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Factors Affecting the Abundance of Phytoplankton in a Restricted Subtropical Lagoon, the Indian River Lagoon, Florida, USA

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Phytoplankton dynamics in the Indian River Lagoon was examined from the point of view of several key controlling factors, including: nutrient limitation, light availability, temperature, wind, hydrodynamic restriction and grazing. Water was collected at eight sampling sites in the lagoon on a monthly basis for a two and a half year period. Samples were analysed for nutrient content and phytoplankton abundance. Site measurements of salinity and light extinction were made at all sites. Regional data on rainfall, wind and water temperature was obtained for correlation analyses. Bioassays were performed to determine nutrient limiting status and a series of preliminary grazing experiments were carried out on selected samples. The results indicate that the Indian River Lagoon is a nutrient-rich environment where phytoplankton standing crops are often held below their potential by several key loss functions, including hydraulic flushing and grazing. Spatial patterns of phytoplankton abundance generally reflected the degree of restriction to water turnover in different regions of the lagoon, with higher mean abundances in restricted regions. Spatial and temporal patterns of nutrient content and limitation suggest that patterns of external nutrient loading also play a significant role in phytoplankton dynamics. High phosphorus levels in the southern portion of the lagoon contribute to the predominance of nitrogen limitation in the region. In contrast, relatively high N/P ratios in the northern portions of the lagoon contribute to greater potential for phosphorus limitation of phytoplankton growth. As might be expected from the subtropical location of the lagoon, temporal patterns of phytoplankton abundance appear to be less strictly dependent on season than in temperate habitats, and more closely linked to variations in weather conditions, like rainfall (including storm events). The latter considerations bring into play issues like temporal variation in salinity and wind-induced mixing. The high light flux and shallow depth in the lagoon also presents the potential for photoinhibition.

Keywords: phytoplankton; lagoon; Florida; nutrients; light; flushing

Introduction

A significant body of literature exists on the spatial and temporal patterns of phytoplankton abundance in estuaries and how these are influenced by physical, chemical and biological factors (Platt & Denham, 1980; Smayda, 1980; Carrick *et al.*, 1993; Kirk, 1994; Cloern, 1996; Lucas *et al.*, 1999*a*, *b*). Among the most frequently discussed factors are those that control algal growth, principally nutrient availability, light availability and temperature, as well as those that contribute to biomass loss, like tidal flushing and grazing. In many cases the impacts of one factor are dependent on other factors. For example, the effects of nutrient loading on phytoplankton abundance in coastal ecosystems is dependent on other factors that affect biomass gains and losses, including: light availability (Hitchcock & Smayda, 1977; Cole & Cloern, 1984; Bledsoe & Phlips, 2000), sedimentation, death, hydraulic flushing (Richardson & Jorgensen, 1996) and grazing (Frost, 1980). Relatively restricted estuarine environments often develop higher phytoplankton standing crops than more open estuaries that receive similar nutrient inputs, due to higher water turnover rates in the latter (Knoppers *et al.*, 1991; Monbet, 1992). In restricted estuaries of elevated trophic status algal blooms can be common and persistent, sometimes leading to problems with hypoxia, toxins and changes in the structure of biological communities (Paerl, 1988; Nixon 1995). In areas of the world subject to significant human development, the process of eutrophication can be accelerated (Smayda, 1989), increasing the frequency and intensity of algal blooms, which in turn can lead to significant changes in the structure and function of the effected ecosystems. This trend is illustrated by the results of research in Chesapeake Bay (Harding, 1994), the Baltic Sea (Rosenberg *et al.*, 1990) and the Wadden Sea (Jonge *et al.*, 1993).

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In this study we examined spatial and temporal trends of phytoplankton standing crops in the Indian River Lagoon, a restricted estuarine ecosystem in Florida subject to increasing pressures of cultural eutrophication. The watersheds feeding in to the lagoon encompass one of the fastest growing population centres in the United States. Historically, the basin has also been the site of major citrus industries. Climatologically, the lagoon is located in the transition region between the tropical environment of the Florida Keys and the temperate environment of the Georgia coast. Tidal flushing is restricted to three major inlets along the 260 km extent of the barrier islands that define the eastern boundary of the lagoon. While there are no major rivers that flow into the lagoon, a number of smaller rivers, canals and municipal discharges are sources of freshwater and nutrients. It has been estimated that up to 50% of nutrient loading may come from non-point sources (Kleppel, 1996).

The narrow (generally <3 km wide) and very long (260 km) structure of the Indian River Lagoon, along with the limited number of inlets to the Atlantic Ocean, together result in significant spatial variation in a number of key physical and chemical parameters; including hydraulic flushing, salinity and nutrient content. In the northern part of the lagoon water exchange rates are very low, with turnover rates that can exceed 1 year (Sheng *et al.*, 1990; Smith, 1993). Over the past few decades major loses of seagrass communities have been documented (Kleppel, 1996; Morris & Tomasko, 1993). It has been hypothesized that anthropogenically-driven eutrophication has elevated levels of phytoplankton (Kleppel, 1996), which contribute to light limitation of benthic plant production. Since these plant communities are the dominant primary producers in the lagoon and support a diverse biological community (Virnstein *et al.*, 1983; Virnstein, 1990, 1995), the dynamic character and controlling factors for phytoplankton communities are major issues of concern. Recent observations of algal blooms in the lagoon involving potentially toxic species (Badylak & Phlips, in preparation) also raise broader concerns about the consequences of eutrophication for ecosystems health.

Our working hypothesis was that patterns in phytoplankton abundance in the lagoon could be interpreted in terms of the degree of hydrodynamic restriction and nutrient availability. The results suggest that a number of other factors may also affect phytoplankton standing crops, including grazing, light flux, temperature and patterns of rainfall and wind.

Methods

Study site description

The Indian River Lagoon is located along the eastern shore of Florida, USA. The lagoon extends from Jupiter in South Florida to near Daytona Beach in Central Florida and is characterized by a number of ecologically distinct basins, which differ considerably in hydrodynamic, chemical, biological and watershed (Kleppel, 1996; Sheng *et al.*, 1990; Smith, 1993). Based largely on hydrodynamic considerations, Glatzel and Da Costa subdivided the Indian River lagoon system into five distinct regions (Kleppel, 1996), which we used to select the locations of seven sampling sites (Figure 1); Northern Indian River Lagoon (Site 2), Banana River (which is directly connected to the Indian River Lagoon near the City of Melbourne) (Site 3), North Central Indian River Lagoon (Sites 4 and 5), South Central Indian River Lagoon (Sites 6 and 7) and South Indian River Lagoon (Site 8). In addition, we added a sampling site in the southern portion of the Mosquito Lagoon (Site 1), which is connected to the northern region of the lagoon.

Field procedures

Water was collected at the eight sampling sites on a monthly basis. Dissolved oxygen ($mg\,l^{-1}$), salinity and temperature (°C) were measured with a YSI Model 895. Water samples were collected with a water column integrator that captures water from the surface to within 0·1 m. of the bottom. Aliquots of sampled water were used for determination of chlorophyll *a*, total phosphorus, soluble reactive phosphorus, total nitrogen, nitrate–nitrite and ammonium. An additional 15 l were collected for subsequent nutrient limitation bioassays.

Laboratory procedures

Water colour was determined from filtered station water (0·3 μm glass-fibre filter). Samples were analysed using platinum cobalt standards from protocols described in Standard methods (APHA, 1989) on a Hitachi U2000 dual beam spectrophotometer. Inorganic nutrient concentrations ($NO_2^- + NO_3^-$, PO_4^+, and NH_4^+) were determined colourimetrically with a Technicon AutoAnalyser (Parsons *et al.*, 1984; APHA, 1989) from filtered aliquots (Gelman A/E glass fibre filters). Silica (SiO_2) was determined using manual colourimetric methods (APHA, 1989). Total nitrogen and total phosphorus were determined using

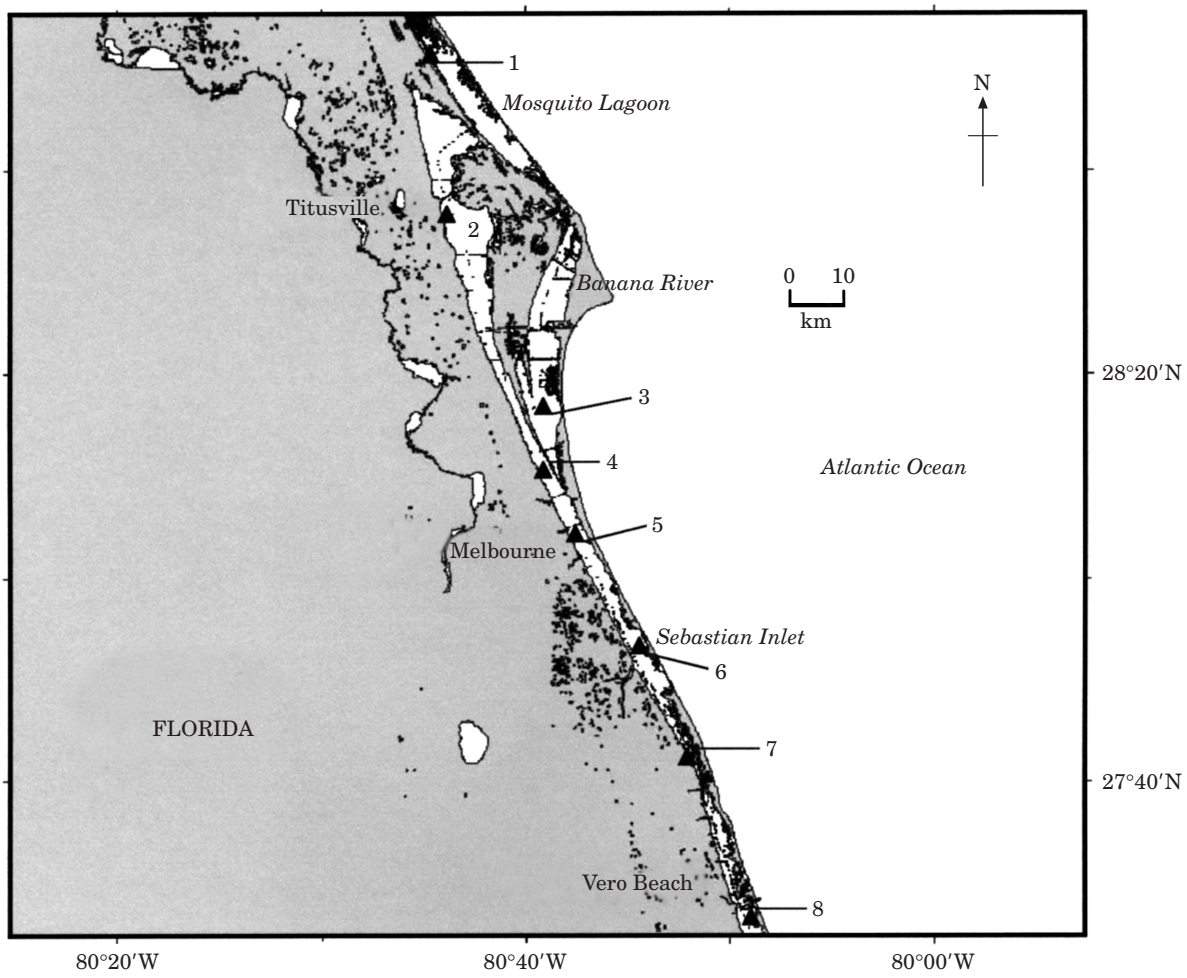


FIGURE 1. Locations of eight sampling sites in the Indian River and Mosquito Lagoons.

the persulfate digestion method (APHA, 1989) and analysed with a Technicon AutoAnalyser. Particulate organic carbon (POC) was determined colourimetrically (APHA, 1989).

