

Climatic Trends and Temporal Patterns of Phytoplankton Composition, Abundance, and Succession in the Indian River Lagoon, Florida, USA

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Abstract This paper describes the results of 10 years of water quality monitoring in the Indian River Lagoon Florida, with special emphasis on the relationships between trends in climatic conditions and the distribution, composition, and abundance of the phytoplankton community. The Indian River Lagoon, which spans 220 km of Florida's east coast, is a region of particular concern because of the rapid rate of human development throughout the region and the hydrologically restricted character of the lagoon, which heightens the potential for algal bloom. Water sampling was carried out on a monthly to twice-monthly basis at six sites located in the northern and central lagoon. The 10-year study included both extended periods of below and above average rainfall. A number of ecologically distinct regions exist within the lagoon, which differ considerably in water exchange properties and watershed inputs. The northern lagoon is characterized by longer water residence times, lower phosphorus concentrations, higher nitrogen concentrations, and more stable salinity conditions than the central lagoon. Mean phytoplankton biovolumes were substantially higher at the sites in the northern lagoon than at the sites in the central lagoon, and algal blooms were more common

and intense in the former region. Inter-annual patterns of phytoplankton biovolume were also different in the northern and central lagoon. In the northern lagoon, phytoplankton biovolumes were lowest during the drought period, from the autumn of 1998 to the spring of 2001. By contrast, algal bloom events in the central lagoon were not only less frequent but were not tied to periods of high rainfall. The most widespread and common bloom formers were the potentially toxic dinoflagellate *Pyrodinium bahamense* var. *bahamense* and two centric diatoms, *Dactyliosolen fragilissimus* and *Cerataulina pelagica*. Many of the biovolume peaks observed over the study period were attributable to these three species. The results of time series modeling of phytoplankton dynamics further highlighted the disparities between the two regions of the lagoon in terms of the suite of parameters that best predict the observed trends in the biomass of phytoplankton. Overall, the outcome of this initial modeling effort in the Indian River Lagoon suggests that time series approaches can help define the factors that influence phytoplankton dynamics.

Keywords Eutrophication · Residence time ·
Dinoflagellates · Diatoms · Cyanobacteria · Sub-tropical

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Introduction

Many aquatic ecosystems throughout the world are experiencing increasing rates of eutrophication and alterations in hydrologic conditions associated with expanding human development and population growth (Nixon 1995; Glibert and Burkholder 2006). One of the consequences of these trends is changes in phytoplankton communities, including increases in the frequency and intensity of algal blooms (Paerl 1988; Nixon 1995; Hallegraeff 2003; Glibert and

Burkholder 2006). Despite these apparent trends, it is often difficult to unequivocally define the direct causal linkages between eutrophication and algal abundance, particularly in marine environments, where the relationships between nutrient load and algal abundance are often less definitive and predictable than in freshwater ecosystems (Cloern 2001). Linking changes in phytoplankton composition and abundance to alterations in nutrient load depends on the ability to define variability in ecosystems related to other environmental factors, such as climatic conditions. In aquatic ecosystems, variability in rainfall affects a wide range of water column conditions related to direct atmospheric and watershed influences, such as nutrient loads, salinity regimes, suspended sediment levels, and general hydrologic conditions (e.g., water residence times and circulation patterns) (Paerl 1997; Cloern 2001; Weise et al. 2002; Phlips et al. 2007). All of these factors can affect the abundance, composition, and distribution of phytoplankton.

This paper describes the results of 10 years of water quality monitoring in the Indian River Lagoon, with special emphasis on the influences of climatic conditions and hydrologic regimes on the distribution, composition, and abundance of the phytoplankton. The Indian River Lagoon, which spans 220 km of Florida's east coast, is a region of particular concern because of the rapid rate of human development throughout the region and the hydrologically restricted character of the lagoon, which heightens the potential for algal blooms (Phlips et al. 2004b). Similar

concerns have been raised for other restricted ecosystems throughout the world (Monbet 1992; Knoppers et al. 1991; Oliveira and Kjerfve 1993) and in Florida, such as Florida Bay (Phlips et al. 1999) and Tampa Bay (Badylak et al. 2007; Badylak and Phlips 2008). The results of the study demonstrate that the specific responses of the phytoplankton community to shifts in rainfall differ by region, as they relate to disparities in water residence times, nutrient loads, and freshwater inflows.

Methods

Site Descriptions

Study Site Description The Indian River Lagoon (IRL) is a geomorphic component of the east coast barrier reef system of Florida, USA (Davis 1997). The northern portion of the lagoon includes a side branch, called the Banana River, which extends from near Eau Gallie northeastward to north of Cape Canaveral, west of the barrier island (Fig. 1). The entire lagoon extends from just north of Titusville to the Jupiter Inlet. The width of the lagoon varies from 0.5 to 5 km and depth averages near 2 m (Table 1). A number of ecologically distinct regions exist within the lagoon, which differ considerably in water exchange properties (Sheng et al. 1990; Virnstein 1990; Smith 1993; Sheng and Davis 2003; Steward et al. 2005) and watershed inputs (Steward et

Fig. 1 Locations of sampling sites in the Indian River Lagoon

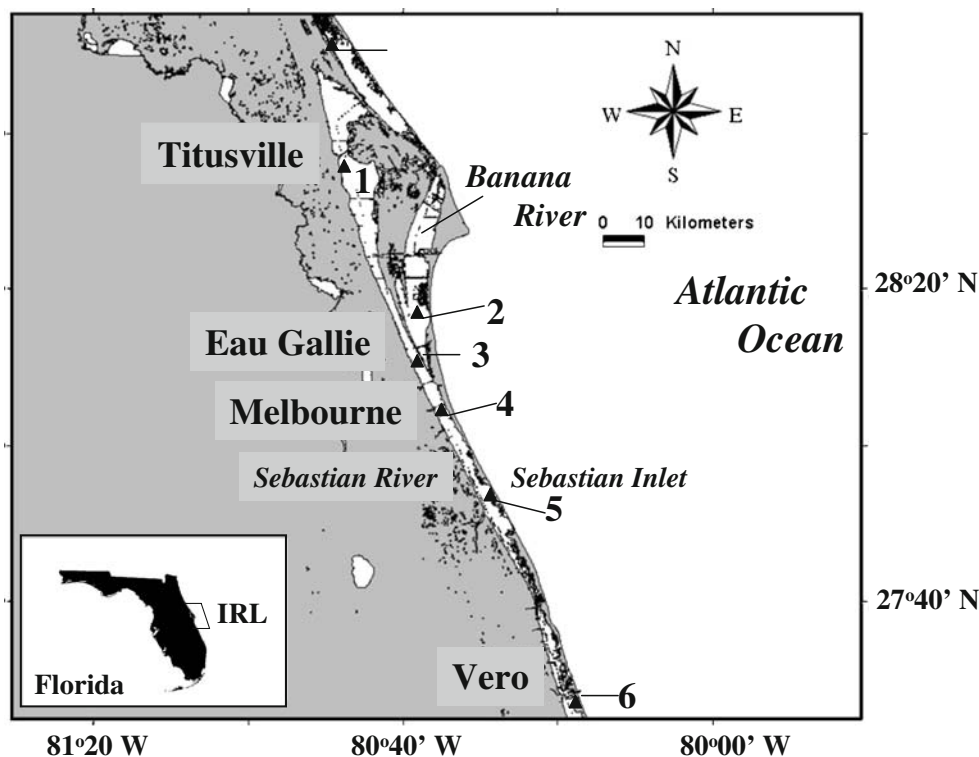


Table 1 Mean depth, watershed land area relative to water area, mean annual watershed freshwater runoff, and water retention time, R_{50} (time required to replace 50% of the water volume) (Steward et al. 2005)

	Northern IRL	Banana River	Central IRL
Mean depth (m)	1.9	1.7	1.7
Land/water area	2.1	1.2	8.1
Mean annual runoff ($\times 10^6$ m ³)	160	111	549
R_{50} (days)	107	156	9

al. 2006). These regions were the basis for the selection of the six sampling sites in this study. The northern-most site in the IRL, Site 1, was located by the city of Titusville (Fig. 1). Site 2 was located in the Banana River. Sites 3 and 4 were located near the cities of Eau Gallie and Melbourne, respectively, in the main stem of the IRL. Sites 1–4 are all located in the northern lagoon where water residence times (i.e., expressed as R_{50} =the time required for 50% turnover of water) are on the order of months (Table 1), due to their considerable distance from the nearest inlet to the Atlantic Ocean, the Sebastian Inlet (Phlips et al. 2002; 2004b; Steward et al. 2005). Site 5 was located in the central region of the IRL, within a few kilometers of the Sebastian Inlet. Site 6 was located in the central lagoon near Vero, between the Sebastian and Ft. Pierce Inlets (Fig. 1). Mean residence times for the central lagoon are on the order of days (Table 1). The approximate rank order of mean water residence times (R_{50}) in the segments of the IRL associated with the six sampling sites is Titusville (Site 1) at 128 days, Banana River (Site 2) at 116 days, Eau Gallie (Site 3) at 85 days, Melbourne (Site 4) at 85 days, Vero (Site 6) at 10 days, and Sebastian at 5 days (Site 5) (Jones, Edmunds and Associates, unpublished data).

