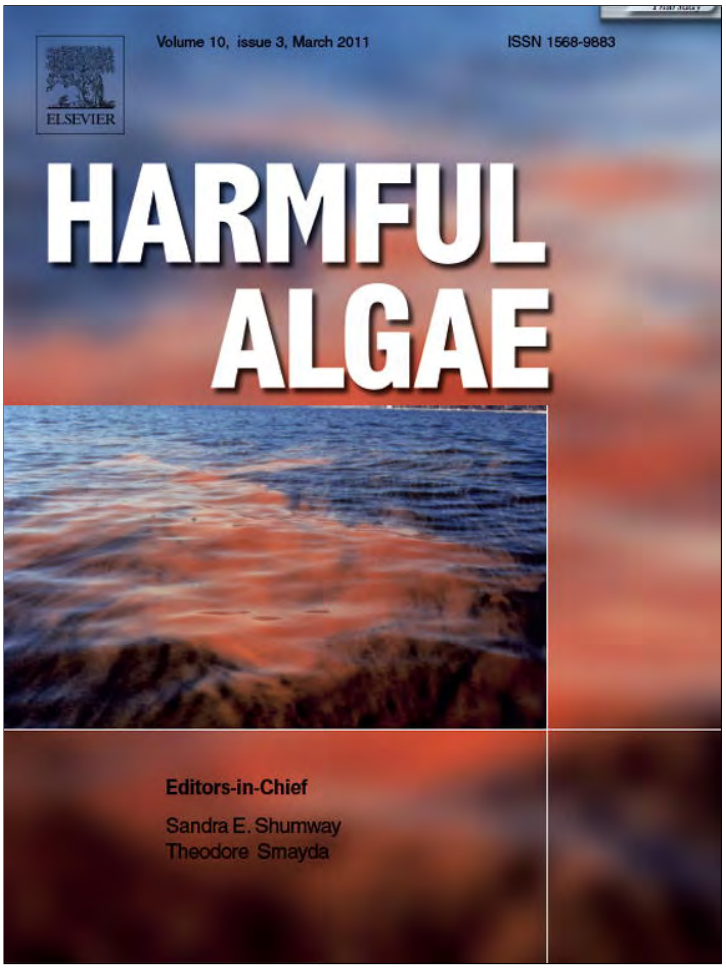

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Scales of temporal and spatial variability in the distribution of harmful algae species in the Indian River Lagoon, Florida, USA

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ABSTRACT

This paper describes the results of a harmful algal bloom (HAB) monitoring effort in the Indian River Lagoon. The goal of the study was to describe spatial and temporal variability in the distribution, frequency of occurrence, and composition of HABs, along with an examination of potential driving factors, such as hydrologic conditions and nutrient concentrations. Six sampling sites in the northern lagoon were selected for the study. The composition and abundance of the phytoplankton community was determined microscopically. Water column parameters measured in the study included salinity, water temperature, Secchi depth, total phosphorus, and total nitrogen.

Dinoflagellates, diatoms or cyanobacteria dominated the phytoplankton communities in terms of biovolume at all six sampling sites. Five potential toxin producing species were observed at bloom levels during the study period, including the diatom *Pseudo-nitzschia calliantha* and the dinoflagellates *Pyrodinium bahamense* var. *bahamense*, *Prorocentrum rathymum*, *Cochlodinium polykrikoides*, and *Karlodinium veneficum*. The saxitoxin-producing dinoflagellate *P. bahamense* var. *bahamense* had the highest biovolume observed over the study period, 33.9×10^6 μm^3 ml^{-1}, and was present in almost half of the samples collected. Three non-toxic HAB species were observed at bloom levels of biovolume, including *Akashiwo sanguinea*, *Peridinium quinquecorne*, and *Kryptoperidinium foliaceum*. As part of this study, a statistical approach to estimating the probability of detecting HAB events was explored, using three common and important HAB species in the IRL, *P. bahamense* var. *bahamense*, *A. sanguinea* and *P. calliantha*, as exemplars. The potential driving factors for HAB events are discussed within the context of the hydrological, meteorological and watershed characteristics of the lagoon.

1. Introduction

Global increases in cultural eutrophication and the potential for climate change, have heightened concerns over future threats to the integrity of coastal phytoplankton communities (Paerl, 1988; Hallegraeff, 2003; Phlips, 2002; Cloern, 2001; Smetacek and Cloern, 2008), such as increases in the frequency and intensity of harmful algal blooms (HABs) (Nixon, 1995; Smayda, 1989, 1997; Anderson et al., 1998; Sellner et al., 2003; Glibert and Burkholder, 2006). In response, long-term monitoring programs have been established to document bloom dynamics in ecosystems at risk, and build data bases of information from which models can be developed to predict future trends in HABs (Andersen, 1996; Smayda, 1997; Sellner et al., 2003; Franks, 2008; Zingone et al., 2010). One of the major challenges in designing such monitoring programs is dealing with variability in HAB events that span a wide range of spatial and temporal scales (Andersen, 1996; Chang and Dickey, 2008; Cullen, 2008).

This paper describes the results of a HAB monitoring study in the northern and central Indian River Lagoon (IRL) in Florida. The

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goal of the study was to describe spatial and temporal variability in the distribution, frequency of occurrence, intensity and composition of HABs, and examine how different spatial and temporal scales of sampling affect the detection of HAB events. The IRL, which spans over 220 km of the east coast of Florida, is characterized by a number of sub-basins with different environmental characteristics and algal populations (Phlips et al., 2002, 2010; Badylak and Phlips, 2004). While HAB events have been observed throughout the IRL, areas subject to long water residence time in the northern lagoon have been particularly prone to intense blooms (Phlips et al., 2004, 2010), and were the focus of this study. Of particular concern is the repeated occurrence of intense blooms of the toxic dinoflagellate *Pyrodinium bahamense* var. *bahamense* (Phlips et al., 2006), which has been linked to the appearance of saxitoxin in the tissues of certain fish species in the IRL (Landsberg et al., 2006; Abbott et al., 2009). The results of the study highlight the importance of differences in growth, longevity and ecological strategies of individual HAB species in defining their distribution and probability of detection. Possible driving factors for HAB events are also discussed, including the importance of meteorological conditions, in relation to shifts in salinity, temperature and nutrient concentration.

2. Methods

2.1. Site description

Six sampling sites were selected for the study, three in the northern and central Indian River Lagoon, and three in adjacent intra-coastal lagoons linked to the IRL via canals and waterways, the Mosquito Lagoon (1 site) and the Banana River (2 sites) (Fig. 1). For simplification the overall study region is described as the Northern Indian River Lagoon, or NIRL. The sampling sites included: (1) in the southern Mosquito Lagoon, near a canal which links the Mosquito Lagoon to the northern-most reach of the IRL; (2) in the IRL, near the city of Titusville; (3) in the northern Banana River, (4) in the IRL, near the city of Cocoa; (5) in the central Banana River, near the city of Cocoa Beach, and (6) in the central IRL, near the city of Melbourne. Mean depths at Sites 1 and 4 were near 1 m. Mean depths at Sites 2, 3, and 5 were 1.7–1.9 m. Mean depth at Site 6 was near 2.5 m.

The entire NIRL region is microtidal and has long water residence times, with average estimated mean water half-lives (standardized to unit volume of water) ranging from several weeks at the southern most site (Site 6), 1–2 months at Sites 1, 2, 4 and 5, and up to five months at Site 3 (Sheng and Davis, 2003; Steward et al., 2005; Reyier et al., 2008; D. Christian, unpublished data).

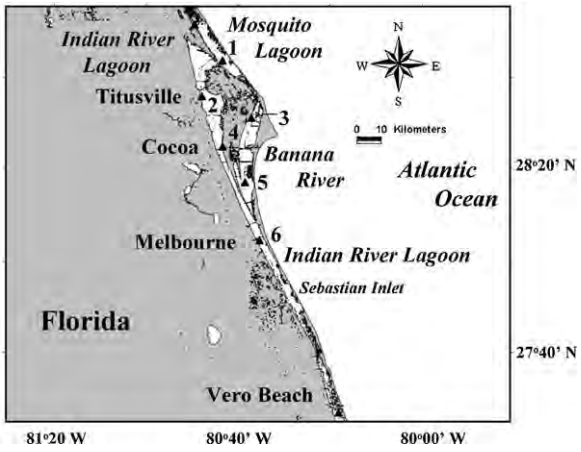

Fig. 1. Locations of the six sampling sites.

Watersheds draining different regions of the IRL basin vary in size and land-use characteristics (Adkins et al., 2004). Sites 1 and 3 are associated with relatively small watersheds, with high waterbody/watershed area ratios, and a high proportion of undeveloped wetlands. Sites 4 and 5 also have relatively high basin/watershed area ratios, but are characterized by significant urban/residential areas and light industry (Steward et al., 2005). Sites 4 and 6 are located in basins associated with somewhat larger watersheds, including urban and agricultural land uses.

2.2. Field and laboratory procedures

Salinity and temperature were measured with YSI or Hach/Hydrolab environmental multi-probes. Water was collected at the sampling sites using a vertical integrating sampling tube that captures water evenly from the surface to within 0.1 m of the bottom. Split phytoplankton samples were preserved on site, one with Lugol's and the other with gluteraldehyde in 0.1 M sodium cacodylate buffer. Additional aliquots of water were frozen for determination of total nitrogen and total phosphorus, using the persulfate digestion method (APHA, 1989; Parsons et al., 1984).

