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Spatial and temporal patterns of phytoplankton composition in a subtropical coastal lagoon, the Indian River Lagoon, Florida, USA

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A 2 year study of the phytoplankton community was carried out in the Indian River Lagoon, USA. In terms of biovolume, the phytoplankton community was generally dominated by dinoflagellates, diatoms or cyanobacteria. Mean phytoplankton standing crops were highest in the most flow-restricted regions of the lagoon, which had the lowest mean salinity values and comparatively high total nitrogen:total phosphorus ratios. In this region, blooms of dinoflagellates were common in the first year of the study, which was characterized by an El Niño event that yielded exceptionally high rainfall levels and freshwater outflow. Picoplanktonic cyanobacteria blooms became more prominent in the second year of the study, which was characterized by below average rainfall conditions. In unrestricted flow regions of the lagoon, located near inlets to the Atlantic Ocean, diatoms were most often the dominant taxa. Regions of intermediate water turnover rates and high external loading of phosphorus had a prevalence of diatom blooms. However, the average phytoplankton standing crops in the latter regions did not reach the levels experienced in the flow-restricted parts of the lagoon. In terms of individual phytoplankton taxa, the most common bloom-forming diatoms in the Indian River Lagoon system included: Skeletonema costatum, Dactyliosolen fragilissimus, Skeletonema menzelii, Cerataulina pelagica, Odontella regia, Chaetoceros lorenzianus, Rhizosolenia setigera and Thalassionema nitzschioides. The major bloom-forming dinoflagellate species included: Pheopolykrikos hartmannii, Akashiwo sanguinea, Prorocentrum micans, the potentially toxic species Pyrodinium bahamense var. bahamense and Prorocentrum minimum. Several picoplanktonic cyanobacteria were also prominent members of the phytoplankton community, including Synechococcus elongates. The spatial and temporal patterns observed in some of these dominant species were attributable to patterns in key environmental variables, including salinity, temperature and nutrient concentrations.

INTRODUCTION

Historically, information on phytoplankton communities in estuaries and lagoons has been most abundant for temperate ecosystems, such as Chesapeake Bay (Harding, 1994), San Francisco Bay (Cloern, 1996) and the near-shore environments of northern Europe (Jonge *et al.*, 1994). However, there is a growing interest in warm-water ecosystems, especially those subject to so-called cultural eutrophication (Knoppers *et al.*, 1991; Oliviera and Kjerfve, 1993). The issue of phytoplankton composition has gained increasing importance as a consequence of this putative increase in eutrophication (Smayda, 1992; Hallegraeff, 1993).

The Indian River Lagoon (IRL) is a physically, chemically and biologically diverse inshore marine habitat located in a region of the south-eastern USA subject to extensive human development (Sheng *et al.*, 1990; Virnstein, 1990). One of the central concerns about the integrity of the IRL has been the occurrence of algal blooms, particularly toxic species (Steidinger *et al.*, 1998; Landsberg *et al.*, 2002; Phlips *et al.*, 2004*a*). The IRL has experienced fish kills associated with blooms of the toxic

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dinoflagellate *Alexandrium monilatum* since the 1950s (Howell, 1953; Norris, 1983). In 1998, fish kills were linked to blooms of the toxic dinoflagellate *Gyrodinium pulchellum* (Steidinger *et al.*, 1998). Most recently, blooms of the dinoflagellate *Pyrodinium bahamense* in the IRL were shown to be associated with the production of saxitoxin (Landsberg *et al.*, 2002). The appearance of toxic forms of *P. bahamense* in the lagoon and the magnitude of recent blooms, with densities as high as 680 000 cells L^{-1} (Phlips *et al.*, 2004*a*), has caused particular concern over the factors that may encourage algal blooms. Despite the concerns about phytoplankton blooms in the IRL over the past 50 years, only a limited amount is known about phytoplankton abundance and composition (Tester and Steidinger, 1979; Hargraves, 2002*a*,*b*). This is unfortunate because the lagoon presents an opportunity to compare phytoplankton populations in an ecosystem composed of ecologically distinct regions.

Biogeographically, the IRL is located in the transition between the tropical habitats of the Florida Keys and the temperate environments of the Carolina Banks. This biogeographic transition is evidenced by the structure of plant and animal communities. The northern region of the lagoon is reflective of more temperate regions and the southern region is more indicative of subtropical regions. For example, salt marshes are concentrated in the north region, whereas mangrove communities are of greater importance in the southern lagoon (Virnstein, 1990; Rey *et al.*, 1991; Gilmore, 1995). Physically, the barrier islands and inlets that define the eastern boundary of the lagoon create a series of subsystems with distinct hydrodynamic characteristics. Water turnover rates in different regions of the lagoon vary from days to over a year depending on the distance from inlets to the Atlantic Ocean (Sheng *et al.*, 1990; Smith, 1993). Chemically, the individual characteristics of different regions of the lagoon are also strongly influenced by the nature of freshwater inflows to the lagoon from the mainland of Florida. Over the past century, the amount and composition of these inflows have changed as a result of rapid human development, including agricultural activities, urbanization and industrialization (Livingston, 1990). For instance, the northern region of the lagoon, which contains the cities of Titusville, Cocoa and Melbourne, has experienced a yearly population increase of over 20 000 persons per year (Brevard County, 1994; De Freese, 1995).

In this study we examined spatial and temporal patterns of phytoplankton composition and abundance (i.e. standing crop) across the various ecologically distinct regions of the IRL, including the Mosquito Lagoon and Banana River, which connect to the northern reach of the IRL. We hypothesized that these distinct regions would exhibit different phytoplankton communities and abundances, and that these differences could be interpreted in terms of key distinguishing features of each region, including water residence time, salinity variation and nutrient regime.

METHOD

Study site description

The IRL is a geomorphic component of the east coast barrier reef system of Florida, USA (Davis, 1997). The entire lagoon extends 252 km from the warm temperate environment near Titusville to the subtropical environment of Jupiter inlet. The width of the lagoon varies from 0.5 to 5 km and depth averages 2 m. A number of ecologically distinct regions exist within the lagoon, which differ considerably in water exchange properties (Sheng *et al.*, 1990; Smith, 1993). These regions were the basis for the selection of the eight sampling sites for this study. Sampling site 1 was located in the Mosquito Lagoon, which is connected to the northern part of the lagoon via the Haulover canal (Figure 1). The northern-most site in the IRL, site 2, was located by the city of Titusville. Three sites were located in the north-central region of the lagoon, sites 3, 4 and 5. Site 3 is located in an extension of the IRL referred to as the Banana River. Sites 4 and 5 are located near the cities of Eau Gallie and Melbourne, respectively. Sites 2–5 have low water turnover rates and the lowest salinities in the lagoon owing to their distance from the nearest inlet to the Atlantic Ocean, the Sebastian Inlet (Phlips *et al.*, 2002). Site 6 is the central region of the IRL in close proximity to the Sebastian Inlet. Sites 7 and 8 are located in the south-central region of the Lagoon. The southern-most sampling site in the study was located near the city of Vero Beach. Water retention times within the regions of the lagoon represented by the eight sampling sites range from days to up to 1 year (Sheng *et al.*, 1990; Smith, 1993). The approximate rank order of retention times, from greatest to least is as follows: Titusville (site 2) > Banana River (site 3) > Eau Gallie (site 4) > Melbourne (site 5) > Vero (site 8) > St John Island (site 7) > Mosquito Lagoon (site 1) > Sebastian (site 6) (Phlips *et al.*, 2004*b*).

Field procedures

Water was collected at each site on a monthly basis for a 2 year period from September 1997 to August 1999. Twenty collections were made over the sampling period. Salinity and temperature were measured with a YSI (Yellow Springs Instrument) Model 85. Water samples were collected with a vertical integrating sampling tube that captures water from the surface to within 0.1 m of

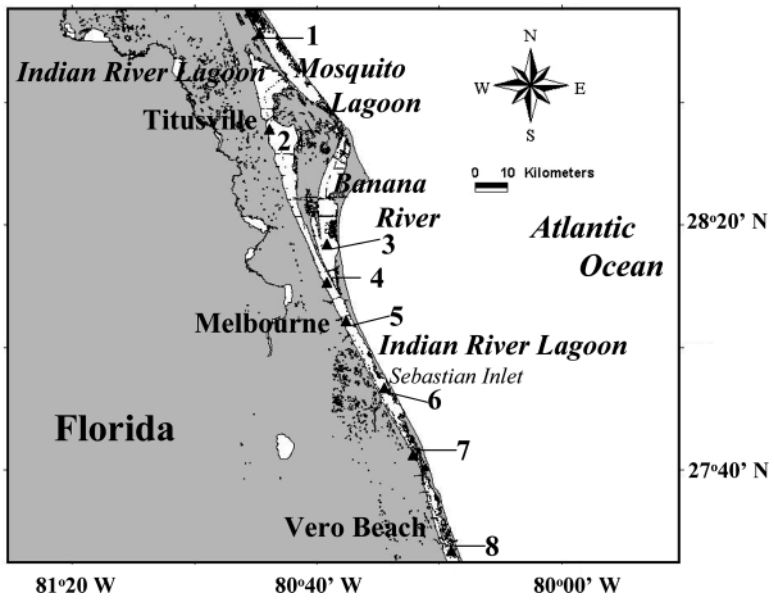

Fig. 1. Locations of eight sampling sites in the Indian River Lagoon, USA.

the bottom. Phytoplankton samples were preserved with Lugol solution and a backup aliquot was preserved with glutaraldehyde in 0.1 M sodium cacodylate buffer.

Phytoplankton analysis

Fluorescence microscopy was used to enumerate picoplanktonic cyanobacteria, e.g. *Synechococcus* (Fahnenstiel and Carrick, 1991). Subsamples of station water were filtered onto 0.2 μm pore Nuclepore 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). Owing to the inherent difficulty in identifying certain species of picoplankton using standard microscopy, some taxa were given letter designations. These include Cyanobacterium A, a phycocyanin-rich spherical unicell of ~3 μm in diameter, and Cyanobacterium B, a phycoerythrin-rich spherical unicell of ~3 μm in diameter.

Numerical abundance of cyanobacteria cells was determined by counting a minimum of five ocular micrometer grids at ×1000. The numbers of grids counted were adjusted according to cell density. Counts were completed upon reaching a minimum of 100 cells.