Watershed inputs to the six regions of the IRL represented by the selected sampling sites are different in source, composition, and volume (Adkins et al. 2004; Steward et al. 2005). Site 1 receives inputs from various small tidal creeks emanating the primarily small urban area of Titusville and undeveloped watersheds, including the protected lands and wetlands of the Kennedy Space Center complex on the barrier island east of the lagoon (Table 2). Site 2 in the Banana River is associated with the smallest watershed runoff in the IRL (Table 1), characterized by urban land-use and natural wetlands. South of Site 2 in the IRL, the size of the watersheds increase. The first significant river inputs are the Eau Gallie River near Site 3 and Crane Creek at Melbourne (Site 4), both of which

have watersheds dominated by urban land-use (Table 2). The central lagoon includes a number of major canal and river inflows, such as the Sebastian River. Watersheds of the central IRL are characterized by significant agricultural influences, including the extensive Indian River citrus industry (Table 2). Due to differences in runoff and land-use characteristics, nutrient load estimates for the three segments of the IRL associated with Sites 4–6 are substantially higher than those associated with the areas of the lagoon associated with Sites 1–3 (Table 3). The relative balance of nitrogen and phosphorus in the freshwater inflows from the watersheds are regionally dependent, with proportionally higher nitrogen than phosphorus in the north than central IRL (Table 3).

Field Procedures

Water was collected at each site on a monthly to twice-monthly basis for a 10-year period September 1997 to October 2007. Salinity and temperature were measured with a YSI Model 85. Water samples were collected with a vertical integrating sampling tube that captures water from the surface to within 0.1 m of the bottom. Phytoplankton samples were preserved with acidic Lugol solution and a backup aliquot was preserved with glutaraldehyde in 0.1 M sodium cacodylate buffer. Samples for chlorophyll *a* analysis were filtered on site onto 0.7 μ m glass fiber filter and kept frozen in the dark.

Chemical Analyses

Total nitrogen was determined using the persulfate digestion method (APHA 1989) and analyzed with a Bran-Luebbe AutoAnalyzer. Total phosphorus was determined using the persulfate digestion method (APHA 1989) and analyzed using a spectrophotometer. Chlorophyll *a* concentration was determined after extraction of the filtered

Table 2 Relative (percent) contributions of different land-use in watersheds associated with different regions of the IRL (Adkins et al. 2004)

	Northern IRL	Banana River	Melbourne/Eau Gallie	Sebastian	Vero
Urban	15	33	48	15	36
Agricultural	9	1	8	30	35
Open land/forest	31	45	28	39	21
Wetland	45	21	16	15	8

Table 3 Mean annual total nitrogen (TN) and total phosphorus (TP) load (kg) from the watershed to different regions of the lagoon (Steward and Green 2007)

	TN	TP
Titusville	45,974	3,428
Banana River	25,310	4,721
Eau Gallie	48,645	7,063
Melbourne	102,987	19,355
Sebastian	147,448	28,706
Vero	108,190	23,538

samples with 90% warm ethanol (Sartory and Grobbelaar 1984), with a Hitachi U2000 dual beam spectrophotometer.

Phytoplankton Analysis

Fluorescence microscopy was used to enumerate picoplanktonic cyanobacteria, e.g., *Synechococcus* (Fahnenstiel and Carrick 1992). Subsamples of station water were filtered onto 0.2- μm -pore nucleopore filters and mounted between a microscope slide and cover slip with immersion oil. These were stored in the freezer and counted within 72 h using a Nikon research microscope equipped with autofluorescence (green light 530–560 nm excitation and >580 nm emission). Numerical abundance of cyanobacteria cells was determined at 1,000 \times by counting a minimum of five ocular micrometer grids. Counts were completed upon reaching a minimum of 100 cells, or 100 grids, whichever came first.

General phytoplankton composition was determined using the Utermöhl method (Utermöhl 1958). Samples preserved with acidic Lugol solution were settled in 19-mm-inner-diameter cylindrical chambers. Phytoplankton cells were identified and counted at 400 \times and 100 \times with a Nikon phase contrast inverted microscope. At 400 \times , a minimum of 100 cells of a single taxa and 30 grids were counted. If 100 cells were not counted by 30 grids, up to a maximum of 100 grids were counted until 100 cells of a single taxa was reached. At 100 \times , a total bottom count was completed for taxa greater than 30 μm . Light microscopy was aided by other techniques to confirm the identification of certain key dinoflagellates and diatoms, such as SEM. One of the prominent species of algae found in the samples was *Pyrodinium bahamense*, recently identified as the variety *bahamense* (Badylak et al. 2004). The related variety *compressum* was not observed during the study. The capability of *Pyrodinium bahamense* var. *bahamense* from the Indian River Lagoon to produce the toxin saxitoxin has been confirmed using HPLC (Landsberg et al. 2006).

The texts and journal articles used most frequently to aid in taxonomic identification were Steidinger and Williams (1970), Tester and Steidinger (1979), Sournia (1986),

Ricard (1987), Hasle and Syvertsen (1996), Steidinger and Tangen (1996), Fryxell et al. (1997), and Hargraves (2002). Recent revisions to the nomenclature for dinoflagellate taxa by Daugbjerg et al. (2000) were incorporated into the results.

Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa. Specific phytoplankton dimensions were measured for at least 30 randomly selected cells. Volumes were calculated for each cell from which a mean value was derived (Smayda 1978). In taxa that exhibited a range of cell sizes, such as occurs with many diatom species, the counts were divided into size classes to provide more accurate estimates of biovolume. The total biovolume per sample was the sum of the estimated cell volumes for each species. The term ‘bloom’ was defined as biovolumes in excess of $2.8 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$, which represented the top 10% of the frequency distribution curve for phytoplankton biovolume.

Statistical Analyses

The focus of the modeling effort was the identification of environmental variables that explain the observed trends in phytoplankton biovolume (i.e., biomass), including the major groups of phytoplankton. In addition, the time series nature of the data was maintained to allow for shifting correlations between biovolume and environmental variables lagged in time. A full multivariate time series analysis could not be performed due to missing observations over the 10 years of the study period. The set of explanatory variables were correlated to one another and a selection procedure used Akaike’s Information Criterion (AIC) (Akaike 1981; Burnham and Anderson 2003) to identify candidate models and then chose the model with the best predictive capability.

The dependent variables were total phytoplankton, dinoflagellate, diatom, cyanobacteria, and “other” (e.g., chlorophytes, cryptophytes, raphidophytes) biovolume. The explanatory variables included water salinity, temperature, Secchi disk depth, total nitrogen, total phosphorus, nitrogen phosphorus ratio, and lagged values (back three time periods). For example, salinity at the current time t , at time $t-1$, at time $t-2$, and at time $t-3$ were used as potential regressors. In addition, year and month were included as categorical variables to capture any additional behavior not explained by the explanatory variables. For the dinoflagellates, the explanatory variables included the natural logarithm of diatom biovolume and the lagged values back three time periods. Similarly, for the diatoms and cyanobacteria and the “other” biovolumes, explanatory variables included the natural logarithm of dinoflagellate biovolume and the lagged values back three time periods. For all variables with lags, lagged values were limited to three time periods; otherwise,

the number of potential explanatory variables was too large, given the length of the time period under analysis.

Initial exploratory mixed models used subsets of the explanatory variables, allowing for temporal autocorrelation in the error terms. Results indicated that the response variables of biomass needed to be log transformed so that the model residuals were normally distributed. No residual temporal autocorrelation was observed in the model when the set of explanatory variables included the lagged values of some of the independent variables. The set of explanatory variables tended to vary from station to station (as expected) and analyses were done separately for each station and each response variable.

Since the number of candidate explanatory variables was very large ($p=28$, excluding month and year), the following model selection procedure was employed. First, an analysis of variance was performed using the response variable Y with main effects year alone or month alone. The residuals were obtained from each ANOVA. This resulted in two sets of residuals, plus the set of original response variable values. Each set (residuals or the original values of Y) was used in a restricted all possible models regression selection procedure, with a maximum of 15 variables being permitted in a model. From these, 420 models with the highest R^2 values and lowest AIC scores were selected. Overall, 1,260 candidate models for each dependent variable were obtained. This approach was used because it was likely that year or month would provide additional information beyond that provided by the environmental variables, thereby requiring comparisons among models with or without year or month included.

For each model, AIC corrected for small sample size was plotted against the parameters in the model (Burnham and Anderson 2003). This was done separately for each subset of the 420 models, since both the AIC and AICC scores were calculated assuming the number of parameters was the number chosen only by the restricted selection procedure, i.e., ignoring whether year and month were in the model. For each set of the 420 models, the lowest AICC values were chosen to allow comparing models with and without the effects of year and month.

Many of the models were within four units of the lowest AICC score, and so use of AICC alone was not sufficient to determine the final choice of a model. The six models with the lowest AICC scores for each combination of year and month were selected for further comparison. For these models, Y was regressed on the selected variables and year and month, if they had been included in the original ANOVA. The correlation between the observed and predicted values of the response was obtained for each candidate model. This allowed us to compare models based on the number of variables in the model, the AICC score, and the predictive capability of the

model. All analyses were done using SAS v9.1 (SAS Institute, Cary, NC, USA).

