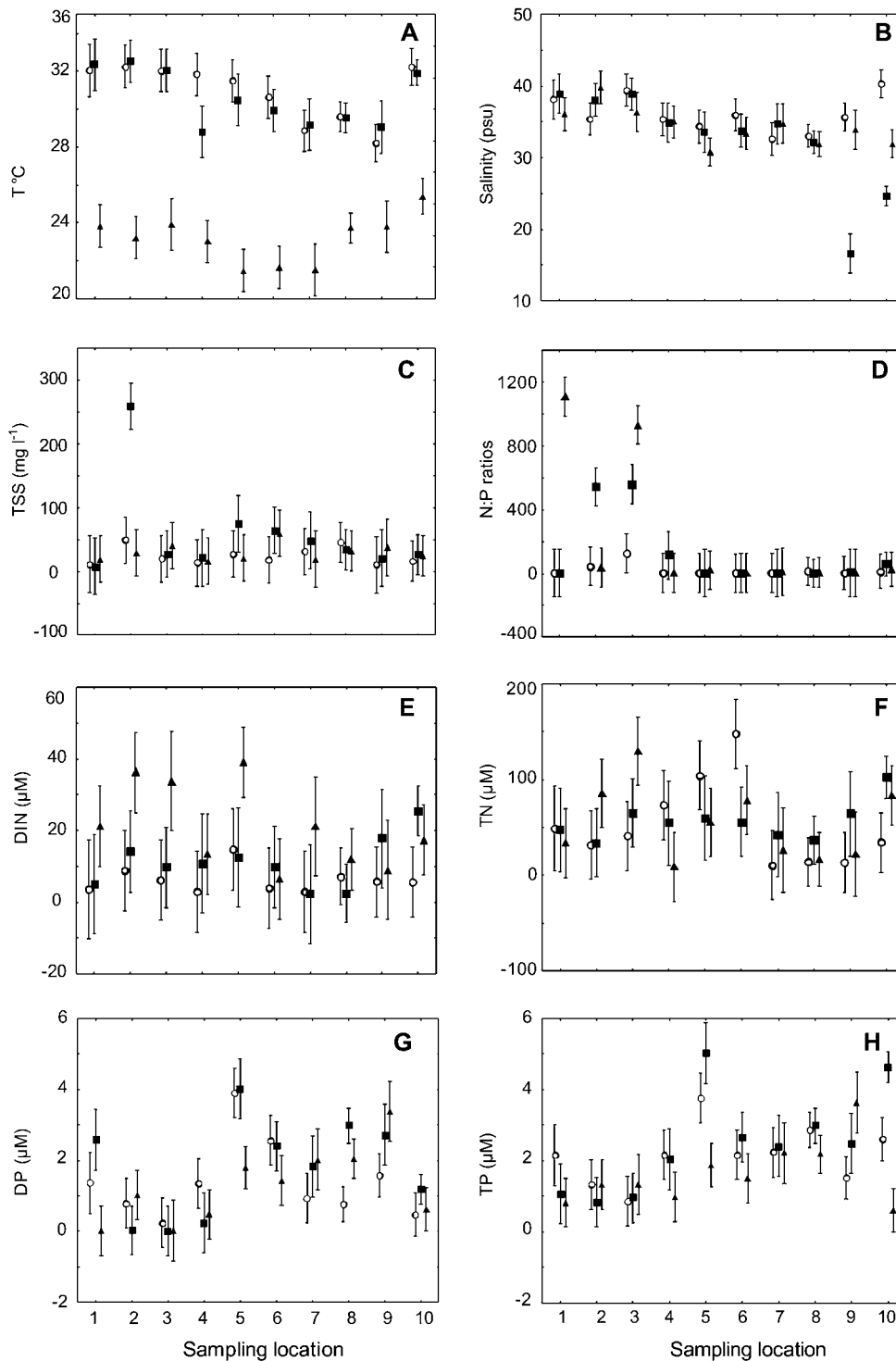


Figure 2 (A–H) Temperature, salinity, total suspended solids (TSS), dissolved inorganic nitrogen (DIN), total nitrogen (TN), dissolved phosphorus (DP), total phosphorus (TP) and N:P ratios at each sampling location during the dry season (○), rainy season (■) and cold season (▲). Vertical bars denote 95% confidence intervals. See Figure 1 for location codes.

location 4 during the cold season, location 8 during all seasons, and locations 9 and 10 during the dry season (Tukey's test, $p < 0.01$; Figure 2F). Mean seawater DP concentrations were significantly higher at location 5 during the dry and rainy seasons (3.9 ± 0.3 and 4.0 ± 1.0 μM , respectively) than at locations 1, 2, 3, 4, 7 and 10 during the dry, rainy and cold seasons (Tukey's test, $p < 0.01$; Figure 2G). Finally, mean seawater TP was significantly higher at location 5 during the dry and rainy seasons

(3.7 ± 0.3 and 5.0 ± 1.0 μM , respectively) than at most of the locations (Tukey's test, $p < 0.05$; Figure 2H).