Chlorophyll *a* was determined from water samples filtered onto Gelman A/E glass-fibre and extracted with 95% ethanol (Sartory & Grobbelaar, 1984). Chlorophyll *a* concentrations were determined with a Hitachi U2000 dual beam spectrophotometer.

Phytoplankton analysis

Fluorescence microscopy was used to enumerate small-celled cyanobacteria from water samples filtered onto 0·2 μm pore Nucleopore filters (Phlips *et al.*, 1999). Numerical abundances of cyanobacteria cells were determined by counting a minimum of five ocular micrometer grids at 1000 × magnification.

Phytoplankton composition was determined microscopically using the Utermohl method (Utermohl, 1958). Lugols preserved water samples were settled in 19 mm diameter cylindrical chambers. Phytoplankton cells were identified and counted at 400 × and 100 × magnification with a Nikon inverted microscope using phase contrast according to methods described by Phlips *et al.*, 1999. Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa (Smayda, 1978).

Light extinction coefficient

Light attenuation (K_t) (m^{-1}) or Lambert-Beer's Law was used to describe the decrease in light penetration with depth. Incident irradiance (I_o) and light intensity at depth z (m), were determined with Li-cor Instruments Inc. (Lincoln, NE, U.S.A.) submersible quantum light probes (cosine corrected) that simultaneously recorded surface and downwelling light (μmole photons m^{-2} s^{-1} of photosynthetically active radiation, PAR) with a data logger. Surface reflection,

based upon the angle and declination of the sun, was subtracted from the surface values.

Partial extinction coefficients caused by components of light attenuation were estimated using conversion factors from the literature. Light attenuation by phytoplankton, K_c, was estimated by multiplying chlorophyll *a* concentrations by $0{\cdot}016\ m^2\ mg^{-1}$ (Reynolds, 1984). Light attenuation by colour, K_{ac}, was estimated by multiplying pt colour units by $0{\cdot}014\ pt^{-1}\ m^{-1}$ (McPherson & Miller, 1987). Light attenuation by seawater, K_w, was set at $0{\cdot}0384\ m^{-1}$ (Lorenzen, 1972). Light attenuation by tripton, K_s, was calculated as $K_t - (K_c + K_{ac} + K_w)$. The mean light flux in the mixed layer, I_m, was estimated after Stefan *et al.* (1976): $I_m = (I_o/K_tZ_m)\ (1 - e^{-K_tZ_m})$, where Z_m is the depth of the mixed layer (m), and I_o is the mean daily surface PAR irradiance as estimated from the literature (Oswald & Gataas, 1957). Z_m was set at the site depth.

Nutrient limitation bioassays

Nutrient limitation status was determined using whole water collected at the eight sampling sites. The experimental design was based on that described by Aldridge *et al.* (1995). Assays were done under controlled laboratory conditions in 500 ml Erlenmeyer flasks containing 300 ml of whole water collected in the field. Treatments (in triplicate) were, N addition ($400\ \mu g\ NO_3^-\ l^{-1}$), P addition ($40\ \mu g\ PO_4\ l^{-1}$), N+P addition ($400\ \mu g\ NO_3^-\ l^{-1} + 40\ \mu g\ PO_4\ l^{-1}$), N+P+Si ($400\ \mu g\ NO_3^-\ l^{-1} + 40\ \mu g\ PO_4 + 400\ \mu g\ Si\ l^{-1}$) and N+P+Si+Trace elements ($400\ \mu g\ NO_3^-\ l^{-1} + 40\ \mu g\ PO_4\ l^{-1} + 400\ \mu g\ Si\ l^{-1} + 4\ \mu g\ Mn\ l^{-1} + 4\ \mu g\ Fe\ l^{-1} + 4\ \mu g\ Mo\ l^{-1}$). Whole water samples without nutrient additions served as the control. Incubations were done in temperature-controlled water baths with bottom illumination. Incubation temperatures were set at ambient temperatures recorded on each sampling date. Light intensity was fixed at 120 μmole photons $m^{-2}\ s^{-1}$. Photoperiod was 12/12 (dark/light). Sub-samples were taken from each flask at 0, 24, 72, 96 and 120 h. Change in algal biomass was estimated in three ways: (1) Net change of *in vivo* fluorescence (*IVF*) of chl-*a* using a Turner Designs Model 10 fluorometer with a 1 cm path length, (2) Change in chlorophyll *a* content over the 72 h incubation period using ethanol-extracted filtered samples and spectrophotometric techniques (APHA, 1989) and (3) Change in particulate organic carbon (POC) over the incubation period using filtered samples analysed for carbon with colourimetric methods.

A nutrient was considered limiting when the addition of that nutrient, or combination of nutrients, resulted in significantly greater growth than the control. When algal growth in the control increased relative to the initial control, it was concluded that surplus bioavailable nutrients were present at the time of sampling. The classification for the growth response was determined using Boolean logic (Aldridge *et al.*, 1995). Estimates of potential sustainable phytoplankton standing crops were determined using the change in POC over the incubation period and the carbon content of the observed phytoplankton biovolume.

Grazing

A serial dilution method was employed to determine phytoplankton growth and grazing losses of a natural assemblage of phytoplankton (Landry & Hassett, 1982). Seawater (50–60 l) was collected with a water column integrating tube and returned immediately to the laboratory for filtration. Water for dilution was filtered through a 0·2 μm Millipore filter. Experiments were conducted in 2 l containers as described in Durbin and Durbin (1992). Excess nutrients in the concentrations of $800\ \mu g\ N\ l^{-1}$, $100\ \mu g\ P\ l^{-1}$, and $800\ \mu g\ Si\ l^{-1}$ were added to each bottle to insure that nutrients were not limiting phytoplankton. The change in phytoplankton over time was estimated by *in vivo* fluorescence (*IVF*) of chl-*a* using a Turner Designs Model 10 fluorometer and by extracted chlorophyll *a* methods (Sartory & Grobbelaar, 1984). Apparent growth rates of phytoplankton were calculated from the exponential equation: $C_t = C_o e^{(k-g)t}$, where k and g are instantaneous coefficients of population growth and grazing losses, respectively calculated from least-squares and linear regression analysis of the relationship between the rate of change of chlorophyll *a* and the fraction of unfiltered seawater in the tanks.

Rainfall, wind and surface water temperature

Rainfall and wind data was obtained from the National Oceanic and Atmospheric Administration's National Climatic Data Center (Asheville, North Carolina, U.S.). Rainfall data were obtained for the Titusville and Vero meteorological stations. Wind data was for the Vero station. Surface water temperature data was obtained from the St. Johns River Water Management District (Palatka, Florida, U.S.) for monitoring sites in Vero and Titusville.

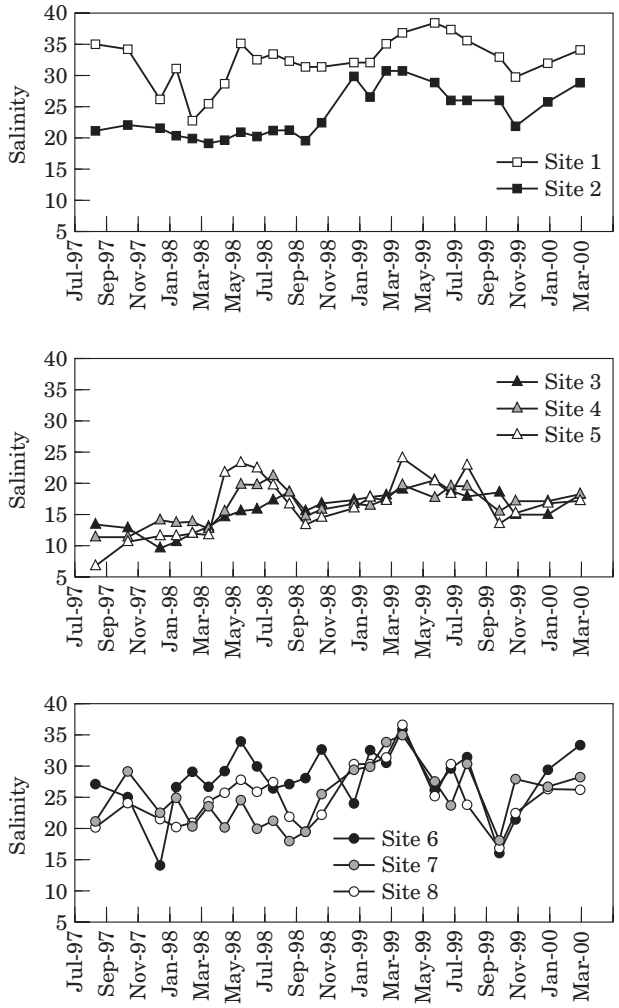


FIGURE 2. Temporal variation in salinity at the eight sampling sites.