Results

Basic Physical–Chemical Characteristics

Some physical and chemical parameters showed similar values at all six sampling sites. Surface water temperatures at all six sites varied seasonally from winter lows of 15–20°C to summer highs near 30°C (Fig. 2). In keeping with the subtropical climate of central Florida, water temperatures typically exceeded 20°C from April through November. Winter lows at the northern-most sites were a few degrees lower than at the southern-most sites. During exceptionally warm winters, such as 2001/2002, water temperatures generally remained above 20°C. Mean Secchi disk depths were similar throughout the lagoon, averaging near 1.5 m (Table 4).

Mean values for other parameters varied between sites (Table 4), as might be expected from previously described spatial differences in hydrologic and watershed characteristics across the sampling region. Mean salinities for the study period ranged from near 20 at Sites 2–4 in the northern lagoon to 28.5 at Site 5 near the Sebastian Inlet (Table 4). All six sites exhibited a wide range of salinities over the sampling period, with disparities between low and high values in excess of 20 (Fig. 3). Declines in salinity occurred in response to increases in local rainfall levels.

The 10-year study included both extended periods of below and above average rainfall. Some of these divergent trends were associated with El Niño and La Niña periods, such as the major El Niño of 1997, and the extended La Niña induced droughts from the autumn of 1998 to the spring of 2001, and autumn of 2006 to the summer of 2007. Other major shifts in rainfall conditions were associated

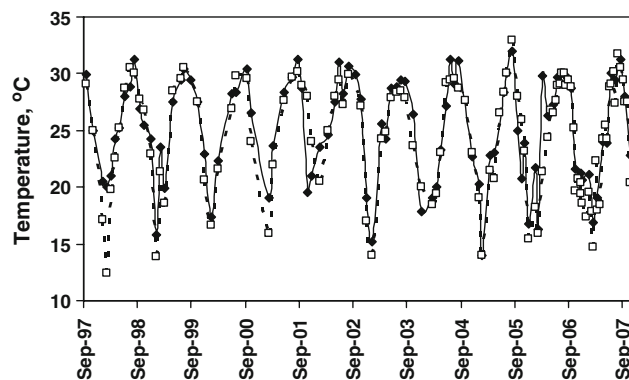


Fig. 2 Surface water temperature over the 10-year study period at Site 1 near Titusville (dashed line with open symbols) and Site 6 near Vero (solid line with filled symbols)

Table 4 Mean values for selected physical and chemical parameters over the 10-year study period

Site	TP (μM)	TN (μM)	TN/TP	Salinity	Secchi depth (m)
1	1.48 (0.61)	70.8 (21.4)	52.1 (20.7)	25.7 (4.8)	1.37 (0.48)
2	1.77 (0.64)	74.5 (19.6)	45.6 (15.7)	20.0 (4.1)	1.33 (0.44)
3	2.00 (0.68)	60.6 (17.2)	33.7 (13.7)	19.9 (4.6)	1.60 (0.57)
4	2.16 (0.74)	55.6 (17.6)	28.6 (12.6)	20.6 (6.0)	1.49 (0.50)
5	1.87 (0.65)	31.9 (11.0)	18.6 (7.7)	28.5 (4.7)	1.38 (0.45)
6	2.74 (1.19)	39.1 (13.6)	15.8 (6.2)	26.4 (5.7)	1.41 (0.50)

Standard deviations are provided in *parentheses*

with storm events, such as the late summer storm of 1999 and the severe hurricane seasons of 2004 and 2005, which directly impacted the east coast of Florida (Steward et al. 2006; Dix et al. 2008).

There were regional differences in the response of salinity to changes in rainfall. For example, at the sites nearest the Sebastian and Ft. Pierce Inlets (i.e., Sites 5 and 6), salinities rebounded rapidly at the end of high rainfall periods to higher values (Fig. 3). By contrast, salinities at the more restricted sites in the northern lagoon (i.e., Sites 1–4) recovered more gradually from rainfall-induced declines. The effect of drought periods were reflected in the high salinities observed from 1998 to 2001, and 2006.

Mean total phosphorus (TP) concentrations were lower in the northern lagoon than in the central lagoon (Table 4). The most dramatic difference was the two-fold higher mean

TP concentration at Site 6, in the central lagoon south of Vero, than at Site 1 in the northern lagoon near Titusville. The opposite trend was observed for mean total nitrogen (TN), with twice as high mean TN values in the northern than central lagoon (Table 4). The contrasting spatial gradients in TN and TP concentrations are reflected in the over three-fold decline in mean TN/TP ratios from Sites 1 to 6 (Table 4), although all the mean ratios equaled or exceeded the Redfield ratio of 16.

Responses of TN and TP concentrations to rainfall varied spatially and temporally. The concentrations of both elements often increased with decreasing salinity, as reflected in the significant negative correlations between salinity and nutrient concentration in both the northern and central lagoon (Table 5), although the specific response of each parameter varied by region and time. TN levels in the

Fig. 3 Surface salinity at the six sampling sites

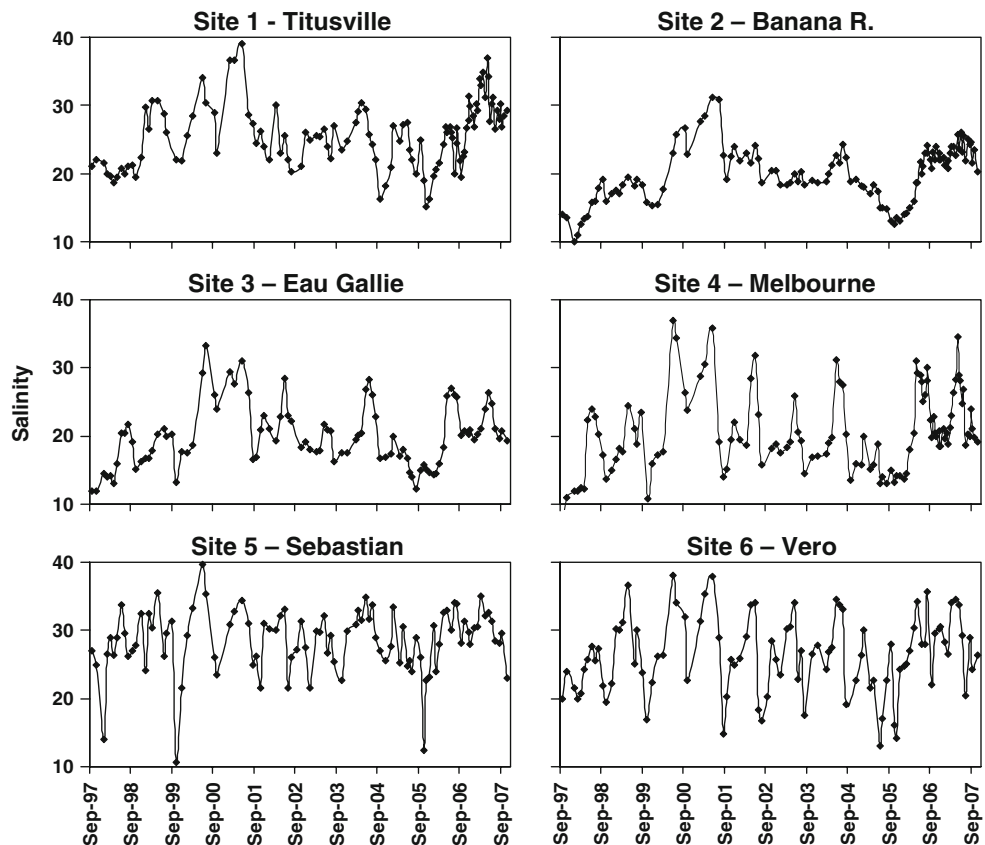


Table 5 Pearson's correlation coefficients for total phytoplankton biovolume (Ln Total), total nitrogen (TN), total phosphorus (TP), water temperature (Temp), and salinity in two regions of the Indian River Lagoon: (1) the northern lagoon (Sites 1–4) and (2) the central lagoon (Sites 5 and 6)

	Ln total	TN	TP	Temp	Salinity
Region 1					
Ln Total	–	0.2507 (<0.0001)	0.3039 (<0.0001)	0.2245 (<0.0001)	–0.1669 (0.0004)
TN	–	–	0.1105 (0.0205)	–0.0789 (0.0986)	–0.1392 (0.0035)
TP	–	–	–	0.0753 (0.1151)	–0.2085 (<0.0001)
Temp	–	–	–	–	0.1658 (0.0005)
Region 2					
Ln Total	–	0.2370 (0.0009)	0.3055 (<0.0001)	0.3392 (<0.0001)	–0.3213 (<0.0001)
TN	–	–	0.5102 (<0.0001)	0.2343 (0.0010)	–0.4809 (<0.0001)
TP	–	–	–	0.3540 (<0.0001)	–0.4588 (<0.0001)
Temp	–	–	–	–	0.0564 (0.4351)

IRL reflected both the degree of marine influence, in terms of the relative proximity of inlets to the Atlantic Ocean, and the character of the watersheds associated with each region. The lowest TN concentrations were observed at the two sites with the greatest tidal water exchange with the Atlantic Ocean, i.e., Sites 5 and 6. All sites except Site 2 in the Banana River showed significant negative correlations between salinity and TN (Table 6), revealing the important role of watershed inputs to nitrogen load. The relationships were strongest at Sites 4 and 6, both of which are located in regions of relatively large freshwater inflows (Table 6). The lack of a significant relationship at Site 2 reflects the unique character of the watershed for the central Banana River, which is isolated from influences of mainland Florida.