2.3. Phytoplankton analysis

General phytoplankton composition was determined using the Utermöhl method (Utermöhl, 1958). Samples preserved in Lugol's were settled in 19 mm diameter cylindrical chambers. Phytoplankton cells were identified and counted at 400× and 100× with a Leica phase contrast inverted microscope. At 400×, a minimum of 100 cells of a single taxon 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 taxon was reached. At 100×, a total bottom count was completed for taxa >30 μm in size. Light microscopy was aided by other techniques for proper identification, such as the squash technique (Steidinger, 1979) and scanning electron microscopy (Badylak et al., 2004).

Fluorescence microscopy was used to enumerate picoplanktonic cyanobacteria at 1000× magnification (Phlips et al., 1999). Subsamples of seawater were filtered onto 0.2 μm Nuclepore filters and mounted between a microscope slide and cover slip with immersion oil. If not analyzed immediately, slides were stored in a freezer and counted at within 72 h.

Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa (Smayda, 1978). Specific phytoplankton dimensions were measured for at least 30 randomly selected cells. Species which vary in size, such as many diatom species, were placed into size categories.

For the purpose of description and discussion, 'blooms' were defined as phytoplankton biovolumes for individual species which fell within the top 5% of biovolumes observed over the study period for all individual species, i.e. $>10^6$ μm^3 ml^{-1}.

2.4. Statistical methods

Basic statistical procedures (i.e. determination of mean values, standard deviations, Pearson Correlation Coefficients) were carried out using SAS v9.2 (SAS Institute, Cary, North Carolina, USA).

As part of this study, a statistical approach was explored for estimating the probability of detecting blooms, given different sampling intervals. When systematic sampling is used, that is when measurements are taken on a regularly recurring schedule, the probability that a particular bloom will be observed during the study is a function of the length of time (L) that the phytoplankton species is at bloom levels, the number and temporal dispersion of the blooms, and the time interval between sampling dates (I). The probability that a systematic sample regime S (the set of dates on

which measurements are taken) at time interval I intersects a bloom in period B (the set of contiguous dates on which the bloom occurs) of length L is given by:

$$P(S \cap B) = \begin{cases} \frac{L}{I} & L < I \\ 1 & L \geq I^* \end{cases}$$

For example, if a 10-day bloom occurs during a study in which a two-week sampling design is used, the probability of the bloom being observed is 0.714 (=10/14) if the start date of the systematic sample is random. To provide approximations for estimating the effect of sampling interval and bloom length on the probability of detecting a HAB event, the observed biovolumes of the dinoflagellate *P. bahamense* var. *bahamense*, *Akashiwo sanguinea*, and the diatom *Pseudo-nitzschia calliantha* were used to predict the daily values for dates on which sampling was not performed. To obtain a complete daily time series for the study period, a non-parametric smoothing function was used to fit a cubic spline to the observed biovolumes for each species at each station. The cubic spline method uses a set of third-degree polynomials spliced together such that the resulting curve is continuous and smooth at the splices (knot points). An example of the predicted time series for a single station for *P. bahamense* is shown in Fig. 11.

Dinoflagellate blooms were defined as biovolumes above 10^6 μm^3 ml^{-1}. For the diatom *P. calliantha* the bloom threshold level was based on the cell density above which health warnings are administered in many countries around the world, i.e. 200 cells ml^{-1} (Andersen, 1996), equivalent to a biovolume of 0.06×10^6 μm^3 ml^{-1}. The simulated bloom lengths for *P. bahamense* over all of the stations were 4, 10, 11, 13, 14, 16, 18, 24, 25, 32, 70, 92, and 149 days. Using the simulated time series which incorporate lengths of blooms as well as the temporal distribution of the blooms, the probability of observing a bloom was estimated by systematically sampling from these daily time series using different intersampling intervals (I). We used intervals of one, two, four and eight weeks. Sampling was done by using every possible start date for a systematic sample of a given intersampling interval so that all possible systematic samples for each I were performed. The probability of intersecting a bloom of a particular length during the study period was calculated using the set of systematic samples with the same interval. All analyses were done using R (R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org).

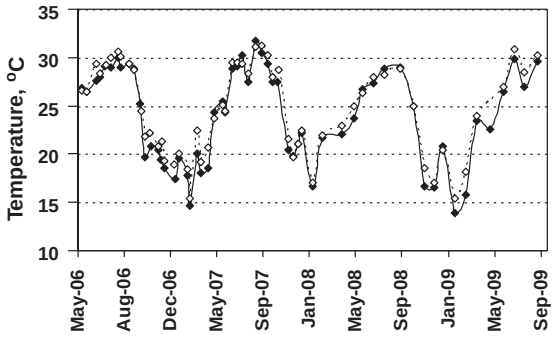

Fig. 2. Surface water temperatures at Sites 2 (closed circles) and 6 (open circles).

GIS images of HAB distribution were generated using the Arc Map Spatial Analyst Extension feature of Arc View 9.3 (ESRI, Redlands, California, USA), to illustrate the spatial distribution of single-species blooms using supplemental monitoring data. Interpolations were done using Inverse Distance Weighting (IDW).

3. Results

3.1. Physical-chemical and meteorological characteristics

Water temperatures over the study period reflected the subtropical climate of central Florida, with temperatures in excess of 20 °C through most of the study period (Fig. 2). In the Spring of 2006 there was an early increase in water temperature due to exceptionally high air temperatures in April station (U. S. National Climate Data Center, www.ncdc.noaa.gov).

Monthly rainfall totals ranged from 0 to 39 cm at the Titusville meteorological station and from 0.2 to 68 cm at the Melbourne meteorological station (U. S. National Climate Data Center, www.ncdc.noaa.gov) (Fig. 3). Rainfall was generally greater from May through October (the wet season) than November through April (the dry season). The wet seasons included in the study period had different rainfall patterns. Monthly rainfall totals in the wet season of 2006 were near, to somewhat above, 'normal' from May through September. In 2007, monthly rainfall totals during

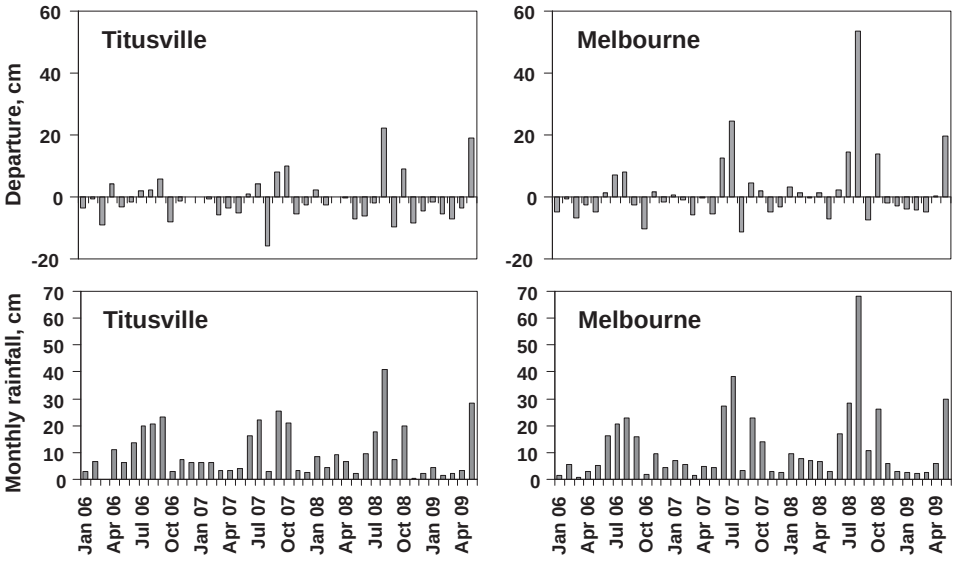

Fig. 3. Monthly rainfall totals (cm) at meteorological stations in Titusville (bottom left frame) and Melbourne (bottom right frame), and departure from normal (cm) in Titusville (top left frame) and Melbourne (top right frame) (after U. S. National Climate Data Center, Florida Climatological Record).

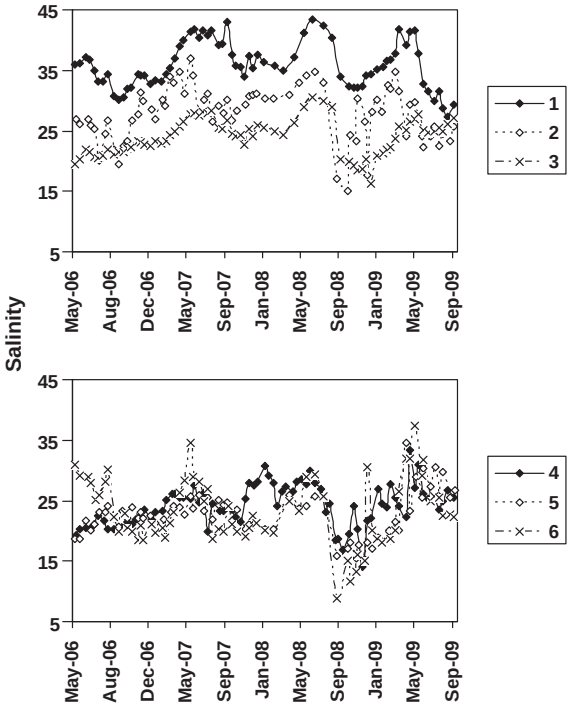

Fig. 4. Surface water salinities at the six sites in the NIRL.

the wet season varied from well-below normal in May, the last month of a six-month drought period, to well above average in June, July and September, particularly at the Melbourne meteorological station, which had large rainfall peaks in June and July. In 2008, monthly rainfall totals were above normal most of the wet season at the Melbourne meteorological station, including well above normal totals in July, August and October. The August peak was associated with the passage of tropical storm Fay. At the Titusville meteorological station rainfall was only above normal in August and October, with the remainder of the wet season being below normal.