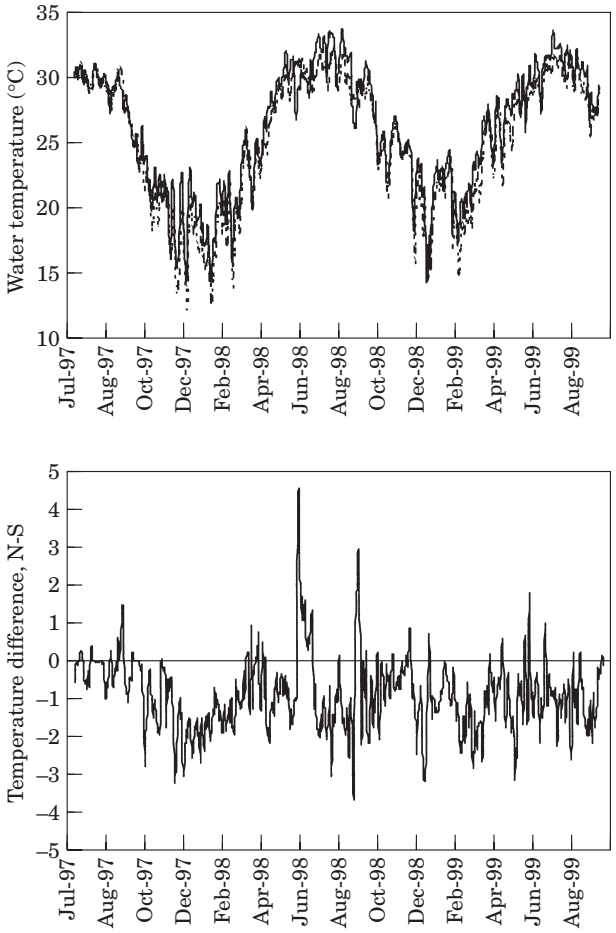


FIGURE 3. Surface water temperatures at two locations in the Indian River Lagoon (top), Titusville (dashed line) and Vero Beach (solid line), and difference in surface water temperatures between the northern (Titusville) and southern (Vero Beach) portions of the lagoon (bottom).

Data analysis

Statistical analysis was performed using the SAS statistical program for personal computers (SAS, 1989). Relationships between different variables were determined using Pearson Correlation Analysis. Tukey's Multiple Range Test was used to determine statistical differences between mean values.

Results

Salinity

Salinity patterns in the lagoon were reflective of both spatial differences in the distance from inlets to the Atlantic Ocean and temporal changes in freshwater inflow (Figure 2). Salinities were highest at Site 1 in the Mosquito Lagoon, located near Ponce De Leon Inlet, and Site 6 located near the Sebastian Inlet. Salinities at both sites were regularly near, or above, 30. Even at these sites, the high rainfall totals experienced during the *El Nino* period (October of 1997 through April of 1998) forced salinities down to as low as 14. North of the Sebastian Inlet salinities in the Indian River Lagoon were relatively low, i.e. generally below 25. Sites 2, 3, 4 and 5 showed distinct salinity minima during the *El Nino*, followed by a rise in salinity at the post *El Nino* period. In contrast, salinities at Sites 7 and 8 were generally higher than at Sites 2–5.

Temperature

Surface water temperatures within the study area ranged from 12·4 °C to 33·0 °C (Figure 3). From April through October temperatures were consistently

TABLE 1. Mean light extinction coefficients K_t (m^{-1}) and per cent contributions of water, tripton, colour and phytoplankton to total light attenuation at the eight sampling sites. Values shown are means for the sampling period. Standard errors are shown in parentheses. Tukey's Multiple Range Test was used to compare mean K_t values observed for the eight sampling sites. Means with the same letter designation were not statistically different

Site	K_t (m^{-1})	Water (%)	Tripton (%)	Colour (%)	Phytoplankton (%)
1	1·80 A	2·4	71·7	17·3	8·6
	(0·17)	(0·2)	(2·1)	(2·2)	(1·6)
2	0·97 B	4·2	61·5	26·3	8·0
	(0·10)	(0·3)	(3·4)	(3·2)	(1·1)
3	1·13 B	3·6	59·7	26·0	10·7
	(0·08)	(0·3)	(3·6)	(2·9)	(1·4)
4	0·96 B	4·2	50·4	29·7	15·7
	(0·07)	(0·3)	(5·1)	(4·2)	(2·7)
5	1·21 B	3·2	50·9	29·7	16·2
	(0·10)	(0·2)	(4·2)	(3·1)	(1·8)
6	1·20 B	3·6	60·6	27·0	8·8
	(0·11)	(0·6)	(6·1)	(5·2)	(1·0)
7	1·75 A	2·4	66·9	22·5	8·2
	(0·15)	(0·2)	(2·1)	(1·7)	(1·5)
8	1·58 A	2·9	60·4	27·4	9·3
	(0·16)	(0·3)	(2·6)	(2·4)	(1·3)

above 25 °C throughout the sampling range. A comparison of water temperatures for the northern- and southern-most sites in the Indian River Lagoon (Sites 2 and 8, respectively) showed slightly higher temperatures at the latter site during the winter months (Figure 3).

Light attenuation, components of extinction and availability

Mean light extinction coefficients (K_t) ranged from 0·5 to 2·5 m^{-1} (Table 1). Overall means for the eight sampling sites were highest at Sites 1, 7 and 8, and may reflect the effect of sediment resuspension in these regions, which are characterized by shallow depths and muddy sediments.

Among the four major components of light attenuation (water, tripton, colour and phytoplankton), tripton (non-algal suspended solids) was the major contributor to light extinction. The estimated contribution of tripton to K_t ranged from 50·4 to 71·7% (Table 1). The highest values were observed at Sites 1 and 7, probably due to the frequent resuspension of sediments, as mentioned above. The next greatest contributor to light extinction was colour, representing an estimated 17·3 to 29·7% of K_t. Organic colour levels in the lagoon were moderate, with mean values for the sampling period ranging from 19·4 to 28·8 Platinum-cobalt Units.

TABLE 2. Mean phytoplankton abundance in terms of biovolume ($\mu m^3\ ml^{-1}$)the eight sampling sites. Standard errors are given in parentheses. Tukey's Multiple Range Test was used to compare mean concentrations observed for the eight sampling sites. Means with the same letter designation were not statistically different

Station	Biovolume (Std. Error)
1	1·58 (0·36) BC
2	2·86 (0·49) AB
3	3·94 (0·59) A
4	3·65 (0·67) A
5	3·16 (0·43) A
6	1·25 (0·19) C
7	1·54 (0·35) BC
8	2·00 (0·56) B

Phytoplankton was also a major component of light extinction, with an estimated contribution of 8 to 16·2% of K_t (Table 1). The highest contributions were at the three sites within the central region of the lagoon (Site 3 in the Banana River, Site 4 near Palm Shores and Site 5 near Melbourne), which were also the sites with the highest chlorophyll levels (Table 2). These contributions may be underestimated because they are based on a conversion coefficient for chlorophyll *a* developed for temperate freshwater ecosystems

TABLE 3. Seasonal and overall chlorophyll/biovolume ratio (micrograms chl *a* mm^{-3}). Standard errors are in parentheses

Site	Autumn 1997	Winter 1997/1998	Spring 1998	Summer 1998	Autumn 1998	Site Mean
1	6·0	12·2	17·8	2·9	7·9	10·0
	(1·6)	(3·3)	(1·2)	(0·4)	(3·9)	(1·9)
2	1·5	1·1	6·4	1·5	2·6	2·9
	(0·4)	(0·1)	(2·7)	(0·1)	(1·2)	(0·9)
3	2·1	2·5	2·3	1·3	3·4	2·4
	(0·8)	(0·6)	(0·6)	(0·5)	(0·6)	(0·3)
4	2·6	4·1	3·5	1·5	3·4	3·1
	(0·2)	(1·5)	(1·8)	(0·3)	(1·0)	(0·5)
5	2·3	6·7	5·4	2·2	3·9	4·2
	(0·5)	(0·4)	(2·8)	(0·2)	(1·2)	(0·8)
6	5·5	8·5	10·9	4·3	6·1	7·3
	(2·2)	(3·3)	(4·6)	(1·8)	(1·4)	(1·4)
7	8·0	13·1	10·0	4·4	5·7	8·2
	(1·3)	(3·0)	(3·2)	(0·8)	(1·6)	(1·3)
8	2·6	8·0	7·1	3·8	8·6	6·3
	(0·2)	(0·1)	(2·7)	(0·7)	(4·0)	(1·2)
Seasonal Mean	3·8 (0·6)	7·0 (1·2)	7·9 (1·3)	2·7 (0·4)	5·2 (0·8)	

(Reynolds, 1984). As noted in previous studies of light extinction in Florida estuaries (McPherson & Miller, 1987; Phlips *et al.*, 1995*a*), low chlorophyll *a* to biovolume ratios found in some high light environments may warrant the use of higher conversion coefficients.

The chlorophyll *a* to biovolume ratios observed in this study were frequently low (<4 μg chl a mm^{-3}) (Table 3). The latter observation may in part be related to the relatively light-rich environment of this shallow lagoon, as indicated by the exceptionally low ratios in the summer season (Table 3). Low ratios may also be related to the strong presence of dinoflagellates. Periods of high dinoflagellate abundance were correlated to low chlorophyll *a*/biovolume ratios (i.e. Pearson Correlation Coefficient = $-0{\cdot}34$, $P>0{\cdot}0007$).

Mean light availability in the water column, I_m, showed considerable spatial and temporal variability (Figure 4), but was generally greater than the threshold for light limitation of phytoplankton production (4–6 mole photons $m^{-2}\,d^{-1}$) suggested by several researchers (Geddes, 1984; Phlips *et al.*, 1995*b*, 1997).

Phosphorus

Mean total phosphorus (TP) concentrations ranged from 35 $\mu g\,l^{-1}$ to 118 $\mu g\,l^{-1}$ (Table 4). All but the two southern most sites (Sites 7 and 8) had mean TP concentrations near 50 $\mu g\,l^{-1}$ (Sites 7 and 8), while mean values at the former sites exceeded 100 $\mu g\,l^{-1}$. TP concentrations generally increased in the late spring and summer at most sites, as demonstrated by observations for two representative sampling sites (Figure 5).

Mean soluble reactive phosphorus (SRP) concentrations followed a spatial pattern similar to TP (Table 4). SRP concentrations were consistently lower in the northern portion of the lagoon than in the southern end. Seasonal patterns of SRP were less definitive than for TP (e.g. Figure 5).

Nitrogen

Mean total nitrogen (TN) concentrations ranged from 366 to 762 $\mu g\,l^{-1}$ (Table 4), with higher mean concentrations in the northern portion of the lagoon (Sites 1–5) than in the southern portion (Sites 6–8). TN concentrations tended to increase in the fall (e.g. Figure 6). Mean nitrate–nitrite concentrations ranged from 5·0 to 26·2 $\mu g\,l^{-1}$ (Table 4). Highest mean nitrate–nitrite concentrations were observed at sites 1, 7 and 8. Mean concentrations of ammonium ranged from 18·0 $\mu g\,l^{-1}$ to 45·4 $\mu g\,l^{-1}$. Ammonium levels showed no consistent spatial pattern or temporal patterns (Figure 6).

