



The occurrence of potentially toxic dinoflagellates and diatoms in a subtropical lagoon, the Indian River Lagoon, Florida, USA

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Abstract

The occurrence of potentially toxic phytoplankton species was examined over a 5-year period in a region of the Indian River Lagoon in Florida that has recently been subject to ecologically significant events, putatively related to algal toxins. The results of the study reveal a significant presence of two species of phytoplankton that have been shown to be toxic in Florida or other regions of world, the dinoflagellate *Pyrodinium bahamense* var. *bahamense* and the diatom *Pseudo-nitzschia pseudodelicatissima*. Concentrations of the former species reached 638,000 cells l⁻¹ and concentrations of the latter reached 23.9 million cells l⁻¹. In addition, the abundance of one of these species, *P. bahamense* var. *bahamense* appears to have increased over the 5-year study period from 1997 to 2002. It may be hypothesized that rainfall events following a regional drought period resulted in a flushing of bioavailable phosphorus and nitrogen into the Indian River Lagoon that stimulated *P. bahamense* var. *bahamense* blooms. The significance of these results is discussed within the context of the ecology of this flow-restricted lagoon.

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1. Introduction

Global concerns over recent trends toward increased rates of coastal eutrophication have drawn attention to the issue of harmful algal blooms (Paerl, 1988; Hallegraeff, 1993; Smayda, 1989, 1992; Nixon, 1995; Richardson and Jorgensen, 1996). Blooms of toxic algae in lagoons and estuaries have been blamed for a range of environmental problems, including fish kills (Smayda, 1992; Steidinger et al., 1998), shellfish die-offs (Shumway, 1990), and marine mammal deaths (Landsberg and Steidinger, 1997). However, defining the more general role of specific harmful algal species

in highly dynamic coastal ecosystems can often be a challenging task due to the lack of long-term monitoring information on phytoplankton composition.

In this paper, we present the results of a 5-year effort to examine phytoplankton dynamics in a region of the Indian River Lagoon in Florida that has recently been subject to ecologically significant phenomena, putatively related to algal toxins. These phenomena include saxitoxin found in local pufferfish (Landsberg et al., 2002) and unexplained losses of clam larvae in regional hatcheries that use the lagoon as a source of water (L. Sturmer, personal communication). Many of the regions of the lagoon subject to these observations are flow-restricted environments with slow turnover rates of water (Sheng et al., 1990; Smith, 1993). It is well known that coastal ecosystems subject to

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low water turnover rate are especially prone to the buildup of high algal biomass, given the presence of sufficient nutrients (Knoppers et al., 1991; Monbet, 1992). The Indian River Lagoon is subject to high nutrient concentrations (Phlips et al., 2002) and is characterized by periodic blooms of dinoflagellates, diatoms and blue-green algae (Steidinger et al., 1998; Phlips et al., 2002; Badylak and Phlips, 2003). The goal of this study was to evaluate the abundance of potentially toxic phytoplankton species within a key region of concern within the lagoon, near the city of Titusville. The results of the study reveal a significant presence of two species of phytoplankton that have been shown to be toxic in Florida or other regions of the United States, the dinoflagellate *Pyrodinium bahamense* (Landsberg et al., 2002) and the diatom *Pseudo-nitzschia pseudodelicatissima* (Martin et al., 1990; Hallegraeff, 1993; Fryxell et al., 1997; Parsons et al., 1999; Pan et al., 2001; Hargrave and Maranda, 2002; Stehr et al., 2002). In addition, the abundance of one of these species, *P. bahamense* appears to have increased over the 5-year study period. The significance of these results is discussed within the context of the ecology of the lagoon.

2. Methods

2.1. Study site description

The Indian River Lagoon is a geomorphic component of the east coast barrier reef system of Florida, USA. The lagoon extends 252 km from the warm temperate environment of Ponce de Leon Inlet near Daytona Beach to the subtropical region of Jupiter Inlet near Ft. Pierce. The width of the lagoon varies from 0.2 to 5 km and depths in the lagoon are generally less than 3 m. A number of ecologically distinct regions exist within the lagoon, which differ considerably in water exchange properties (Sheng et al., 1990; Smith, 1993). Hydrodynamic considerations are a large component in the subdivision of the lagoon into different regions. The study site for this research was located in the northern part of the lagoon adjacent to the city of Titusville (Fig. 1). It is characterized by very long water residence times, which can exceed 1 year (Sheng et al., 1990; Smith, 1993). Due to the severe restriction to water exchange within the study region, changes in rainfall patterns can lead to large shifts in salinity (Phlips et al., 2002).