General phytoplankton composition was determined using the Utermohl method (Utermohl, 1958). Lugol solution preserved samples were settled in 19 mm inner diameter cylindrical chambers. Phytoplankton cells were identified and counted at ×400 and ×100 with a Nikon phase contrast inverted microscope. At ×400, a minimum of 100 cells of a single taxa and 30 grids were counted. If 100 cells were not counted within 30 grids, up to a maximum of 100 grids were counted until 100 cells of a single taxa was reached. At ×100 a total bottom count was completed for taxa >30 μm. For comparative purposes within this study, bloom levels were defined as a phytoplankton biovolume that exceeds 2 mm^3 L^{-1} of a single taxon. Light microscopy was aided by other techniques to confirm the identification of certain key dinoflagellates and diatoms. Identifications of the potentially toxic species *P. bahamense* var. *bahamense* and *Pseudonitzschia calliantha* was confirmed using scanning electron microscopy. *Gonyaulax polygramma* and *Scrippsiella trochoidea* were observed using the squash technique (Steidinger, 1979). Sodium thiosulfate was used to de-stain Lugol-preserved samples where it was needed for positive identification. *Protoperidinium* species were identified by cell size, shape and body contour. Small *Gymnodinium* cells <15 μm were put in size categories. *Pleurosigma* and *Gyrosigma* were not separated out. Microflagellates were defined as <15 μm marine flagellates excluding dinoflagellates. In the case of the small picoplanktonic form of green algae observed on numerous occasions in the lagoon, a tentative identification of *Nannochloris c.f.* was used in the absence of more detailed intracellular structure analyses. The texts and journal articles used most frequently to aid in taxonomic identification were: Cupp (1943); Steidinger and Williams (1970); Tester and Steidinger (1979); Dodge (1982); Sournia (1986); Ricard (1987); Hasle and Syvertsen, (1996); Steidinger and Tangen (1996); Fryxell *et al.* (1997); and Lundholm *et al.*

(2003). Recent revisions to the nomenclature for dinoflagellate taxa by Daugbjerg (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 cell volume was derived (Smayda, 1978). The total biovolume per sample was the sum of the estimated cell volumes for each species.

Statistical analyses

Cluster analysis using single linkage and the Euclidean distance metric (Wilkinson, 1993) was used to validate spatial and temporal similarities observed between sites at the level of algal division. The percentage contribution of each algal division to the total biovolume at each site, for each sampling date, was used as the input data.

RESULTS

Basic physical, chemical and biological conditions

Sites 3–5 exhibited lower mean salinity than the rest of the lagoon. Sites nearest the inlets to the Atlantic Ocean (sites 1 and 6) exhibited the highest mean salinities (Table I). Temperatures ranged from summer highs of 32°C to winter lows of 12°C. The period of high water temperature (>25°C) extended from May through to November.

Mean total phosphorus (TP) concentrations were highest in the south-central region at sites 7 and 8 (Table I).

Table I: Mean salinity, total nitrogen (TN), total phosphorus (TP) and TN:TP at the eight sampling sites in the IRL over the 2 year sampling period (after Phlips et al., 2002)

Site	Salinity	TN (μM)	TP (μM)	TN:TP
1	32.4 (4.2)	35.8 (13.9)	1.58 (0.68)	22.7
2	23.9 (4.2)	63.7 (20.3)	1.26 (0.36)	50.6
3	17.6 (4.2)	63.7 (22.6)	1.84 (0.61)	34.6
4	18.7 (5.1)	50.6 (13.3)	1.74 (0.71)	29.1
5	18.7 (6.9)	47.7 (13.3)	1.97 (0.55)	24.2
6	27.8 (6.0)	26.3 (9.4)	1.65 (0.48)	15.9
7	25.8 (5.5)	33.4 (14.7)	3.45 (2.10)	9.7
8	25.9 (5.3)	35.9 (11.8)	2.98 (1.23)	12.0

Standard deviations are shown in parentheses.

Mean total nitrogen (TN) concentrations were highest in the northern end of the IRL (Table I). As a result of the spatial patterns of TN and TP concentrations the TN:TP ratios were higher in the northern lagoon than the central and south-central lagoon (Table I).

Phytoplankton standing crops were higher in the northern region of the lagoon, as indicated by the phytoplankton biovolume (Figure 2). Certain taxa reached bloom levels over a wide range of salinities, such as the diatom *Skeletonema costatum*, which reached high abundances at salinities from 15 to 34 (Figure 3). By contrast, the cyanobacterium *Synechococcus elongatus* was present over a wide range of salinities, but was only observed at bloom levels at salinities between 15 and 20 (Figure 3). In terms of temperature, some species were observed at high concentrations over a wide range, such as the diatom *Skeletonema menzelii* (Figure 4). Other species were present over a wide temperature range, but only formed blooms at higher temperatures, such as *S. costatum* (Figure 4). By contrast, some species showed a very narrow temperature range, particularly the dinoflagellates *P. bahamense* var *bahamense*, which only occurred at temperatures >25°C (Figure 4).

Phytoplankton biovolume

Among the eight sampling locations included in this study, the IRL north site (site 2) and north-central sites (sites 3–5) of the lagoon had the highest average total biovolumes over the sampling period (Table II). This pattern is also evident in terms of the frequency of phytoplankton blooms (i.e. biovolume >2 mm^3 L^{-1}) (Table III). This threshold level was established using a 25% exceedence criterion, i.e. the biovolume level that was exceeded on <25% of the sampling dates at the sampling site in the IRL with the lowest average total biovolume, site 6 (see Figure 2). In the flow-restricted region of the lagoon (sites 2–5), total phytoplankton biovolumes exceeded 2 mm^3 L^{-1} on 11, 17, 10 and 15 of the 20 sampling dates during the 2 year research period at sites 2, 3, 4 and 5, respectively (Figure 2). This contrasts with the less flow-restricted regions of the lagoon (sites 1, 6, 7 and 8) where total phytoplankton biovolumes only achieved these levels four to six times in the 20 sampling dates (Table III). From a temporal perspective, the highest frequency of bloom conditions at most of the sampling sites occurred in the summer and autumn of 1998, following the El Niño flood of the winter of 1997/98. The exception to this pattern was site 3 in the Banana River region of the IRL, where blooms of cyanobacteria were observed in the winter and spring of the second year of sampling (Figure 2). Cyanobacteria and green algae blooms were also a prominent feature at site 2 in the spring and summer of the second year.

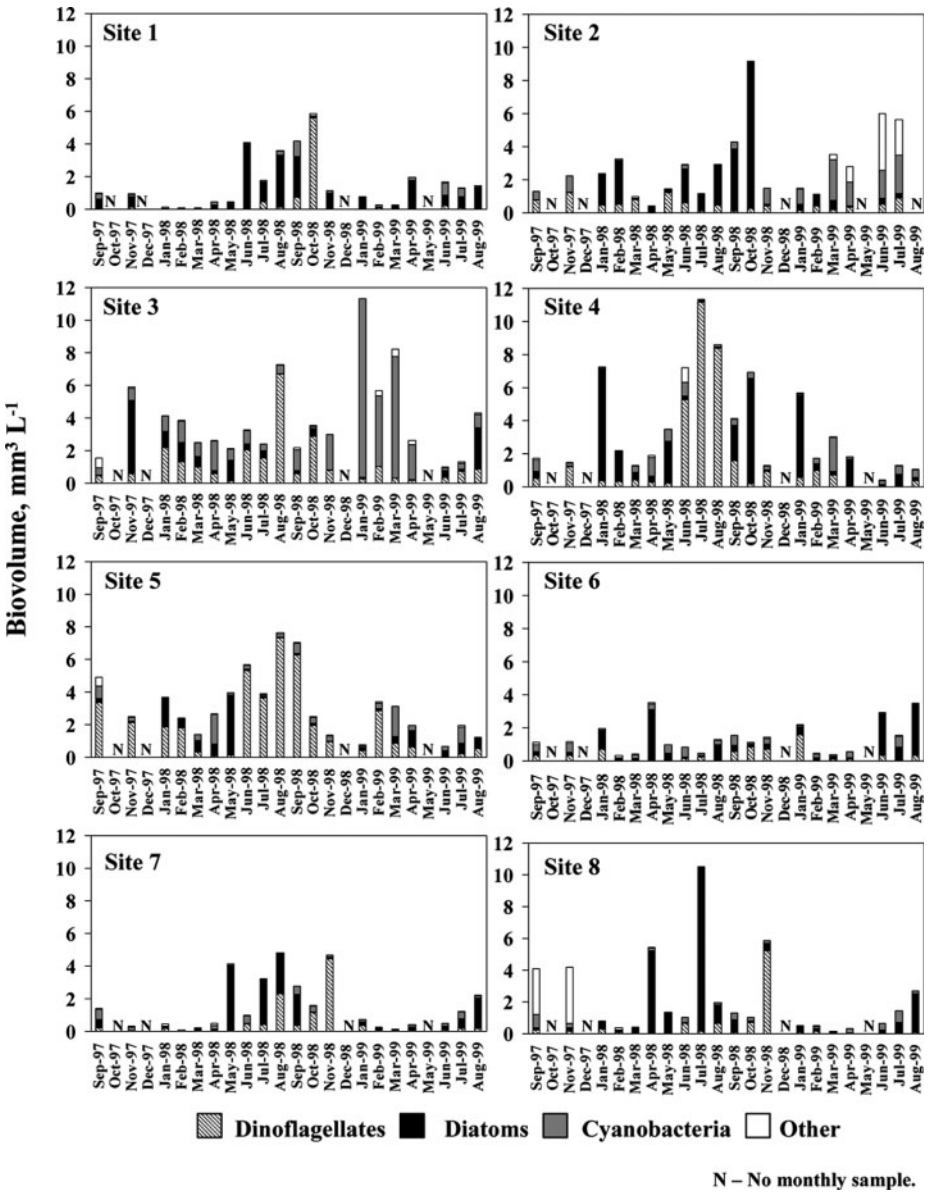

Fig. 2. Biovolumes of the major phytoplankton taxa encountered at the eight sampling sites. The top figure for each site is the biovolume as μm^3 mL^{-1}. The bottom figure shows the relative contribution of the major taxonomic groups to total biovolume, on a percentage basis.

The major algal groups that contributed to phytoplankton biovolume in the IRL included cyanobacteria (i.e. blue–green algae or Cyanophyceae), dinoflagellates (Dinophyceae), diatoms (Bacillariophyceae), cryptophytes (Cryptophyceae), green algae (Chlorophyceae), euglenoids (Euglenophyceae) and small unidentified marine microflagellates (not including dinoflagellates) (Table IV). In addition, the ebridian *Hermesinum adriaticum* (Hargraves, 2002*a*) was observed during the microscopic analyses. In most cases, diatoms, dinoflagellates or cyanobacteria dominated the phytoplankton community on a biovolume basis (Figure 2).

Dinoflagellates

Phytoplankton communities were dominated (i.e. represented the highest percentage of total biovolume) by dinoflagellates in at least 1 month during the 2 year sampling period at all eight sampling sites in the lagoon (Figure 2). However, the greatest frequency of dinoflagellate domination was observed in the north-central region, sites 3–5 (Table V). At sites 3, 4 and 5, dinoflagellates dominated the phytoplankton community in 9, 7 and 12 of the 20 months sampled during the study (Table V).