Salinities for the study period ranged from near 10 at Site 6 near Melbourne to 42 at Sites 1 in the Mosquito Lagoon (Fig. 4). The timing and extent of salinity variation differed between sites. The most prominent feature shared by all sites was a sharp decline in salinity associated with very high rainfall in the summer/fall of 2008.

Mean water column transparency values, expressed as Secchi disk depths, were near 1.5 m at all sites except Site 4. Mean Secchi depth at Site 4 was 0.6 m, reflecting the shallow depth (<1.0 m) and high potential for sediment re-suspension.

Mean total nitrogen (TN) concentrations at Sites 1 through 6 were 1070 $\mu g\ N\ l^{-1}$ (Std = 298), 1083 $\mu g\ N\ l^{-1}$ (Std = 313), 1226 $\mu g\ N\ l^{-1}$ (Std = 280), 1134 $\mu g\ N\ l^{-1}$ (Std = 303), 1167 $\mu g\ N\ l^{-1}$ (Std = 318), and 809 $\mu g\ N\ l^{-1}$ (Std = 298), respectively. Temporal patterns of TN concentration were similar at all sites, with declining values through the drought period from the fall of 2006 through the Spring of 2007. Increases in TN in the summer and fall of 2007 coincided with increases in rainfall. Increases in TN concentrations also coincided with high rainfall experienced in the late summers/early fall of 2008 at all six sites. The positive relationships between TN concentration, rainfall and freshwater inflow were reflected in the significant negative correlations between salinity and TN at most sites (Table 1).

Mean total phosphorus (TP) concentrations at Sites 1 through 6 were 38 $\mu g\ P\ l^{-1}$ (Std = 17), 45 $\mu g\ P\ l^{-1}$ (Std = 16), 39 $\mu g\ P\ l^{-1}$ (Std = 13), 93 $\mu g\ P\ l^{-1}$ (Std = 48), 48 $\mu g\ P\ l^{-1}$ (Std = 16), and 55 $\mu g\ P\ l^{-1}$ (Std = 19), respectively. Temporal variability of TP concentration was less predictable than TN concentration.

Table 1
Pearson correlation coefficients for relationships between salinity, chlorophyll *a*, total phosphorus (TP), and total nitrogen (TN) at the six sampling sites. Coefficients shown in italics were not significant at the $p = 0.05$ level.

Site	Salinity ×		Chlorophyll *a* ×	
	TN	TP	TN	TP
1	*−0.04*	0.26	0.20	*0.16*
2	−0.47	−0.28	0.34	0.46
3	−0.42	*0.12*	0.21	0.34
4	*−0.15*	*−0.08*	0.27	0.43
5	−0.45	*0.16*	*0.11*	0.51
6	−0.46	0.21	0.38	*0.06*

Correlations between TP and salinity varied by site and were not significant at Sites 3–5 (Table 1), suggesting that other factors may significantly contribute to variability in TP, such as internal loading processes (e.g. sediment resuspension).

Mean chlorophyll *a* concentrations at Sites 1 through 6 were 6.2 $\mu g\ l^{-1}$ (Std = 35), 8.0 $\mu g\ l^{-1}$ (Std = 5.6), 8.6 $\mu g\ l^{-1}$ (Std = 5.7), 16.4 $\mu g\ l^{-1}$ (Std = 12.2), 10.0 $\mu g\ l^{-1}$ (Std = 7.7), and 11.9 $\mu g\ l^{-1}$ (Std = 9.3), respectively. Chlorophyll *a* concentrations were positively correlated to TP and TN at Sites 2–5 (Table 1), but the correlation coefficients for TN were lower than for TP. At Sites 1 and 6, chlorophyll *a* concentrations were only correlated to TN.

3.2. Phytoplankton biomass

Mean total phytoplankton biovolumes at Sites 1 through 6 were $2.31 \times 10^6\ \mu m^3\ ml^{-1}$ (Std = 2.45×10^6), $2.68 \times 10^6\ \mu m^3\ ml^{-1}$ (Std = 3.15×10^6), $3.58 \times 10^6\ \mu m^3\ ml^{-1}$ (Std = 2.88×10^6), $4.91 \times 10^6\ \mu m^3\ ml^{-1}$ (Std = 5.69×10^6), $5.21 \times 10^6\ \mu m^3\ ml^{-1}$ (Std = 7.14×10^6), and $4.23 \times 10^6\ \mu m^3\ ml^{-1}$ (Std = 19×10^6), respectively. The mean values for all six sites were subject to large standard deviations, reflecting the periodic appearance of blooms (Fig. 5). Dinoflagellates, diatoms or cyanobacteria dominated the phytoplankton communities during bloom conditions in terms of biomass (i.e. expressed as biovolume), as illustrated by the time series of phytoplankton biovolume (Fig. 5). Although major blooms were relatively rare at Site 1, they were typically dominated by diatoms, including *P. calliantha*, *Chaetoceros simplex* and *Dactyliosolen fragilissimus* (Fig. 5). At Site 2, the largest blooms were dominated by dinoflagellates, typically involving the HAB species *P. bahamense* var. *bahamense* and *A. sanguinea* (Fig. 5). A mixture of dinoflagellate and diatom blooms was observed at Site 3, including the dinoflagellates *P. bahamense* var. *bahamense* and *A. sanguinea*, and the diatoms *P. calliantha*, *D. fragilissimus* and *Corataulina pelagica*. As in the case of Site 2, blooms at Site 4 were dominated either by the diatom *D. fragilissimus* or by the dinoflagellates *P. bahamense* var. *bahamense*, *Karlodinium veneficum*, *Kryptoperidinium foliaceum*, *Peridinium quinquecorne* and *Prorocentrum rathymum*. At Site 5, the highest phytoplankton biovolumes observed over the study period frequently involved the dinoflagellate *P. bahamense* var. *bahamense* and three diatom species, i.e. *C. pelagica*, *D. fragilissimus* and *Rhizosolenia setigera* (Fig. 5). At Site 6, many of the peaks in phytoplankton biovolume were dominated by diatoms, including *Leptocylindrus minimus*, Leptocylindrus danicus, *C. pelagica*, *D. fragilissimus* and *R. setigera* (Fig. 5). Several blooms of *P. bahamense* var. *bahamense* and *A. sanguinea* were also observed at Site 6 in 2006.

3.3. HAB species

Twenty-four phytoplankton taxa that appear on major lists of harmful algal bloom (HAB) species (Landsberg, 2002; FWC, 2009; IOC, 2009) were observed over the study period (Table 2). Among the 24 HAB species, 16 are considered potential toxin producers, while the remaining eight have been associated with other harmful

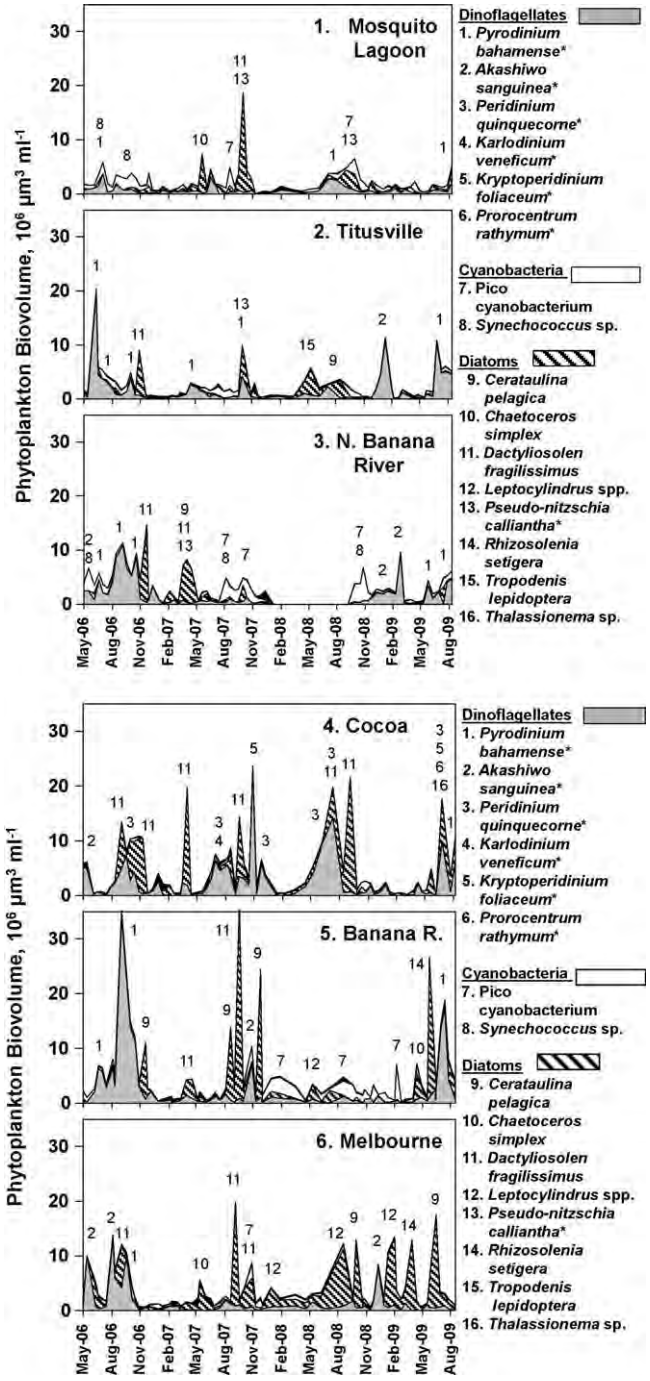

Fig. 5. Biovolume contribution of the major phytoplankton groups to total phytoplankton biovolume. The major groups include dinoflagellates (grey), diatoms (cross hatch) and cyanobacteria (white), and other (black), which includes the remainder of the phytoplankton taxa observed in each sample. The species associated with some of the major peaks in biovolume are shown as numbers above the peaks. Species with '*' indicates a HAB species.

effects, such as hypoxia. Eight of the HAB species were observed at bloom levels of biomass (defined as biovolumes $> 10^6\ \mu m^3\ ml^{-1}$); including the diatom *P. calliantha*, and the dinoflagellates *P. bahamense* var. *bahamense*, *A. sanguinea*, *P. quinquecorne*, *K. foliaceum*, *K. veneficum*, *Cochlodinium polykrikoides* and *P. rathymum* (Table 2).