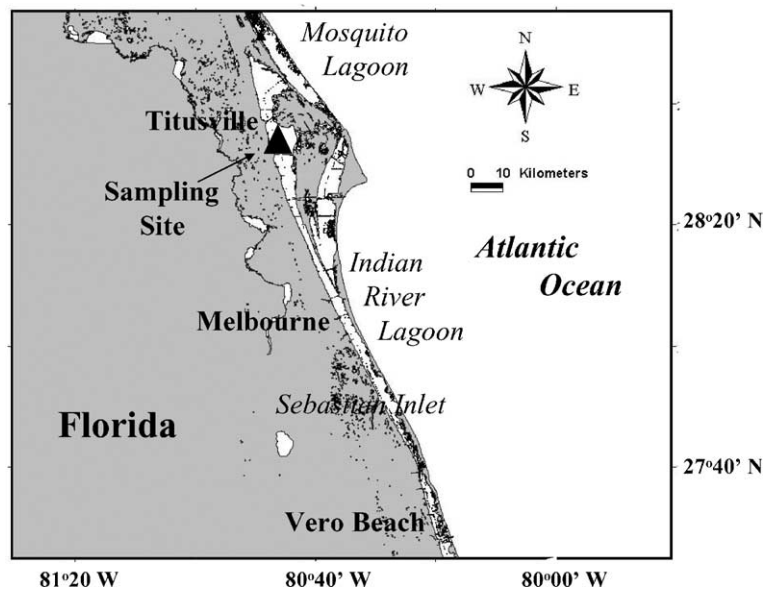


Fig. 1. Location of sampling site near Titusville in the Indian River Lagoon.

2.2. Field procedures

Water was collected at the sampling site for 5 years on roughly a monthly basis. Thirty-seven collections were made over the sampling period. Dissolved oxygen, salinity, and temperature were measured with a YSI Model 85. Water samples were collected with a vertical integrating sampling tube that captures water from the surface to within 0.1 m of the bottom. Phytoplankton samples were preserved with Lugols and a backup aliquot was preserved with glutaraldehyde in 0.1 M sodium cacodylate buffer.

2.3. Laboratory procedures

Total nitrogen and total phosphorus were determined colorimetrically using the persulfate digestion method (APHA, 1989; Parsons et al., 1984).

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

2.4. Phytoplankton analysis

Fluorescence microscopy was used to enumerate picoplankton cyanobacteria (Philips et al., 1999). Sub-samples of station water were filtered onto 0.2 μm pore nucleopore filters and mounted between a microscope slide and cover slip with immersion oil. These were counted within 72 h using a Nikon research microscope equipped with autofluorescence (green light 530–560 nm excitation and >580 nm emission). Numerical abundance of cyanobacteria cells was determined by counting a minimum of five ocular micrometer grids at 1000 \times . The number of grids counted was adjusted for cell density. Counts were completed upon reaching a minimum of 100 cells.

General phytoplankton composition was determined using the Utermohl method (Utermohl, 1958). Lugols preserved samples were settled in 19 mm i.d. cylindrical chambers. Phytoplankton cells were identified and counted at 400 \times and 100 \times with a Nikon phase contrast inverted microscope. At 400 \times , a minimum of 100 cells of a single 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 \times a total bottom count was completed for taxa greater than 30 μm . Light microscopy was aided by other techniques to properly identify dinoflagellates and diatoms. Identifications of *Gonyaulax polygramma* and *Scrippsiella trochoidea* were confirmed using the squash technique (Steidinger, 1979). Sodium thiosulfate was used to de-stain Lugols preserved samples where it was needed for positive identification. *Protoperidinium* species were identified by cell size, shape, and body contour. Small *Gymnodinium* cells were put in size categories. Certain diatom taxa were identified after clearing the cells with hydrogen peroxide. The texts and journal articles used most frequently to aid in taxonomic identification were Steidinger and Williams (1970), Tester and Steidinger (1979), Sournia (1986), Ricard (1987), Hasle et al. (1996), Tomas (1997), and Fryxell et al. (1997).