Macroalgal seasonal changes

A total of 10 "important" species (biomass > 0.1 g m^{-2} DW) was recorded in the macroalgal blooms, six Chlorophyta and four Rhodophyta; no species of Phaeophyta were found. Cyanobacteria were also measured because

Table 2 Mean biomass (g m^{-2}) (SE) of species at each sampling location in six lagoons on the coast of Sinaloa.

Species	Sampling location									
	1	2	3	4	5	6	7	8	9	10
Chlorophyta										
<i>Caulerpa sertularioides</i> (S.G. Gmelin) M. Howe	121.5 (37.3)	-	-	-	-	-	27.0 (17.4)	-	-	-
<i>Rhizoclonium riparium</i> (Roth) Harvey	-	-	-	-	0.03 (0.02)	-	-	-	-	-
<i>Ulva clathrata</i> (Roth) C. Agardh	-	-	-	-	-	-	-	-	1.1 (0.7)	-
<i>U. intestinalis</i> Linnaeus	-	-	-	0.8 (0.5)	-	-	-	0.1 (0.0)	-	-
<i>U. lactuca</i> Linnaeus	-	-	-	0.1 (0.1)	0.2 (0.1)	-	-	-	-	-
<i>U. prolifera</i> O.F. Müller	-	-	-	-	-	-	-	0.2 (0.2)	-	-
Rhodophyta										
<i>Gracilaria vermiculophylla</i> (Ohmi) Papenfuss	-	1.3 (0.5)	1.0 (0.5)	7.0 (4.1)	72.4 (44.6)	23.2 (11.5)	0.3 (0.2)	60.3 (25.9)	54.4 (38.2)	56.7 (28.0)
<i>Hypnea spinella</i> (C. Agardh) Kützinger	5.4 (3.6)	-	-	-	-	1.6 (0.8)	1.4 (1.1)	-	0.1 (0.2)	1.1 (0.6)
<i>H. valentiae</i> (Turner) Montagne	4.1 (2.0)	-	-	-	-	0.1 (0.1)	-	-	-	-
<i>Spyridia filamentosa</i> (Wulfen) Harvey	17.9 (11.6)	4.9 (2.1)	0.8 (0.2)	-	-	-	0.1 (0.0)	-	-	-
Cyanobacteria										
<i>Microcoleus lyngbyaceus</i> (Kützinger) P.L. Crouan et H.M. Crouan	-	-	-	-	-	-	4.7 (1.8)	-	-	-

See Figure 1 for location codes.

Microcoleus lyngbyaceus contributed a large amount of biomass (Table 2). During the annual cycle, macroalgal blooms in the lagoons of Ohuira (1) and one in Altata-Ensenada (8) had a species composition different from the other lagoons. In both, *Gracilaria vermiculophylla* was absent during the times of sampling and *Caulerpa sertularioides* was important during the rainy season. In terms of biomass, the sampling locations with the lowest biomass during the entire annual cycle, compared with the rest of the locations, were locations 2 and 3 in Nava-chiste (Figure 1, Table 2; range from 0.3 to 13.7 g m^{-2}). Total biomass of macroalgal blooms increased from the dry season (140.4 g m^{-2}) to the rainy season (1,138.6 g m^{-2}) and decreased during the cold season (220.5 g m^{-2}). The most abundant species were *Spyridia filamentosa*, *G. vermiculophylla*, and *C. sertularioides* during the dry, rainy and cold seasons, respectively.

Changes in biomass and species composition

Mean biomass values of important species in the macroalgal blooms ranged from 0.1 to 291.0 g m^{-2} during the sampling period. The number of important species in each macroalgal bloom varied from 1 to 3 (Figure 3). Biomass of important species changed according to season.

During the dry season, the species with highest biomass was *Spyridia filamentosa* with $57.5 \pm 17.8 \text{ g m}^{-2}$ (mean $\pm$ SE) at location 1. After *S. filamentosa*, *Gracilaria vermiculophylla* contributed more biomass ($20.0 \pm 2.1 \text{ g m}^{-2}$) at location 4 than the rest of the species (Figure 3A). These two species contributed more than 70.0% of the biomass: *G. vermiculophylla* at locations 2, 3, 4, 5, 8 and 9 (relative abundance ranged from 72.0% to 100.0%), and *S. filamentosa* at location 1 with a relative abundance of 70.0% (Figure 4A).