The spatial trends in TP concentrations were less clear than for TN. Only Site 6 showed a strong negative relationship between salinity and TP due to the large phosphorus-rich freshwater inflows to the region (Table 6). Significant but weaker correlations were observed at Sites 1 and 2.

Phytoplankton Biovolume and Community Composition

Mean phytoplankton biovolumes were substantially higher at the sites in the northern lagoon than at the sites in the central lagoon (Table 7), and algal blooms were more common and intense in the former region (Fig. 4, Table 8). From a broad intra-annual perspective, dinoflagellates were the dominant group in the northern Indian River Lagoon (Sites 1–4) throughout the year, in terms of mean relative biovolume (Table 7). The importance of dinoflagellates increased in the warm season, exceeding 40% of mean relative biovolume at all four sites, reflecting the numerous blooms observed in the spring and summer. Conversely, diatoms, the next most important group in the northern lagoon, were on the average somewhat more important in the cold season, except at Site 2, where cyanobacteria took on added importance in the cold season. Cyanobacteria,

primarily consisting of picoplanktonic species, were also periodically major components of the phytoplankton biovolume at the other three sites (1, 3, and 4), such as in the cold seasons of 1998/1999 and 2003/2004 (Fig. 4). The 'other' components of the phytoplankton community, which primarily consisted of small cryptophytes and chlorophytes, typically represented less than 10% of the mean relative biovolume in either the cold or warm season, with substantially higher values in the former season (Table 7).

The most common successional pattern for major phytoplankton groups in the northern lagoon was spring–summer dinoflagellate blooms followed by late summer–fall diatom maxima (Fig. 4). However, exceptions to this pattern were observed. For example, in 2005, spring blooms at Sites 2, 3, and 4 were dominated by diatoms (Fig. 4).

The relative biovolume contribution of the major phytoplankton groups at the two sites in the central lagoon (Sites 5 and 6) was more balanced than in the northern lagoon (Table 7). Diatoms took on a more important role in the phytoplankton community than dinoflagellates, comprising over 30% of mean relative biovolume in both the cold and warm seasons. The relative importance of dinoflagellates increased in the warm season at both sites,

Table 6 Pearson correlation coefficients for the relationship between salinity and total nitrogen and total phosphorus at the six sampling sites

Site	TN	TP
Site 1—Titusville	–0.2622 (0.0050)	–0.2404 (0.0103)
Site 2—Banana River	0.0998 (0.2909)	–0.2400 (0.0100)
Site 3—Eau Gallie	–0.2564 (0.0108)	0.1595 (0.1168)
Site 4—Melbourne	–0.4566 (<0.0001)	–0.0949 (0.3149)
Site 5—Sebastian	–0.3057 (0.0021)	–0.0175 (0.8639)
Site 6—Vero	–0.5549 (<0.0001)	–0.6278 (<0.0001)

The *p* values are shown in parentheses

Table 7 Mean relative biovolume of the major phytoplankton groups in the cold and warm seasons

Site	Season	Total biovolume	% Dino	% Diatom	% Cyano	% Other
1	Cold	1.49	36.4	29.6	22.3	11.8
	Warm	5.26	44.1	25.8	23.9	6.2
2	Cold	4.14	38.3	23.3	34.6	3.8
	Warm	6.54	41.2	30.8	24.04.1	
3	Cold	3.71	33.1	37.6	20.6	8.7
	Warm	4.61	42.2	34.9	18.1	4.8
4	Cold	2.84	38.4	30.2	23.0	8.4
	Warm	5.12	46.9	28.7	19.4	5.0
5	Cold	1.19	21.8	32.3	23.9	22.0
	Warm	2.22	30.2	30.9	25.1	13.8
6	Cold	1.12	14.2	31.6	20.0	34.2
	Warm	2.12	20.3	34.4	26.3	19.0

Mean total biovolume is presented as $10^6 \mu\text{m}^3 \text{ml}^{-1}$

but in contrast to sites in the northern lagoon, did not exceed the mean relative biovolume of diatoms. Cyanobacteria were also strongly represented, with mean relative biovolumes between 20% and 30%. One of the most prominent differences between the northern and central lagoon in terms of the relative importance of different phytoplankton groups was the strong representation of microflagellates in the central lagoon, as reflected in the high mean relative biovolume of the ‘other’ group, reaching 34% in the warm season at Site 6.

Inter-annual patterns of phytoplankton biovolume were also different in the northern and central lagoon (Fig. 4). In the northern lagoon, phytoplankton biovolumes were lowest

during the prolonged drought period, from the autumn of 1998 to the spring of 2001 (Fig. 4). Periods of significantly above average rainfall were often associated with peaks in phytoplankton biovolume, as illustrated by the relationship between the maximum phytoplankton biovolume observed in the summer and the deviation from normal rainfall for the season (Fig. 5). At Sites 1 and 4 in the northern lagoon, peak summer phytoplankton biovolumes were associated with summers of above average rainfall. By contrast, algal bloom events in the central lagoon (Sites 5 and 6) were not tied to periods of high rainfall (Fig. 5).

In terms of species composition, 25 species of phytoplankton were observed at bloom levels over the study

Fig. 4 Phytoplankton biovolume at the six sampling sites, including a breakdown of the contributions of dinoflagellates (*Dino*), diatoms (*Diatom*), cyanobacteria (*Cyano*), and all other taxa (*Other*; e.g., chlorophytes, cryptophytes, unidentified microflagellates)