The identifications of the potentially toxic diatom *Pseudo-nitzschia pseudodelicatissima* and dinoflagellate *Pyrodinium bahamense* var. *bahamense* were confirmed using scanning electron microscopy (Fig. 2). *Pseudo-nitzschia pseudodelicatissima* were prepared for SEM observation by using 0.1% (w/v) poly-L-lysine in water solution (Sigma Diagnostics, St. Louis, MO) on membrane filters. The samples were fixed in 2% glutaraldehyde, dehydrated in a graded ethanol series, and critical point dried. While light microscopy and preliminary SEM analyses indicated that the diatom in question was either *P. pseudodelicatissima* or *P. delicatissima*, more detailed SEM examination revealed that the dominant species observed in the lagoon exhibited several features consistent with the former designation (Hasle et al., 1996; Fryxell et al., 1997), including: (1) presence of central inner space, (2) striae with squarish poroids with hymenate sectors (Fig. 2), (3) transapical axis averaging 1.8 μm , (4) average apical axis of 63 μm , (5) an average of 36 striae in 10 μm , and (6) an average of 19 fibulae in 10 μm .

Glutaraldehyde fixed *P. bahamense* var. *bahamense* were deposited onto three aminopropyltriethoxysilane-treated cover slips (Angerer and Angerer, 1991), then fixed with 1% osmium tetroxide, and dehydrated in a graded ethanol series. After dehydration, the samples were dried using hexamethyldisilazane and observed on a Hitachi S-4000 scanning field emission electron microscope (Hitachi High Technologies America,

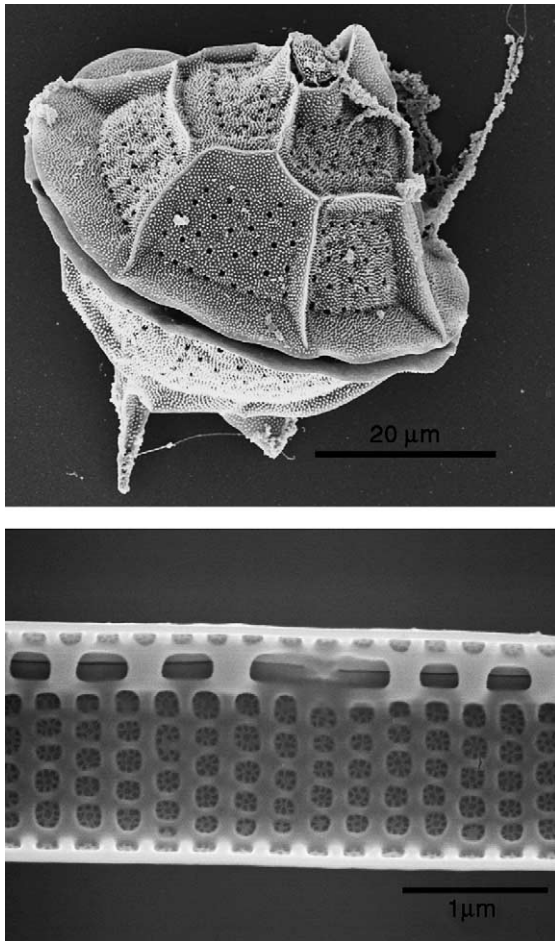


Fig. 2. SEM images of *Pyrodinium bahamense* var. *bahamense* (top) and *Pseudo-nitzschia pseudodelicatissima* (bottom) from samples collected at bloom sites in the Indian River Lagoon in 2002.

Inc., Pleasanton, CA). After light and SEM (Fig. 2) examination of size, shape, and plate counts the *P. bahamense* observed in the samples from the Indian River Lagoon were given the varietal designation *bahamense*, in accordance with the re-description of the species in the Atlantic region by Steidinger et al. (1980). It should be noted that this varietal designation has been disputed by Balech (1985).

Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxon. 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.