Phytoplankton standing crop

Mean phytoplankton abundances were highest at Sites 3, 4 and 5 (Table 2). Temporal patterns of phyto-

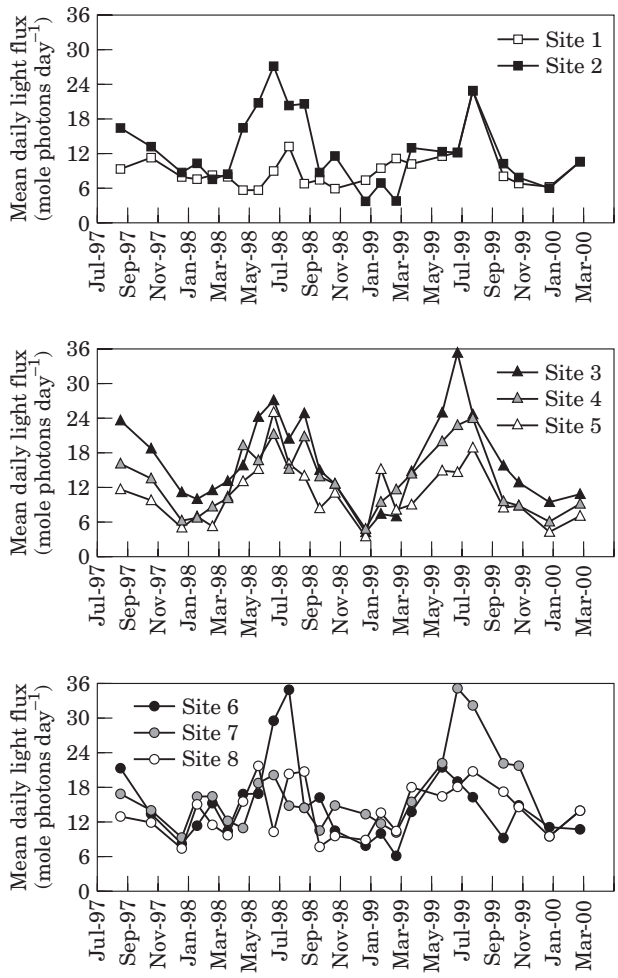


FIGURE 4. Temporal variation in mean light availability in the water column, I_m, at the eight sampling sites.

plankton abundance and composition exhibited significant spatial differences (Figure 7). All sites showed elevated standing crops of phytoplankton in the summer. In addition, standing crops also showed winter peaks at Sites 2–6. Spring peaks in phytoplankton abundance were observed at the four southern-most sites (Sites 5–8), most prominently at Site 8.

While chlorophyll *a* and biovolume manifested similar trends in phytoplankton abundance the chlorophyll to biovolume ratios varied spatially and temporally (Table 3). These variations may, in part, reflect temporal and spatial differences observed in the composition of the phytoplankton community (Badylak & Phlips, in preparation). Diatoms were the dominant phytoplankton division in the winter and early spring at many sites. In the summer and early fall dinoflagellates became increasingly important, forming significant blooms at certain sites.

Nutrient limitation

The nutrient limiting status of phytoplankton growth in the Indian River Lagoon was examined in two ways: (1) Comparison of nitrogen to phosphorus ratios with the Redfield ratio (approximately 7:1 by weight for nutrient sufficient phytoplankton) (Redfield *et al.*, 1963) and (2) Nutrient enrichment bioassays. Total nitrogen to total phosphorus ratios varied spatially and temporally. In the northern part of the lagoon (Sites 1–5) TN/TP values were frequently greater than the Redfield ratio, as shown for Site 2 (Figure 8). High TN/TP ratios are generally indicative of phosphorus limitation. At Site 6, near the Sebastian Inlet, TN/TP values were close to the Redfield ratio throughout the sampling period. By contrast, south of Site 6, TN/TP values were substantially below the Redfield ratio in the spring and summer, e.g. Site 8 (Figure 8), indicating the potential for nitrogen limitation of phytoplankton growth.

Nutrient limitation bioassays provided a more complex picture of the nutrient limiting status of the lagoon (Table 5). Of the 120 bioassays performed during this study, seventy-five showed the presence of sufficient nitrogen and phosphorus to support phytoplankton growth, indicating that . Among the forty-five remaining bioassays, forty-three showed immediate nitrogen limitation (including four that were co-limited by phosphorus) of phytoplankton growth. Five bioassays showed immediate phosphorus limitation (including four that were co-limited by nitrogen). In almost all of the bioassays nitrogen became a growth-limiting element within the 72-h incubation period (Table 5). In the northern portion of the lagoon (Sites 1–5) phosphorus became a limiting nutrient in many of the bioassays over the 72-h incubation period, while in the southern part of the lagoon phosphorus limitation was observed less frequently (Table 5). The relative severity of nutrient limitation in different regions of the lagoon is reflected by the frequency of nitrogen and/or phosphorus limitation within the first 24 h of incubation. Sites in the restricted portion of the lagoon (Sites 3 and 5) exhibited the highest percentage of bioassays where nutrient limitation set in immediately.

While the primary limiting nutrient status identified in nutrient enrichment bioassays did not reveal as distinct a picture of the spatial patterns of phosphorus and nitrogen limitation as indicated by the TN to TP ratios, examination of secondary and tertiary limiting nutrient did reveal a trend. At Sites 3 and 5 phosphorus became limiting within 24 h 27 of fifty bioassays (i.e. phosphorus was the primary limiting nutrient or became limiting after the depletion of

TABLE 4. Mean concentrations of total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), nitrate+nitrite (NO_3+NO_2) and ammonium (NH_4) ($\mu g\,l^{-1}$) at the eight sampling sites over the sampling period. Standard errors are in parentheses. Tukey's Multiple Range Test was used to compare mean concentrations observed for the eight sampling sites. Means with the same letter designation were not statistically different

Site	TP	SRP	TN	NO_3+NO_2	NH_4
1	54 B	9·1 B	563 B	26·2 A	34·4 AB
	(6)	(2·0)	(42)	(11·2)	(7·1)
2	35 C	4·6 C	762 A	6·7 BC	45·4 A
	(2)	(0·9)	(67)	(2·1)	(18·3)
3	54 B	2·9 C	760 A	5·0 C	28·0 B
	(5)	(0·8)	(56)	(1·0)	(5·0)
4	59 B	3·7 C	667 A	7·7 BC	18·2 B
	(7)	(1·1)	(43)	(2·4)	(2·5)
5	68 B	5·0 C	667 A	13·5 AB	29·2 AB
	(5)	(1·6)	(50)	(4·5)	(4·8)
6	55 B	12·5 B	366 C	9·8 BC	18·0 B
	(4)	(3·1)	(40)	(2·4)	(3·4)
7	118 A	45·3 A	458 B	19·8 A	40·4 A
	(21)	(8·4)	(68)	(7·9)	(13·5)
8	101 A	36·9 A	530 B	18·3 A	23·7 B
	(11)	(5·6)	(54)	(6·0)	(4·5)

surplus nutrients) (Table 5). Furthermore, forty-nine of fifty bioassays showed some degree of phosphorus limitation by the end of the full 72-h incubation period. At Site 8 phosphorus was the first nutrient to become limiting in only one of twenty-five bioassays and only twelve of twenty-five bioassays showed some degree of phosphorus limitation within the 72-h incubation.

Rainfall and wind

One of the noteworthy features of environmental variability in the Indian River Lagoon during our study period was the change in rainfall, from the flood conditions of the *El Nino* to the relative drought of the post-*El Nino* period. This variation is evident from the monthly rainfall totals (Figure 5) and ' departures from normal ' (Figure 9) for two selected meteorological stations located within the drainage basin of the Indian River Lagoon. The most dramatic features were the impact of *El Nino*, which drove rainfall totals well above normal in the winter and early spring of 1997/98, and the above average rainfall totals in the summer and fall of 1999 associated with storm events.

Wind speed on the east coast of Florida is seasonal, with generally higher monthly totals in the winter and spring (National Oceanic and Atmospheric Administration's National Climatic Data Center). Tropical storm events during the summer and fall are obvious exceptions to this general trend. To examine the relationship between wind and phytoplankton abundance, linear regression relationships were generated between chlorophyll *a* concentrations and wind speed on the day of sampling at each of the eight sampling sites. R^2 were 0·007, 0·013, 0·003, 0·087, 0·196, 0·184, 0·155 and 0·008 for Sites 1–8 (n=21 for each site), respectively. Five of the eight regression relationships exhibited a small negative slope.

Grazing

The three grazing experiments performed in this study all yielded significant grazing rates (Table 6). In two of the experiments there was a net accumulation of phytoplankton biomass. In the third experiment, the grazing intensity was sufficient to result in a net decline of phytoplankton.

Discussion

Our initial hypothesis was that spatial and temporal patterns of phytoplankton abundance could be most readily explained in terms of hydrodynamic restriction (i.e. rates of water turnover) and nutrient availability. While the results of our research generally support the importance of the latter factors, it is clear that phytoplankton dynamics in the Indian River lagoon must be viewed within the broader context of other controlling factors, including biomass loss processes