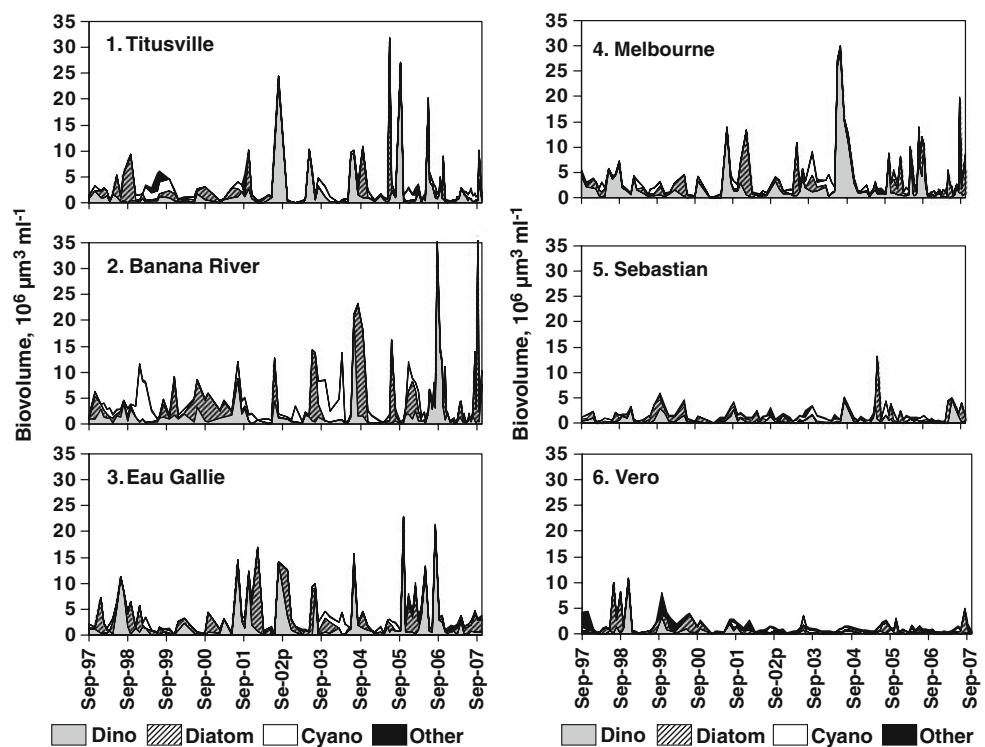


Table 8 Bloom species of phytoplankton at the six sampling sites

Bloom species	Maximum biovolume	Bloom freq.
Site 1		
<i>Pyrodinium bahamense</i>	26,422,647	12
<i>Dactyliosolen fragilissimus</i>	27,785,208	3
<i>Cerataulina pelagica</i>	4,040,035	2
<i>Chlorella/Nannochloris</i>	3,427,705	1
<i>Pseudo-nitzschia calliantha</i>	7,240,968	1
<i>Thalassionema nitzschioides</i>	3,310,490	1
<i>Pyramimonas</i> spp.	3,885,017	1
Site 2		
<i>Pyrodinium bahamense</i>	33,942,714	10
<i>Cerataulina pelagica</i>	13,003,863	8
<i>Dactyliosolen fragilissimus</i>	35,252,732	5
<i>Synechococcus</i> sp.	11,002,539	5
<i>Pseudo-nitzschia</i> sp.	7,366,432	3
<i>Spherical picocyanobacterium</i>	7,839,134	3
<i>Akashiwo sanguinea</i>	6,272,876	1
cf. <i>Chaetoceros danicus</i>	4,198,286	1
<i>Thalassionema nitzschioides</i>	5,413,108	1
Site 3		
<i>Pyrodinium bahamense</i>	20,116,910	7
<i>Akashiwo sanguinea</i>	19,594,347	3
<i>Cerataulina pelagica</i>	7,414,535	3
<i>Pheopolykrikos hartmannii</i>	10,890,766	2
cf. <i>Skeletonema menzeli</i>	3,099,669	2
<i>Pseudo-nitzschia</i> sp.	3,095,303	2
<i>Prorocentrum micans</i>	2,917,577	1
<i>Chaetoceros lorenzianus</i>	3,168,250	1
<i>Odontella regia</i>	2,809,521	1
cf. <i>Skeletonema costatum</i>	5,273,117	1
<i>Navicula</i> spp.	2,910,045	1
<i>Dactyliosolen fragilissimus</i>	4,439,189	1
<i>Spherical picocyanobacterium</i>	3,063,625	1
Site 4		
<i>Pyrodinium bahamense</i>	28,361,185	9
<i>Akashiwo sanguinea</i>	6,548,583	6
<i>Dactyliosolen fragilissimus</i>	15,065,270	4
<i>Pheopolykrikos hartmannii</i>	5,960,922	3
<i>Cerataulina pelagica</i>	7,911,736	2
<i>Spherical picocyanobacterium</i>	4,380,984	2
<i>Gonyaulax polygramma</i>	5,313,322	1
<i>Cyclotella</i> spp.	2,967,591	1
<i>Pseudosolenia calcar-avis</i>	9,014,250	1
<i>Chaetoceros tenuissimus</i>	3,964,269	1
<i>Odontella regia</i>	3,154,550	1
Pennate diatom spp.	3,744,800	1
<i>Pseudo-nitzschia calliantha</i>	3,017,045	1
Site 5		
<i>Pyrodinium bahamense</i>	4,323,307	2

Table 8 (continued)

Bloom species	Maximum biovolume	Bloom freq.
<i>Dactyliosolen fragilissimus</i>	5,417,518	1
<i>Cerataulina pelagica</i>	5,891,718	1
Site 6		
cf. <i>Nannochloris</i>	3,487,560	2
<i>Rhizosolenia setigera</i>	4,342,333	2
<i>Prorocentrum micans</i>	9,743,712	1
<i>Cerataulina pelagica</i>	9,091,194	1

The maximum biovolume ($\mu\text{m}^3 \text{ml}^{-1}$) observed for each species is shown along with the number of times biovolume exceeded $3 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$

period (i.e., biovolume $>2.8 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$, as defined for this study, see ‘Methods’). The composition and frequency of blooms varied by sampling site (Table 8). The most widespread and common bloom formers were the potentially toxic dinoflagellate *Pyrodinium bahamense* var. *bahamense* and two centric diatoms, *Dactyliosolen fragilissimus* and *Cerataulina pelagica*. Many of the biovolume peaks observed in Fig. 4 were attributable to these three species. Picoplanktonic cyanobacteria were observed at relatively high cell densities in almost all samples, and were observed at bloom levels in terms of biovolume on a number of sampling dates, particularly at Site 2 in the Banana River (Table 8). Blooms of the diatom *Pseudo-nitzschia calliantha* and the dinoflagellate *Akashiwo sanguinea* were also noteworthy because of their potential harmful impacts on ecosystems (Hallegraeff 2003; Landsberg 2002). The spatial distribution of blooms was not uniform within the lagoon, with lower frequency of occurrence at Sites 5 and 6 in the central lagoon than in the northern lagoon (Sites 1–4) (Fig. 4), although the species associated with blooms were similar in both regions.

Modeling Outcomes

Results of the time series modeling of phytoplankton dynamics in the IRL yielded some basic regional differences in the primary parameters driving the model outcome, as exemplified by the outputs for Site 1 in the northern lagoon and Site 5 in the central lagoon (Table 9). Examples of the predicted versus observed phytoplankton biovolume levels at Sites 1 and 5 are shown in Fig. 6. The most consistent difference in the selected model parameters was the importance of salinity in the models for the central lagoon, in contrast to the northern lagoon. TN concentration was consistently important in models of phytoplankton dynamics in the northern lagoon, while TP was more important in the central lagoon. Another consistent difference between

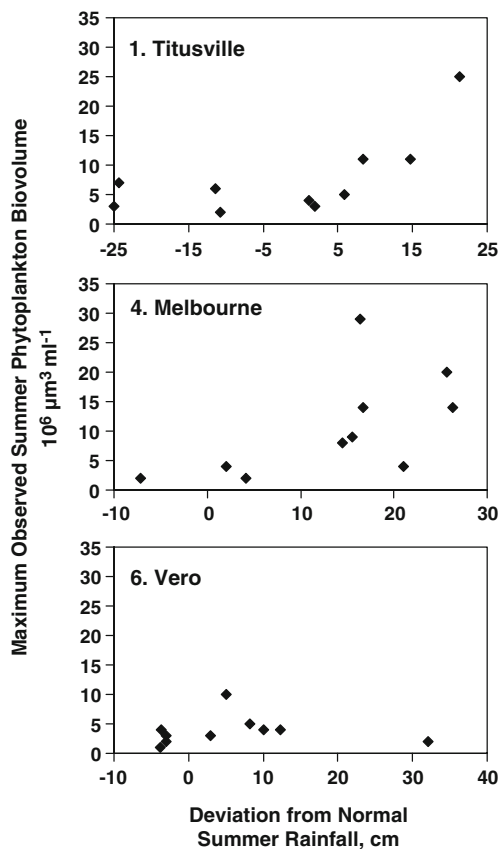


Fig. 5 Relationship between the deviation from normal summer rainfall totals in different regions and the maximum observed summer phytoplankton biovolume at three sampling sites: Sites 1 and 4 in the northern lagoon and Site 6 in the central lagoon

regions was the importance of ‘year’ in the models for the northern lagoon, while month was the key temporal scale parameter in the central lagoon. The latter outcome reflects the greater inter-annual variability of phytoplankton biovolume in the northern than central lagoon.

Discussion

The driving factors for the spatial and temporal differences in the composition and abundance of phytoplankton observed in the Indian River Lagoon (IRL) can be viewed from two perspectives, (1) regional differences in basic ecosystem characteristics and (2) temporal changes in climate, to which specific regions within the lagoon respond differently.

Regional Differences

In some respects, all the regions of the IRL included in this study share important structural elements, such as uniformly shallow depth and relatively narrow profile. By contrast,

there are other characteristics that are markedly different between regions and help to explain some of the spatial disparities in phytoplankton composition and dynamics. One important area of distinction involves hydrologic regimes. The northern portion of the lagoon (Sites 1–4) is severely restricted in terms of tidal water exchange (Sheng et al. 1990; Sheng and Davis 2003), due to the considerable distance from the nearest inlet to the Atlantic Ocean (i.e., the Sebastian Inlet) as well as physical barriers to water circulation, such as shoals, vehicular causeways, and bridges. In addition, the absence of major river inputs to the lagoon north of Melbourne further diminishes flushing rates. As a result of these features, water residence times in the northern lagoon are very long, with a mean value of 107 days for R_{50} in parts of the main stem of the IRL and 156 days in the side branch, i.e., the Banana River (Phlips et al. 2004b; Steward et al. 2005). By contrast, the central lagoon (Sites 5 and 6) is more directly influenced by water exchange with the Atlantic Ocean, via the Sebastian and Ft. Pierce Inlets. The central lagoon is also subject to inputs of fresh water from rivers and canals fed by watersheds of relatively substantial size and human influence (Adkins et al. 2004; Phlips et al. 2004b; Steward and Green 2007). Tidal influences and freshwater inputs in the central lagoon are reflected in higher mean salinities than the northern region and rapid shifts in salinity in response to rainfall events, resulting in shorter water residence times, with a mean R_{50} of 9 days (Phlips et al. 2004b; Steward et al. 2005).

One of the major factors contributing to the high frequency and intensity of algal blooms encountered in the northern IRL is long water residence time (Phlips et al. 2004b, 2006). Similar observations have been made for other restricted microtidal ecosystems around the world (Monbet 1992; Knoppers et al. 1991; Phlips et al. 1999; Badylak et al. 2007). Even in more open environments, conditions which elevate water residence times can yield enhanced phytoplankton standing crops (Seliger et al. 1970; Trainer et al. 2002; Bledsoe et al. 2004; Vila and Masó 2005). By contrast, major episodic pulses of fresh water into the central lagoon during high rainfall periods not only decrease water residence times but can also temporarily depress phytoplankton standing crop potential through the osmotic stress imposed during mixing, on both the incoming fresh water phytoplankton community and the resident marine taxa (Rijstenbil 1988; Weise et al. 2002; Shikata et al. 2008).