During the rainy season, *Gracilaria vermiculophylla* had the maximum biomass ($291.0 \pm 20.5 \text{ g m}^{-2}$) at location 5. It was the only species at locations 5, 6, 8, 9 and 10; the lowest amount of biomass ($64.0 \pm 5.4 \text{ g m}^{-2}$) was at location 6. This species replaced *Ulva lactuca* at location 5, *Ulva intestinalis* at location 8, and *Hypnea spynella* at location 10. *Caulerpa sertularioides* followed in rank with highest biomasses at locations 1 ($154.4 \pm 40.9 \text{ g m}^{-2}$) and 7 ($96.0 \pm 15.6 \text{ g m}^{-2}$) (Figure 3B). No algae were found at location 4. Two red and one green macroalgal species contributed more than 70.0% relative abundance in the blooms, namely, *G. vermiculophylla* at locations 5, 6, 8, 9 and 10 (100.0%), *Caulerpa sertularioides* at locations 1 (100.0%) and 7 (86.0%), while *Spyridia filamentosa* was the “important” species at locations 2 (85.0%) and 3 (72.0%) (Figure 4B).

During the cold season, the species with the highest biomass was *Caulerpa sertularioides* ($180.1 \pm 41.2 \text{ g m}^{-2}$) at location 1. Except for this location, biomass values were low ($< 14.0 \text{ g m}^{-2}$). The green algal species *Ulva prolifera* and *U. clathrata* were present only during the cold season (Figure 3C). No algae were found at locations 7 and 10. In this season, six species made up more than 80.0% of the relative abundance, namely, *Spyridia filamentosa* at locations 2 (95.0%) and 3 (100.0%), *Gracilaria vermiculophylla* at locations 5 (100.0%) and 6 (100.0%), *C. sertularioides* at location 1 (95.0%), *U. intestinalis* at location 4 (100.0%), *U. prolifera* at location 8