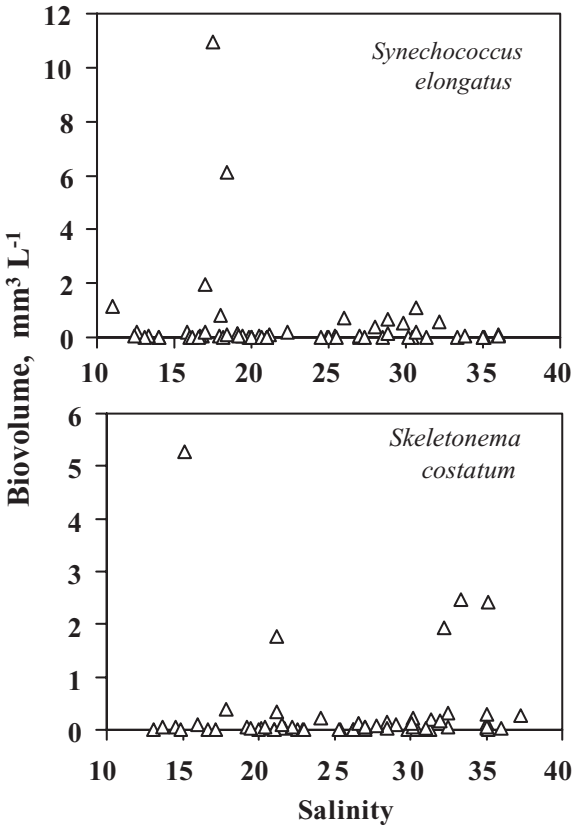

Fig. 3. Salinity versus biovolume for two selected species of phytoplankton encountered at the eight sampling sites.

A further indication of the importance of dinoflagellates at sites 3–5 was the observation that total dinoflagellate biovolume reached bloom levels on a number of dates (Figure 2; Table III). From a temporal perspective, the summer and autumn of 1998 was a period of particular dinoflagellate prominence throughout the IRL (Figure 2).

A number of individual dinoflagellate taxa reached high biovolume levels during our sampling period (Table IV). *Pheopolykrikos hartmannii* was among the most common bloom-forming species, reaching bloom levels at the north-central sites of the lagoon on multiple occasions. Blooms of *P. hartmannii* were observed in a number of samples: (i) site 3 in January 1998; (ii) site 4 in November 1997 and June and July 1998; and (iii) site 5 in November 1997 and February, June, July and September 1998.

Akashiwo sanguinea and *Prorocentrum micans* also reached bloom proportions in the lagoon at several sites on numerous occasions. *Akashiwo sanguinea* reached bloom concentrations at sites 1, 3 and 5 in October 1998, and at site 4 in August 1998. *Prorocentrum micans* reached bloom levels at sites 7 and 8 in November 1998, and near bloom levels at site 6 in January 1999.

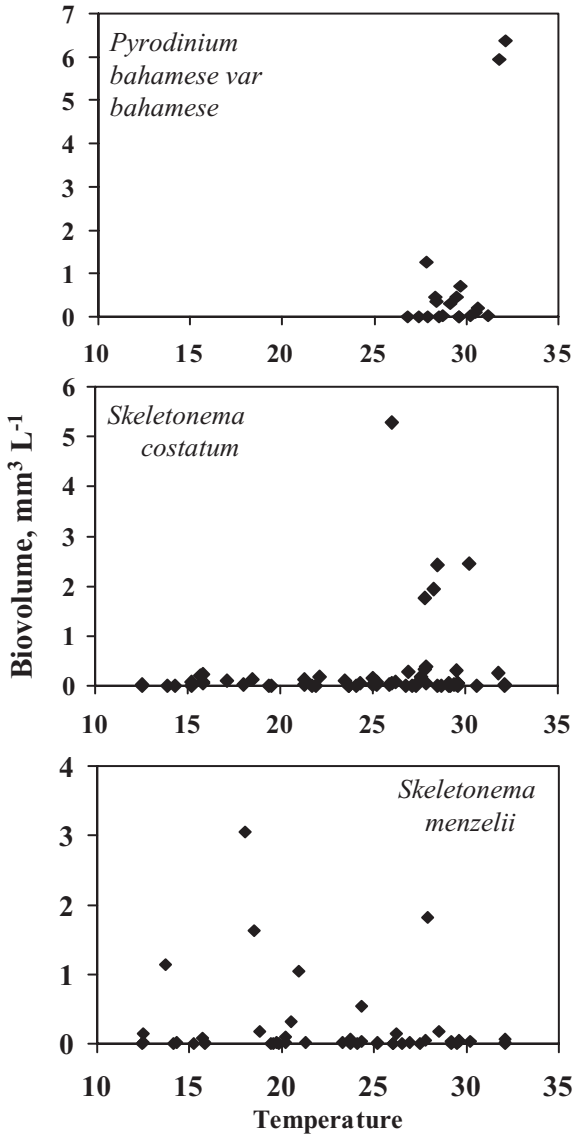

Fig. 4. Temperature versus biovolume for three selected species of phytoplankton encountered at the eight sampling sites.

A number of other dinoflagellate taxa periodically contributed prominently to phytoplankton biovolume in the lagoon, including *P. bahamense var. bahamense*, *Polykrikos schwartzii*, *S. trochoidea* and *Prorocentrum minimum*. *Pyrodinium bahamense* var. *bahamense* was most abundant during the summer months, and reached bloom levels at site 3 in June and August 1998 and at site 5 in August 1998. The other three species were observed at elevated concentrations at site 5; i.e. *Polykrikos schwartzii* in January 1998, *S. trochoidea* in May 1997 and *Prorocentrum minimum* in February 1998.

Diatoms

As with dinoflagellates, diatoms were biovolumetrically dominant during at least 1 month of the sampling period

Table II: Mean biovolume of major algal taxa at the eight sampling sites in the Indian River Lagoon

	Site							
	1	2	3	4	5	6	7	8
Diatoms	0.963	1.349	0.682	1.483	0.590	0.582	0.779	1.017
Dinoflagellates	0.384	0.498	1.226	1.674	2.037	0.339	0.531	0.454
Cyanobacteria	0.195	0.638	1.915	0.457	0.452	0.294	0.196	0.201
Green algae	0.001	0.341	0.063	0.000	0.001	0.001	0.003	0.317
Cryptophytes	0.028	0.026	0.044	0.033	0.035	0.025	0.024	0.023
Euglena	0.002	0.000	0.001	0.002	0.029	0.004	0.001	0.000
Microflagellates	0.001	0.003	0.002	0.002	0.002	0.008	0.003	0.005
Total	1.574	2.855	3.933	3.651	3.146	1.253	1.537	2.017

Mean values are for the entire sampling period and are presented as million $\mu m^3\ mL^{-1}$.

Table III: Frequency of algal blooms at the eight sampling sites in the Indian River Lagoon region

Site	Frequency of blooms (out of 20)				
	Diatoms	Dinoflagellates	Cyanobacteria	Green	Total
1	3	1	0	0	4
2	6	0	2	2	11
3	2	4	6	0	17
4	5	3	1	0	10
5	1	8	1	0	15
6	3	0	0	0	4
7	2	2	0	0	6
8	3	1	0	2	6

The frequency with which total biovolume of the four major algal divisions observed during our study reached $2 \times 10^6\ m^3\ mL^{-1}$ was used as a measure of bloom frequency. A column is also provided to show the frequency at which total phytoplankton biovolume exceeded $2 \times 10^6\ m^3\ mL^{-1}$ at the eight sampling sites. The numbers shown are out of a total of 20 sampling dates at the eight sampling sites from September 1997 to August 1999.

at all sampling sites (Figure 2). There was a general trend of greater diatom dominance in the Mosquito lagoon (site 1) and in the north (site 2) and south-central (sites 7 and 8) regions of the lagoon (Table V).

Blooms of diatoms were observed at various times and locations during the study. Bloom levels of diatoms were observed in one to six of the 20 monthly samples at the eight sampling sites in the study (Table III).

Several individual species of diatoms reached high biovolume levels during the study period (Table IV). *Skeletonema costatum*, a common diatom species in the estuaries along the east coast of the USA, was observed at bloom concentrations on multiple occasions in the Mosquito Lagoon (site 1) and northern region of the lagoon (site 2), during the summer of 1998. Other bloom-forming species included *Dactyliosolen fragilissimus*, *Skeletonema menzelii*, *Cerataulina pelagica*, *Odontella regia*, *Chaetoceros lorenzianus*, *Rhizosolenia setigera* and *Thalassionema nitzschioides*. *Dactyliosolen fragilissimus* was observed at bloom levels at site 2 in January, February, June, August and October 1998, as well as at sites 4 and 5 in May of 1998. Blooms of *S. menzelii* were observed at sites 4, 5, and 6 in January of 1998 and again at site 4 in February and September 1998. *Cerataulina pelagica* was observed at bloom levels in November 1997 at site 3, January 1998 at site 4, October 1998 at site 2, July 1998 at site 8 and January 1999 at site 4. Other diatom blooms included: *O. regia* at site 4 in April 1999, *Chaetoceros lorenzianus* at site 4 in January 1998, *T. nitzschioides* at site 6 in June 1999, *Thalassiosira* (10 μm diameter) at site 7 in May 1998, a 15 μm centric diatom at site 7 in September 1998 and pennate diatoms (with a transapical axis <5 m) at sites 3 and 6 in August 1999.

Cyanobacteria

The third algal group regularly encountered in high abundance in the IRL was cyanobacteria. On a cell population basis (cells mL^{-1}) cyanobacteria were usually the most numerous algae in the lagoon. However, due to their small size, cyanobacteria were often less important on a biovolume basis than diatoms or dinoflagellates.

Cyanobacteria cell populations were greatest at site 3 in the Banana River, where *Synechococcus elongates*, Cyanobacterium A and B dominated the phytoplankton community in seven of the 20 monthly samples (Table V). At the remaining sites (1, 2, 4, 5, 6, 7 and 8), cyanobacteria were the dominant phytoplankton group in 0, 4, 3, 3, 4, 1 and 2 of the monthly samplings, respectively.

Cyanobacteria biovolume at site 3 reached bloom in 6 of the 20 months sampled (Figure 2; Table III). Other observations of cyanobacteria blooms were made at sites 2, 4 and 5 (Figure 2).

The most common cyanobacteria observed in the lagoon consisted of Cyanobacterium A, Cyanobacterium B and *S. elongates*. Cyanobacterium A reached the highest levels in the Mosquito Lagoon, and the north and north-central regions of the IRL. *Synechococcus elongates* reached the highest levels at sites 2 and 3.