3. Results and discussion

3.1. General trends in phytoplankton abundance and composition

A number of features of the Indian River Lagoon make it a candidate for algal blooms. Long residence times, shallow depth, and high nutrient concentrations all contribute to algal biomass potential in large portions of the lagoon (Phlips et al., 2002), characteristics it shares with other restricted lagoonal ecosystems around the world (Monbet, 1992; Knoppers et al., 1991). The region of the lagoon near Titusville, examined in this paper, exhibits all these characteristics. As might be expected, high phytoplankton standing crops were regularly observed at the sampling site (Fig. 3). In this case, high standing crops are defined as phytoplankton biovolumes in excess of 2 million $\mu\text{m}^3 \text{ml}^{-1}$, or roughly equivalent to $10 \mu\text{g l}^{-1}$ of chlorophyll *a*. The highest standing crops were observed in 2001 and 2002, with values up to 43.86 million $\mu\text{m}^3 \text{ml}^{-1}$ (Fig. 3).

From an intra-annual perspective, the results of this study support the existence of a seasonal pattern of phytoplankton abundance (Phlips et al., 2002), with the highest standing crops during the warm-wet season from June through October. Mean phytoplankton biovolume for the warm-wet season over the study period was $7.15 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$ (range: 1.17×10^6 to $43.86 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$), compared to $1.58 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$ for the remainder of the year, i.e. November to May (range: 0.40×10^6 to $3.58 \times 10^6 \mu\text{m}^3 \text{ml}^{-1}$). However, since the Indian River Lagoon is located in the transition region between the tropical environment of South Florida and the temperate environments of the mid-Atlantic coast of the United States, temperature and light conditions during the winter do not preclude the development of elevated phytoplankton standing crops, as seen in the El Nino winter of 1997/1998 (Fig. 3).

The results of this study also showed temporal shifts in the dominant algal groups within the phytoplankton community. Diatoms generally dominated

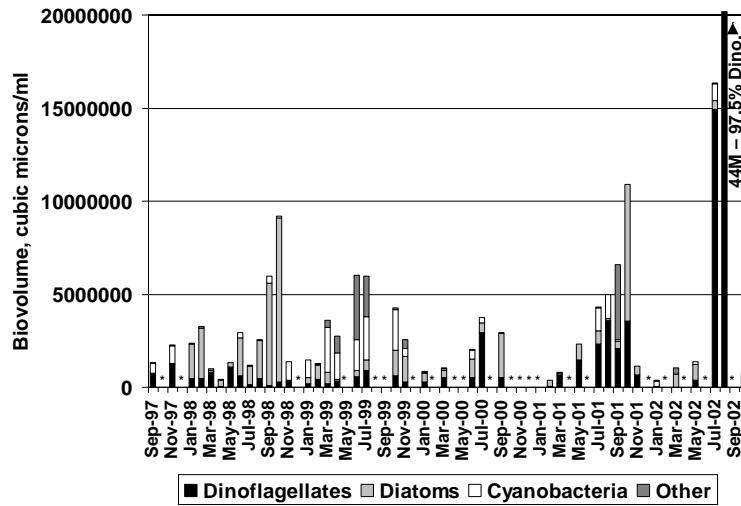


Fig. 3. Biovolume of major algal groups at the Titusville sampling site. Asterisk indicates that a monthly sample was not collected.

phytoplankton biomass in the first year of the study (Fig. 3). In the second year, cyanobacteria and green algae took on a position of greater prominence. In subsequent years, dinoflagellates were most often the dominant algal group, at least from a biovolume perspective. Among the algae encountered at the study site there were two taxa which warrant special consideration because of their potential toxicity and prominence during the study period, the dinoflagellate *P. bahamense* var. *bahamense* and the diatom *P. pseudodelicatissima*.

3.2. *Pyrodinium bahamense* var. *bahamense*

One of the most distinctive features of the phytoplankton record over our 5-year study period was the exceptionally high phytoplankton standing crops observed in the summer of 2001 and even more dramatically in the summer of 2002 (Fig. 3). The potential significance of these high standing crops is accentuated by the predominance of dinoflagellates during these time periods. While the long-term historical record of phytoplankton communities in the Indian River Lagoon is relatively limited, there are indications that dinoflagellate blooms are a recurring feature of the Lagoon. Reports of dinoflagellate blooms in the lagoon include the toxic species *Alexandrium monilatum* (formerly *Gonyaulax monilata*) in the early

1950s (Howell, 1953) and late 1970s (Norris, 1983) and *Gymnodinium pulchellum* in 1996 (Steidinger et al., 1998). Both of these species were encountered in this study and a previous study of the lagoon in general (Badylak and Phlips, 2003), but not at bloom levels. The dominant bloom-forming dinoflagellate encountered in our 5-year study of the Titusville region was *P. bahamense* var. *bahamense* (Figs. 2 and 4). During the algal blooms observed in 2001 and 2002, *P. bahamense* var. *bahamense* comprised up to 97.5% of total phytoplankton biovolume (Table 1).