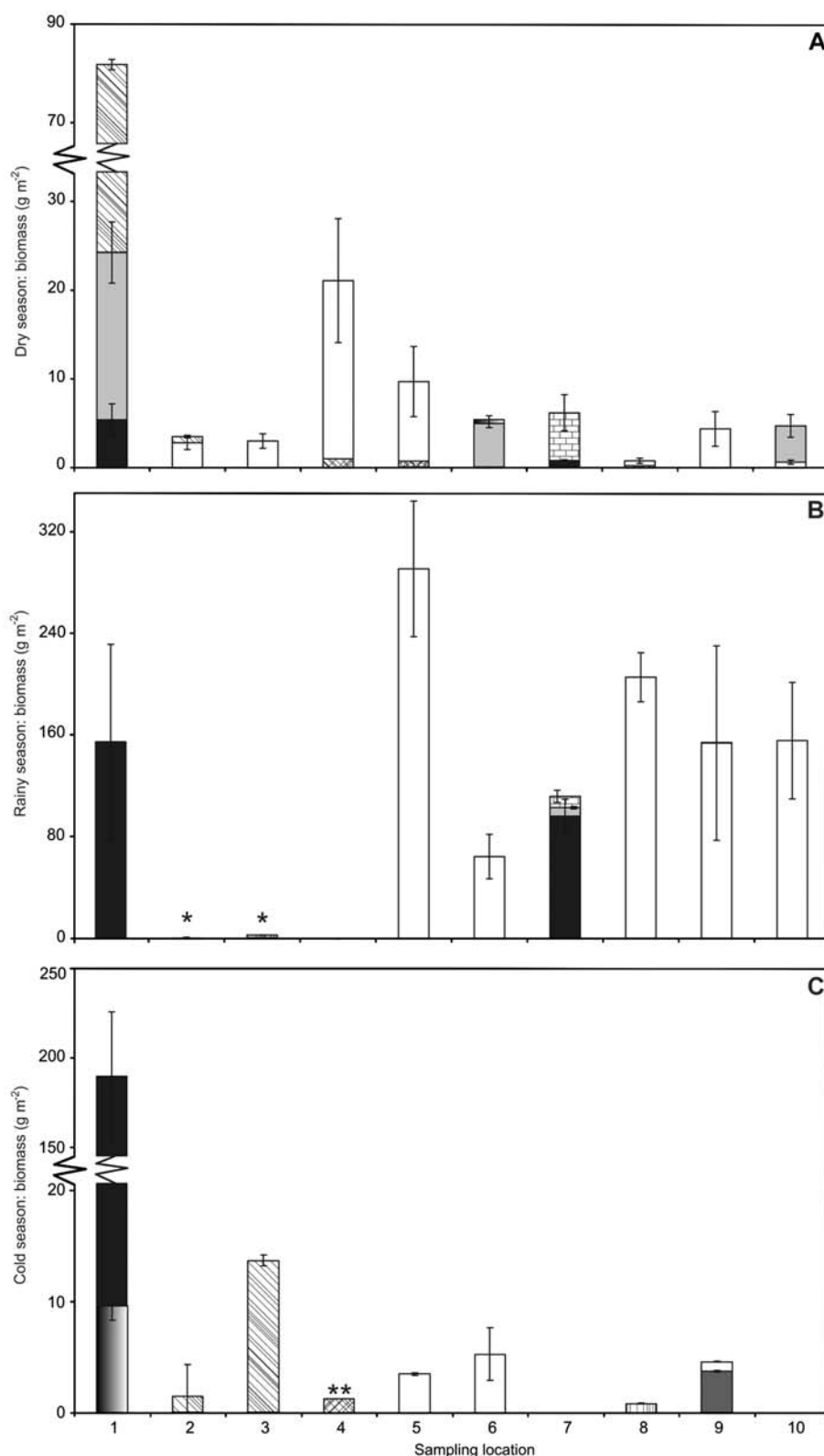


Figure 3 Species biomass ($\pm$ SE) found at each location in each season (see Figure 1 for location codes and Table 2 for means across locations).

(A) Dry season, (B) rainy season, (C) cold season. *Caulerpa sertularioides*, *Rhizoclonium* sp., *Ulva clathrata*, *U. intestinalis*, *U. lactuca*, *U. prolifera*, *Gracilaria vermiculophylla*, *Hypnea spinella*, *H. valentiae*, *Spyridia filamentosa*, *Mycrocoleus lyngbyaceus*. **S. filamentosa* and *G. vermiculophylla* species present at these locations with relatively low values of biomass (<2.0 g m⁻²). **Absence of or small SE bars means that error values are lower than <0.1 g m⁻². Blank spaces indicate absence or biomass <0.1 g m⁻² of important species.