Other taxonomic divisions

Other than dinoflagellates, diatoms and cyanobacteria there were few instances where taxa of other algal

Table IV: List of species observed in the Indian River Lagoon over the two-year sampling period

	Site							
	1	2	3	4	5	6	7	8
Cyanobacteria – Cyanophyceae								
Merismopedia sp.		c	c	r	r	r	r	r
Oscillatoria Vaucher ex Gomont	r	r	r	r		r	r	r
Cyanobacterium A (phycocyanin)	c[1]	c[3]	c[2]	c[2]	c	c	c	
Cyanobacterium B (phycoerythrin)	c	c	c	c	c	c	c	c
Synechococcus elongatus Nageli	c	c[1]	c[4]	c	r	c	c	
Unidentified 4 μm filamentous		r			r	r		
Dinoflagellates – Dinophyceae								
Akashiwo sanguinea[c] (Hirasaka) Hansen & Moestrup	r[1]	r	c[1]	c[1]	c[1]	c	c	r
Alexandrium monilatum[a,b] (Howell), F.J.R. Taylor								r
Amphidinium operculatum[b] Claparede & Lachmann	r	c	c	c	c	c	c	r
Ceratium furca (Ehrenberg) Claparede & Lachmann				r				
Ceratium fusus (Ehrenberg) Dujardin	r	c	c	r	r			
Ceratium hircus Schroder	c	c	c	c	c	c	c	c
Cochlodinium citron Kofoid & Swezy							r	
Coolia monotis c.f.[b] Meunier	r	c	r		r	r		r
Corythodinium tesselatum (Stein) Loeblich Jr & Loeblich III		r				r	r	r
Cryptoperidiniopsoid sp.[a]						r		r
Dinophysis caudata[a,b] Saville-Kent		r				r	r	r
Dinophysis caudata var. *acutiformis* Kofoid and Skoogsberg	r	c	c	c	c	c	c	c
Dinophysis A			r		r	r	c	r
Dinophysis B	r	r	r	r	r	r	r	r
Gambierdiscus toxicus[a,b] Adachi & Fukuyo	r	c	r		r	r	r	
Gonyaulax digitale (Pouchet) Kofoid					r	r	r	
Gonyaulax scrippsae Kofoid	r	r	r	r	r	r	r	r
Gonyaulax spinifera[a] (Claparede & Lachmann) Diesing	r	c	c	r	c	c	r	r
Gonyaulax polygramma[a] Stein	c	c	c	c	c	c	c	r
Gymnodinium A	c	c	c	c	c	c	c	c
Gymnodinium B	r	c	r	c	c	c	c	c
Gymnodinium C	r	r	c	c	r	c		r
Gymnodinium D	c	c	c	c	c	c	c	c
Gymnodinium E	r	r	r	c	c	c	r	
Gymnodinium F	r	r	r	r		r	r	r
Gyrodinium estuariale Hulbert	c	c	c	c	c	c	c	c
Gyrodinium instriatum[a] Freudenthal & Lee	r	r	r			r	r	r
Gyrodinium spirale (Bergh) Kofoid & Swezy	c	r	r	r	r	c	c	r
Heterocapsa niei[a] (Loeblich) Morrill & Loeblich III	c	c	c	c	c	c	c	r
Katodinium glaucum (Lebour) Loeblich III	c	c	c	c	c	c	c	c
Katodinium rotundatum (Lohmann) Loeblich III				r	r	r		r
Katodinium sp.	r							
Oxyphysis oxytoxoides[a] Kofoid	r	c		r	r	r		r
Oxyrrhis marina Dujardin			r	r		r		
Oxytoxum scolopax Stein	r	r				r	r	
Phalacroma argus Stein					r			r
Pheopolykrikos hartmannii (Zimmerman) Matsuoka & Fukuyo	r		c[1]	c[3]	c[5]	c	r	r
Polykrikos schwartzii Butschli	r	r	c	c	c[1]	c	r	r

(Continued)

Table IV: Continued

	Site							
	1	2	3	4	5	6	7	8
Prorocentrum arcuatum Issel						r		
Prorocentrum balticum (Lohmann) Loeblich III	r		r	r	c	r		r
Prorocentrum dentatum Stein			r	r				
Prorocentrum emarginatum[a,b] Fukuyo	r				r	r		
Prorocentrum gracile Schutt	r			r		c		
Prorocentrum lima[a,b] (Ehrenberg) Dodge			r	r	r		r	
Prorocentrum mexicanum[a,b] Tafall					r		r	r
Prorocentrum micans[a] Ehrenberg	c	c	c	c	c	c[1]	c[1]	c[1]
Prorocentrum minimum[b] (Pavillard) Schiller	r	c	c	c	c[1]	c	c	r
Prorocentrum scutellum Schroder					r	r	r	r
Prorocentrum triestinum Schiller			r	r	r		r	
Prorocentrum sp.	r	r						
Protoperidinium claudicans (Paulsen) Balech		r	r			r	r	
Protoperidinium conicum (Gran) Balech		r		r				
Protoperidinium depressum (Bailey) Balech	r	r	r			r	r	r
Protoperidinium divergens (Ehrenberg) Balech		c	c	r	c	r	r	r
Protoperidinium leonis (Pavillard) Balech		r	r		r	r	r	r
Protoperidinium oceanicum (Van Hoffen) Balech		r	r					
Protoperidinium pellucidium Bergh	r	c	r	c	r	c	r	c
Protoperidinium pentagonum (Gran) Balech		r	r				r	r
Protoperidinium punctulatum (Paulsen) Balech			r	r		r		r
Protoperidinium sp.			r				r	
Pyrodinium bahamense var. *bahamense* Plate	r	c	c[2]		r[1]		r	
Pyrophacus horologium Stein	r	c	c	r	r	c	r	r
Pyrophacus steinii (Schiller) Wall and Dale	r	r	r	r		r	c	r
Scrippsiella trochoidea (Stein) Loeblich III	r	r	c	c	c[1]	c	c	r
Torodinium teredo (Pouchet) Kofoid & Swezy						r	r	
Dinoflagellate chain	r	r		r		r		r
Diatoms – Bacillariophyceae								
Asterionellopis glacialis (Castracane) Round	c	r		r		c	r	r
Bacillaria paxillifera (O.F. Mueller) Hendry	c	r		r	r	c	c	c
Bellerochea sp.	r			r				
Biddulphia pulchella (Smith) Boyer				r	r			r
Biddulphia tuomeyi (Bailey) Roper						r		
Campylosira cymbelliformis (A. Schmidt) Grunow			r					
Centric diatom, 5–10 μm	c	c	c	c	c	c	c	c
Centric diatom, 10–50 μm	c	c	c	c	c	c	c[1]	c
Centric diatom, >50 μm <200 μm	c	c	c	c	c	c	c	c
Cerataulina pelagica (Cleve) Hendey	c	c[1]	c[1]	r[1]	r	c	r	r[1]
Chaetoceros aequatorialis Cleve	r	r	r			r	r	
Chaetoceros affinis Lauder		r	r	r		r		
Chaetoceros anastomosans Grunrow in Van Heurck			r					
Chaetoceros atlanticus Cleve						r		
Chaetoceros compressus Lauder		r				r	r	r
Chaetoceros costatus Pavillard		r						
Chaetoceros curvisetus Cleve	c	r				r		r

(Continued)

Table IV: Continued

	Site							
	1	2	3	4	5	6	7	8
Chaetoceros danicus Cleve		r			r	r		r
Chaetoceros diadema (Ehrenberg) Gran		r				r		
Chaetoceros didymus Ehrenberg		r	r	r		r	r	r
Chaetoceros diversus Cleve	r							
Chaetoceros decipiens Cleve	r	r		r		r		
Chaetoceros lorenzianus Grunrow	c	r		r[1]				
Chaetoceros minimus (Levander) Marino, Giuffre, Montresor, & Zingone	r	r	c	c	c	r	r	
Chaetoceros simplex Ostenfeld	c	c	r	r	c	c	c	c
Chaetoceros subtilis Cleve	r	r	r	r	r	c	r	
Chaetoceros wighamii Brightwell	r	c	r	r	r	r		r
Chaetoceros A	r	r						
Chaetoceros B	r	c		r	r		r	r
Chaetoceros, 5 μm	r	r			r	r		r
Chaetoceros, 10 μm	c	c	r	r	r	c	r	r
Chaetoceros, 20 μm	r	r		r				
Corethron Castracane	r	r	c	r				r
Coscinodiscus granii Gough	r	r		r	r		r	r
Coscinodiscus sp.	r	r	r	r	r	r	r	c
Dactyliosolen fragilissimus (Bergon) Hasle comb. Nov.	c	c[5]	r	r[1]	c[1]	c	r	r
Ditylum brightwellii (West) Grunrow in Van Heurck	r			r				
Grammatophora marina (Lyngbye) Kutzing	r						r	
Guinardia delicatula (Cleve) Hasle comb. Nov	r							
Guinardia striata (Stolterfoth) Hasle com. nov.	c			r				
Guinardia sp.	r			r	r			
Hemiaulus hauckii Grunrow in Van Heurck		c					r	
Hemiaulus sinensis Greville	r							
Leptocylindrus danicus Cleve	r					r		
Licmophora gracilis (Ehrenberg) Grunrow	r						r	
Lithodesmium sp.	r							
Navicula sp.	c	r	c	c	c	c	c	c
Nitzschia closterium (Ehrenberg) W. Smith	c	c	c	c	c	c	c	c
Nitzschia A	r	r	r	r	r	r	r	r
Nitzschia B					r			
Nitzschia C	r		r					
Odontella aurita (Lyngbye) C.A. Agardh	r	r						
Odontella mobiliensis (Bailey) Grunow	c	c	r	r	r	r		
Odontella regia (Schultze) Simonsen	r	r	r	c[1]	c	r		
Paralia sulcata (Ehrenberg) Cleve	c	r	r	r	c	c	c	c
Pennate diatom <5 μm transapical axis	c	c	c	c	c	c	c	c
Pennate diatom <5 μm transapical axis >100 and <150 μm apical axis	r		r[1]			c[1]	r	
Pennate diatom >5 μm transapical axis	c	c	c	r	r	c	c	c
Pennate diatom 20 μm transapical axis		r					r	r
Pleurosigma/Gyrosigma	c	c	c	c	c	c	c	c
Pseudo-nitzschia	c	c	r	r	r	r		

(Continued)