While the presence of *P. bahamense* var. *bahamense* in the Titusville region was not unexpected, since it has been observed throughout the lagoon (Badylak and Phlips, 2003) and other estuaries in Florida, like Florida Bay (Phlips and Badylak, manuscript in preparation), the intensity of the blooms in 2001 and 2002 is noteworthy. A close relative of *P. bahamense* var. *bahamense*, *P. bahamense* var. *compressum*, has long been known for its ability to produce the neurotoxin saxitoxin (Hallegraeff, 1993), associated with paralytic shellfish poisoning (i.e. PSP). *Pyrodinium bahamense* var. *compressum* has been associated with numerous toxic bloom events around the world and is responsible for more reported PSP cases than any other dinoflagellate species (Azanza and Taylor, 2001). However, *P. bahamense* var. *bahamense* had not been identified as a potential toxin producer

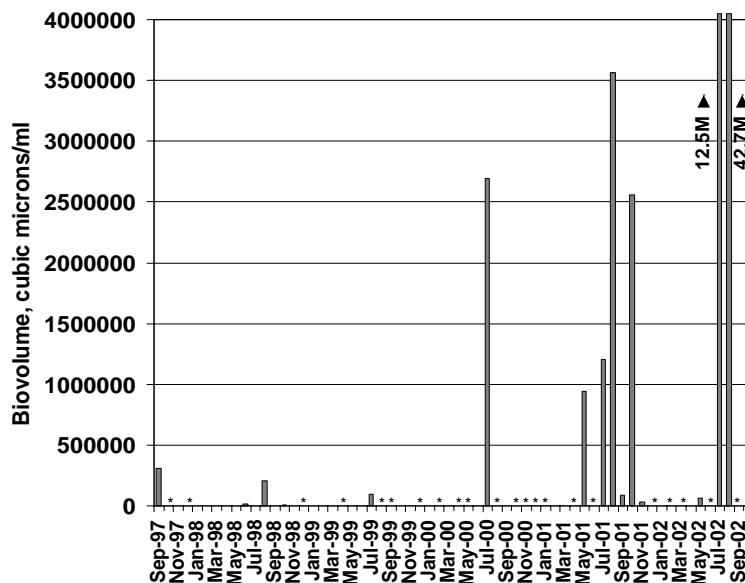


Fig. 4. Biovolume of *Pyrodinium bahamense* var. *bahamense* at the Titusville site. Asterisk indicates that a monthly sample was not collected.

until recently. Landsberg et al. (2002) first observed saxitoxin production by *P. bahamense* in samples collected from the Indian River Lagoon in 2001. The latter research was carried out in relation to observations of high concentrations of saxitoxin in pufferfish collected from the Titusville region of the Indian River Lagoon. While a direct link between *P. bahamense* var. *bahamense* blooms and the saxitoxin in pufferfish has yet to be confirmed, the temporal and spatial coincidence of these two phenomena provides a hypothetical link between the two phenomena. Given the information currently available on saxitoxin production by *P. bahamense* from the Indian River Lagoon it is only possible to speculate whether the cell densities observed in this study should be considered harmful. The current guideline used to establish risk levels for *P. bahamense* var. *compressum* by several nations is 200 cells l^{-1} (Andersen, 1996). The latter threshold was exceeded on 14 dates during our study (Table 2). The cell numbers encountered in 2001 and 2002 (i.e. up to $638,000 \text{ cells l}^{-1}$) are especially noteworthy and warrant further study in terms of the potential ecological and human health implications. But as noted by Smayda (1997a,b) cell numbers are not the only criteria for defining the risk of specific algal pop-

ulations. The size and toxin production capacity of individual strains of potentially toxic species must be evaluated for the prevailing environmental conditions in the ecosystem in question. It is well known that toxin production is under the control of both genotypically and phenotypically based modes of regulation (Smayda, 1997a,b; Smayda and Reynolds, 2001).