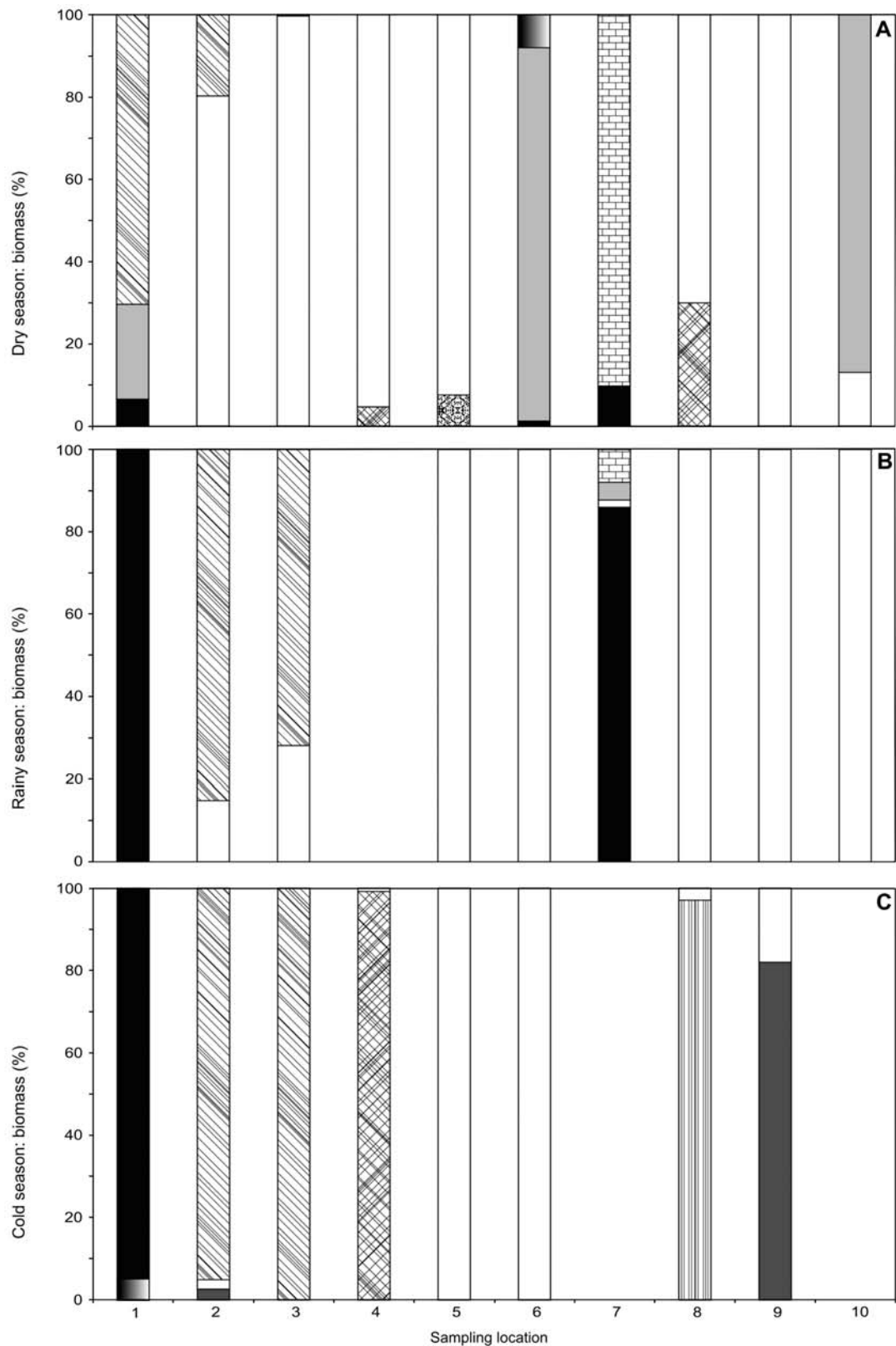


Figure 4 Relative abundance of macroalgae found at each location in each season (see Figure 1 for location codes).

(A) Dry season, (B) rainy season, (C) cold season. *Caulerpa sertularioides*, *Rhizoclonium* sp., *Ulva clathrata*, *U. intestinalis*, *U. lactuca*, *U. prolifera*, *Gracilaria vermiculophylla*, *Hypnea spinella*, *H. valentiae*, *Spyridia filamentosa*, *Mycrocoleus lyngbyaceus*. Blank spaces indicate absence of macroalgal blooms.

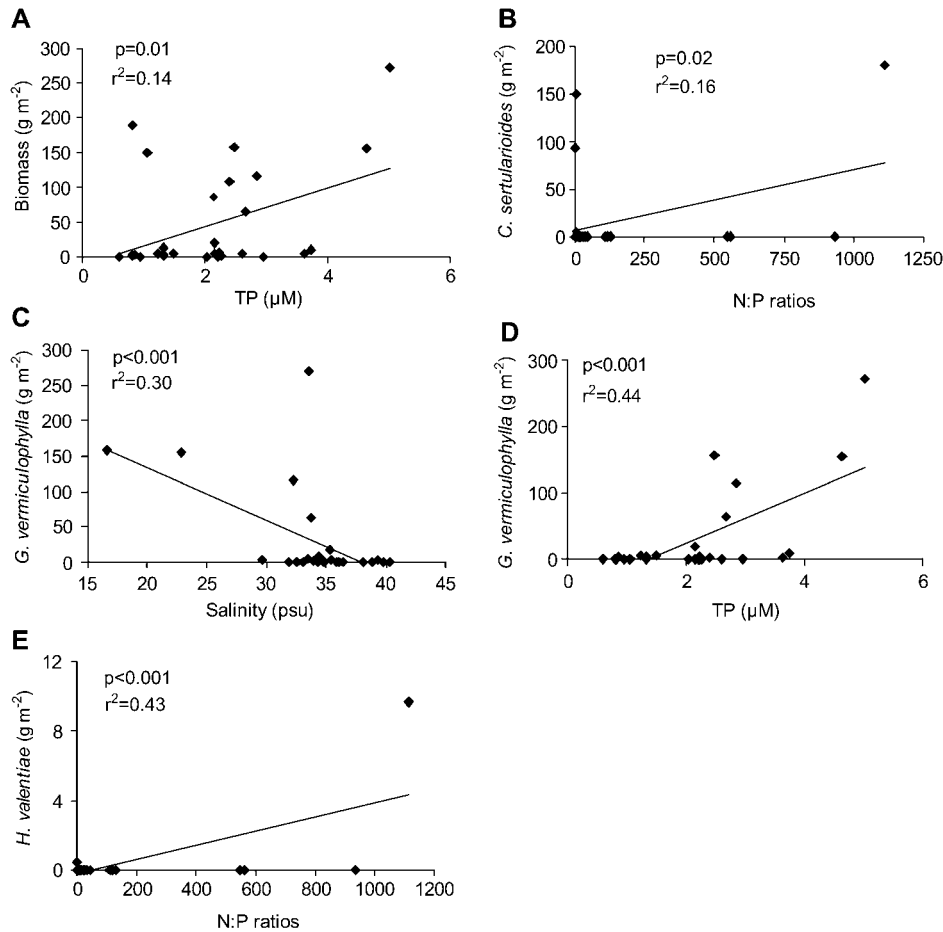


Figure 5 Significant ($p<0.01$) correlations between physicochemical parameters and species biomass.