Table IV: Continued

	Site							
	1	2	3	4	5	6	7	8
Pseudo-nitzschia calliantha[a,b] Lundholm, Moestrup, Hasle		c	c	r	r	r	r	r
Pseudosolenia calcar-avis (Schultze) Sundstrom	c		c	r				
Rhabdonema adriaticum Kutzing					r			
Rhizosolenia imbricata Brightwell	r							
Rhizosolenia setigera Brightwell	c	c	r	c	c	c	c[1]	c
Skeletonema costatum (Greville) Cleve	c[3]	c[1]	r	c[1]	c	c	c	c
Skeletonema menzellii Guillard, Carpenter & Reimann	c	c	c	c[3]	c[1]	c[1]	c	c
Stictocyclus stictodiscus (Grunrow) Ross	r							
Striatella unipunctata (Lyngbye) C.A. Agardh		r						
Thalassionema nitzschioides (Grunrow) Mereschkowsky	c	c	c	r	c	c[1]	c	
Thalassiosira chain	c	r	c	c	c	c	c[1]	c
Trigonium sp.			r					
Unidentified pennate sp. A	c	r	c	c	c	c	r	c
Unidentified pennate sp. B						r		r
Unidentified pennate sp. C	r							
Cryptophytes – Cryptophyceae								
Unidentified Cryptophyte	c	c	c	c	c	c	c	c
Green algae – Chlorophyceae								
Nannochloris c.f.	c	c[2]	c	r	c	c	r	c[2]
Euglena – Euglenophyceae								
Euglena sp.	r	c	c	c	c	c	c	r
Unidentified microflagellates								
Not including dinoflagellates <5 μm	c	c	c	c	c	c	c	c
Zooflagellates – Zoomastigophora								
Hermesinum adriaticum Zacharias	r	r	c		c	c	r	r

The letter 'r' indicates species that appeared 'rarely', i.e. in less than three samples. The letter 'c' indicates species that were 'common', i.e. appeared in more than three samples. A numerical superscript indicates the number of samplings in which the species appeared at biovolume in excess of 10^{-6} μm mL^{-1} levels. Superscript letters by the species names indicates that they appeared in the FMRI[a] or IOC[b] reference lists of potentially toxic or harmful algal species (IOC, 2002; FMRI, 2002) or identified by Bockstahler and Coats (Bockstahler and Coats, 1993)[c] as potentially toxic.

groups were major contributors to total phytoplankton biovolume. One exception to the general dominance of the latter three algal groups was the small (<5 μm) spherical green alga *Nannochloris c.f.*, which periodically appeared at bloom levels at sites 2 and 8 (Figure 2; Table IV).

Cluster analysis

Cluster analysis using single linkage and the Euclidean distance metric confirmed the existence of spatial and temporal similarities in the relative divisional biovolume between sites (Figure 5). In the winter seasons of 1998 and 1999 the closest linkages were between the Mosquito Lagoon (site 1) and site 8 in the south-central region of the IRL. Diatoms were the dominant taxa during the winter at both sites. Site 3 had the greatest distance from all other sites for both winters. Site 3 exhibited dinoflagellate and cyanobacteria codominance in the winter of 1998, and cyanobacteria dominance in the winter of 1999.

During the summer season of 1998, the north-central sites 4 and 5 were closely linked, both being dominated by dinoflagellates. Sites 1 and 2 were also closely linked, with diatom domination throughout the summer. Sites 7 and 8

Table V: Frequency of dominance of major algal groups at the eight sampling sites in the Indian River Lagoon region

Site	Frequency of dominance (out of 20)			
	Diatoms	Dinoflagellates	Cyanobacteria	Green
1	16	1	2	0
2	9	4	4	3
3	4	9	7	0
4	8	7	5	0
5	5	12	3	0
6	7	4	9	0
7	12	4	4	0
8	12	3	3	2

Frequency of dominance is defined as the number of dates out of a total of 20 sampling dates at the eight sampling sites from September 1997 to August 1999 during which the taxonomic group represented the highest percentage of total phytoplankton biovolume.

had dinoflagellate dominance during one of the summer months and diatom dominance the remaining summer months. In the summer of 1999, overall phytoplankton abundance was down from the first year and all sites showed more mixed populations in terms of algal divisions.

DISCUSSION

The results of this study reveal distinct spatial and temporal patterns in phytoplankton composition and abundance in the IRL, including the distribution of potentially harmful species. There were a number of species classified as potentially toxic or harmful in the IRL phytoplankton taxa. Species found in the lagoon which appear in the 'harmful algal bloom' list of the Intergovernmental Oceanographic Commission of UNESCO included the dinoflagellates *Dinophysis caudata*, *Alexandrium monilatum*, *Gambierdiscus toxicus*, *Prorocentrum emarginatum*, *Prorocentrum lima*, *Prorocentrum mexicanum*, *Prorocentrum minimum* and

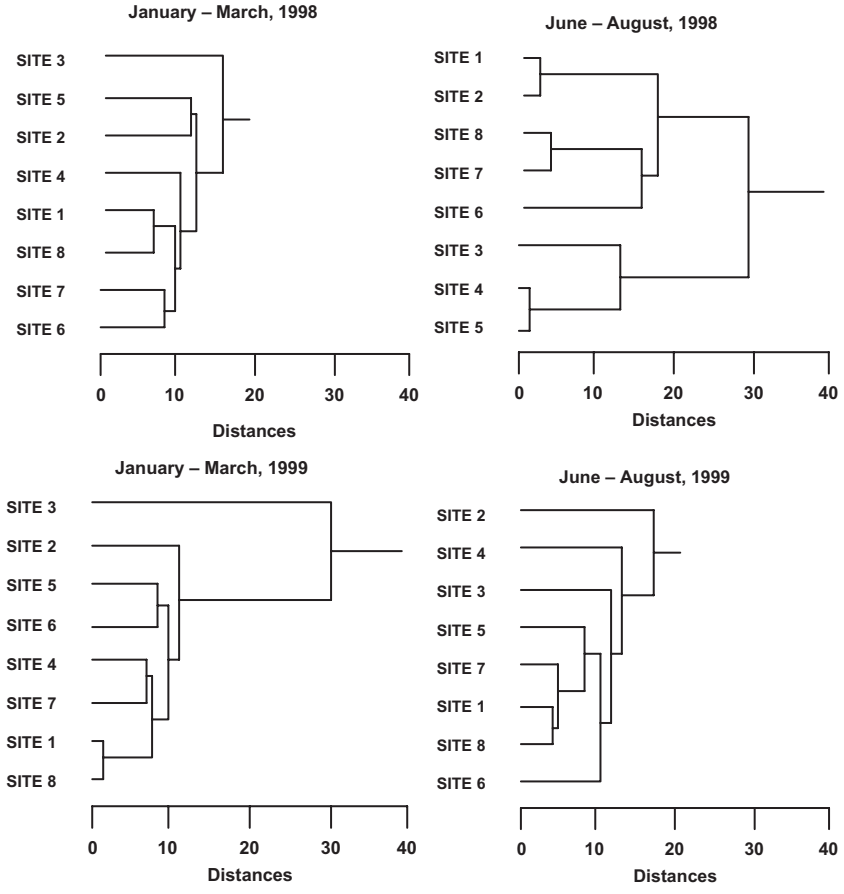

Fig. 5. A comparison of the dominance structure of algal divisions at the eight sampling sites using cluster analysis was used with single linkage with Euclidean distance. The analyses were performed for 3 months within the winter/dry season (January, February and March) and summer/wet season (June, July and August) of 1998 and 1999.

Amphidinium operculatum (IOC, 2002). In addition, a dinoflagellate tentatively identified as *Coolia monotis c.f.* is on the UNESCO list and was observed at low densities on rare occasions. Among the potentially toxic diatoms, *Pseudo-nitzschia calliantha* (formerly known as *Pseudo-nitzschia pseudodelicatissima)* (Lundholm *et al.*, 2003) was widely observed in the lagoon, sometimes at high concentrations. Several additional species observed in this study have been identified by the Florida Marine Research Institute (FMRI, 2002) as potentially 'harmful algal species' including *Gonyaulax polygramma*, *Gonyaulax spinifera*, *Gyrodinium instriatum*, *Heterocapsa niei*, *Oxyphysis oxytoxoides* and *Prorocentrum micans*. Most recently, one species of dinoflagellate found in bloom proportions in the IRL, *Pyrodinium bahamense* (Phlips *et al.*, 2004*a*) has been reported to be toxic (Landsberg *et al.*, 2002).

In terms of the more general phytoplankton community, certain overall spatial and temporal patterns in composition and abundance were apparent from the results. The north-central portion of the lagoon, defined by sites 3, 4 and 5, was frequently dominated by dinoflagellates and/or cyanobacteria. In the rest of the sampling region, including the Mosquito Lagoon (site 1), north IRL (site 2) central IRL (site 6), and south-central IRL (sites 7 and 8), diatoms were more often the dominant taxa. From a temporal perspective, phytoplankton abundances were generally higher during the first year of the study, a high rainfall El Niño period, than the second year, a drought period. The spatial differences between regions were most pronounced during the summer El Niño period. These general spatial and temporal patterns were corroborated by the results of cluster analyses. Some important insights into the factors that may be driving these patterns can be achieved by discussing the observations from a spatial point of view and then applying a temporal perspective.

Spatial patterns in phytoplankton structure and abundance

There are two factors that distinguish the north and north-central regions of the IRL from the rest of the lagoon and Mosquito Lagoon: the exceptionally long water residence times and the unique watershed characteristics (Phlips *et al.*, 2004*b*). It is well known that high residence time can contribute to biomass accumulation and high phytoplankton standing crops (Knoppers *et al.*, 1991; Monbet, 1992). The most restricted parts of the IRL can experience water residence times of up to a year, while regions near inlets can have residence times in the order of days (Sheng *et al.*, 1990; Smith, 1993). Since doubling times for phytoplankton can be in the order of days, such large differences in water residence times can have a major impact on the build-up of phytoplankton biomass. In a recent complementary study of phytoplankton standing crops in the IRL, it was shown that the north-central region had the highest mean phytoplankton biomass (Phlips *et al.*, 2002).

In terms of the phytoplankton community, one of the prominent features of the north central sites of the IRL was the frequent domination of the community by dinoflagellates and cyanobacteria. Among the individual phytoplankton species that reached bloom concentrations (i.e. biovolume >2 mm^3 L^{-1}) in the north central sites of the lagoon there were five dinoflagellates: *Akashiwo sanguinea*, *Pheopolykrikos hartmannii*, *Polykrikos schartzii*, *Prorocentrum minimum*, *Pyrodinium bahamense* var. *bahamense* and *Scrippsiella trochoidea*. Historically, blooms of the toxic dinoflagellate *Alexandrium monilatum* (i.e. *Gonyaulax monilata*) have been observed in the northern region of the lagoon (Howell, 1953; Norris, 1983), but were only observed at relatively low concentrations in our study. Two cyanobacteria were also observed at bloom concentrations: the picoplanktonic species *Synechococcus elongatus* and the spherical Cyanobacterium A.

Water residence time does not, by itself, explain the importance of dinoflagellates and cyanobacteria in the north-central region of the IRL. This point is exemplified by the fact that diatom and green algae were periodically observed at bloom levels in the north IRL (site 2), the most flow-restricted region of the sampling reach. It is important to consider the potential impact of other factors correlated to low water turnover rates, as well as the specific character of regional watersheds. The long residence times observed in the northern region have implications for a number of key environmental variables, including nutrient concentrations, salinity variation (Phlips *et al.*, 2002) and tidal mixing energy (Sheng *et al.*, 1990; Smith, 1993). The watershed characteristics of the northern region result in higher TN:TP ratios and greater potential for phosphorus limitation of phytoplankton growth than in the rest of the lagoon (Phlips *et al.*, 2002), possibly impacting the character of the phytoplankton community (Kilham and Hecky, 1988).