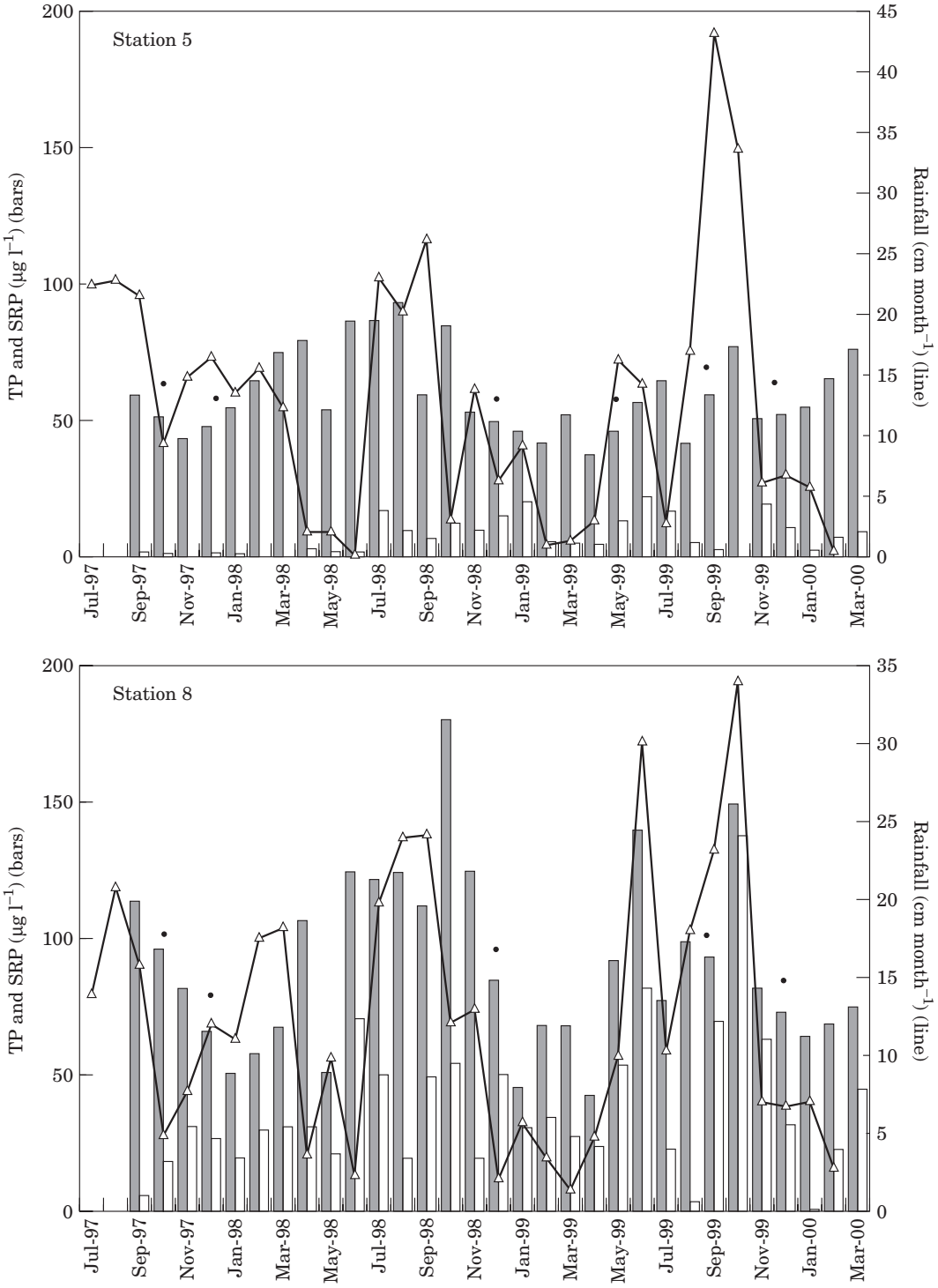


FIGURE 5. Temporal variation in monthly rainfall, total phosphorus concentration (TP, filled bars) and soluble reactive phosphorus concentration (SRP, open bars) at two representative sampling sites in the Indian River Lagoon; Site 5 in the northern half of the lagoon and Site 8 in the Southern portion of the lagoon. Phosphorus values with dots above them are interpolated values due to the unavailability of data for that date.

like grazing and sedimentation, as well as, regulators of primary production like light flux, temperature and salinity.

Hydrodynamic factors

The degree of tidal water exchange between the Indian River Lagoon and the Atlantic Ocean is

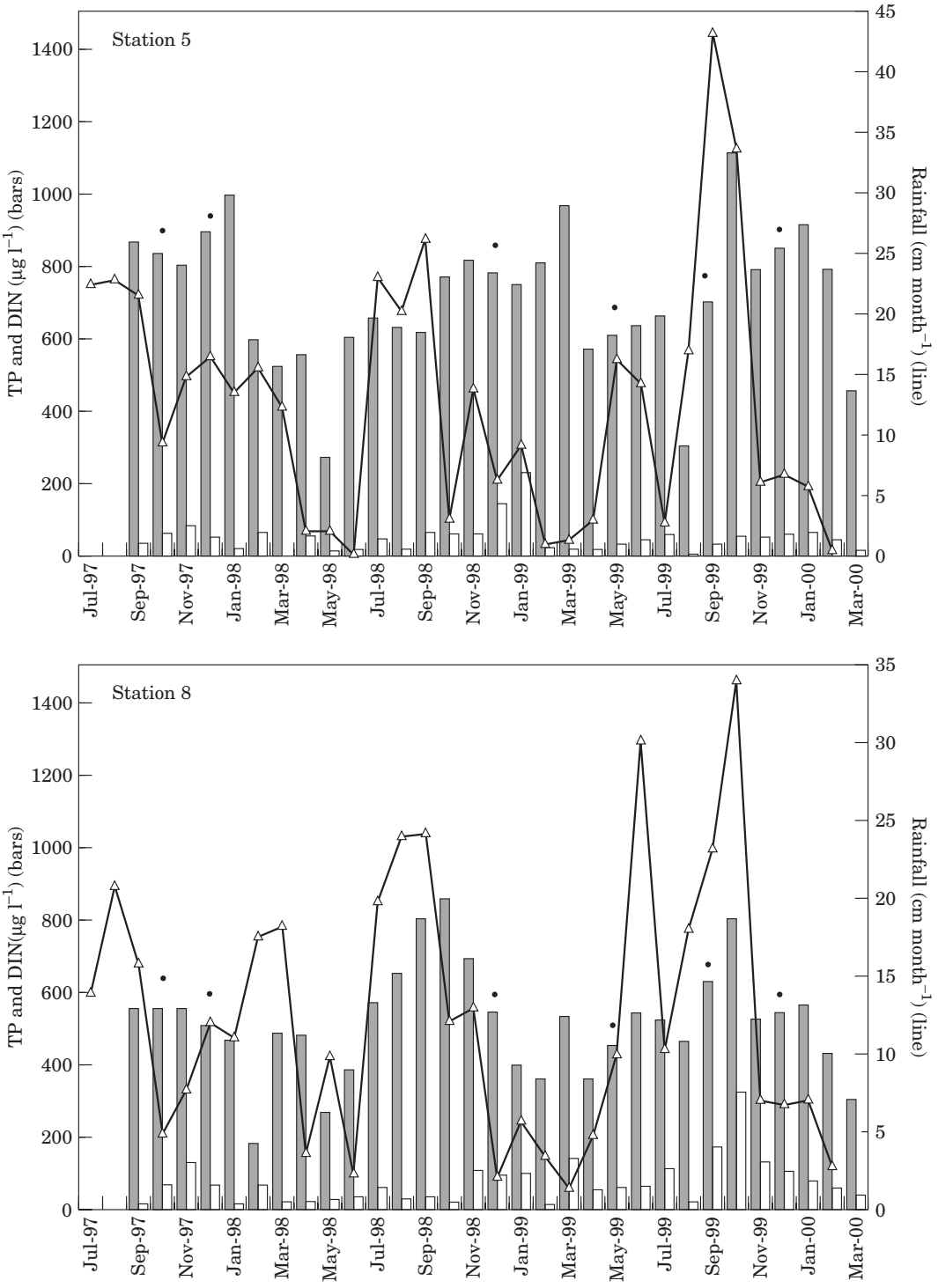
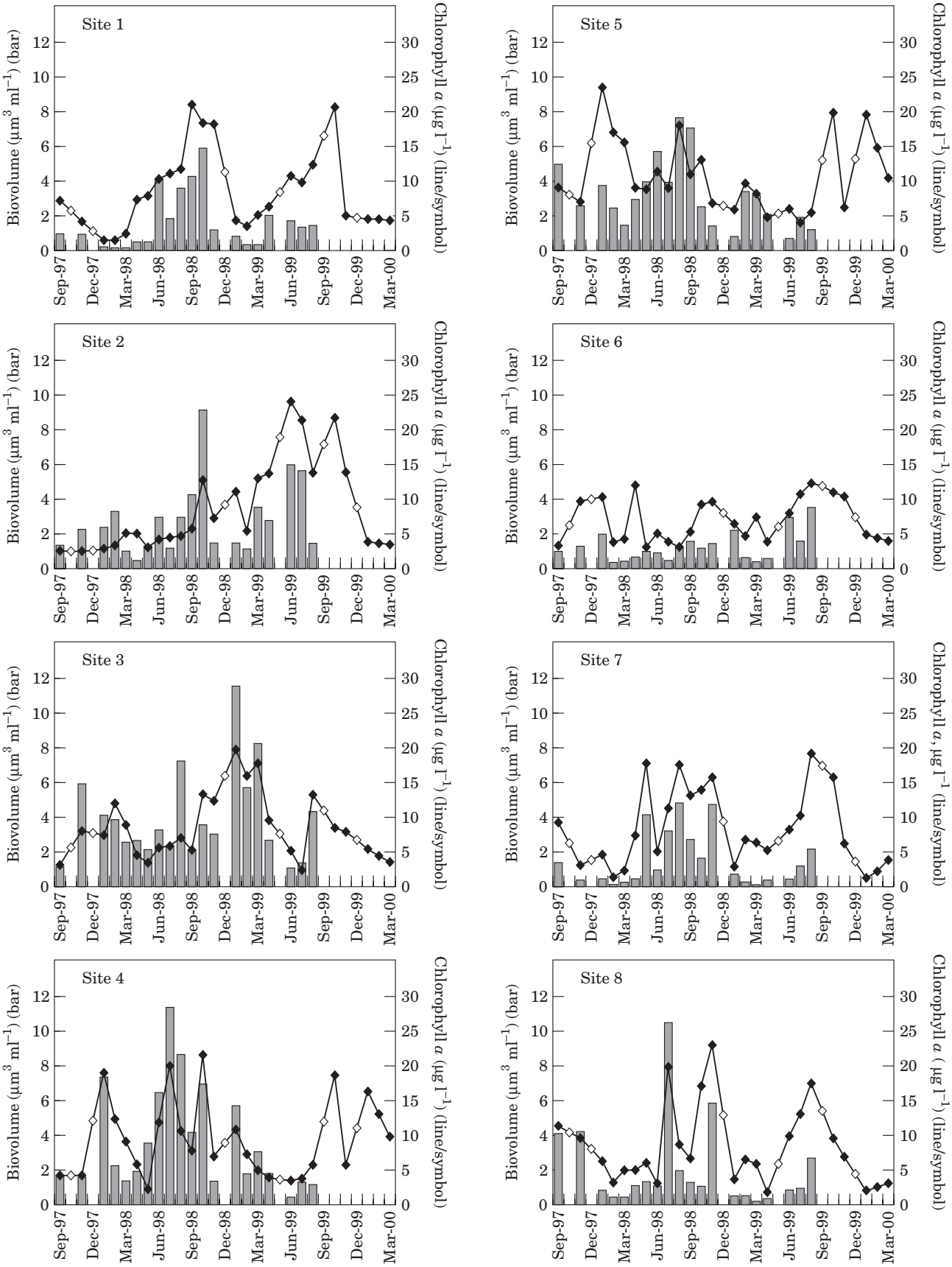