The HAB species most commonly observed at bloom levels of biovolume was *P. bahamense* var. *bahamense* (Table 2). The saxitoxin-producing dinoflagellate had the highest biovolume observed over the study period, $33.9 \times 10^6\ \mu m^3\ ml^{-1}$, and was observed at bloom levels in 51 samples, primarily during the summer and fall of 2006 and 2008 (Fig. 5). *A. sanguinea* was the HAB species with the second largest number of bloom observations, i.e. 17 (Table 2). The most intense blooms of *A. sanguinea* were observed in three time windows, the spring of 2006, fall of 2007 and winter of 2009 (Fig. 5). The only HAB diatom commonly observed at bloom levels was *P. calliantha* (Table 2), a potential domoic acid producing diatom (Landsberg, 2002). *K. veneficum*, a dinoflagellate associated with the production of the icthyotoxic karlotoxins (Landsberg, 2002), was the most frequently observed HAB species during the study period, appearing in 272 of 419 samples (Table 2), but seldom reached bloom levels.

Five other HAB species were observed at cell densities greater than 100 cells ml^{-1}; including the dinoflagellates *Prorocentrum minimum* and *Takayama tasmanica*; the diatom *Pseudo-nitzschia turgidula*; and the haptophytes *Chrysochromulina* spp. and *Prymnesium* spp. (Table 2). None of the latter five species were observed at bloom levels of biovolume, although *Chrysochromulina* spp. came close at Site 4 in the Summer of 2007, with a biovolume of $0.88 \times 10^6\ \mu m^3\ ml^{-1}$.

A number of potentially toxic species were occasionally observed, generally at densities below 100 cells ml^{-1}. Included in this list were two potentially toxic species from the genus *Karenia*, i.e. mikimotoi and brevis, as well as the potentially toxic raphidophyte *Chattonella* spp. (Table 2). The potential PSP-producing species *Alexandrium monilatum* was observed in four samples, but at densities below 10 cells ml^{-1}. Although cell densities for these HAB species were relatively low, there were some observations that exceeded thresholds of concern established by management organizations. For example, the observation of *K. brevis* at 50 cells ml^{-1} on June 9, 2007 at Site 1 is 10-fold higher than the alert threshold established by the Florida Fish and Wildlife Commission (FWC, 2009).

3.4. The distribution of major bloom-forming species

Many of the major bloom-forming phytoplankton species were widely distributed through the NIRL, but bloom events of certain species were more spatially restricted. The most prominent HAB dinoflagellate *P. bahamense* var. *bahamense*, was observed at bloom levels at all six sites (Fig. 6). Blooms of *A. sanguinea* were also widely distributed, appearing at Sites 2–6 (Fig. 6). Similarly, blooms of the major non-HAB diatoms and cyanobacteria were widely distributed throughout the NIRL, as exemplified by the distribution of *D. fragilissimus* and picoplanktonic cyanobacteria (Fig. 6). Some other bloom-forming HAB species showed spatially biased distribution. The HAB diatom *P. calliantha* was only observed at bloom levels at Sites 1–3. Some HAB dinoflagellates were only observed at bloom levels at Site 4, including *K. veneficum*, *K. foliaceum*, and *P. quinquecorne* (Fig. 6).

From an ecophysiological perspective, many of the bloom-forming phytoplankton in the NIRL were observed over a wide range of salinities, as exemplified by the HAB species *P. bahamense* var. *bahamense*, *A. sanguinea*, *P. calliantha*, and *P. quinquecorne* (Fig. 7). The major non-HAB diatoms, such a *D. fragilissimus*, and picoplanktonic cyanobacteria were also euryhaline in their distribution (Fig. 7). Peak levels of biomass were commonly observed at mid-range salinities (i.e. 20–30 psu) (Fig. 7).

The distribution of major bloom-forming phytoplankton species according to water temperature showed some disparities (Fig. 8). The tropical dinoflagellate *P. bahamense* var. *bahamense* was not observed at significant concentrations below 20 °C, and blooms were generally confined to temperatures above 25 °C. Blooms of *P. quinquecorne* were similarly most abundant above 25 °C. By contrast, blooms of *A. sanguinea* were observed at temperatures from 12 to 30 °C, as were blooms of picoplanktonic cyanobacteria and the diatom *D. fragilissimus*.

Table 2
Species of phytoplankton observed during the study period, which appear on Harmful Algal Bloom lists (FWC, 2009; IOC, 2009). First column shows the number of samples containing the species, out of a total of 410 samples. The second column shows the highest biovolume observed for each species and the third column the highest cell density. The final column shows the number of 'bloom' ($>10^6$ μm^3 ml^{-1}) observations for each species. The first column shows group identities; 'Df' for dinoflagellates (*Dinophyceae*), 'Di' for diatoms (*Bacillariophyceae*), 'R' for raphidiophytes (*Raphidophyceae*) and 'H' haptophytes (*Prymnesiophyceae*).

HAB species	Group	Obs.	Maximum biovolume 10^6 μm^3 ml^{-1}	Maximum density cells ml^{-1}	Bloom Obs.
Pyrodinium bahamense[a]	Df	198	33.94	928	51
Akashiwo sanguinea[b]	Df	186	12.55	176	17
Peridinium quinquecorne[a]	Df	44	10.35	1,556	11
Pseudo-nitzschia calliantha[a]	Di	90	5.07	16,780	5
Kryptoperidinium foliaceum[b]	Df	34	22.66	3848	5
Karlodinium veneficum[a]	Df	274	3.93	4485	3
Prorocentrum rathymum[a]	Df	39	16.68	944	1
Cochlodinium polykrikoides[a]	Df	56	1.21	39	1
Gonyaulax polygramma[b]	Df	97	0.50	11	0
Prorocentrum minimum[a]	Df	72	0.48	302	0
Gyrodinium instriatum[b]	Df	52	0.14	5	0
Oxyphysis oxytoxides[b]	Df	50	0.39	26	0
Takayama tasmanica[a]	Df	39	0.25	127	0
Chrysochromulina spp.[a]	H	35	0.88	5980	0
Pseudo-nitzschia turgidula[a]	Di	23	0.52	2431	0
Takayama pulchella[a]	Df	17	0.12	60	0
Gonyaulax spinifera[b]	Df	13	0.02	2	0
Chattonella spp.[a]	R	12	0.12	20	0
Prorocentrum lima[a]	Df	11	0.03	1	0
Prymnesium spp.[a]	H	9	0.01	290	0
Karenia mikimotoi[a]	Df	6	0.13	30	0
Alexandrium monilatum[a]	Df	5	0.05	3	0
Karenia brevis[a]	Df	2	0.22	50	0
Gyrodinium impudicum[b]	Df	1	0.01	1	0

[a] Refers to potentially toxic species.
[b] Refers to species associated with other harmful effects, such as fish kills not necessarily associated with toxins.

In addition to the more general distribution patterns of bloom-forming species, the frequent and widespread presence of *P. bahamense* var. *bahamense* provided an opportunity to examine more specific spatial issues. For example, in a limited test of vertical stratification of HAB species, the distribution of *P. bahamense* var. *bahamense* was examined on several sampling dates during a bloom event at Site 2. On the first sampling date, clear skies prevailed, and *P. bahamense* var. *bahamense* densities were four-fold higher in the bottom water sample (depth = 2 m) than in the surface or mid-column (depth = 1 m) water samples

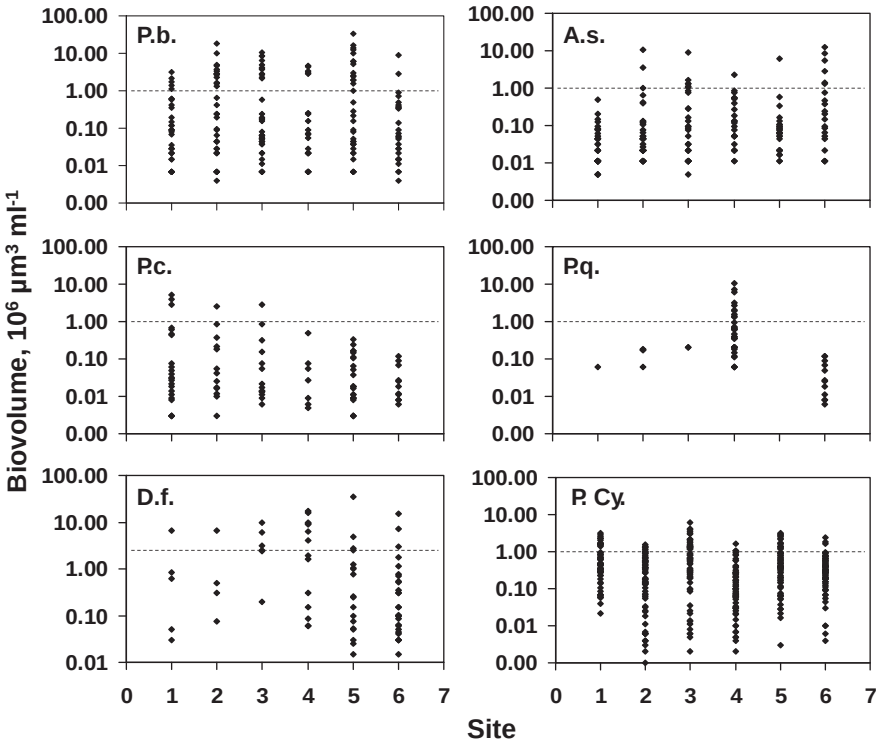

Fig. 6. Spatial distribution of observations of four HAB species (P.b., *Pyrodinium bahamense* var. *bahamense*; A.s., *Akashiwo sanguinea*; P.c., *Pseudo-nitzschia calliantha*; P.q., *Peridinium quinquecorne*), and two non-HAB taxa (D.f., *Dactyliosolen fragilissimus*; P.cy., *Picoplanktonic cyanobacteria*), in terms of biovolume.