The causes of the observed *P. bahamense* var. *bahamense* blooms in the Indian River Lagoon in 2001 and 2002 remain unresolved. The 5-year period included in this study was characterized by three major shifts in meteorological conditions. The first year of the study was highlighted by an El Niño event that brought exceptionally high rainfall to the Indian River Lagoon watershed. The impact of the El Niño can be detected in the low salinities observed in the first year of the project (1997/1998) (Fig. 5). Although *P. bahamense* var. *bahamense* was observed in samples from this period of time it did not play a dominant role in the overall phytoplankton community from a biovolume perspective (Table 1). The subsequent 2 years of the study were associated with a severe drought. The paucity of rainfall during these years is reflected in the elevated salinities observed in the lagoon. *P. bahamense* var. *bahamense* was observed during the

Table 1
Total phytoplankton biovolume ($\mu\text{m}^3 \text{ml}^{-1}$) and the percent contributions of *Pyrodinium bahamense* and *Pseudo-nitzschia pseudodelicatissima* to total biovolume

Date	Total biovolume	% <i>Pyrodinium</i>	% <i>Pseudo-nitzschia</i>
September 18, 1997	1327412	23.4	1.5
November 13, 1997	2255498	0.0	1.1
January 5, 1998	2386088	0.0	0.2
February 9, 1998	3275867	0.0	0.4
March 2, 1998	989043	0.0	0.0
April 6, 1998	434337	0.0	0.0
May 4, 1998	1338533	0.0	0.0
June 9, 1998	2925288	0.5	0.4
July 13, 1998	1172195	0.0	1.2
August 10, 1998	2567524	8.1	29.8
September 14, 1998	5977450	0.0	33.3
October 19, 1998	9184430	0.1	0.0
November 30, 1998	1395672	0.0	0.0
January 11, 1999	1486937	0.0	0.0
February 8, 1999	1257239	0.0	11.5
March 8, 1999	3587764	0.0	0.0
April 26, 1999	2768067	0.0	0.0
June 28, 1999	6032485	0.1	0.1
July 16, 1999	5960178	1.6	5.3
October 11, 1999	4266008	0.0	9.5
November 29, 1999	2563414	0.0	0.0
January 10, 2000	869497	0.0	0.0
March 17, 2000	1043291	0.0	0.0
June 1, 2000	2040618	0.0	0.0
July 7, 2000	3736077	72.2	8.3
September 14, 2000	2918498	0.0	36.9
February 7, 2001	400163	0.0	0.0
March 14, 2001	802430	0.0	1.7
May 22, 2001	2331889	40.3	10.2
July 20, 2001	4308480	28.0	3.3
August 23, 2001	4979974	71.6	0.0
September 25, 2001	6602311	1.3	0.0
October 30, 2001	10906817	23.5	66.4
November 28, 2001	1158921	2.9	8.8
January 23, 2002	399683	0.0	0.0
March 21, 2002	1062384	0.0	0.0
May 2, 2002	1397030	4.8	0.0
July 2, 2002	16333092	76.7	2.1
August 6, 2002	43868616	97.5	0.0
October 30, 2002	772924	12.1	0.0

latter period of time but at relatively low concentrations. The drought ended in the late spring of 2001, as manifested by the coincidental drop in salinity (Fig. 5). In the following summer *P. bahamense* var. *bahamense* took on bloom proportions. The post-drought period of 2001/2002 was also associated with significant increases in total phosphorus concentrations not

observed during the previous high rainfall period of 1997/1998 (Fig. 6). Total nitrogen levels were elevated during both high rainfall periods (Fig. 6). It may be hypothesized that rainfall events following the drought period of 1999/2000 resulted in a flushing of bioavailable phosphorus and nitrogen into the Indian River Lagoon that stimulated *P. bahamense* var. *bahamense* blooms. A similar argument was made by Anton et al. (2000), who noted that blooms of *P. bahamense* var. *compressum* in Malaysia appeared to coincide with periods of elevated rainfall and nutrient-rich runoff. From broader temporal and biogeographical perspectives, Maclean (1989) has proposed that blooms of *P. bahamense* var. *compressum* in the Indo-Pacific are linked to El Nino events that alter the vertical and geographical distribution of warm water masses. The results of this study, as well as a previous study of the Indian River Lagoon (Badylak and Phlips, 2003), indicate that *P. bahamense* var. *bahamense* is restricted to temperatures in excess of 25 °C (Figs. 3 and 5), which is indicative of the tropical nature of this species.