Salinity is a primary candidate in the list of potential regulating factors for phytoplankton composition. Adaptation to osmotic stress is a major factor in dictating the success of specific species in estuarine environments, and can have broad impacts on phytoplankton composition and standing crops (Kennish, 1990). Over the course of this study, salinity in the north-central region varied from 7 to 25. Sites 3–5 exhibited lower average salinity than the rest of the lagoon. The latter three sites were the most frequently dominated by dinoflagellates and cyanobacteria. It is not surprising that many of the major phytoplankton species found at these sites have been previously characterized as euryhaline, including the dinoflagellates

Akashiwo sanguineum, *Prorocentrum micans*, *Prorocentrum minimum* and *Scrippsiella trochoidea* (Braarud, 1951; Kain and Fogg, 1960; Qasim *et al.*, 1972; Brand, 1984; Grzebyk and Berland, 1996) and the diatoms *Skeletonema costatum* and *Skeletonema menzelii* (Guillard *et al.*, 1974; Brand, 1984). The euryhaline character of the latter two diatoms was corroborated by the salinity ranges observed for these taxa in this study. Among the prominent cyanobacteria, *Synechococcus elongates* was also a major bloom forming species in the north-central IRL. *Synechococcus elongatus* has been shown to have broad salinity tolerance in other estuarine environments subject to a wide range in salinity, like Florida Bay. In Florida Bay, *S. elongatus* blooms were observed at salinities from 15–50 (Phlips *et al.*, 1999) and exhibited the ability to grow under laboratory conditions at salinities <10 and >65 (Phlips and Badylak, 1996). Like *S. elongatus*, some of the most important phytoplankton species encountered in the north-central IRL reached bloom levels within the mesohaline range, including the dinoflagellates *Prorocentrum minimum*, *Pheopolykrikos hartmannii*, *Akashiwo sanguinea* and *Pyrodinium bahamense*, as well as the diatoms *Dactyliosolen fragilissimus* and *Cerataulina pelagica*.

Site 2, the other site located in the flow-restricted region, deviated from sites 3, 4 and 5 by having less variation in salinity and a distinct phytoplankton assemblage. It is clear from a comparison of salinity regimes that sites 3, 4 and 5 are subject to greater freshwater inflows from local watersheds than site 2, despite similar residence times. The nutrient inputs from the watershed to the regions of the lagoon defined by sites 3 through 5, along with long residence times, apparently provide the resources and conditions needed to sustain frequent blooms of dinoflagellates and cyanobacteria, whereas diatoms dominated the blooms at site 2. However, this distinction is not a static feature, as indicated by the results of subsequent studies of the Titusville region, which revealed large blooms of dinoflagellates, particularly the potentially toxic species *Pyrodinium bahamense*, in 2001 and 2002 (Phlips *et al.*, 2004*a*).

Another factor that may contribute to the success of dinoflagellates and cyanobacteria species in the north-central region of the IRL is the low tidal mixing energy, particularly during the summer when wind-mixing energy is at a minimum. It has been suggested by several researchers that motile phytoplankton are selectively favored in environments where vertical mixing energy is limited, because of their ability to access the resources needed for growth and survival, principally light and nutrients (Margalef, 1978, 1997; Smayda and Reynolds, 2001). Dinoflagellates certainly fall within this category. The cyanobacterium *S. elongatus* can also regulate its position in the water column by adjusting gas vesicles content. The latter trait has been hypothesized to aid *S. elongatus* in dominating the phytoplankton community of another flow-restricted environment in Florida, Florida Bay (Phlips *et al.*, 1999). A similar argument may be made for the flow-restricted northern IRL.

From a nutrient resource point of view, there are aspects of the north-central IRL that may play a role in the relative importance of dinoflagellates and cyanobacteria. A recent study of nutrient limitation in the IRL using bioassay methods showed that the potential for nutrient limitation of phytoplankton growth was greater in the north-central region than other areas of the lagoon (Phlips *et al.*, 2002). Overall, N was the most frequently limiting nutrient throughout the lagoon; however, there was a greater potential for P limitation in the north and north-central IRL. The results of these bioassay experiments were corroborated by water chemistry analyses that showed lower P concentrations, higher N concentrations and higher TN:TP ratios in the north-central of the lagoon than other regions. These conditions may favor picoplanktonic species, such as *S. elongatus*, which have been shown to compete very effectively for P at low concentrations (Richardson, 2001). It has been suggested by several researchers that a number of dinoflagellate species also have a selective advantage in N-limited ecosystems (Harrison, 1976), owing in part to their ability to take up N at night (Paache *et al.*, 1984), store significant amounts of N (Sciandra, 1991) and migrate through the water column in search of N sources (Olsson and Granelli, 1991). Similar reasons have been given to explain the dominance of cyanobacteria in certain aquatic ecosystems, including their competitive advantage under N-limiting conditions and ability to regulate their position in the water column (Phlips *et al.*, 1999).

It has also been shown that mixotrophic dinoflagellates can meet their demand for nutrients by feeding on smaller algae and bacteria. The latter phenomenon has been demonstrated for a number of dinoflagellates common to the IRL, including *Prorocentrum minimum*, *Prorocentrum micans*, *Akashiwo sanguineum* and *Scrippsiella trochoidea* (Bockstahler and Coats, 1993; Jacobson and Anderson, 1996; Li *et al.*, 1996; Skovgaard, 1996; Stoecker *et al.*, 1997).

In contrast with the flow-restricted character of the north-central IRL, two regions in the sampling range of this study are characterized by high rates of tidal water exchange with the Atlantic Ocean: site 1 in the Mosquito Lagoon and site 6 near the Sebastian Inlet in the central IRL. Tidal water exchange in these regions is reflected in the higher average salinity at the latter sites in comparison with the rest of the lagoon. In tidally mixed regions, oceanic water containing relatively low phytoplankton biomass can significantly dilute phytoplankton standing

crops in lagoons and estuaries. The relatively high level of diatom dominance in regions of the lagoon that are well-mixed may in part be attributable to tidal mixing energy and tidal water in flux. Diatoms are often more dependent on and tolerant of environments characterized by strong vertical mixing energy, while the turbulence of the water column at these sites may have a negative impact on the relative success of dinoflagellates (Wyatt and Horwood, 1973; Margalef, 1978; Margalef *et al.*, 1979; Smayda and Reynolds, 2001).

At the species level, another feature of tidally mixed regions of the lagoon is the presence of a significant complement of phytoplankton taxa considered oceanic or neritic. For example, *Thalassionema nitzschioides*, a cosmopolitan neritic and oceanic diatom (Marshall, 1982) was observed at bloom levels in tidally mixed regions of the IRL. Two other oceanic/neritic diatoms, *Cerataulina pelagica* and *Dactyliosolen fragilissimus*, commonly co-occurred in the lagoon, as observed in other ecosystems (Hasle and Syvertsen, 1996).

Several other species of diatoms normally considered oceanic or neritic appeared throughout the lagoon, rather than predominantly in tidally mixed regions. *Skeletonema menzelii*, found in the western Sargasso Sea and west coast of Florida (Guillard *et al.*, 1974), and cosmopolitan species *Skeletonema costatum*, both occurred in bloom proportions throughout the lagoon. The small size and structural configuration of these species diminish the mixing energy needed to keep these species suspended in the water column. *Skeletonema costatum* is a common centric diatom in many estuarine/coastal environments of Florida and is also a major component of phytoplankton communities in many coastal ecosystems around the world. *Skeletonema costatum* is well known for its adaptability to a wide range of salinities (Rijstenbil, 1988). Laboratory studies indicate that *S. costatum* is capable of significant growth at salinities from 5 to 40 (Brand, 1984). In this study *S. costatum* reached bloom levels at salinities from 15 to 34.

Another characteristic of tidally mixed regions of the study range was the presence of benthic pennate diatoms in the water column. Their presence in the water column can be indicative of wind and tidal resuspension. The presence of high concentrations of large pennate diatom associated with wind-induced benthic resuspension has been observed in estuaries such as the Peel–Harvey estuary in south-west Australia (Lukatelich and McComb, 1986).

The south central region of the IRL is distinguishable from the northern region by the presence of high P concentrations (Phlips *et al.*, 2002, 2004*b*). This gradient in P concentration is related to differences in loading rates from specific watersheds associated with different regions of the lagoon (Sigua and Tweedale, 2002). Based on P concentration gradients alone, one might expect the highest standing crops of phytoplankton to occur at the southernmost sampling sites (sites 7 and 8). However, overall phytoplankton standing crops observed in our study were higher in the northern region of the lagoon, even though mean TP concentrations were only half those observed at the southern sites. The disparity between the regions was even more pronounced in terms of soluble reactive P, with a 10-fold difference in mean concentration, e.g. 1.2 M at site 8 and 0.12 M at site 4 (Phlips *et al.*, 2002). The impact of the P gradient is further manifested by the higher frequency and intensity of nutrient limitation of phytoplankton growth in the northern region compared with the southern region (Phlips *et al.*, 2002). The high concentrations of soluble reactive P commonly observed in the southern part of the IRL highlight the fact that high water turnover rates, as well as other processes that limit algal standing crops (e.g. grazing or N limitation), can restrict standing crops below the potential represented by the bioavailable P present (Phlips *et al.*, 2004*b*).

The question of how these nutrient gradients impact phytoplankton species composition is a complex issue. All sites within the IRL, with the exception of site 6 near the Sebastian Inlet, were subject to periodic blooms of dinoflagellates, diatoms and cyanobacteria. The most pronounced distinction between regions was the high frequency of dinoflagellate and cyanobacteria blooms observed at sites 3–5 in the north-central region of the lagoon, compared with the prevalence of diatom blooms in the rest of the sampling regions. The factors besides P availability that may promote dinoflagellates and cyanobacteria dominance in the former region include: (i) lower average salinity; (ii) lower tidal mixing energy; and (iii) differential grazing activity.

The potential significance of grazing in the regulation of phytoplankton standing crops in the IRL is suggested by the results of recent preliminary research showing high grazing rates in the lagoon (Phlips *et al.*, 2002). The role of grazing in molding phytoplankton community structure in the lagoon is presently not known. Research in other estuarine ecosystems has shown that certain species of dinoflagellates and cyanobacteria may be subject to relatively low grazing pressure, owing to their toxicity or other palatability issues. For example, inhibition of grazing by zooplankton has been demonstrated for *Akashiwo sanguinea* (Ukeles and Sweeney, 1969; Fiedler, 1992), a species found in the IRL at bloom levels. These observations provide support for the hypothesis that factors affecting feeding selectivity play an important role in phytoplankton community structure. Similar arguments have been made for the prominence of certain cyanobacteria in other aquatic ecosystems (Fulton and Paerl, 1987; DeMott and Moxter, 1991).