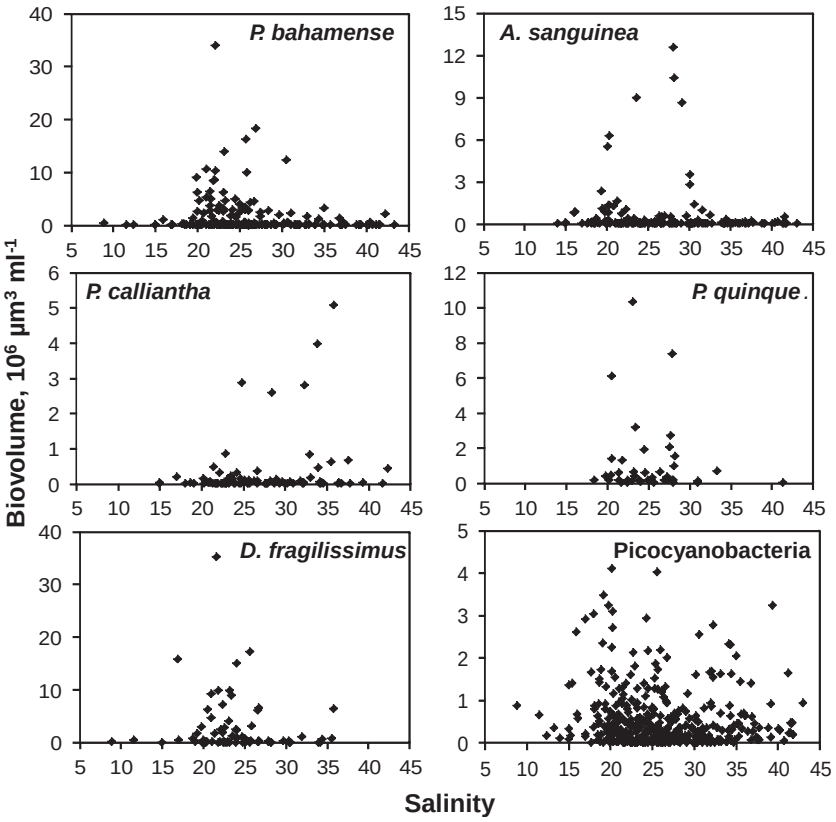

Fig. 7. Distribution of observations of four HAB species (*Pyrodinium bahamense* var. *bahamense*, *Akashiwo sanguinea*, *Pseudo-nitzschia calliantha*, and *Peridinium quinquecorne*), and two non-HAB taxa (*Dactyliosolen fragilissimus* and *Picoplanktonic cyanobacteria*) in relation to salinity.

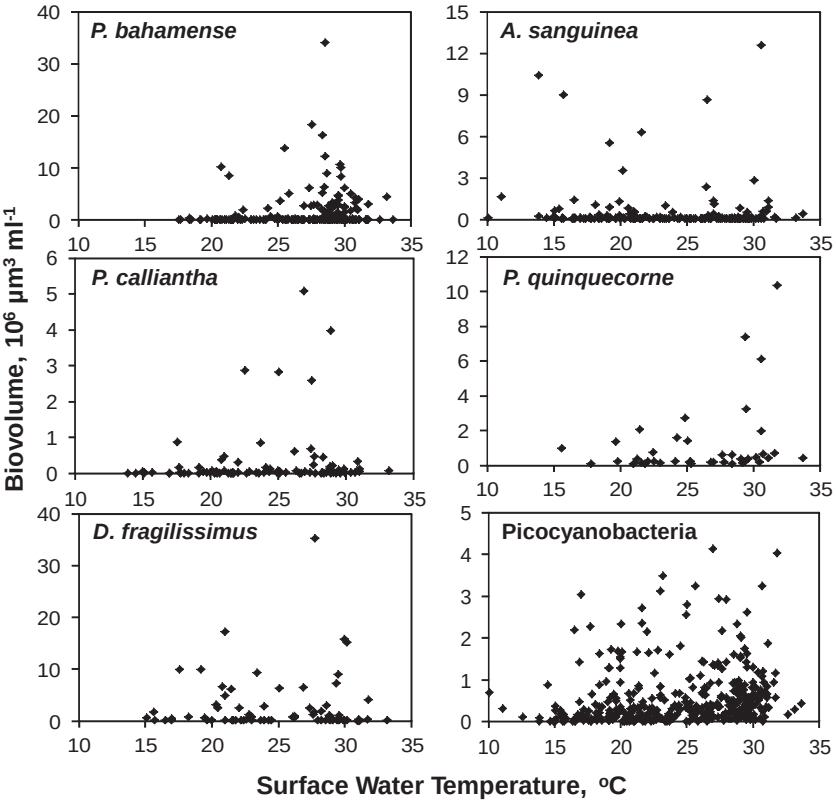

Fig. 8. Distribution of observations of four HAB species (*Pyrodinium bahamense* var. *bahamense*, *Akashiwo sanguinea*, *Pseudo-nitzschia calliantha*, and *Peridinium quinquecorne*), and two non-HAB taxa (*Dactyliosolen fragilissimus* and *Picoplanktonic cyanobacteria*) in relation to water temperature.

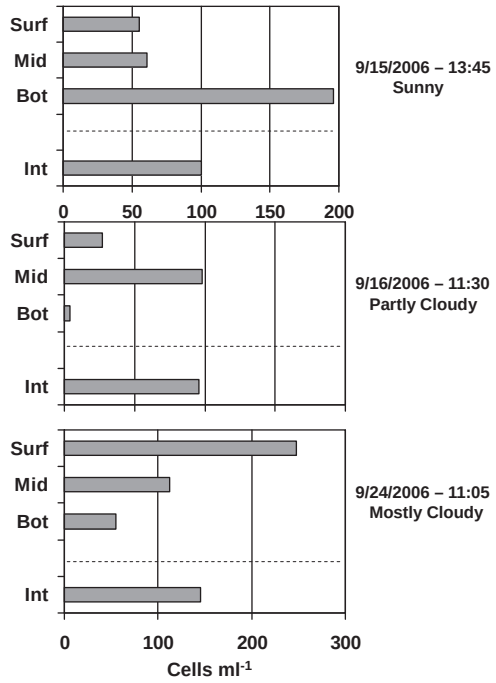

Fig. 9. The distribution of *Pyrodinium bahamense* var. *bahamense* cells (cells ml^{-1}) in the water column at Site 2. The mid-water column (Mid) was at 1 m and the bottom (Bot) at 2 m. The integrated value (Int) was determined from a whole water column sample.

(Fig. 9). On the second sampling date conditions were partly cloudy, and *P. bahamense* var. *bahamense* were highest in the mid-water column sample. On the third sampling date mostly cloudy conditions prevailed, and *P. bahamense* var. *bahamense* densities

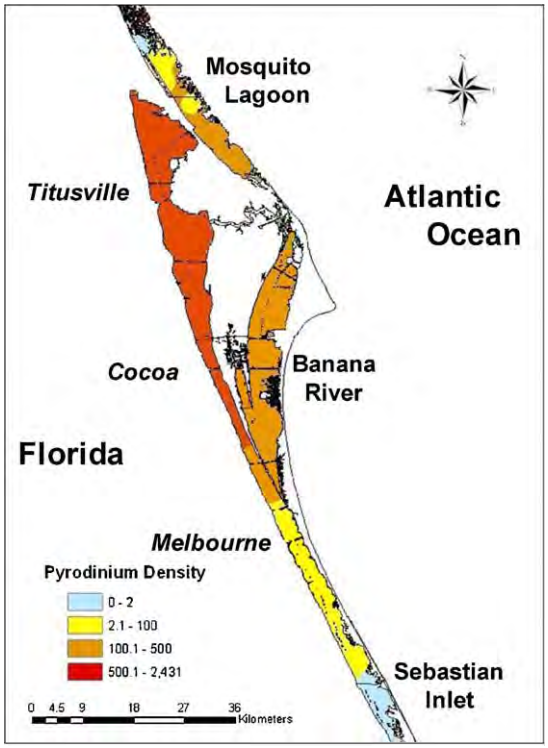

Fig. 10. Spatial distribution of *Pyrodinium bahamense* var. *bahamense* blooms in the northern Indian River Lagoon, Banana River and southern Mosquito Lagoon from July to October 2009. Maximum cell densities over the time period at 19 sites distributed around the study region were used to generate the GIS contours.

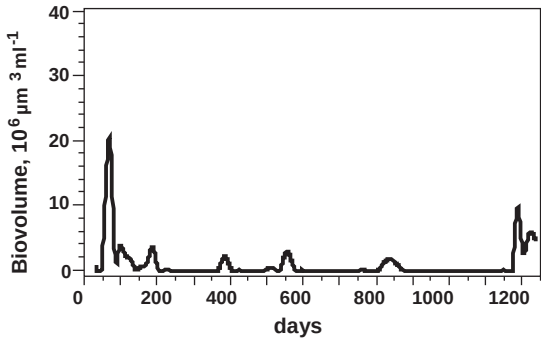

Fig. 11. Predicted daily time series of biovolume (10^6 μm^3 ml^{-1}) for *Pyrodinium bahamense* var. *bahamense* at Station 2 using cubic splines. The cutoff for blooms is defined as a biovolume greater than 10^6 μm^3 ml^{-1}.

were highest in the surface water sample. *P. bahamense* var. *bahamense* densities in integrated water column samples were relatively similar on all three sampling dates, indicating that the overall densities were similar throughout the 10-day test period.