The prominence of *P. bahamense* var. *bahamense* in the Titusville region of the Indian River Lagoon, as well as the overall importance of dinoflagellates in the Indian River Lagoon (Badylak and Phlips, 2003), supports the contention that certain taxa within this algal division are good competitors in nutrient-rich and flow-restricted estuaries, as suggested by Smayda and Reynolds (2001). However, *P. bahamense* var. *bahamense* does not appear to fall into the category of small-celled dinoflagellate species identified by Smayda and Reynolds (2001) as high nutrient, i.e. “C” selected taxa, i.e. species with high growth rates at high nutrient levels. There is clearly much to be learned about the factors that dictate species succession in the lagoon (Badylak and Phlips, 2003). At the present time, it is only possible to formulate causal hypotheses from empirical observations of key environmental parameters, like trends in phosphorus concentration.

3.3. *Pseudo-nitzschia pseudodelicatissima*

While many of the algal toxin-related events in marine environments are associated with dinoflagellates there are other algal divisions which contain toxic taxa. One of the most prominent of these is the diatom

Table 2

Cell densities (cells l⁻¹) for *Pyrodinium bahamense* var. *bahamense* and *Pseudo-nitzschia pseudodelicatissima*

<i>Pyrodinium bahamense</i> var. <i>bahamense</i>		<i>Pseudo-nitzschia pseudodelicatissima</i>	
September 18, 1997	4630	September 18, 1997	65000
June 9, 1998	200	November 13, 1997	85500
August 10, 1998	3100	January 5, 1998	18200
October 19, 1998	100	February 9, 1998	45300
June 28, 1999	50	June 9, 1998	41000
July 16, 1999	1400	July 13, 1998	45000
July 7, 2000	40200	August 10, 1998	2532000
May 22, 2001	14000	September 14, 1998	6588000
July 20, 2001	18000	February 8, 1999	480000
August 23, 2001	53200	June 28, 1999	22800
September 25, 2001	1300	July 16, 1999	1041900
October 30, 2001	38200	October 11, 1999	1344700
November 28, 2001	500	July 7, 2000	1020100
May 2, 2002	1000	September 14, 2000	3563600
July 2, 2002	186800	March 14, 2001	45000
August 6, 2002	637800	May 22, 2001	787200
October 30, 2002	1400	July 20, 2001	463600
		October 30, 2001	23945000
		November 28, 2001	336700
		July 2, 2002	1152600

genus *Pseudo-nitzschia*, known for the production of the neurotoxin domoic acid, responsible for amnesiac shellfish poisoning (ASP). ASP events have been most common in the northwest Pacific coast (Hallegraeff, 1993; Fryxell et al., 1997; Stehr et al., 2002) and to a lesser extent in the North Atlantic (Martin et al.,

1990; Hargrave and Maranda, 2002). However, potentially toxic species of *Pseudo-nitzschia* have been observed in many regions of the world, including the Gulf of Mexico (Hallegraeff, 1993; Dortch et al., 1997; Parsons et al., 1999; Pan et al., 2001) and the Indian River Lagoon (Hargrave, 2002). Our

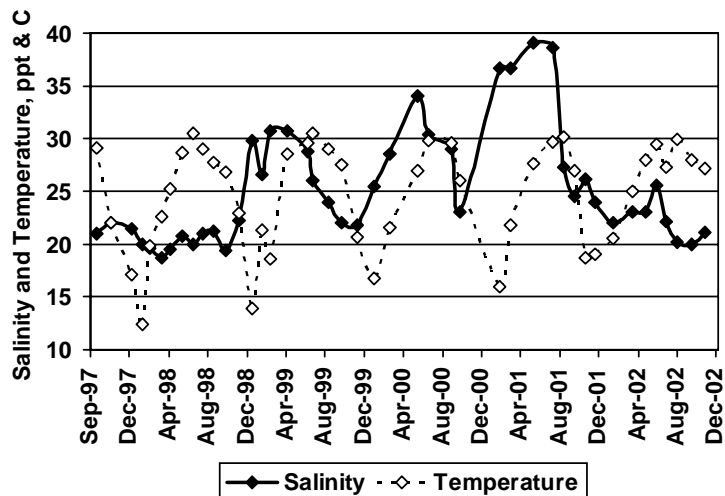


Fig. 5. Temperature and salinity over the sampling period.