(A) Total algal biomass, (B) *Caulerpa sertularioides* biomass, (C and D) *Gracilaria vermiculophylla* biomass, (E) *Hypnea valentiae* biomass.

(97.0%), and *U. clathrata* at location 9 (82.0%) (Figure 4C).

Regression and multivariate analysis

Linear regression analyses showed that biomasses of some of the important species were correlated with some of the environmental parameters studied. Overall, total biomass showed a positive correlation with TP concentrations (Figure 5A). *Caulerpa sertularioides* biomass showed a positive linear correlation with N:P ratios (Figure 5B). The correlation analysis indicated an inverse relationship between salinity and the biomass of *Gracilaria vermiculophylla* (Figure 5C) and a positive correlation with TP concentrations (Figure 5D). The biomass values for *Hypnea valentiae* showed a positive correlation with the N:P ratios (Figure 5E). No correlations were found between biomasses of other species and any of the parameters.

The PCA extracted three factors (eigenvalue >1) from the variables included in the data sets (the environmental parameters and the species biomass) that accounted for 68.7% of the total variation. Factor 1 (eigenvalue 2.4) explained 31.0% of the total variation and included a positive correlation with DIN and N:P ratios, but a neg-

ative correlation between DP, TP and *Gracilaria vermiculophylla* biomass and the cumulative biomass of all sampled species. Factor 2 (eigenvalue 1.7) explained 22.3% of the total variation and included a positive correlation with temperature and salinity, but a negative correlation between TN, DIN and the biomass of *G. vermiculophylla*. Factor 3 (eigenvalue 1.1) explained 17.7% of the total variation. Only factors 1 and 2 included correlations with the biomass of important species and are the only ones shown in Figure 6A (53.3% of the total variation).

The plot of scores shows the correlations obtained from the PCA for the sampling locations (Figure 6B). Associations between sampling locations in the dry and rainy seasons are shown. Locations 4 and 9 during the dry season and locations 1, 7, 8 and 9 during the dry and rainy seasons were characterized by high concentrations of DP and TP, and high temperature and salinity values. Some of the highest values for *Caulerpa sertularioides* and *Gracilaria vermiculophylla* biomass were found at these sampling locations. Locations 5, 6 and 9 sampled during the dry and rainy seasons and location 10 during the rainy season had the same characteristics, but had low salinity and the highest biomass of *Gracilaria vermiculophylla*. Locations 2 and 3 during the dry and

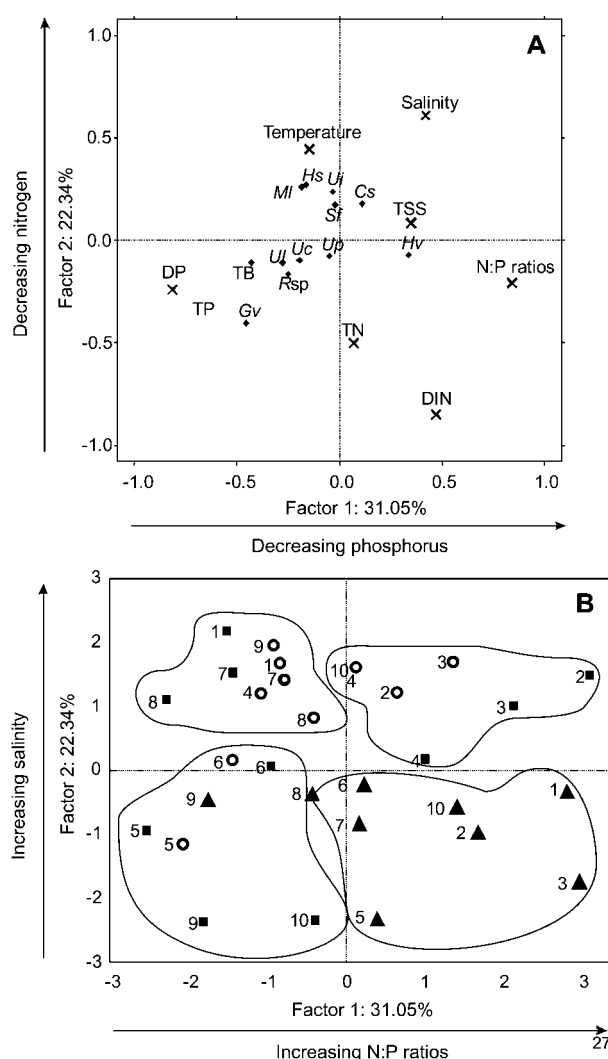


Figure 6 Multivariate analyses.