FIGURE 6. Temporal variation in monthly rainfall, total nitrogen concentration (TN, filled bars) and dissolved inorganic nitrogen (DIN, open bars) at two representative sampling sites in the Indian River Lagoon; Site 5 in the northern half of the lagoon and Site 8 in the Southern portion of the lagoon. Nitrogen values with dots above them are interpolated values due to the unavailability of data for that date.

reflected in the level and variability of salinity in different regions of the lagoon. The regions of lowest salinity, represented by Sites 2–5, are the most restricted parts of the lagoon (Sheng *et al.*, 1990; Smith, 1993). During periods of high rainfall the restriction to tidal water exchange result in low salinities for


Site 1
Site 2
Site 3
Site 4
Site 5
Site 6
Site 7
Site 8
Biovolume (µm^3 ml^{-1}) (bar)
Chlorophyll *a* (µg l^{-1}) (line/symbol)
Sep-97
Dec-97
Mar-98
Jun-98
Sep-98
Dec-98
Mar-99
Jun-99
Sep-99
Dec-99
Mar-00

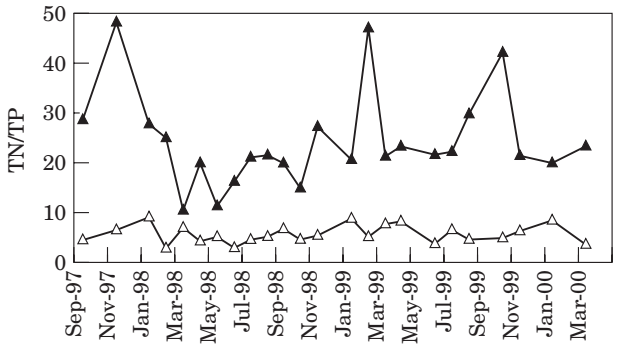


FIGURE 8. Total nitrogen to total phosphorus ratios at two selected sampling sites, Site 2 in the northern end of the Indian River Lagoon and Site 8 at the southern end of the lagoon. ▲ Site 2 △ Site 8

extended periods of time in the latter regions, as seen during the *El Nino* flood period of 1997/98 (October 1997–March 1998). In contrast, the relatively high salinities observed at Sites 1, 6 and 8 are indicative of the close proximity of the Ponce De Leon, Sebastian and Ft. Pierce Inlets to these sites, respectively. Water turnover times in these less restricted regions can be on the order of days. Based on the principal that water residence time is a major factor in the control of phytoplankton standing crops, it is fitting that the highest mean phytoplankton standing crops observed in this study were associated with the former ' restricted ' sites (Table 2). Conversely, the region of highest water turnover, represented by Site 6, exhibited the lowest phytoplankton standing crops. This conclusion is further supported by the results of nutrient limitation bioassays and light extinction measurements which demonstrate the presence of sufficient nutrients and light to support higher than observed phytoplankton standing crops in regions of higher water turnover.

Regional differences in phytoplankton populations in the Indian River Lagoon are not limited to standing crops, but extend to community structure. At three sites in the most restricted part of the Indian River Lagoon (Sites 3, 4 and 5) dinoflagellates were a major, and in many cases dominant, element of the phytoplankton community (Badylak & Phlips, in preparation). Outside of the ' restricted ' regions of the Indian River Lagoon the relative importance of diatoms increased, along with regionally and seasonally dependent pulses of green algae and blue-green algae (i.e. cyanobacteria). The prominence of dinoflagellates in flow restricted regions of the Indian River Lagoon fits within the more general observations of other researchers that low water exchange rates and shallow depths promote the importance of dinoflagellates in lagoonal habitats (Anderson & Keafer, 1985; Smayda, 1989). Dinoflagellates reach bloom proportions (i.e. biovolumes in excess of 1 million $\mu m^3\,ml^{-1}$) in the Indian River Lagoon, including the potentially toxic species *Prorocentrum minimum* (Luckenbach *et al.*, 1993; Badylak & Phlips, in preparation). The presence of these species may be important in light of their potentially negative effects on benthic filter-feeding macroinvertebrates (Luckenbach *et al.*, 1993), which are major components of the Indian River Lagoon's benthic biota. High standing crops of toxic dinoflagellates in certain flow-restricted estuarine habitats has become an issue of concern along the eastern seaboard of the U.S. (Paerl, 1988; Smayda, 1989; Burkholder *et al.*, 1992).

In addition to water exchange rates, vertical mixing processes have been shown to play a role in the regulation of phytoplankton structure and abundance (Lucas *et al.*, 1999*a*). Vertical mixing can have a direct affect on phytoplankton abundance in shallow ecosystems by redistributing biomass through the water column (Cloern, 1991). In one shallow lake in Florida wind speed was shown to be strongly correlated to chlorophyll *a* due to wind resuspension of meroplankton (Carrick *et al.*, 1993). While no significant relationships between wind speed and chlorophyll *a* were observed for any of the sites examined in this study, it seems likely that wind resuspension of sedimented algae plays some role in the vertical distribution of algae in the Indian River Lagoon considering the shallowness of the environment. The periodic presence of benthic diatoms in water samples from the lagoon supports this notion (Badylak & Phlips, in preparation). There was, however, insufficient data to probe this issue in greater detail.

Affects of nutrient limitation

With mean total phosphorus concentrations from $35\,\mu g\,l^{-1}$ to $118\,\mu g\,l^{-1}$ the Indian River Lagoon would be classified as nutrient-rich. The results of

FIGURE 7. Temporal changes in phytoplankton abundance at the eight sampling sites. Abundance is presented in the form of total phytoplankton biovolume (bar), $\mu m^{-3}\,ml^{-1} \times 10^6$, and chlorophyll *a* concentration (solid lines), $\mu g\,l^{-1}$. Chlorophyll values with open symbols are interpolated values due to the unavailability of data for that date.

TABLE 5. Results of nutrient enrichment bioassays. The ' initial response ' indicates the growth response of the control and enrichment treatment groups in the first 24 h of the bioassays. Growth (i.e. increase in chlorophyll *a*) in the control group is interpreted as a ' presence of bioavailable nutrients '. The ' primary limiting nutrient ' indicates the nutrient enrichment treatment group that first shows greater growth response than the control group (i.e. no nutrient addition). The ' intensity of nutrient limitation ' indicates the number of bioassays which show nutrient limitation within the first 24 h of the bioassay

A.	Initial response:	1	3	5	6	8
	Presence of bioavailable nutrients (of 24)	17	8	14	18	18
	Immediate nutrient limitation (of 24)	7	16	10	6	6
B.	Primary limiting nutrient, including double countfor co-limitation:					
	Nitrogen	20	20	21	24	24
	Phosphorus	9	7	5	2	0
C.	Intensity of nutrient limitation:					
	Nitrogen limitation within 24h	17	17	20	19	16
	Phosphorus limitation within 24 h	13	16	11	7	1

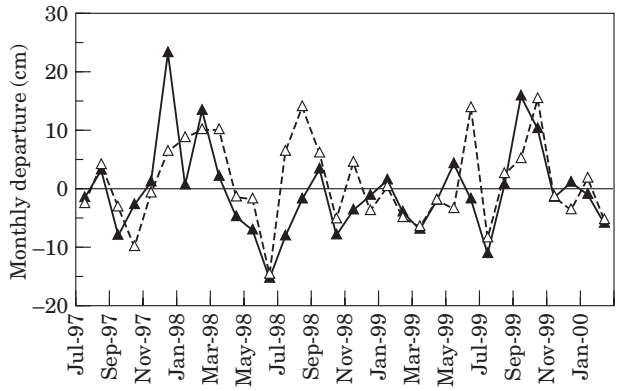


FIGURE 9. Departure from normal for monthly rainfall totals for two meteorological stations located within the Indian River Lagoon watershed. Titusville is in the northern part of the watershed and Vero Beach in the southern end of the watershed. ▲ Titusville △Vero

TABLE 6. Grazing rates and apparent growth rates observed in three experiments for water samples from the Indian River Lagoon

	Grazing rate (/day)	Growth rate (dbl/day)
Experiment 1	0·236	0·205
Experiment 2	0·314	0·436
Experiment 3	0·332	− 0·035

correlation analyses suggest that there are regional differences in nutrient availability within the Indian River Lagoon. In the northern and central regions of the lagoon chlorophyll *a* concentrations were most strongly correlated to total phosphorus concentrations (Table 7), suggesting a role for phosphorus limitation. In contrast, chlorophyll *a* concentrations were more strongly correlated to total nitrogen in the southern region, suggesting the potential for nitrogen limitation.

The results of the bioassay experiments shed further light on the nature and extent of nutrient limitation in the Indian River Lagoon. The observation that seventy-five of one hundred and twenty nutrient enrichment bioassays showed the presence of varying amounts of surplus bioavailable nitrogen, phosphorus and silica suggests that processes of nutrient input and regeneration in the lagoon often exceed the instantaneous demand of the resident phytoplankton community. This is further indicated by the low chlorophyll/TP and chlorophyll/TN ratios observed in the lagoon. Chlorophyll/TP averaged 0·17 (Std. Err.=0·008, n=118) in the northern portion of the lagoon (Sites 1–5) and 0·09 (Std. Err.=0·007, n=45) in the southern portion. Chlorophyll/TN averaged 0·014 (Std. Err.=0·001, n=118) in the northern portion of the lagoon (Sites 1–5) and 0·018 (Std. Err.=0·002, n=45) in the southern portion. These observations also suggest the presence of other important loss or growth regulating factors that keep nutrient demand down.