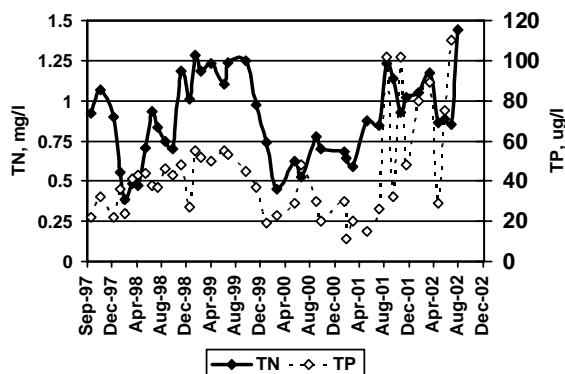


Fig. 6. Total nitrogen and total phosphorous concentrations.

quantitative information on *P. pseudodelicatissima* abundance over the past 5 years in the Indian River Lagoon indicates that this potentially toxic species is a prominent member of the phytoplankton community (Fig. 7 and Table 1). Concentrations of *P. pseudodelicatissima* exceeded the risk guidelines of 500,000 cells l⁻¹ used by many countries (Andersen, 1996) on nine dates during the sampling period (Table 2). Since no studies of domoic acid production by *P. pseudodelicatissima* from the Indian River La-

goon have been carried out, it would be premature to estimate the environmental risk associated with these observations.

The results of our study indicate that the *P. pseudodelicatissima* was a major feature of the phytoplankton community in the Titusville region on over half of the 37 sampling dates over the 5-year study period. It was observed in every season, although it was most prolific in the summer and early fall. It is unclear what factors promote the abundance of *P. pseudodelicatissima*. Given its broad temporal distribution, it is apparently an adaptable species, a conclusion shared by Fryxell et al. (1997), who concluded that *P. pseudodelicatissima* appears to be able to act as either an r- or k-selected species, depending on the prevailing environmental conditions. Fryxell et al. (1997) examined long-term data on the distribution of *P. pseudodelicatissima* in the Pacific northwest, as well as the results of culture experiments, and concluded that cells can shift from fast growth mode under high nutrient conditions to slow growth nutrient conserving mode during periods of low nutrient availability. This may help to explain why the *P. pseudodelicatissima* observed in our study showed peaks of abundance throughout the study period, irrespective of flood or drought conditions.

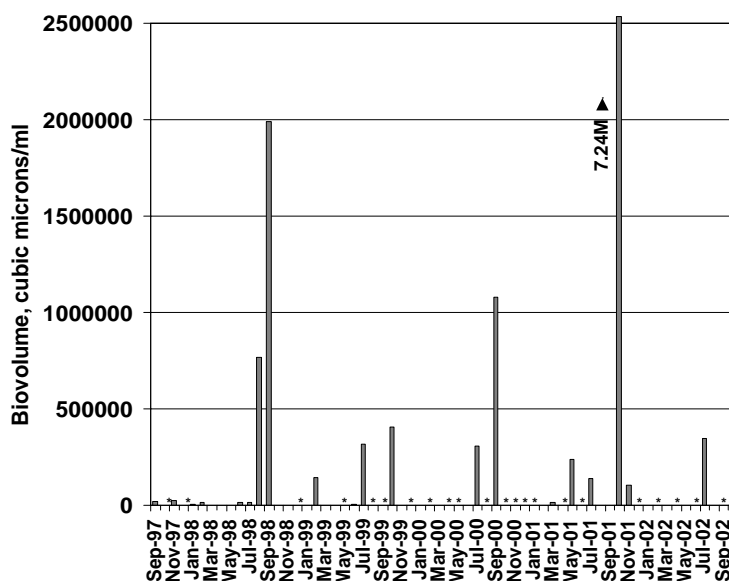


Fig. 7. Biovolume of *Pseudo-nitzschia delicatissima* at the Titusville site. Asterisk indicates that a monthly sample was not collected.

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