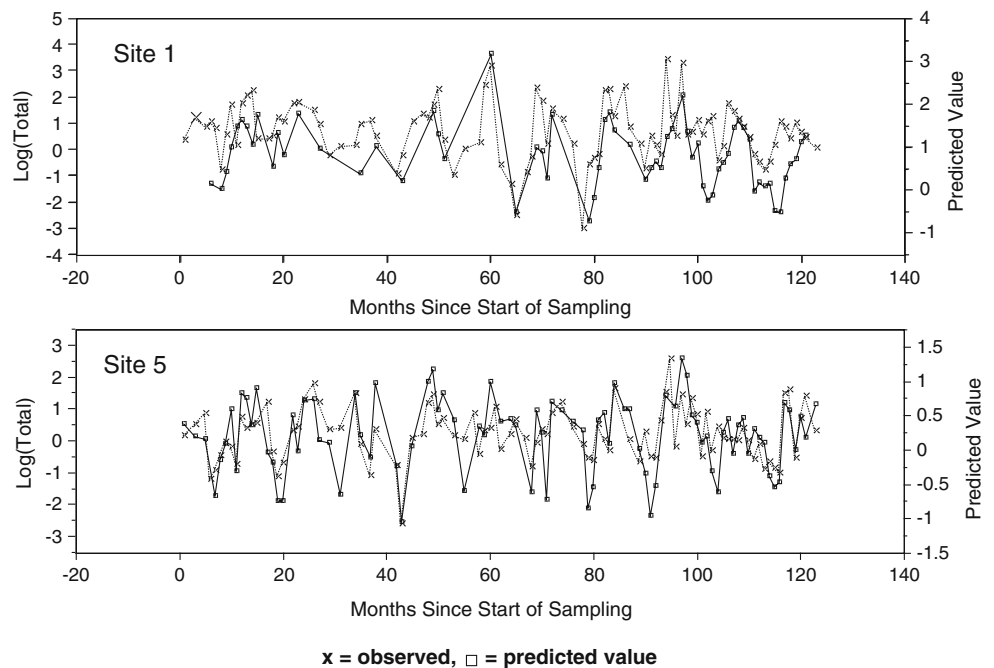
The manner in which regional differences in hydrology and nutrient composition in the IRL translate into disparities in phytoplankton composition can be viewed from the context of the inherent adaptive strategies of the dominant taxa observed in each region. It is useful to employ the ‘C-S-R’ framework developed by Reynolds and Smayda (Reynolds and Smayda 1998; Smayda and Reynolds 2001; Reynolds 2006) to define

Table 9 Parameters that play a significant role in predicting total phytoplankton, dinoflagellate, diatom, and cyanobacteria biovolume at Site 1 in the northern Indian River Lagoon and Site 5 in the central lagoon from the time series model

	Site 1	Site 5
Total phytoplankton	Temperature, lag 1 (+) TN (+) TP, lag 3 (-) Secchi, lag 3 (+) Year $R^2=0.47$	Salinity, lag 1 (-) TP (+) Secchi, lag 1 (-) Month $R^2=0.46$
Dinoflagellate	Temperature (+) TN, lag 2 (+) Secchi, lag 1 (+) Diatoms (-) Year $R^2=0.43$	Salinity, lag 1 (-) TP (+) Secchi (-) Month $R^2=0.48$
Diatom	TN (-) N/P ratio (-) Secchi, lag 2 (+) Dinoflagellates, lag 2 (+) Year $R^2=0.50$	Salinity, lag 3 (-) TN, lag 1 (+) TP, lag 1 (-) N/P ratio (-) Secchi (-) Dinoflagellates (+) Month and year $R^2=0.41$
Cyanobacteria	Temperature (-) TN (+) Secchi (-) Year $R^2=0.59$	Temperature (-) Salinity, lag 3 (-) TN (-) TP (+) Month $R^2=0.58$

The symbol in parentheses indicates the nature of the relationship

Fig. 6 Example of the time series model outputs for total phytoplankton biovolume at Site 1 near Titusville (top) and Site 5 near Sebastian (bottom). The values predicted by the model are shown as open squares and the observed values as 'x'



strategic groups of phytoplankton. On a broad spatial and temporal scale, the northern lagoon is a region of relatively stable hydrologic conditions, in terms of low rates of tidal water exchange, long water residence times, and relatively small volumes of fresh water inputs (Phlips et al. 2004b; Steward et al. 2005). These conditions should favor ‘S’ strategists, which are defined as large-celled species, with low potential for grazing loss and the ability to survive episodic periods of reduced inorganic nutrient availability (Phlips et al. 2006; Reynolds 2006). In keeping with this hypothesis, large ‘S’ type dinoflagellates such as *Pyrodinium bahamense* var. *bahamense* and *Akashiwo sanguinea* are the dominant bloom-forming phytoplankton species in the northern lagoon, particularly in the warm season, from late spring through early autumn, when the concentration of inorganic bioavailable nutrients can become growth limiting between rainfall events. *P. bahamense* var. *bahamense* may also benefit from a resistance to grazing pressure, in terms of negative selectivity by both zooplankton and benthic filter-feeding invertebrates (Badylak and Phlips 2008), as observed for some other species of toxic algae (Turner 2006). Given the shallow depth and subtropical climate of the IRL, it is likely that grazing is an important element of phytoplankton dynamics. However, there is currently insufficient information on food web structure and dynamics in the lagoon to evaluate whether top-down processes are as important to phytoplankton dynamics, as observed in some other ecosystems (Turner and Granéli 2006; Smetacek and Cloern 2008), such as San Francisco Bay (Cloern 1996).

Unlike the late spring and summer, the autumn through early spring in the IRL is characterized by high wind-induced turbulence in the water column and reduced light availability, which should favor ‘R’ strategists (Reynolds 2006). In accordance with this concept, three species of diatoms, often classified as ‘R’ strategists, are common bloom-forming taxa from the autumn and early spring in the northern lagoon, i.e., *Dactyliosolen fragilissimus*, *Cerataulina pelagica*, and *Pseudosolenia calcar-avis*. These diatoms may also benefit from the ability to store nutrients and prosper in environments where nutrients are available in pulses (Pinckney et al. 1999; Tozzi et al. 2004; Katz et al. 2005), as encountered in the northern lagoon.

In contrast to the relatively ‘stable’ hydrodynamic conditions in the northern IRL, the central lagoon is characterized by considerably higher rates of tidal water exchange and shortened water residence times, attributable to the proximity of the Sebastian and Ft. Pierce Inlets (Phlips et al. 2004b; Steward et al. 2005). The central region is also subject to larger inputs of phosphorus-rich fresh water (Adkins et al. 2004; Steward and Green 2007). The combination of less water column stability and higher phosphorus availability should favor ‘C’ strategists within the phytoplankton community, which are opportunistic

species of small size and high growth rates (Reynolds 2006). This hypothesis is supported by the high relative biomass of small microflagellates (e.g., cryptophytes), small chlorophytes (e.g., cf. *Nannochloris*), picoplanktonic cyanobacteria, and small-celled centric diatoms (e.g., *Cyclotella* spp.) in the central lagoon. Fast growing species can not only outcompete ‘S’ and ‘R’ species under conditions of short water residence times but can also recover quickly from rainfall flushing events, which cause short-term and rapid fluctuations in salinity (Shikata et al. 2008). This is illustrated by the *Nannochloris* bloom at Site 6 after the 1999 summer storm event. Many estuarine microflagellates are tolerant of a wide range of salinities (Qasim et al. 1972; Brand 1984; Watanabe et al. 1991; Yamaguchi et al. 1997). Together, these groups average over 50% of total relative biovolume in the central lagoon.

Climatic Influences and Temporal Trends

One of the distinguishing climatic features of the IRL is its location in the transition zone between the tropical environment of the Florida Keys and the warm temperate regime of the northeast Florida coast. In terms of species composition, the subtropical climate in the IRL is reflected in the appearance of tropical species in the warm season. A prominent example of this trend is the dinoflagellate *Pyrodinium bahamense* var. *bahamense*, which is only present in significant numbers in the warm season, and largely disappears from the water column for most of the cold season. The IRL is the northern-most location along the Atlantic coast of North America where major blooms of *P. bahamense* have been observed (Phlips et al. 2006). There is also recent evidence that *P. bahamense* blooms in the IRL are associated with observations of high levels of saxitoxins in certain local fish species (Landsberg et al. 2006). It is possible to speculate that future increases in temperatures associated with global warming may lead to the northward expansion of *Pyrodinium* blooms. Conversely, some species of phytoplankton normally associated with blooms in temperate environments also appear in the Indian River Lagoon at bloom levels, such as the diatoms *Pseudo-nitzschia calliantha*, particularly from the late fall through winter (Phlips et al. 2004a).

Another climatic factor that appears to play an important role in defining the composition and dynamics of phytoplankton in the IRL is rainfall. It is well known that rainfall patterns impact a variety of factors that directly or indirectly effect phytoplankton productivity and standing crop in estuarine ecosystems, such as nutrient load, salinity variation and water flushing rates (Weise et al. 2002). All of these factors also play an important role in guiding species composition and succession (Margalef 1978; Smayda 1980; Smayda and Reynolds 2001; Anderson and Rengefors 2006; Reynolds 2006). The effects of shifts in

rainfall regime from drought to flood conditions on the phytoplankton community in the IRL are different by region, due in large part to inherent spatial disparities in hydrologic and watershed characteristics.