In the forty-five nutrient bioassays where immediate limitation for phytoplankton growth was observed, nitrogen proved to be the most frequently limiting nutrient throughout the lagoon. In terms of phosphorus limitation, there was a disparity between the northern and southern parts of the lagoon. Based on the observed patterns of secondary and tertiary limitation, the potential for phosphorus limitation is greater in the northern half of the lagoon. This spatial pattern is further indicated by the high TN/TP ratios in the northern region (Figure 7). The latter gradient

TABLE 7. Pearson Correlation Coefficients for the relationship between chlorophyll *a* concentration and five key ecological parameters; total phosphorus (TP), total nitrogen (TN), silica (Si), mean light availability in the mixed layer (I_m) and temperature. Coefficients are shown for four regions within the Indian River Lagoon; Northern (Sites 1 and 2, n=53), Central (Sites 3, 4 and 5, n=81), Sebastian Inlet (Site 6, n=26) and South (Sites 7 and 8, n=52). Coefficients for the combined data set (n=212) are also included

Region	TP	TN	Si	I_m	Temperature
Northern	0·765	0·652	0·472	− 0·250	0·446
	(0·0001)	(0·0001)	(0·0002)	(0·0906)	(0·0017)
Central	0·591	0·386	0·318	− 0·469	− 0·480
	(0·0001)	(0·0004)	(0·0038)	(0·0001)	(0·0001)
Sebastian Inlet	0·481	0·491	0·501	− 0·329	0·232
	(0·0130)	(0·0127)	(0·0107)	(0·1685)	(0·2650)
Southern	0·160	0·412	0·054	− 0·097	0·400
	(0·2567)	(0·0024)	(0·7020)	(0·5110)	(0·0044)
Combined	0·207	0·436	0·132	− 0·073	0·050
	(0·0088)	(0·0001)	(0·0982)	(0·3747)	(0·5520)

may reflect the varying character of freshwater runoff in different regions of the lagoon. Previous studies of the lagoon have shown that the southern half is subject to greater phosphorus-rich freshwater inflows than the northern half (Kleppel, 1996), helping to explain the high phosphorus levels at the two southern most sites (Sites 7 & 8).

From a temporal perspective, our results indicate an increase in nutrient concentrations in the lagoon during the summer and fall. It is likely that this temporal pattern is influenced by seasonal patterns of rainfall, the latter period being the wet season. The observation that total and soluble reactive phosphorus concentrations track rainfall amounts (Figure 5), particularly in the southern part of the lagoon, support the regional importance of watershed inputs of phosphorus.

Seasonal variation in certain biological processes may further impact patterns of nutrient availability. The high temperatures and reduced oxygen levels characteristic of the summer and fall seasons enhance both pelagic and benthic processes of nutrient regeneration. The late summer–autumn period also coincides with the die-back of the extensive drift algae populations that develop in the lagoon during the spring (Virnstein & Carbonara, 1985), thereby adding to the pool of recyclable nutrients. The importance of recycled nutrients in phytoplankton production has been recognized in a variety of estuaries (Dugdale & Goering, 1967; Boynton *et al.*, 1982). It is also probable that grazing by both zooplankton and benthic filter-feeding invertebrates contribute to both consumption of primary production and regeneration of nutrients.

Affects of grazing

The results of the grazing and bioassay experiments manifest a potential role for planktonic grazers in the control of phytoplankton abundance, as demonstrated for some other estuaries (Frost, 1980). While it is difficult to derive a precise loss-term attributable to planktonic grazers from the limited number of grazing experiments done in this study, the results show that grazing rates can be high enough to overcome phytoplankton growth rates, resulting in a net loss in standing crop. The results of bioassay experiments further support the potential importance of grazing. In over 20% of the bioassays there were loses of chlorophyll *a* content from the beginning to the end of the 72 h incubation periods in the control groups (i.e. no nutrient additions), despite simultaneous increases in particulate organic carbon (Phlips *et al.*, in preparation). These observations suggest that phytoplankton biomass is declining over the bioassay period due to grazing. Differential grazing pressures in various regions of the lagoon may help to explain some of the spatial and temporal patterns of phytoplankton abundance and composition. For example, the dominance of dinoflagellates in flow restricted regions of the lagoon may in part be a consequence of resistance to grazing loss, as observed for dinoflagellates in some estuaries (Turner & Tester, 1989).

Besides planktonic grazers, benthic invertebrate filter-feeders can contribute substantially to phytoplankton losses (Officer *et al.*, 1982; Cloern, 1982; Lucas *et al.*, 1999*b*). These organisms are widely abundant throughout the Indian River Lagoon (Virnstein, 1990), as indicated by the major clam

harvesting industry that currently exits in the region. The uniformly shallow depths and restricted nature of the lagoon increase the probability that benthic filter-feeders play a role in the dynamics of plankton populations, although no research has been done to measure the magnitude of the effect in the Indian River Lagoon.

Affects of light availability, temperature and salinity

There are a number of physical and chemical factors that can have direct and indirect affects on the growth and physiology of algae and thereby have a bearing on phytoplankton abundance. This study examined three such factors, light, temperature and salinity. Light availability has been shown to be important in controlling phytoplankton standing crops in a number of estuarine environments (Hitchcock & Smayda, 1977; Cole & Cloern, 1984; Bledsoe & Phlips, 2000). The potential for light limitation in the Indian River Lagoon was examined using estimates of mean light availability in the mixed layer, I_m. The results of other studies of aquatic ecosystems indicate that 2–6 mole photons $m^{-2} d^{-1}$ is the threshold range for I_m that defines the boundary between light-sufficient and light-limited conditions for phytoplankton production (Geddes, 1984; Phlips *et al.*, 1995*b*). Most of the I_m values determined for this study were above this threshold, suggesting that light availability does not routinely limit phytoplankton standing crops in the Indian River Lagoon. The low potential for light limitation is in large part attributable to the shallow depth of the lagoon (i.e. <4 m). This conclusion is, however, dependent on the assumption of a well-mixed water column. Under conditions of low wind and tidal mixing energy algal cells sinking to the bottom of the water column may experience a greater potential for light limitation. This factor may further help to explain the importance of dinoflagellates and blue-green algae in restricted parts of the lagoon (Badylak & Phlips, in preparation), since both have the ability to regulate their position in the water column, the former through motility and the latter through buoyancy control.

In contrast to light limitation, primary production in shallow water ecosystems can also be negatively impacted by excessive light energy, i.e. photoinhibition (Kirk, 1994). Since large areas of the Indian River Lagoon are very shallow in depth (i.e. <2 m) the possibility of photoinhibition, particularly in the summer months, can not be overlooked. Given the relatively small light extinction coefficients observed for the lagoon (i.e. 1–2 m^{-1}) and peak summer light fluxes of approximately 2300 μmole photons $m^{-2} s^{-1}$, mid-day light fluxes within the top metre of the water column could fall within the photoinhibition range for photosynthesis reported for a number of phytoplankton populations in other ecosystems (Kirk, 1994). The low chlorophyll/biovolume ratios observed for phytoplankton populations in the lagoon in the summer provide some indication that the phytoplankton communities are exposed to high light fluxes. Whether these light fluxes actually limit primary production and standing crop require further investigation.

Temperature is another factor that has been widely investigated in phytoplankton ecology (Eppley, 1972; Smayda, 1980). Although seasonal variation of temperature in the Indian River Lagoon is modest by comparison to that experienced in many temperate ecosystems its significance to phytoplankton dynamics can not be discounted. In the northern and southern regions of the lagoon chlorophyll *a* concentrations were positively correlated to temperature (Table 7). In contrast, the central region exhibited a negative relationship. It may be hypothesized that the shorter residence times of water in the former two regions accentuate the affects of low winter temperatures on the relationship between algal growth rates and standing crop. Alternatively, the apparent relationships between chlorophyll and temperature may be autocorrelated to nutrient limitation caused by reduced freshwater runoff in the winter dry season. The relative importance of temperature and rainfall variation to phytoplankton dynamics may vary annually depending on the severity of winter temperatures and trends in rainfall abundance (i.e. drought versus flood periods) in individual years.

Another factor linked to rainfall is salinity. It is well-established that salinity variation in estuarine environments affects both algal growth and physiology (Smayda, 1980). Rapid changes in salinity can be a stress factor for phytoplankton communities and therefore result in changes of both algal abundance and composition. Since the Indian River Lagoon is subject to large and sometimes rapid changes in salinity it is important to include this factor in the discussion of factors that control phytoplankton abundance. For example, the observed drop on phytoplankton abundance at Sites 3, 4 and 5 in the Spring of 1998 coincided with a period of rapid increase in salinity. Similarly, the storm-induced decrease in salinity observed in the late Summer of 1999 at Sites 7 and 8 also coincided with a decrease in phytoplankton abundance. Whether these observations demonstrate a causal relationship remains hypothetical. For example, the latter observation could be attributed as much to dilution as osmotic stress.

Conclusions

The general picture of phytoplankton dynamics in the Indian River Lagoon emerging from this study is one of a nutrient-rich environment where phytoplankton standing crops are frequently held below their potential by several key loss functions, including tidal flushing, freshwater dilution and grazing. Regional differences in the degree of restriction to water turnover help to explain the spatial patterns of mean phytoplankton abundance observed in the study. Specific spatial and temporal patterns of algal abundance may also be impacted by patterns of nutrient availability. While nitrogen appears to be the most widely limiting nutrient in the lagoon, phosphorus availability appears to play a relatively important role in the northern half of the lagoon, where the literature indicates that phosphorus loading from the watershed is less pronounced. There is also inter-annual variation in phytoplankton abundance that can be hypothetically attributed to variations in nutrient loading from the watershed caused by changes in rainfall totals. As might be expected from the subtropical location of the lagoon, temporal patterns of phytoplankton abundance appear to be less strictly dependent on season than in temperate habitats, and more closely linked to variations in weather conditions, like rainfall (including storm events). The latter considerations bring into play issues like temporal variation in salinity and wind-induced mixing, because of the restricted and shallow nature of the lagoon. The high light flux and shallow depth in the lagoon also presents the potential for photoinhibition.

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References

Aldridge, F. J., Phlips, E. J. & Schelske, C. L. 1995 The use of nutrient enrichment bioassays to test for sp[atial and temporal distribution of limiting factors affecting phytoplankton dynamics in Lake Okeechobee, Florida, USA. *Ergebnisse der Limnologie* **45,** 177–190.

Anderson, D. M. & Keafer, B. A. 1985 Dinoflagellate cyst dynamics in coastal and estuarine waters. In *Toxic Dinoflagellates* (Anderson, D. M., White, A. W. & Baden, D. G., eds). Proceedings of the III International Conference on Toxic Dinoflagellates, St. Andrews, Canada, June 8–12, 1985, UNESCO, pp. 219–222.

APHA 1989 *Standard Methods for the Analysis of Water and Wastewater*, 17th edition. American Public Health Association, Washington, D.C., USA, pp. 1067–1074.

Bledsoe, E. L. & Phlips, E. J. 2000 Correlation of phytoplankton standing crop in the Suwannee River and estuary to physical and chemical gradients. *Estuaries* **23,** 458–473.

Boynton, W. R., Kemp, V. M. & Keefe, C. W. 1982 A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In *Estuarine Comparisons* (Kennedy, V., ed.). Academic Press, New York, N.Y., USA, pp. 69–98.

Burkholder, J. M., Noga, E. J., Hobbs, C. H. & Glasgow, H. B. 1992 New ' phantom ' dinoflagellate is the causitive agent of major estuarine fish kills. *Nature* **358,** 407–410.