The availability of supplemental phytoplankton monitoring data for the late summer and early fall of 2009 provided an opportunity to examine in greater detail the geographical extent of a *P. bahamense* var. *bahamense* bloom in the NIRL in greater detail (Fig. 10). The GIS contour image of the peak cell densities for the August through October bloom period of 2009 revealed a region of peak cell densities in the northern IRL proper, from near Cocoa northward, although significant densities (i.e. >100 cells ml^{-1}) extended into the southern Mosquito Lagoon, the Banana River Lagoon, to near Site 6.

The occurrence of peak *P. bahamense* var. *bahamense* abundances in the NIRL and sharp decline south of Melbourne (Site 6) has been a repeating pattern since 2001 (Phlips et al., 2006, 2010), but not without exception. In the summer of 2004 a *P. bahamense* var. *bahamense* bloom uncharacteristically appeared in the Sebastian Inlet region of the IRL, well south of Melbourne, just after the passage of Hurricane Charley. On July 22 no *P. bahamense* var. *bahamense* cells were observed in the region, while cell densities were 775 cells ml^{-1} at Melbourne (Site 6). One week after Hurricane Charley on August 25 concentrations dropped to 391 cells ml^{-1} at Melbourne and went up to 100 cells ml^{-1} near the Sebastian Inlet. It is likely that the bloom near the Sebatian Inlet was not a local event, but resulted from wind-driven displacement of *P. bahamense* var. *bahamense* from the Melbourne region southward to Sebastian during the hurricane. This observation highlights the potential importance of wind-driven circulation on the distribution of blooms.

A similar non-indigenous HAB event was observed in the fall of 2007, when the toxic dinoflagellate *Karenia brevis* was observed in the Mosquito Lagoon (Site 1), as a result of tidally driven incursion of coastal water containing a bloom of the alga.

3.5. Detecting HAB species and bloom events

Three of the most prominent HAB species in the IRL were included in a test of bloom detection probabilities using a non-parametric smoothing function to fit a cubic spline to the observed biovolumes or cell densities at each site, as described in the methods section; i.e. the dinoflagellates *P. bahamense* var. *bahamense* and *A. sanguinea*, and the diatom *P. calliantha*. To determine the effects of sampling interval and bloom period length on the probability of detecting HAB events, daily time series were generated for blooms of the three selected HAB species. Dinoflagellate blooms were defined as biovolumes above 10^6 μm^3 ml^{-1}. For the diatom *P. calliantha* the bloom threshold

Table 3
Predicted number of blooms (count), mean and standard deviation (Std) of the length of a bloom, standard error of the mean (SEM) bloom length, and the proportion of days (*P*) during the study period which met the definition of a bloom event. Daily biovolumes or cells ml^{-1} were predicted at each of the six stations over the study period, May 2006 to August 2009, using cubic splines (see text) fitted to biweekly observations. Blooms were identified as the days when the predicted value exceeded the cutoff for an event where an event is defined as a biovolume over 1×10^6 μm^3 ml^{-1} for *P. bahamense* and *A. sanguinea* and over 200 cells ml^{-1} for *P. calliantha*.

Statistic	*P. bahamense*	*A. sanguinea*	*P. calliantha*
Count	22	11	27
Mean	40.27	26.09	28.48
Std	31.15	12.53	20.61
SEM	6.64	3.78	3.97
Min	12	2	2
Max	151	42	94
P	0.123	0.040	0.106

level was based on the cell density above which health warnings are administered in many countries around the world, i.e. 200 cells ml^{-1} (Andersen, 1996), equivalent to a biovolume of 0.06×10^6 μm^3 ml^{-1}. An example of a predicted time series is shown in Fig. 11. The mean bloom lengths and timing of the blooms are shown in Table 3. Mean lengths of time over which the three species exceeded the bloom thresholds were 26.09, 28.48, and 40.27 days for *A. sanguinea*, *P. calliantha*, and *P. bahamense* var. *bahamense*, respectively.

The probability of observing a bloom of a given length was strongly influenced by sampling interval (Fig. 12). The effect of sampling interval was inversely related to the mean length of

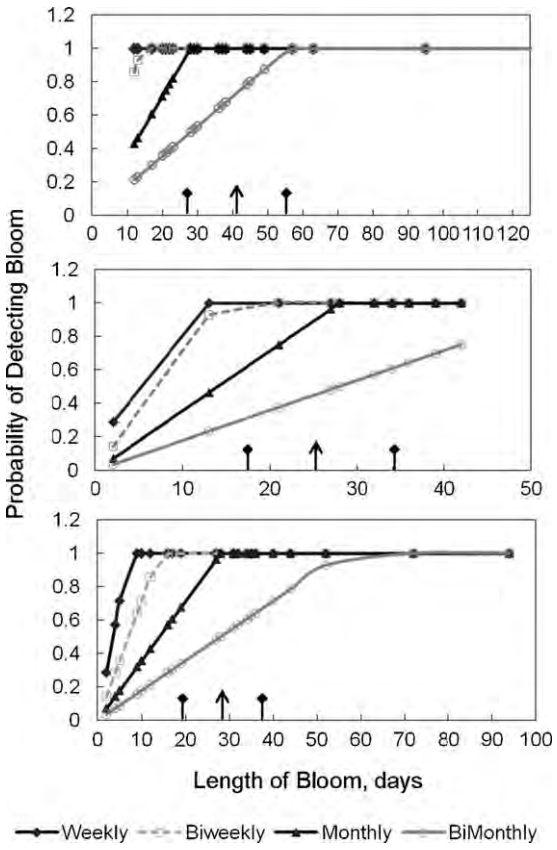

Fig. 12. Plot of the probability of a bloom being observed as a function of the length of time the bloom exists and the time interval between systematic samples. The three panels are for *Pyrodinium bahamense* var. *bahamense* (top), *Akashiwo sanguinea* (middle), and *Pseudo-nitzschia calliantha* (bottom). The arrows indicate the mean bloom length and the diamond markers are the 95% confidence intervals around the means.

blooms. Using the 95% confidence interval around the mean values for bloom length, the probability of detecting a *P. bahamense* var. *bahamense* bloom was 1.00 for sampling intervals of 1–2 weeks, and 0.85–1.00 for monthly sampling intervals (Table 3). At a sampling interval of two months (bi-monthly), the probability of detection went down to 0.45–1.00. For *A. sanguinea*, a species with shorter–lived blooms, the probability of detection was 0.95–1.00 for one and two-week sampling intervals, 0.55–1.00 for monthly sampling intervals, but only 0.20–0.55 for bi-monthly sampling intervals. The probabilities of bloom detection for *P. calliantha* were similar to *A. sanguinea*; 1.00 for one- to two-week sampling intervals, 0.70–1.00 for monthly sampling intervals, and 0.25–0.70 for bi-monthly sampling intervals.

Precisely defining the probability of detecting blooms of species that did not span more than one sampling date in a row over the sampling period was not feasible. For example, *K. foliaceum* appeared at bloom levels several times at Site 4, but bloom levels were never sustained for more than one sampling date. Hence for some of the HAB species observed in this study, we have likely missed several short duration blooms due to the two-week sampling interval. The probability that all blooms of such species would be missed during the study is a complicated calculation that depends not only on the sampling interval and the lengths of the blooms but also on the number of blooms and the number of days between blooms. The resolution of this problem would require a longer–term data series.

4. Discussion

Spatial and temporal variability in the abundance and composition of phytoplankton during bloom events can be viewed on various levels of taxonomic organization, but for the purpose of this discussion it is useful to begin by examining variability of total phytoplankton biomass at the sub-basin scale, before proceeding toward an examination of the dominant bloom-forming groups and harmful algae bloom (HAB) species. Spatial and temporal variability can also be viewed from the perspective of the probability of detecting bloom events involving different species, given different monitoring strategies.

4.1. Temporal and spatial patterns in phytoplankton biomass

From a temporal perspective, phytoplankton blooms in the northern Indian River Lagoon (NIRL) were most abundant from the late spring to early fall, but winter blooms were common, reflecting the subtropical character of central Florida's climate. A similar lack of consistent seasonal periodicity of blooms has been observed in other south Florida ecosystems, such as Florida Bay (Phlips et al., 1999; Brinceño and Boyer, 2010; Winder and Cloern, 2010). Seasonal changes in light availability and temperature, which are major factors in defining phytoplankton production and biomass in temperate and boreal ecosystems (Cushing, 1959; Sommer et al., 1986), are less critical in controlling seasonal biomass potential in sub-tropical ecosystems (Harris, 1986; Winder and Cloern, 2010), and their role may be more important in guiding species composition and succession than setting biomass thresholds.

One of the driving factors for temporal trends of phytoplankton biomass in the NIRL is rainfall. Elevated rainfall totals during the wet season are associated with increased nutrient loads in the NIRL, as indicated by the negative relationship between salinity and concentrations of total nitrogen. In regions of the lagoon with high hydraulic residence time, such periods of increased load are correlated to bloom intensity, while in regions with short water residence time, such as near the Sebastian Inlet, changes in load have less impact on phytoplankton biomass (Phlips et al., 2004, 2010).