The issue of grazing impacts on phytoplankton in the Indian River Lagoon is not limited to zooplankton, but extends to the benthic community of filter and suspension feeders. The very shallow nature of the lagoon, along with the extensive populations of benthic filter-feeding macroinvertebrates found in the lagoon (e.g. clams), make benthic grazing an important issue. The role of the benthic community in regulating phytoplankton dynamics has been demonstrated in a number of estuaries (Gaston *et al.*, 1997; Lucas *et al.*, 1999). As in the case of zooplankton, the presence of taxa that are avoided by benthic grazers, or harmful to them, presents the potential for altering the structure of the community (Shumway, 1990; Luckenbach *et al.*, 1993; Wikfors and Smolowitz, 1995). Without further research it is difficult to estimate the specific impact of differential grazing by benthic invertebrates on temporal and spatial patterns of phytoplankton community structure and abundance.

Temporal variability in phytoplankton structure and abundance

From a temporal perspective, the IRL is characterized by seasonal and inter-annual differences in phytoplankton composition and abundance. In the most general sense, the highest phytoplankton standing crops occurred in the warmer months of the year, i.e. May to November (Phlips *et al.*, 2002). However, the location of the IRL in the Florida peninsula limits the range of water temperatures normally encountered over the year. In comparison with many temperate ecosystems, temperature variation in the lagoon may be viewed as relatively modest in magnitude (Karentz and Smayda, 1998). However, the impact of the observed seasonal variation in temperature on phytoplankton communities in the lagoon can not be discounted owing to the presence of many warm water taxa. Although bloom concentrations of phytoplankton were encountered in every month of the sampling period somewhere in the lagoon, the frequency of blooms was higher in the warm season, when temperatures generally exceeded 25°C.

Examples of species that appear to be restricted to warm months of the year include the potentially toxic species *Pyrodinium bahamense* (Landsberg *et al.*, 2002; Phlips *et al.*, 2004*a*), bioluminescent dinoflagellate common in tropical waters (Smayda, 1980). This species was observed only during the summer season in the IRL, when it occasionally reached bloom concentrations. This could be an indication that the low temperatures experienced during the winter months are too cold for such tropical species. By contrast, *P. bahamense* var *bahamense* was found throughout the year in Florida Bay, located just south of the IRL in the Florida Keys (Badylak and Phlips, manuscript in preparation). This observation provides further evidence for the transitional nature of the lagoon from a biogeographical standpoint.

On the other hand, some of the important phytoplankton species in the IRL, such as the diatoms *Skeletonema menzelii*, *Dactyliosolen fragilissimus*, *Cerataulina pelagica* and *Odontella regia*, as well as the cyanobacterium *Synechococcus elongatus*, were observed to reach bloom levels over the entire temperature range encountered in the lagoon. Other important phytoplankton species encountered in the lagoon occurred over a broad range of temperatures, but reached bloom levels at higher temperatures, as exemplified by the diatom *Skeletonema costatum*. The latter pattern was shared by the dinoflagellates *Pheopolykrikos hartmannii*, *Prorocentrum micans* and *Akashiwo sanguineum*, as well as the unicellular green algae. Overall, there was a general tendency for dinoflagellates to bloom during the warm season, while the dominant diatoms bloomed over a broader temperature range. A similar tendency has been noted in other ecosystems (Goldman and Carpenter, 1974).

The complexities of temperature preferences of different species of phytoplankton in the IRL highlight the danger of viewing this issue from a univariate perspective (Smayda, 1980). Other studies indicate that phytoplankton community structure is frequently not a consequence of a single controlling factor, but a combination of factors that change over time (Smayda, 1980; Karentz and Smayda, 1984; Bledsoe and Phlips, 2000). This is supported by the fact that the phytoplankton communities observed in the IRL differed from one year to the next, despite similar patterns in temperature. For example, dinoflagellates dominated the flow-restricted regions of the lagoon in the first year of the study, but were much less prominent in the second year. The first year of this study was characterized by exceptionally high watershed inputs of water and nutrients resulting from the flood period associated with an El Niño event (winter 1997/98) (Phlips *et al.*, 2002). The latter inputs may have provided the additional nutrient inputs needed to drive the spring and summer phytoplankton blooms observed during the first year of the study. The second year of the study was characterized by below average rainfall conditions, which may help to explain the reduction in spring/summer phytoplankton biomass.

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LITERATURE CITED

Bledsoe, E. L. and Phlips, E. J. (2000) Relationships between phytoplankton standing crop and physical, chemical, and biological gradients in the Suwannee River and plume region, USA. *Estuaries*, **23**, 458–473.

Bockstahler, K. R. and Coats, D. W. (1993) Grazing of the mixotrophic dinoflagellate *Gymnodinium sanguineum* on ciliate populations in Chesapeake Bay. *Mar. Biol.*, **116**, 477–487.

Braarud, T. (1951) Salinity as an ecological factor in marine phytoplankton. *Physiol. Plant.*, **4**, 28–32.

Brand, L. E. (1984) The salinity tolerance of forty-six marine phytoplankton isolates. *Estuarine Coastal Shelf Sci.*, **18**, 543–556.

Brevard, County (1994) The Brevard County data abstract. *Geographic Research Division*, Brevard County, Florida, 60 pp.

Cloern, J. E. (1996) Phytoplankton bloom dynamics in coastal ecosystems: a review with some general lessons from sustained investigation of San Francisco Bay, California. *Rev. Geophy.*, **34**, 127–168.

Cupp, E. E. (1943) *Marine Plankton Diatoms of the West Coast of North America, Vol. 5*. University of California Press, Los Angeles, CA, pp. 1–238.

Daugbjerg, N., Hansen, G., Larsen, J. and Moestrup, Ø. (2000) Phylogeny of some of the major genera of dinoflagellates based on ultrastructure and partial LSU r DNA sequence data, including the erection of three new genera of unarmored dinoflagellates. *Phycologia*, **39**, 302–317.

Davis, R. A. (1997) Geology of the Florida coast. In Randazzo, R. F. and Jones D. S. (eds), *The Geology of Florida*, The University Press of Florida, Gainesville, FL, pp. 155–168.

De Freese, D.E. (1995) Land acquisition: a tool for biological diversity protection in the Indian River Lagoon, Florida. *Bull. Mar. Sci.*, **57**, 14–27.

DeMott, W. R. and Moxter, F. (1991) Foraging on cyanobacteria by copepods: responses to chemical defenses and resource abundance. *Ecology*, **72**, 1820–1834.

Dodge, J. D. (1982) *Marine Dinoflagellates of the British Isles*. Her Majesty's Stationery Office, London, pp. 1–303.

Fahnenstiel, G. L. and Carrick, H. J. (1992) Phototrophic picoplankton in Lakes Huron and Michigan: abundance, distribution, composition and contribution to biomass and production. *Can. J. Fish. Aquat. Sci.*, **49**, 379–388.

Fiedler, P. C. (1992) Zooplankton avoidance and reduced grazing response to *Gymnodinium splendens*. *Limnol. Oceanogr.*, **27**, 961–965.

FMRI (2002) Florida Marine Research Institute, HAB Species subcategory of the harmful algal blooms and red tides. Available at www.floridamarine.org/redtide, last accessed June 12, 2002.

Fryxell, G. A., Villac, M. C. and Shapiro, L. P. (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.

Fulton, R. S., III and Paerl, H. W. (1987) Toxic and inhibitory effects of the blue-alga *Microcystis aeruginosa* on herbivorous zooplankton. *J. Plankton Res.*, **9**, 837–855.

Gaston, G. R., Cleveland, C. M., Brown, S. S. and Rakocinski, C. F. (1997) Benthic-pelagic coupling in Northern Gulf of Mexico estuaries: do benthos feed directly on phytoplankton. *Gulf Res. Rep.*, **9**, 231–237.

Gilmore, G. R. (1995) Environmental and biogeographic factors influencing ichtyofaunal diversity: Indian River Lagoon. *Bull. Mar. Sci.*, **57**, 153–170.

Goldman, J. C. and Carpenter, E. L. (1974) A kinetic approach to the effect of temperature on algal growth. *Limnol. Oceanogr.*, **19**, 756–766.

Grzebyk, D. and Berland, B. (1996) Influences of temperature, salinity and irradiance on growth of *Prorocentrum minimum* (Dinophyceae) from the Mediterranean Sea. *J. Plankton Res.*, **18**, 1837–1849.

Guillard, R. R. L., Carpenter, E. J. and Reimann, B. E. F. (1974) *Skeletonema menzelii* sp. Nov., a new diatom from the western Atlantic Ocean. *Phycologia*, **13**, 131–138.

Hallegraeff, G. M. (1993) A review of harmful algal blooms and their apparent global rise. *Phycologia*, **32**, 79–99.

Harding, L. W. (1994) Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow. *Mar. Ecol. Prog. Ser.*, **104**, 267–291.

Hargraves, P. E. (2002*a*) The ebridian flagellates *Ebria* and *Hermesinum*. *Plankton Biol. Ecol.*, **49**, 9–16.

Hargraves, P. E. (2002*b*) Diatoms of the Indian River Lagoon, Florida: an annotated account. *Florida Sci.*, **65**, 225–244.

Harrison, W. G. (1976) Nitrate metabolism of the red tide dinoflagellate *Gonyaulax polyedra* Stein. *J. Exp. Mar. Biol. Ecol.*, **21**, 9–209.

Hasle, G. R. and Syvertsen, E. (1996) Marine diatoms. In Tomas, C. R. (ed.), *Identifying Marine Diatoms and Dinoflagellates*. Harcourt & Brace, San Diego, CA, pp. 5–386.

Howell, J. R. (1953) *Gonyaulax monilata* sp. Nov., the causative dinoflagellate of a red tide on the east coast of Florida in August–September, 1951. *Trans. Am. Microsc. Soc.*, **72**, 153–156.

IOC (2002) IOC taxonomic reference list of toxic algae. Intergovernmental Oceanographic Commission of UNESCO. Available from: www.ioc.unesco.org/hab, last accessed June 12, 2002.

Jacobson, D. M. and Anderson, D. M. (1996) Widespread phagocytosis of ciliates and other protists by marine mixotrophic and heterotrophic thecate dinoflagellates. *J. Phycol.*, **32**, 279–285.

Jonge, V. N., Boynton, W., D'Elia, C. F., Elmgren, R. and Welsh, B. L. (1994) Responses to developments in eutrophication in four different North Atlantic estuarine systems. In Dyer, K. R. and Orth, R. J. (eds), *Changes in Fluxes in Estuaries*. Olsen & Olsen, Fredensborg, Denmark.

Kain, J. M. and Fogg, G. E. (1960) Studies on the growth of marine phytoplankton. III. *Prorocentrum micans*. *J. Mar. Biol. Assoc. UK*, **39**, 33–50.