Carrick, H. J., Aldridge, F. J. & Schelske, C. L. 1993 Wind influences phytoplankton biomass and composition in a shallow, productive lake. *Limnology and Oceanography* **38,** 1179–1192.

Cloern, J. E. 1982 Does the benthos control phytoplankton biomass in south San Francisco Bay. *Marine Ecology Progress Series* **9,** 191–202.

Cloern, J. E. 1991 Tidal stirring and phytoplankton bloom dynamics in an estuary. *Journal of Marine Research* **49,** 203–221.

Cloern, J. E. 1996 Phytoplankton bloom dynamics in coastal ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. *Reviews of Geophysics* **34,** 127–168.

Cole, B. E. & Cloern, J. E. 1984 Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Marine Ecology Progress Series* **36,** 299–305.

Dugdale, R. C. & Goering, J. J. 1967 Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography* **12,** 196–206.

Durbin, E. G. & Durbin, A. G. 1992 Effects of temperature and food abundance on grazing and short-term weight change in the marine copepod *Acartia hudsonica*. *Limnology and Oceanography* **37,** 361–378.

Eppley, R. W. 1972 Temperature and phytoplankton growth in the sea. *Fisheries Bulletin* **70,** 1063–1085.

Frost, B. W. 1980 Grazing. In *The Physiological Ecology of Phytoplankton* (Morris, I., ed.). University of California Press, Berkeley, California, USA, pp. 465–492.

Geddes, M. C. 1984 Limnology of Lake Alexandrina, River Murray, South Australia and the effects of nutrients and light on the phytoplankton. *Australian Journal of Marine and Freshwater Research* **35,** 399–415.

Harding Jr, L. W. 1994 Long-term trends in the distribution of phytoplankton in Chesapeake Bay: Roles of light, nutrients and streamflow. *Marine Ecology Progress Series* **104,** 267–291.

Hecky, R. E. & Kilham, P. 1988 Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence of enrichment. *Limnology and Oceanography* **33,** 796–822.

Hitchcock, G. L. & Smayda, T. J. 1977 The importance of light in the initiation of the 1972–73 winter-spring bloom in Narragansett Bay. *Limnology and Oceanography* **22,** 126–131.

Jonge, V. N. de, Essink, K. & Boddeke, R. 1993 The Dutch Wadden Sea: A changed ecosystem. *Hydrobiologia* **265,** 45–71.

Kirk, J. T. O. 1994 *Light and photosynthesis in aquatic ecosystems*, second edition. Cambridge University Press, 509 pp.

Kleppel, G. S. 1996 The State of Florida's estuaries and future needs in estuarine research. The Florida Sea Grant College Program, Technical Paper 85, pp. 43–51. Florida Sea Grant College Program, University of Florida, Gainesville, Florida.

Knoppers, B., Kjerfve, B. & Carmouze, J. P. 1991 Trophic state and water turn-over time in six choked coastal lagoons in Brazil. *Biogeochemistry* **14,** 147–166.

Landry, M. R. & Hassett, R. P. 1982 Estimating the grazing impact of marine micro-zooplankton. *Marine Biology* **67,** 283–288.

Lorenzen, C. J. 1972 Extinction of light in the ocean by phytoplankton. *Journal du Conseil* **34,** 262–267.

Lucas, L. V., Koseff, J. R., Cloern, J. E., Monismith, S. G. & Thompson, J. K. 1999*a* Processes governing phytoplankton blooms in estuaries. I: The local production-loss balance. *Marine Ecology Progress Series* **187,** 1–15.

Lucas, L. V., Koseff, J. R., Cloern, J. E., Monismith, S. G. & Thompson, J. K. 1999*b* Processes governing phytoplankton blooms in estuaries. II: The role of horizontal transport. *Marine Ecology Progress Series* **187,** 17–30.

Luckenbach, M. W., Sellner, K. G., Shumway , S. E. & Greene, K. 1993 Effects of two bloom-forming dinoflagellates, *Prorocentrum minimum and Gyrodinium uncatenum,* on the growth and survival of the eastern oyster, *Crassostrea virginica*. *Journal of Shellfish Research* **12,** 411–415.

McPherson, B. F. & Miller, R. L. 1987 The vertical attenuation of light in Charlotte Harbor, a shallow, subtropical estuary, southwestern Florida. *Estuarine Coastal and Shelf Science* **25,** 721–737.

Monbet, Y. 1992 Control of phytoplankton biomass in estuaries: A comparative analysis of microtidal and macrotidal estuaries. *Estuaries* **15,** 563–571.

Mullin, M. M., Sloan, P. R. & Eppley, R. W. 1966 Relationship between carbon content, cell volume and area in phytoplankton. *Limnology and Oceanography* **11,** 307–311.

Nixon, S. W. 1995 Coastal marine eutrophication: A definition, social consequences and future concerns. *Ophelia* **41,** 199–220.

Officer, C. B., Smayda, T. J. & Mann, R. 1982 Benthic filter feeding: A natural eutrophication control. *Marine Ecology Progress Series* **9,** 203–210.

Oswald, W. J. & Gataas, H. B. 1957 Photosynthesis in sewage treatment. *Transactions of the American Society of Civil Engineers* **122,** 73–97.

Paerl, H. W. 1988 Nuisance phytoplankton blooms in coastal, estuarine and inland waters. *Limnology and Oceanography* **33,** 823–847.

Parsons, T. R., Maita, Y. & Lalli, C. M. 1984 *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, New York, N.Y., USA, 173 pp.

Phlips, E. J., Lynch, T. C. & Badylak, S. 1995*a* Chlorophyll *a*, tripton, color and light availability in a shallow tropical inner shelf lagoon, Florida Bay. *Marine Ecology Progress Series* **127,** 223–234.

Phlips, E. J., Aldridge, F. E., Schelske, C. L. & Crisman, T. L. 1995*b* Relationship between light availability, chlorophyll *a* and tripton in a large shallow sub-tropical lake. *Limnology and Oceanography* **40,** 416–421.

Phlips, E. J., Badylak, S. & Lynch, T. L. 1999 Blooms of the picoplanktonic cyanobacterium Synechococcus in Florida Bay. *Limnology and Oceanography* **44,** 1166–1175.

Phlips, E. J., Cichra, M., Havens, K., Hanlon, C., Badylak, S., Rueter, B., Randall, M. & Hansen, P. 1997 The control of phytoplankton abundance and structure by nutrient and light availability in a shallow subtropical lake. *Journal of Plankton Research* **19,** 319–342.

Platt, T. & Denham, K. 1980 Patchiness in phytoplankton distribution. In *The Physiological Ecology of Phytoplankton* (Morris, I., ed.). University of California Press, Berkeley, California, pp. 465–492.m

Redfield, A. C., Ketchum, B. H. & Richards, F. A. 1963 The influence of organisms on the composition of sea water. In *The Sea*, volume 2 (Hill, M. N., ed.). Wiley-Interscience, New York, NY, pp. 26–77.

Reynolds, C. S. 1984 *The ecology of freshwater phytoplankton*. Cambridge University Press, Cambridge.

Richardson, K. & Jorgensen, B. B. 1996 Eutrophication, definition, history and effects. In *Eutrophication in Coastal Marine Ecosystems* (Jorgensen, B. B. & Richardson, K.). American Geophysical Union, Washington, D.C., pp. 1–20.

Rosenberg, R., Elmgren, E., Fleischer, S., Jonsson, P., Persson, G. & Dahlin, H. 1990 Marine eutrophication studies in Sweden. *Ambio* **19,** 102–108.

SAS 1989 *SAS/STAT User's Guide*, Version 6, 3rd edition. SAS Institute.

Sartory, D. P. & Grobbelaar, J. U. 1984 Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia* **114,** 177–187.

Sheng, Y. P., Peene, S. & Lui, Y. M. 1990 Numerical modeling of tidal hydrodynamics and salinity transport in the Indian River Lagoon. *Florida Scientist* **50,** 49–61.

Sloan, P. R. & Eppley, R. W. 1966 Relationship between carbon content, cell volume and area in phytoplankton. *Limnology and Oceanography* **11,** 307–311.

Smayda, T. J. 1978 From phytoplankters to biomass. In *Phytoplankton Manual* (Sournia, A., ed.). UNESCO, Paris, pp. 273–279.

Smayda, T. J. 1980 Phytoplankton species succession. In *The Physiological Ecology of Phytoplankton* (Morris, I., ed.). University of California Press, Berkeley, California, USA, pp. 493–570.

Smayda, T. J. 1989 Primary production and the global epidemic of phytoplankton blooms in the sea: a linkage? In *Novel Phytoplankton Blooms* (Cosper, E. M., Bricelj, V. M. & Carpenter, E. J., eds). Springer-Verlag, New York, N.Y., pp. 449–484.

Smith, N. P. 1993 Tidal and non-tidal flushing of Florida's Indian River Lagoon. *Estuaries* **16,** 739–746.

Stefan, H., Skoglund, T. & Megard, R. O. 1976 Wind control of algal growth in eutrophic lakes. *American Society of Civil and Environmental Engineering Division* **102,** 1201–1213.

Turner, J. T. & Tester, P. A. 1989 Zooplankton feeding ecology: Copepod grazing during an expatriate red tide. In *Novel Phytoplankton Blooms* (Cosper, E. M., Bricelj, V. M. & Carpenter, E. J., eds). Springer-Verlag, New York, N.Y., pp. 359–374.

Utermohl, H. 1958 Zur vervollkommnung der quatitativen phytoplankton-methodik. *Mitteilungen-Internationale Vereinigung fur Theoretische und Angewandte Limnologie* **9,** 1–38.

Virnstein, R. W. 1990 The large spatial and temporal biological variability of Indian River Lagoon. *Florida Scientist* **53,** 249–256.

Virnstein, R. W. 1995 Seagrass landscape diversity in the Indian River Lagoon, Florida: The importance of geographic scale and pattern. *Bulletin Marine Science* **57,** 67–74.

Virnstein, R. W. & Carbonara, P. A. 1985 Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River Lagoon, Florida. *Aquatic Botany* **23,** 67–82.

Virnstein, R. W., Mikkelsen, P. S., Cairns, K. D. & Capone, M. A. 1983 Seagrass beds versus sand bottoms: The trophic importance of their associated benthic invertebrates. *Florida Scientist* **46,** 363–381.

Author Queries

Page	Query
2	Please provide reference for Morris & Tomasko 1993.
17 & 18	The following references were not cited in the text: Hecky & Kilham 1988, Mullin et al 1966 and Sloan & Eppley, 1996.