From a spatial perspective, differences in average phytoplankton biovolumes among the six sampling sites in the NIRL can be viewed in terms of both basin and watershed characteristics. The southern Mosquito Lagoon (Site 1) had the lowest average phytoplankton biovolume and bloom frequency. The region is fed by water inflows from relatively small and pristine watersheds, yielding lower nutrient loads than other regions of the NIRL (Adkins et al., 2004). The region is also characterized by shallow mean depths (i.e. <1.5 m) and extensive seagrass populations (Fletcher and Fletcher, 1995), increasing competition for nutrients by algal populations associated with seagrass, which can reach high biomass levels in the early spring (Virnstein and Carbonara, 1985). Virnstein and Carbonara (1985) observed drift algae standing crops as high as 400 g dry wt. m^{-2}, along with seagrass biomass of up to 300 g dry wt. m^{-2} in the IRL.

The Mosquito Lagoon, as well as the rest of the NIRL, also contain significant populations of clams, mussels and other filter-feeding invertebrates (Mikkelsen et al., 1995), as reflected by the presence of a bivalve harvesting industry (Busby, 1986). Concentrations of certain filter-feeding bivalves, such as clams and mussels, can be particularly high in seagrass communities of the NIRL (Mikkelsen et al., 1995). From a spatial perspective, the Mosquito Lagoon is one of the regions in the NIRL with high bivalve densities (http://www.dep.state.fl.us/coastal/sites/mosquito/management/public_use.htm). These benthic communities represent a potential source of top-down pressure on phytoplankton populations in the NIRL. The importance of benthic grazers on phytoplankton dynamics has been demonstrated for other shallow ecosystems, such as San Francisco Bay (Cloern, 1982). In terms of the importance of zooplankton grazing in the NIRL, preliminary evidence suggests that rates are lower than phytoplankton growth potential (Phlips et al., 2002). The specific magnitude of planktonic and benthic grazing pressures in the NIRL is difficult to quantify due to the lack of sufficient faunal abundance and composition data.

The sites with the next to highest mean phytoplankton biovolumes were Site 2 near Titusville and Site 3 in the Northern Banana River. Both sites are located in regions with shallow mean depths (i.e. around 2 m) and significant seagrass and drift algae populations, but are also characterized by very long water residence times (i.e. average half water replacement rate, or $R_{50} > 100$ days), and watersheds with moderate human influence (Adkins et al., 2004; Reyier et al., 2008; Gao, 2009). Nitrogen and phosphorus loads to most of the NIRL have increased by at least 30% and 50%, respectively since the 1940s (Steward and Green, 2007), likely contributing to bloom potential.

The three sites with the highest mean phytoplankton biovolume and greatest frequency of bloom events during the study period, Sites 4–6, were located in regions of the IRL with markedly different physical characteristics. Site 4 was located in an isolated very shallow (i.e. 1 m) embayment, Site 5 was located in a broad shallow (i.e. 2 m) basin in the central Banana River Lagoon, and Site 6 was located in a broad, somewhat deeper (i.e. 2–3 m), basin with lower seagrass densities and subject to inflows from a major tidal creek, as reflected by the exceptionally variable salinities. Despite these distinctions, the three regions share one important feature, their close proximity to watersheds with significant human development and associated anthropogenic enhancement of nutrient inputs (Adkins et al., 2004; Gao, 2009). Nutrient loads in the central Banana River Lagoon and central Indian River Lagoon (which includes Site 6) have experienced larger increases of nitrogen (TN) and phosphorus (TP) loads since the 1940s than the rest of the NIRL, i.e. 85% for TN and 161–183% for TP (Steward and Green, 2007). Estimates of TN and TP loads per acre of basin area in the regions containing Sites 4, 5 and 6 are three-fold higher than in the basins associated with Sites 2 and 3 (Gao, 2009).

In summary, the spatial and temporal patterns of total phytoplankton biomass in the NIRL reflect the variable influences of watershed nutrient loads, climatic variability and water residence time. In line with the general hypothesis forwarded by Cloern and Jassby (2010), the high frequency of bloom events in the southern half of the NIRL is suggestive of the influence of nutrient-enriched inputs from the watershed. The inter-annual variability in the intensity of blooms in the NIRL over the past decade reflect shifts in climatic conditions, principally rainfall, which affect the intensity of nutrient loads and freshwater flushing rates (Phlips et al., 2004, 2010). For example, a study of water residence times in the north-central Indian River Lagoon (Site 6) from 1997 to 1998 showed an R_{50} (50% water exchange) of five days during a high rainfall period in 1997 (a strong El Niño year), to an R_{50} of 20 days in the low rainfall summer of 1998 (David Christian, unpublished data). Underlying the spatial and temporal differences in nutrient loads and water residence time, the very shallow bathymetry and extensive communities of benthic flora and fauna in the NIRL represent a significant potential for top-down control of phytoplankton and nutrient competition for planktonic primary producers.

4.2. Temporal and spatial patterns in bloom composition

Interest in defining the ecological basis for spatial and temporal differences in phytoplankton community structure has grown out of the observations of a number of researchers in the 1960s and 1970s (Hutchinson, 1961; Grime, 1977; Tilman, 1977; Margalef, 1978; Smayda, 1980). The ability to divide phytoplankton taxa into functional groups, which relate to their adaptability to different environmental scenarios, is a valuable tool in defining the causes of blooms and developing predictive capacity. Recent efforts to classify phytoplankton according to their ecophysiological "traits" have focused attention on both autogenic and allogenic considerations, such as differences in nutrient acquisition, light adaptation, temperature preference, susceptibility to grazing, and reproductive strategies (Riegman, 1998; Sommer et al., 1986; Grover, 1991; Burkholder et al., 2008; Litchman and Klausmeier, 2008; Smayda, 2008). It is useful to view variability in the composition of phytoplankton blooms in the NIRL from the perspective of the relationships between key traits and shifting environmental conditions.

Two environmental features that help define the dominant bloom-forming phytoplankton taxa in the NIRL are wide salinity variation and pulsed nutrient inputs. Salinities in most of the NIRL vary between 10 and 35 psu, except at Site 1 in the southern Mosquito Lagoon. It is therefore not surprising that the major bloom-forming species in the NIRL are euryhaline. Blooms were often associated with mid-range salinities (i.e. 20–30 psu), which likely reflects the positive influence of freshwater inputs from the watershed on nutrient loads and the concurrence of the wet season with warmer water temperatures.

The pulsed nature of nutrient loads to the NIRL is a product of relatively small size of the watersheds that feed the estuary, resulting in episodic loads of small to moderate size, depending on rainfall conditions. Such conditions should favor species with nutrient storage capacity (Grover, 1991; Litchman and Klausmeier, 2008), or mixotrophic capabilities which provide access to organic sources of nutrients (Burkholder et al., 2008). It is generally believed that diatoms have greater storage capacities than dinoflagellates, chlorophytes or cyanobacteria, particularly in terms of nitrogen (Litchman and Klausmeier, 2008), which is a commonly limiting nutrient in the NIRL, particularly in the north-central (Site 6), central and southern IRL (Phlips et al., 2002). Based on this observation, it might be expected that diatoms would play a dominate role in blooms, however, both diatoms and dinoflagel-

lates play major roles in phytoplankton blooms, and picoplanktonic cyanobacteria are periodically important (Phlips et al., 2010). In 2006 large-celled dinoflagellates dominated most blooms at all sampling sites in the NIRL, but from 2007 to 2009 shifts in dominance between diatoms and dinoflagellates varied by region and year. Clearly, the forces that define competition between phytoplankton groups in the NIRL vary over time and space, including the potential for phosphorus limitation in the NIRL (Phlips et al., 2002), which is reflected in the observed correlations between concentrations of chlorophyll *a* and TP.

It is possible to speculate on the environmental factors that contributed to the widespread dominance of dinoflagellates during blooms throughout the NIRL in 2006. Two coinciding climatic conditions in 2006 are noteworthy, an early spring increase in water temperature, related to well-above average air temperatures in April, and relatively moderate summer storm activity compared to 2007 and 2008, which yields lower freshwater flushing rates and more stable water column conditions. Most of the dinoflagellate blooms of 2006 were dominated by one of two HAB species, *P. bahamense* var. *bahamense* and *A. sanguinea*. Both species are common features of phytoplankton communities in the NIRL (Phlips et al., 2010; Badylak et al., 2004). The two species share several important features; i.e. large size (40–60 μm in diameter), low maximum growth rates (near or below one doubling per day) (Phlips unpublished data; Usup and Azanza, 1998; Matsubara et al., 2007), motility, tolerance to a wide range of salinities (Phlips et al., 2006; Matsubara et al., 2007), and the ability to form resting cysts (Sombrito et al., 2004; Badylak and Phlips, unpublished data). The existence of seed banks of the two species in the NIRL, combined with the early Spring warm up of 2006, may have provided a jump start for the dinoflagellate blooms, in terms of the germination of cysts. This may be particularly true for the dominant dinoflagellate in the NIRL, *P. bahamense* var. *bahamense*, which is a tropical species that prefers water temperature greater than 25 °C (Phlips et al., 2006). Anomalous warm temperature periods have been associated with dinoflagellate blooms in other ecosystems, such as San Francisco Bay (Cloern et al., 2005) and the Neuse River estuary in North Carolina (Hall et al., 2008).

The importance of *P. bahamense* and *A. sanguinea* through the summer of 2006 was also promoted by more stable hydrologic conditions and longer water residence times than in 2007–2008, providing a favorable environment for these slower growing dinoflagellates. The success of dinoflagellates in 2006 also indicates their ability to compete for pulses of nutrients or revert to alternative sources of nutrition. Although dinoflagellates are not generally considered to have as large a storage capacity for nutrients as diatoms (Litchman and Klausmeier, 2008), the large size of *P. bahamense* and *A. sanguinea* may make them better competitors than smaller dinoflagellate species. This hypothesis is supported by the concept that internal nutrient reserve capacities are not just correlated to the physiological characteristics of different species, but also their size (Grover, 1991; Stolte and Riegman, 1996). *P. bahamense* and *A. sanguinea* also exhibit other characteristics which may provide selective advantages under nutrient-limited conditions, such as the mixotrophic growth capabilities of *A. sanguinea* (Burkholder et al., 2008), and the presence of alkaline phosphatase activity in *P. bahamense* (Gonzáles-Gil et al., 1998), allowing it to maintain substantial growth using polyphosphates, rather than just orthophosphate.