In the northern lagoon, high rainfall levels increase nutrient load from the watershed, but do not result in short water residence times, due to the small size of the watersheds and large distance from inlets to the ocean. The latter conditions favor the development of algal blooms. Conversely, during drought periods, bloom activity is depressed, despite long water residence times, most probably due to increased potential for nutrient limitation (Phlips et al. 2002, 2004b). Phytoplankton dynamics in the central lagoon are fundamentally different than in the northern lagoon, in larger part due to short water residence times and variable salinities. As a result, phytoplankton blooms are infrequent in the central lagoon, despite relatively high nutrient loads.

Modeling Phytoplankton Dynamics

Differences in the dynamics of phytoplankton populations in the northern and central lagoon highlight the importance of the links between hydrology and watershed characteristics in defining the response of phytoplankton communities of coastal ecosystems to changes in nutrient load and climate. The results of time series modeling of phytoplankton dynamics further highlight the disparities between the two regions of the lagoon in terms of the suite of parameters that best predict the observed temporal trends in phytoplankton biovolume. The most consistent difference between regions was the importance of salinity for predicting phytoplankton biovolume in the central lagoon, as exemplified by the model output variables for Site 5. By contrast, salinity did not rank as an important predictive parameter in the northern lagoon. This result supports the aforementioned hypothesis that phytoplankton dynamics in the central lagoon is more strongly influenced by tidal mixing with Atlantic water and freshwater inputs from the watershed than in the northern lagoon.

The importance of different parameters in the prediction of temporal patterns of phytoplankton biomass varied by region and algal group. For example, temperature was one of the important parameters for predicting dinoflagellate and total phytoplankton biovolume at Site 1 in the northern lagoon, reflecting the dominance of warm-water dinoflagellates, such as *Pyrodinium bahamense* var. *bahamense*, in summer blooms. By contrast, temperature was not an important component of the model for dinoflagellate and total phytoplankton biovolume at Site 5 in the central lagoon, reflecting the less predictable seasonal distribution of dinoflagellates. At each site, there were also differences in the predictive parameters for specific phytoplankton

groups. For example, while temperature was positively related to dinoflagellate biovolume at Site 1, it was negatively related to cyanobacteria biovolume, reflecting the relatively higher biovolume of the latter group in winter months.

Overall, the outcome of this initial modeling effort in the Indian River Lagoon suggests that time series approaches can help define regulatory factors associated with phytoplankton dynamics. At the same time, the process of modeling manifested important goals for improving future efforts. A number of key elements were lacking in the database used, such as estimates of grazing pressure. The modeling was also sensitive to gaps in the time series, pointing out the importance of maintaining temporal consistency of monitoring, preferably on time scales relevant to the basic dynamics of phytoplankton growth. The monthly to twice-monthly data available for this study clearly involves the potential for missing some bloom events, but the long time series of data provides some relief from the potential for making large errors in interpreting major spatial and temporal trends.

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References

- Adkins, M., M. Mao, M. Taylor, W. Green, C. Basci, M. Bergman, and D. Smith. 2004. *Watershed model development for the Indian River Lagoon basin: providing simulated runoff and pollution load to the Indian River Lagoon pollution load reduction model*. St. Johns River Water Management District Technical Memorandum 50. Palatka: St. Johns River Water Management District.
- Akaike, H. 1981. Likelihood of a model and information criteria. *Journal of Econometrics* 16: 3–14. doi:10.1016/0304-4076(81)90071-3.
- Anderson, D.M., and K. Rengefors. 2006. Community assembly and seasonal succession of marine dinoflagellates in a temperate estuary: the importance of life cycle events. *Limnology and Oceanography* 51: 860–873.
- APHA. 1989. *Standard methods for the analysis of water and wastewater*, 17th ed. Washington, D.C.: American Public Health Association.
- Badylak, S., and E.J. Phlips. 2004. Phytoplankton communities of a restricted subtropical lagoon, the Indian River Lagoon, Florida, USA. *Journal of Plankton Research* 26: 1–22. doi:10.1093/plankt/fbh114.
- Badylak, S., K. Kelly and E.J. Phlips. 2004. A description of *Pyrodinium bahamense* from the Indian River Lagoon, Florida, USA. *Phycologia* 43: 653–657.
- Badylak, S., and E.J. Phlips. 2008. Spatial and temporal patterns of zooplankton distribution in Tampa Bay, Florida, USA. *Journal of Plankton Research* 55: 70–81.

- Badylak, S., E.J. Phlips, P. Baker, J. Fajans, and R. Boler. 2007. Distributions of phytoplankton in Tampa Bay, USA. *Bulletin of Marine Science* 80: 295–317.
- Bledsoe, E., E.J. Phlips, C.E. Jett, and K.A. Donnelly. 2004. The relationships among phytoplankton biomass, nutrient loading and hydrodynamics in an inner-shelf estuary, the Suwannee River estuary, Florida, USA. *Ophelia* 58: 29–47.
- Brand, L.E. 1984. The salinity tolerance of forty-six marine phytoplankton isolates. *Estuarine, Coastal and Shelf Science* 18: 543–556. doi:10.1016/0272-7714(84)90089-1.
- Burnham, K.P., and D. Anderson. 2003. *Model selection and multi-model inference*, 2nd ed. New York: Springer.
- 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. doi:10.1029/96RG00986.
- Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210: 223–253. doi:10.3354/meps210223.
- Daughbjerg, N., G. Hansen, J. Larsen, and Ø. Moestrup. 2000. Phylogeny of some of the major genera of dinoflagellates based on ultrastructure and partial LSU rDNA sequence data, including the erection of three new genera of unarmoured dinoflagellates. *Phycologia* 39: 302–317.
- Davis, R.A. 1997. Geology of the Florida coast. In *The geology of Florida*, ed. R.F. Randazzo, and D.S. Jones, 155–168. Gainesville: The University Press of Florida.
- Dix, N., E.J. Phlips, and R. Gleeson. 2008. Water quality changes in a tidal creek within the Guana Tolomato Matanzas National Estuarine Research Reserve, Florida, associated with the four tropical storms of 2004. *Journal of Coastal Research, Special Issue* 55: 70–81.
- Fahnenstiel, G.L., and H.J. Carrick. 1992. Phototrophic picoplankton in Lakes Huron and Michigan: abundance, distribution, composition and contribution to biomass and production. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 379–388. doi:10.1139/f92-043.
- Fryxell, G.A., M.C. Villac, and L.P. Shapiro. 1997. The occurrence of the toxic diatom genus *Pseudo-nitzschia* (Bacillariophyceae) on the west coast of the USA, 1920–1996: a review. *Phycologia* 36: 419–437.
- Glibert, P.M., and J.M. Burkholder. 2006. The complex relationships between increases in fertilization of the earth, coastal eutrophication and proliferation of harmful algae blooms. In *Ecology of Harmful Algae*, ed. E. Granéli, and J.T. Turner, 341–354. Berlin: Springer-Verlag.
- Hallegraeff, G.M. 2003. Harmful algal blooms: a global overview. In *Manual on harmful marine microalgae*, ed. G.M. Hallegraeff, D. M. Anderson, and A.D. Cembella, 25–49. Paris: UNESCO.
- Hargraves, P.E. 2002. Diatoms of the Indian River Lagoon, Florida: an annotated account. *Florida Scientist* 65: 225–244.
- Hasle, G.R., and E. Syvertsen. 1996. Marine diatoms. In *Identifying marine diatoms and dinoflagellates*, ed. C.R. Tomas, 5–386. California: Harcourt & Brace.
- Katz, M.E., Z.V. Finkel, D. Grzebyk, A.H. Knoll, and P.G. Falkowski. 2005. Evolutionary trajectories and biogeochemical impacts of marine eukaryotic phytoplankton. *Annual Reviews of Ecology and Systematics* 35: 523–556.
- Knoppers, B., B. Kjerfve, and J.P. Carmouze. 1991. Trophic state and water turn-over time in six choked coastal lagoons in Brazil. *Biogeochemistry* 14: 149–168.
- Landsberg, J.H. 2002. The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science* 10: 113–390.
- Landsberg, J.H., S. Hall, J.N. Johannessen, K.D. White, S.M. Conrad, L.J. Flewelling, R.H. Dickey, F.M. Dolah, M.A. Quilliam, T.A. Leighfield, Z. Yinglin, C.G. Baudry, W.R. Richardson, K. Hayes, L. Baird, R.A. Benner, P.L. Rogers, J. Abbot, D. Tremain, D. Heil, R. Hammond, D. Bodager, G. Mcrae, C.M. Stephenson, T. Cody, P.S. Scott, W.S.M. Arnold, H. Schurz-Rogers, A.J. Haywood, and K.A. Steidinger. 2006. Saxitoxin puffer fish poisoning in the United States, with the first report of *Pyrodinium bahamense* as the putative toxin source. *Environmental Health Perspectives* 114: 1502–1507.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1: 493–509.
- Monbet, Y. 1992. Control of phytoplankton biomass in estuaries: a comparative analysis of microtidal and macrotidal estuaries. *Estuaries* 15: 563–571.
- Nixon, S. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199–219.
- Oliviera, A.M., and B. Kjerfve. 1993. Environmental responses of a tropical coastal lagoon system to hydrological variability: Mundaú-Manguaba, Brazil. *Estuarine, Coastal and Shelf Science* 37: 575–591.
- Paerl, H.W. 1988. Nuisance phytoplankton blooms in coastal, estuarine and inland waters. *Limnology and Oceanography* 33: 823–847.
- Paerl, H.W. 1997. Coastal eutrophication and harmful algae blooms: importance of atmospheric deposition and groundwater as ‘new’ nitrogen and other nutrient sources. *Limnology and Oceanography* 42: 1154–1165.
- Phlips, E.J., S. Badylak, and T.C. Lynch. 1999. Cyanobacterial blooms in Florida Bay. *Limnology and Oceanography* 44: 1166–1175.
- Phlips, E.J., S. Badylak, and T. Grosskopf. 2002. Factors affecting the abundance of phytoplankton in a restricted subtropical lagoon, the Indian River Lagoon, Florida, USA. *Estuarine, Coastal and Shelf Science* 55: 385–402.
- Phlips, E.J., S. Badylak, S. Youn, and K. Kelley. 2004a. The occurrence of potentially toxic dinoflagellates and diatoms in a subtropical lagoon, the Indian River Lagoon, Florida, USA. *Harmful Algae* 3: 39–49.
- Phlips, E.J., N. Love, S. Badylak, P. Hansen, J. Lockwood, C. John, and R. Gleeson. 2004b. A comparison of water quality and hydrodynamic characteristics of the Guana Tolomato Matanzas National Estuarine Research Reserve and the Indian River Lagoon of Florida. *Journal of Coastal Research, Special Issue* 45: 93–109.
- Phlips, E.J., S. Badylak, E.L. Bledsoe, and M. Cichra. 2006. Factors influencing the distribution and abundance of *Pyrodinium bahamense* in coastal ecosystems of Florida. *Marine Ecology Progress Series* 322: 99–115.
- Phlips, E.J., J. Hendrickson, E.L. Bledsoe, and M. Cichra. 2007. Meteorological influences on algal bloom potential in a nutrient-rich blackwater river. *Journal of Freshwater Biology* 52: 2141–2155.
- Pinckney, J.L., H.W. Paerl, and M.B. Harrington. 1999. Responses of the phytoplankton community growth rate to nutrient pulses in variable estuarine environments. *Journal of Phycology* 35: 1455–1463.
- Qasim, S.Z., P.M. Bhattathiri, and V.P. Devassy. 1972. The influence of salinity on the rate of photosynthesis and abundance of some tropical phytoplankton. *Marine Biology* 12: 200–206.
- Reynolds, C.S. 2006. *Ecology of phytoplankton*. Cambridge: Cambridge University Press.
- Reynolds, C.S., and T.J. Smayda. 1998. Principles of species selection and community assembly in the phytoplankton: further explorations of the Mandala. In *Harmful algae*, ed. B. Reguera, J. Blanco, M. Fernández, and T. Wyatt, 8–10. Santiago de Compostela: Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO.
- Ricard, M.I. 1987. *Atlas Du Phytoplancton Marin, Diatomophycées Volume 2*. Anatole, France: Editions Du Centre National De La Recherche Scientifique.
- Rijstenbil, J.W. 1988. Selection of phytoplankton species in culture by gradual salinity changes. *Netherlands Journal of Sea Research* 22: 291–300.