(A) PCA showing correlations between physicochemical parameters (x) and species biomass (♦). Total suspended solids (TSS), dissolved inorganic nitrogen (DIN), total nitrogen (TN), dissolved phosphorus (DP), total phosphorus (TP), *Ulva clathrata* (Uc), *U. intestinalis* (Ui), *U. lactuca* (Ul), *U. prolifera* (Up), *Gracilaria vermiculophylla* (Gv), *Hypnea spinella* (Hs), *H. valentiae* (Hv), *Spyridia filamentosa* (Sf), *Mycrocoleus lyngbyaceus* (Mi). (B) Plot of scores showing aggregations of sampling locations (see Figure 1 for location codes) in dry season (○), rainy season (■) and cold season (▲).

rainy seasons and location 10 during the dry season had high temperature and salinity values, while TN concentrations were low. Locations 1, 2, 3, 5, 6, 7, 8 and 10 during the cold season had low temperatures with high concentrations of DIN and TN.

Discussion

Our findings provide a comprehensive description of macroalgal blooms in shallow coastal waters along the coast of Sinaloa. A single macroalgal species or *Mycrocoleus lyngbyaceus* contributed >70% of biomass during at least one of the three seasons (*Ulva clathrata*, *U. intestinalis*, *U. prolifera*, *Caulerpa sertularioides*, *Hypnea spinella*, *Gracilaria vermiculophylla*, *Spyridia filamentosa*).

Only *C. sertularioides*, *H. spinella*, *G. vermiculophylla* and *S. filamentosa* were always present. These species are consistent with genera previously reported as bloom-formers in nutrient-rich coastal waters. For example, Lotze and Schram (2000) and McGlathery (2001) stated that ephemeral green species (i.e., *Ulva* spp.) and red algae of the genus *Gracilaria* were important in macroalgal blooms. Fletcher (1996) reported *Caulerpa*, *Ulva*, *Gracilaria*, and *Hypnea* as characteristic of eutrophic waters and Cyanobacteria under anaerobic conditions and low pH. In general, the mean values of seasonal biomass for the most important species were higher than those previously reported for important species in macroalgal communities in the Gulf of California (Cruz-Ayala et al. 1998, Casas-Valdez et al. 2000, Carballo-Cenizo et al. 2002), but were consistent with those reported for macroalgal blooms in locations favoring growth, such as areas with nutrient enrichment from natural (Pacheco-Ruiz et al. 2002) or anthropogenic (Ochoa-Izaguire et al. 2002, Scanlan et al. 2007) sources.

Some of the most important species found in macroalgal blooms are in the genus *Ulva*. In our surveys, however, very little biomass was contributed by *Ulva*. It is possible that it was present but had become detached from the substratum (Pacheco-Ruiz et al. 2002) and drifted to areas outside the sampling locations so that no correlations or trends were found with any of the parameters. In the region of the present study, *Ulva* species were the most abundant green algae in Laguna San Ignacio (Nuñez and Casas 1998). This abundance was related to the lower temperatures prevailing during the winter and to nutrient enrichment, although the authors did not measure nutrient concentrations. Sfriso and Marcomini (1997) reported biomass production of *Ulva* of ~2.4 kg m⁻² DW in Venice lagoon, Italy in association with the nutrient loads of anthropogenic origin.

Macroalgal blooms are known to be excessive, and extensive growths of macroalgae dominated by few taxa and often associated with nutrient-rich waters (Valiela et al. 1997, Lotze and Schramm 2000). We found that nutrient concentrations in the locations sampled were comparable and sometimes higher than those reported for other coastal lagoons and estuaries, indicating nutrient enrichment from various sources in localized pulses. For example, our high concentrations of DIN at some locations (>50 µM) are comparable to those found by Hernández-Ayón et al. (1993) in the Gulf of California region resulting from groundwater inputs (above 60 µM). A patchy distribution of macroalgae can be associated with these localized pulses of nutrients, such as the mats of *Ulva*, *Gracilaria*, and *Cladophora* (biomass >40 g m⁻²) found in a shallow back barrier lagoon on Hog Island Bay, USA, which were distributed in patches associated with localized pulses of N (10–35 µM; Havens et al. 2001).