Karentz, D. and Smayda, T. J. (1984) Temperature and seasonal occurrence patterns of 30 dominant phytoplankton species in Narragansett Bay over a 22-year period (1959–1980). *Mar. Ecol. Prog. Ser.*, **18**, 277–293.

Karentz, D. and Smayda, T. J. (1998) Temporal patterns and variations in phytoplankton community organization and abundance in Narragansett Bay during 1959–1980. *J. Plankton Res.*, **20**, 145–168.

Kennish, M. J. (1990) *Ecology of Estuaries*. CRC Press, Boca Raton, Florida.

Kilham, P. and Hecky, R. E. (1988) Comparative ecology of marine and freshwater phytoplankton. *Limnol. Oceanogr.*, **33**, 776–796.

Knoppers, B., Kjerfve, B. and Carmouze, J. P. (1991) Trophic state and water turn-over time in six choked coastal lagoons in Brazil. *Biogeochemistry*, **14**, 149–168.

Landsberg, J. H., Hall, S., Johannessen, J. N., White, K. D., Conrad, S. M., Flewelling, L. J., Dickey, R. W. *et al.* (2002) Pufferfish poisoning: widespread implications of saxitoxin in Florida. Abstracts of the International Harmful Algal Bloom Conference, October 21–26, 2002, St Petersburg, Florida.

Li, A., Stoecker, K., Coats, D. W. and Adams, E. J. (1996) Ingestion of fluorescently labeled and phycoerythrin-containing prey by mixotrophic dinoflagellates. *Aquat. Microb. Ecol.*, **10**, 139–147.

Livingston, R. J. (1990) Inshore marine habitats. In Meyers R. L. and Ewel J. J. (eds), *Ecosystems of Florida*. The University of Central Florida Press, Florida.

Lucas, L. V., Koseff, J. R., Cloern, J. E., Monismith, S. G. and Thompson, J. K. (1999) Processes governing phytoplankton blooms in estuaries. I. The local production-loss balance. *Mar. Ecol. Prog. Ser.*, **187**, 1–15.

Luckenbach, M. W., Sellner, K. G., Shumway, S. E. and 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* (Gmelin 1791). *J. Shellfish Res.*, **12**, 411–415.

Lukatelich, R. J. and McComb, A. J. (1986) Distribution and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. *Mar. Ecol. Prog. Ser.,* **27**, 287–297.

Lundholm, N., Moestrup O., Hasle G. R. and Hoef-Emden, K. (2003) A study of the *Pseudo-nitzschia pseudodelicatissima/cuspidata* complex (Bacillariophyceae): what is *P. pseudodelicatissima*? *J. Phycol.*, **39**, 797–813.

Margalef, R. (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta*, **1**, 493–509.

Margalef, R. (1997) Red tides and ciguatera as successful ways in the evolution and survival of an admirable old phylum. In Reguera, B., Blanco, J., Fernandez, L. and Wyatt, T. (eds), *Harmful Algae.* Proceedings of the VIII International Conference on harmful algae, Vigo, Spain, June 25–29, 1997, pp. 3–7.

Margalef, R., Estrada, M. and Blasco, D. (1979) Functional morphology of organisms involved in red tide as adapting to decaying turbulence. In Taylor, D. L. and Seliger, H. H. (eds), *Toxic Dinoflagellate Blooms.* Elsevier, New York, pp. 89–94.

Marshall, H. G. (1982) The composition of phytoplankton within the Chesapeake Bay plume and adjacent waters off the Virginia Coast. *Estuarine Coastal Shelf Sci.*, **15**, 29–43.

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

Norris, D. R. (1983) The occurrence of a toxic dinoflagellate in the Indian River system. *Florida Sci.*, **46**, 150–153.

Olsson, P. and Granelli, E. (1991) Observations on diurnal vertical migration and phased cell division for three coexisting marine dinoflagellates. *J. Plankton Res.*, **13**, 1313–1324.

Oliviera, A. M. and Kjerfve, B. (1993) Environmental responses of a tropical coastal lagoon system to hydrological variability: Mundau-Manguaba, Brazil. *Estuarine Coastal Shelf Sci.,* **37**, 575–591.

Paache, E., Bryceson, I. and Tangen, K. (1984) Interspecific variation in dark nitrogen uptake by dinoflagellates. *J. Phycol.*, **20**, 394–401.

Phlips, E. J. and Badylak, S. (1996) Spatial variability in phytoplankton standing crop and composition in a shallow inner shelf lagoon, Florida Bay, Florida. *Bull. Mar. Sci.*, **58**, 203–206.

Phlips, E. J., Badylak, S. and Lynch, T. C. (1999) Cyanobacterial blooms in Florida Bay. *Limnol. Oceanogr.*, **44**, 1166–1175.

Phlips, E. J., Badylak, S. and Grosskopf, T. (2002) Factors affecting the abundance of phytoplankton in a restricted subtropical lagoon, the Indian River Lagoon, Florida, USA. *Estuarine Coastal Shelf Sci.*, **55**, 385–402.

Phlips, E. J., Badylak, S., Youn, S. and Kelley, K. (2004*a*) 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., Love, N., Badylak, S., Hansen, P., Lockwood, J., John, C. and Gleeson, R. (2004*b*) A comparison of water quality and hydrodynamic characteristics of the Guana Tolomato Matanzas National Estuarine Research Reserve and the Indian River Lagoon of Florida. *J. Coast. Res.*, in press.

Qasim, S. Z., Bhattathiri, P. M. A. and Devassy, V. P. (1972) The influence of salinity on the rate of photosynthesis and abundance of some tropical phytoplankton. *Mar. Biol.*, **12**, 200–206.

Rey, J. T., Kain, T. and Stahl, R. (1991) Wetland impoundments of east-central Florida. *Florida Sci.*, **54**, 33–40.

Ricard, M. I. (1987) *Atlas Du Phytoplancton Marin, Diatomophycées vol. 2.* Editions Du Centre National De La Recherche Scientifique, Anatole, France, pp. 1–297.

Richardson, W. (2001) Florida Bay microalgal blooms: competitive advantage of dominant species. Abstracts 2001 Florida Bay Science Conference, Key Largo, Florida. Florida Sea Grant, Gainesville, Florida.

Rijstenbil, J. W. (1988) Selection of phytoplankton species in culture by gradual salinity changes. *Neth. J. Sea Res.*, **22**, 291–300.

Sciandra, A. (1991) Coupling and uncoupling between nitrate uptake and growth rate in *Prorocentrum minimum* under different frequencies of pulsed nitrate supply. *Mar. Ecol. Prog. Ser.*, **72**, 261–269.

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

Shumway, S. E. (1990) A review of the effects of algal blooms on shellfish and aquaculture. *J. World Aquaculture Soc.*, **21**, 65–104.

Sigua, G. C. and Tweedale, W. A. (2003) Watershed scale assessment of nitrogen and phosphorus loadings in the Indian River Lagoon basin, Florida. *J. Environ. Man.*, **67**, 363–372.

Skovgaard, A. (1996) Mixotrophy in *Fragilidium subglobosum* (Dinophyceae): growth and grazing response as functions of light intensity. *Mar. Ecol. Prog. Ser.*, **143**, 247–253.

Smayda, T. J. (1978) From phytoplankton to biomass. In Sournia, A. (ed.), *Phytoplankton Manual.* United Nations Educational, Scientific and Cultural Organization, Paris, pp. 273–279.

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

Smayda, T. J. (1992) Global epidemics of noxious phytoplankton blooms and food chain consequences in large ecosystems. In Sherman, K., Alexander, L. M. and Gold, D. G. (eds), *Food Chains, Models and Management of Large Marine Ecosystems.* Westview Press, San Francisco, California, pp. 275–307.

Smayda, T. J. and Reynolds, C. S. (2001) Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *J. Plankton. Res.*, **23**, 447–461.

Smith, N. P. (1993) Tidal and nontidal flushing of Florida's Indian River Lagoon. *Estuaries*, **16**, 739–746.

Sournia, A. (1986) *Atlas du phytoplancton marin. Vol. 1. Introduction, Cyanophycees, Dictyochophycees, Dinophycees, et Raphidophycees.* Centre National de la Recherche Scientifique, Paris, pp. 1–219.

Steidinger, K. A. (1979) Collection, enumeration and identification of free-living marine dinoflagellates, In Taylor, D. L. and Seliger, H. H. (eds), *Toxic Dinoflagellate Blooms.* Elsevier, New York, pp. 435–442.

Steidinger, K. A. and Tangen, K. (1996) Dinoflagellates. In Tomas C. R. (ed.) *Identifying Marine Diatoms and Dinoflagellates*. Academic Press, New York, pp. 387–598.

Steidinger, K. A. and Williams, J. (1970) *Dinoflagellates 'Memoirs of the Hourglass Cruises', Vol. 2*. Florida Department of Natural Resources Marine Research Laboratory, St Petersburg, Florida.

Steidinger, K. A., Landsberg, J., Truby, E. W. and Roberts, B. S. (1998) First report of *Gymnodinium pulchellum* (Dinophyceae) in North America and associated fish kills in the Indian River, Florida. *J. Phycol.*, **34**, 431–437.

Stoecker, D. K., Li, A., Coats, D. W., Gustafson, D. E. and Nannen, M. K. (1997) Mixotrophy in the dinoflagellate *Prorocentrum minimum* (Dinophyceae). *Mar. Ecol. Prog. Ser.*, **152**, 1–12.

Tester, L. A. and Steidinger, K. A. (1979) Phytoplankton. In Walker, L. M. and Steidinger, K. A. (eds), *Nearshore Marine Ecology at Hutchinson Island, Florida: 1971–1974*. Florida Marine Research Publication 34, Florida Dept. of Natural Resources, St Petersburg, Florida, pp. 16–61.

Ukeles, R. and Sweeney, B. M. (1969). Influence of dinoflagellate trichocysts factors on the feeding of *Crassostrea virginica* larvae on *Monochrysis lutheri*. *Limnol. Oceanogr.*, **14**, 403–410.

Utermohl, H. (1958) Zur vervollkommnung der quantitativen phytoplankton-methodik. *Mitt. Int. Ver. Theo. Angew. Limnol.*, **9**, 1–38.

Virnstein, R. W. (1990) The large temporal and spatial variability of the Indian River Lagoon. *Florida Sci.*, **53**, 249–256.

Wikfors, G. H. and Smolowitz, R. M. (1995) Experimental and histological studies of four life-history stages of the eastern oyster, *Crassostrea virginica*, exposed to a cultured strain of the dinoflagellate *Prorocentrum minimum*. *Biol. Bull.*, **188**, 313–328.

Wilkinson, L. (1993) Systat for desktop analysis. Chapman & Hall Publications, New York.

Wyatt, T. and Horwood, J. (1973) A model which generates red tides. *Nature*, **244**, 238–240.