- Sartory, D.P., and J.U. Grobbelaar. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia* 114: 177–187.
- Seliger, H.H., J.H. Carpenter, M. Loftus, and W.D. McElroy. 1970. Mechanisms for the accumulation of high concentrations of dinoflagellates in a bioluminescent bay. *Limnology and Oceanography* 15: 234–245.
- Sheng, Y.P., and J.D. Davis. 2003. *Indian River Lagoon pollution load reduction (IRLPLR) model development. Final report to the St. Johns River Water Management District, Volume 1: A 3-D IRL hydrodynamic/salinity model (UF-CH3D)*. Palatka: St. Johns River Water Management District.
- Sheng, Y.P., S. Peene, and Y.M. Lui. 1990. Numerical modeling of tidal hydrodynamics and salinity transport in the Indian River Lagoon. *Florida Scientist* 50: 49–61.
- Shikata, T., S. Nagasoe, S. Oh, T. Matsubara, Y. Yamasaki, Y. Shimasaki, Y. Oshima, and T. Honjo. 2008. Effects of down- and up-shocks from rapid changes of salinity on survival and growth of estuarine phytoplankters. *Journal of the Faculty of Agriculture of Kyushu University* 53: 81–87.
- Smayda, T.J. 1978. From phytoplankton to biomass. In *Phytoplankton manual*, ed. A. Sournia, 273–279. Paris: United Nations Educational, Scientific and Cultural Organization.
- Smayda, T.J. 1980. Phytoplankton species succession. In *The physiological ecology of phytoplankton*, ed. I. Morris, 493–570. Berkeley: University of California Press.
- Smayda, T.J., and C.S. Reynolds. 2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *Journal of Plankton Research* 23: 447–461.
- Smetacek, V., and J. Cloern. 2008. On phytoplankton trends. *Science* 319: 1346–1348.
- Smith, N.P. 1993. Tidal and non-tidal flushing of Florida's Indian River Lagoon. *Estuaries* 16: 739–746.
- Sournia, A. 1986. *Atlas Du Phytoplancton Marin. Volume 1. Introduction, Cyanophycees, Dictyochophycees, Dinophycees, et Raphidophycees*. Paris: Centre National de la Recherche Scientifique.
- Steidinger, K.A., and K. Tangen. 1996. Dinoflagellates. In *Identifying marine diatoms and dinoflagellates*, ed. C.R. Tomas. New York: Academic.
- Steidinger, K.A., and J. Williams. 1970. *Dinoflagellates "Memoirs of the Hourglass Cruises" Vol. 2*. St. Petersburg: Florida Department of Natural Resources, Marine Research Laboratory.
- Steward, J.S., and W.C. Green. 2007. Setting load limits for nutrients and suspended solids based upon seagrass depth-limit targets. *Estuaries and Coasts* 30: 657–670.
- Steward, J.S., R.W. Virnstein, L.J. Morris, and E.F. Lowe. 2005. Setting seagrass depth, coverage, and light targets for the Indian River Lagoon System, Florida. *Estuaries* 28: 923–935.
- Steward, J.S., R.W. Virnstein, M.A. Lasi, L.J. Morris, J.D. Miller, L.M. Hall, and W.A. Tweedale. 2006. The impacts of the 2004 hurricanes on hydrology, water quality, and seagrass in the central Indian River Lagoon, Florida. *Estuaries and Coasts* 29: 954–965.
- Tester, L.A., and K.A. Steidinger. 1979. Phytoplankton. In *Nearshore marine ecology at Hutchinson Island, Florida: 1971–1974. Florida Marine Research Publication 34*, ed. L.M. Walker, and K.A. Steidinger, 16–61. St. Petersburg, Florida: Florida Department of Natural Resources.
- Tozzi, S., O. Schofield, and P. Falkowski. 2004. Historical climate change and ocean turbulence as selective agents for key phytoplankton functional groups. *Marine Ecology Progress Series* 274: 123–132.
- Trainer, V.L., B.M. Hickey, and R.A. Horner. 2002. Biological and physical dynamics of domoic acid production off the Washington coast. *Limnology and Oceanography* 47: 1438–1446.
- Turner, J.T. 2006. Harmful algae interactions with marine planktonic grazers. In *Ecology of harmful algae*, ed. E. Granéli, and J.T. Turner, 341–354. Berlin: Springer-Verlag.
- Turner, J.T., and E. Granéli. 2006. "Top-down" predation control on marine harmful algae. In *Ecology of harmful algae*, ed. E. Granéli, and J.T. Turner, 355–366. Berlin: Springer-Verlag.
- Utermöhl, H. 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik. *Mitteilungen-Internationale Vereinigung für Theoretische und Angewandte Limnologie* 9: 1–38.
- Vila, M., and M. Masó. 2005. Phytoplankton functional groups and harmful algae species in anthropogenically impacted waters of the NW Mediterranean Sea. *Scientia Marina* 69: 31–45.
- Virnstein, R.W. 1990. The large temporal and spatial variability of the Indian River Lagoon. *Florida Scientist* 53: 249–256.
- Watanabe, M., K. Kohata, and T. Kimura. 1991. Diel vertical migration and nocturnal uptake of nutrients by *Chattonella antiqua* under stable stratification. *Limnology and Oceanography* 36: 593–602.
- Weise, A.M., M. Levasseur, J. Saucier, S. Senneville, E. Bonneau, S. Roy, G. Sauve, S. Michaud, and J. Fauchot. 2002. The link between precipitation, river runoff, and blooms of the toxic dinoflagellate *Alexandrium tamarense* in the St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 464–473.
- Yamaguchi, M., S. Itakura, K. Nagasaki, Y. Matsuyama, T. Uchida, and I. Imai. 1997. Effects of temperature and salinity on the growth of the red tide flagellates *Heterocapsa circularisquama* and *Chattonella verruculosa*. *Journal of Plankton Research* 19: 1167–1174.