Even when regression analyses explained little of the variation of the biomass, multivariate analysis (PCA) explained more than 50% of this variation and some trends can be inferred. Multivariate analysis showed that nutrients explain more of the correlations than temperature, but they showed no clear seasonal and/or spatial pattern. This is similar to results obtained by Nixon and Pilson (1983) and Hernández-Ayón et al. (1993) for nutri-

ents at sites in the Gulf of California. Nevertheless, some seasonality was observed in the abundance of the most "important" species, which might be related to variations in temperature and salinity as observed previously for some of these species in the region (Carballo-Cenizo et al. 2002, Ochoa-Izaguirre et al. 2002).

The genus *Gracilaria* is characteristic of tropical and temperate environments (Abbott and Hollenberg 1976) and is widely distributed (Casas-Valdez et al. 2000). In the present study we found *G. vermiculophylla* at most locations in most seasons, through a wide range of temperatures (21.5–32.5°C) and salinities (16.6–40.5 psu) consistent with a wide distribution. Multivariate analysis showed that the abundance of *G. vermiculophylla* is related to phosphorus concentrations and low salinity values. This species originates from the northwestern Pacific Ocean and is an invader in the eastern Pacific Ocean (Bellorin et al. 2004). Its success as an invader in shallow estuaries of Hog Island was suggested to be related to its association with the ubiquitous polychaete *Diopatra cuprea* (Bosc), its efficient recruitment on hard substratum, its high tolerance of dessication, grazing, burial by sediment, low light, low and high temperatures, and its long-term persistence as both small and large vegetative fragments [as *G. verrucosa* (Huds.) Papenfuss, Thomsen 2004a,b, Thomsen et al. 2005]. We also found it in high abundance where high concentrations of phosphorus were present. This positive correlation suggests that this might be the limiting nutrient for this species. This was observed also for *Gracilariopsis sjostedtii* in the southeastern part of the Gulf of California that reached biomass peaks during the rainy season, which is characterized by high concentrations of phosphorus and low salinities (Ochoa-Izaguirre 1999). Chuan-Chuan et al. (2005) found that the growth of *G. coronopifolia* J. Ag. in a region of Taiwan was P-limited for biomass values higher than 40 g m⁻². In Florida, sewage-driven eutrophication in the early 1980s led to drift macroalgal blooms (with biomass levels >600 g m⁻²) that included the red algae *Gracilaria*, *Spyridia*, *Hypnea*, and *Agardhiella*, and the green algae *Ulva* and *Caulerpa* (Avery 1997 in Lapointe and Bedford 2007). We found the highest values of *Gracilaria* biomass associated with locations 5 and 6, locations which had the highest TP content due to upwelling sewage from El Estero del Tule, and location 9 which is affected by a shrimp farm.

The green alga *Caulerpa sertularioides* was the most abundant species during the cold season. Its abundance in this region has been related to inter-annual differences in temperature (Scrosati 2001). In other areas, it was the most abundant species during the autumn, which has been explained by thermal plasticity and tolerance to decreases in sunlight (Cruz-Ayala et al. 1998). However, species of the same genus in other areas of the world are considered invasive and can reach more than 800 g m⁻² in the Mediterranean Sea and 100 g m⁻² in California, USA (Hill et al. 1998). The PCA showed that its abundance was correlated with an increase in nitrogen and lower values of phosphorus, suggesting that it develops well in nitrogen-rich waters, such as at the stations where we found it. This is consistent with species of the genus *Caulerpa* in the Indian River Lagoon in Florida where they

are highly productive due to nutrient enrichment (Gacia et al. 1996).

In the case of *Hypnea valentiae*, we found a positive correlation between N:P ratio and its biomass, but a negative correlation with TP. The genus *Hypnea* has been found to increase its biomass when nutrients are present, but only if temperature is optimal for its growth (22°C) (Friedlander and Zelikovitch 1984). Finally, the abundance of *Spyridia filamentosa* has been particularly related to seawater temperature, with abundance peaks when temperature is high across the Gulf of California (Mateo-Cid et al. 1993, Núñez-López 1996, Casas-Valdez et al. 2000). In this study, biomass values were high only during the dry season at location 1 (>50 g m⁻²), which suggests that local factors are also influencing its abundance, but no correlations were found with environmental parameters.

In general, N:P ratios found in this study were variable but comparable to those previously established in other Mexican lagoons (De la Lanza 1994). This suggests that nutrients are not limiting factors for the development of macroalgae (Ochoa-Izaguirre et al. 2002); however, our correlation analyses indicated that some limitation was present. Overall, our results demonstrate that the biomass of algae is limited by the availability of nitrogen and phosphorus, as in the case of *Caulerpa sertularioides* (nitrogen limited) and *Gracilaria vermiculophylla* (phosphorus limited), and that the type and severity of nutrient limitation varies depending on habitat, species and season (Pedersen and Borum 1996).

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