Another important consideration in the competition between diatoms and dinoflagellates in the NIRL is top-down control. Resistance to grazing can be an important element in the success of HAB species (Turner and Tester, 1997; Turner, 2006; Smayda, 2008). The effects of differences in growth potential between species can be significantly amplified or counteracted by differences in susceptibility to grazing (Riegman, 1998). The large size and motility of *P. bahamense* var. *bahamense* and *A. sanguinea* may provide some resistance to grazing pressure. In addition, the toxin production capabilities (Landsberg et al., 2006; Abbott et al., 2009) and armored character of *P. bahamense* var. *bahamense* may further decrease loss rates due to grazing. A recent study of plankton dynamics in Tampa Bay on the west coast of Florida provides preliminary indications that the abundance of certain zooplankton species may be depressed during major blooms of *P. bahamense* var. *bahamense* (Badylak and Phlips, 2008), supporting the importance of top-down issues in their dynamics. Resistance to grazing losses may help to explain the observed longevity of *P. bahamense* var. *bahamense* blooms relative to other bloom species in the NIRL (see Section 4.4), and Tampa Bay (Badylak and Phlips, 2008).

Regional differences in the relative importance of dinoflagellates and diatoms in blooms after 2006 can be viewed from the perspective of the unique characteristics of individual basins within the NIRL and regional differences in rainfall during the study period. The southern Mosquito Lagoon (Site 1) has the most pristine watershed among the sub-basins in the NIRL (Adkins et al., 2004), which helps to explain the low bloom intensity observed at Site 1. The region is also characterized by the highest mean salinity, and the smallest variability in salinity, which may have contributed to the success of certain marine HAB diatoms, such as the HAB diatom *P. calliantha*.

Moving further south in the NIRL, into regions of increasing human influence, shifts in dominant species from mostly dinoflagellates in 2006 to a mixture of diatoms and dinoflagellates in 2007 and 2008, particularly in the central Banana River Lagoon (Site 5) and the north-central Indian River Lagoon (Site 6), coincided with an increase in the intensity of wet season rainfall events. It may be hypothesized that the increasing frequency of diatom dominance in blooms at Sites 5 and 6 in 2007 and 2008 was related to increased nutrient loads and flushing rates associated with rainfall events, providing a favorable environment for faster growing diatoms. A similar increase in rainfall events was not observed in the northern end of the NIRL (i.e. Sites 2 and 3) in 2007 and 2008. In terms of nutrient availability there are also preliminary indications that temporal and regional differences in silica levels may play a role in the competition between diatoms and dinoflagellates. Nutrient data from the late 1990s indicates that silica concentrations during extended low rainfall periods dip below 1 mg l^{-1}, suggesting a potential for limitation of diatom growth, while concentrations during high rainfall periods exceeded 10 mg l^{-1}, primarily in the central Banana River Lagoon (Site 5) and north-central Indian River Lagoon (Site 6).

In conclusion, defining the causes for the periodicity and species shifts in bloom events involves a wide range of potential driving factors, and is thereby a "challenging task" (Winder and Cloern, 2010). In the NIRL, the relatively small temporal variation in temperature and light availability, along with very shallow depths and little influence from tidal water exchange with the open ocean, focuses attention on the roles of climatic variability, watershed characteristics and differences in the structure of key biological components, such as seagrasses, benthic algae and benthic filter-feeding invertebrates, as driving factors for phytoplankton succession.

4.3. Other HAB species

Three HAB dinoflagellates, *P. quinquecorne*, *K. veneficum* and *K. foliaceum*, were only observed at bloom levels at Site 4, indicating a unique set of driving factors. From a physical perspective, the site is located in the shallowest and most hydrologically isolated bays included in this study. The very shallow depth and restricted horizontal mixing of water the rest of the NIRL provide the

hydrologically stable conditions conducive for dinoflagellate blooms (Margalef, 1978; Smayda and Reynolds, 2001). The site also had twice the mean TP concentration as the other five sites in the study, suggesting the presence of local sources of nutrients or organic material, including internal sources associated with the sediments. The unique bloom characteristics at Site 4 may also reflect the distribution of dinoflagellate cyst banks.

Among the other HAB species observed in the IRL, small unarmored dinoflagellates and flagellates were well represented, and occasionally numerically abundant, although they were not observed at bloom levels of biovolume; including *Takayama* spp., *Prymnesium* spp., *Chrysochromulina* spp., *Karenia* spp., *Chattonella* spp. and *K. veneficum*. Some of these taxa have been categorized as r-selected, in part due to their small size and relatively high growth rates (Smayda, 1997; Reynolds, 2006). However, in terms of dominance during major bloom events they appear to be generally outcompeted by larger-celled dinoflagellate or diatom species, as described above. They also compete with other, even smaller, fast growing picoplanktonic cyanobacteria or small-celled centric diatoms, both of which are common features in the IRL (Badylak and Phlips, 2004; Phlips et al., 2010), and other shallow estuaries in Florida (Phlips et al., 1999; Murrell and Lores, 2004). The overall dominance of larger-celled forms is related to several characteristics of the NIRL, including long water residence times and pulsed nutrient inputs. The dominance hierarchy may also be influenced by the greater susceptibility of smaller taxa to grazing losses associated with zooplankton and benthic filter feeding invertebrates (Turner and Tester, 1997; Turner, 2006), which are abundant in the IRL.

4.4. Detecting HAB events

HAB monitoring efforts are faced with the challenge of defining sampling regimes that have a reasonable probability of discovering important species and detecting bloom events within specified spatial and temporal boundaries (Andersen, 1996; Smayda, 1997; Chang and Dickey, 2008; Cullen, 2008; Franks, 2008). Due to the shallowness of the NIRL, it was possible to use a water column integrating device for sampling, thereby limiting the potential of missing key phytoplankton in the water column due to vertical stratification, as observed in this study for *P. bahamense* var. *bahamense*.

In terms of geographical differences in the distribution of HAB species, basin specific disparities in the composition and intensity of blooms were observed in the NIRL. For example, the largest blooms of the potentially toxic diatom *P. calliantha* were observed in the Mosquito Lagoon. Blooms of the HAB species *P. quinquecorne*, *K. veneficum* and *K. foliaceum* were only observed at one of six sites (i.e. Site 4). Conversely, the spatial distribution of *P. bahamense* var. *bahamense* blooms extended over most of the NIRL, by contrast to the general absence of blooms in the central and southern regions of the Indian River Lagoon (Phlips et al., 2006, 2010). However, major climatic events or trends can result in departures from the more typical spatial distributions of HAB species. The importance of this caveat is illustrated by the sudden appearance of a *P. bahamense* var. *bahamense* bloom in the central IRL following the passage of Hurricane Charley in 2004, likely due to wind and rain-driven movement of water in the lagoon from north to south.

From a temporal perspective, sampling intervals obviously affect the probability of detecting HABs. Bloom-forming HAB species have maximum growth rates ranging from 0.25 to 3.5 doublings per day (Smayda, 1997; Stolte and Garcés, 2006; Burkholder et al., 2008), therefore species can reach bloom levels, starting from baseline concentrations, within 2–4 weeks, assuming ideal growth conditions, and no major loss processes. Given these assumptions biweekly sampling should provide a reasonable probability of capturing a bloom event, although absolute peaks of abundance may be missed. However, the dynamics of phytoplankton are related to more than just growth potential, and include a myriad of factors which impact the timing, and length of bloom events, such as nutrient limitation, sub-saturating light flux, grazing and other loss processes, such as dilution or export of phytoplankton biomass or premature death of cells due to pathogens (Smayda, 1997, 2008).

The importance of growth cycle characteristics of individual species in defining the probability of detecting blooms is illustrated by a comparison of three important HAB species in the IRL; *P. bahamense* var. *bahamense*, *A. sanguinea* and *P. calliantha*. The mean length of *P. bahamense* var. *bahamense* blooms in the NIRL is almost twice that of either *P. calliantha* or *A. sanguinea* blooms. In the case of *P. calliantha*, comparatively high growth rate may lead to more rapid depletion of bioavailable nutrients and collapse of blooms. In addition, both *P. calliantha* and *A. sanguinea* may be more strongly influenced by top-down control by zooplankton and benthic invertebrate filter feeders than *P. bahamense* var. *bahamense*.

As part of this study, a statistical approach was explored to estimate the probability of detecting HAB events given different sampling intervals. The probability is related to the characteristic longevity of blooms, frequency of bloom events, and the seasonal preferences of different species. The tropical species *P. bahamense* var. *bahamense* is largely absent from the NIRL during mid-winter months, but is a common feature in the northern lagoon from late spring through summer (Phlips et al., 2006, 2010). The application of probability statistics to *P. bahamense* var. *bahamense* blooms shows that twice monthly or monthly sampling yield high probabilities of detecting bloom events (i.e. >0.85). By contrast, blooms of *A. sanguinea* and *P. calliantha* were generally shorter in duration, lowering the probability of detection at one month sampling intervals to as low as 0.50 and 0.70, respectively. The power of the statistical approach to defining the probability of detecting HAB events depends on the availability of information on the characteristic seasonality, longevity and frequency of blooms of specific species. Therefore, the power of the approach can be improved over time with the availability of long time series data and improved understanding of the ecological strategies and capabilities of key species in specific ecosystems.

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