From Red Tides to Green and Brown Tides: Bloom Dynamics in a Restricted Subtropical Lagoon Under Shifting Climatic Conditions

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Abstract Relationships between shifts in climatic and other environmental conditions and changes in the character and dynamics of phytoplankton blooms were examined in three interconnected subtropical lagoons on the east coast of Florida, i.e., Mosquito Lagoon, Indian River Lagoon, and Banana River Lagoon, from 1997 to 2013. Phytoplankton blooms were a common feature through most of the study period in two of the lagoons. From 1997 to 2009, blooms in the latter two lagoons were typically dominated by dinoflagellates in the warm wet season and diatoms in the cool dry season. Blooms of the dominant bloom-forming dinoflagellate species *Pyrodinium bahamense* were positively correlated to rainfall levels, indicating a link to enhanced external nutrient loads. In 2011–2013, major blooms were observed in all three lagoons, but unlike the previous 14 years, they were dominated by picoplanktonic eukaryotes, including a chlorophyte, Pedinophyceae sp., and the brown tide species *Aureoumbra lagunensis*. The results suggest that extreme climatic conditions, including record cold winter water temperatures and low rainfall levels, were major driving factors in this state shift in the character of blooms, through a wide range of effects including die-offs of benthic flora and fauna, suppression of grazer populations, alteration of nutrient regimes, and uncharacteristic water column conditions, such as elevated salinities and light attenuation.

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Introduction

Increases in the frequency and intensity of phytoplankton blooms in many coastal environments around the world have focused attention on the importance of defining the factors that control bloom dynamics. The link between increases in nutrient loads and phytoplankton blooms has been demonstrated for a number of estuarine ecosystems (Sellner et al. 2003; Glibert and Burkholder 2006; Anderson et al. 2008; Heisler et al. 2008), while in other systems, the responses of phytoplankton biomass and composition to changes in load are complicated by the influence of other driving factors, such as high rates of water turnover, light limitation, or grazing losses (Cloern 2001; Smayda 2008; Phlips et al. 2004, 2011; Sunda and Shertzer 2012). Overlying these issues, recent indications of global changes in climate have heightened attention on climatic influences on phytoplankton structure and dynamics (Rhodes et al. 1993; Hales et al. 1998; Belgrano et al. 1999; Reid et al. 1998; Belgrano et al. 2002; Paerl and Paul 2012; Phlips et al. 2010; Zingone et al. 2010; O'Neil et al. 2012). One of the major challenges in defining the effects of climatic variability on phytoplankton dynamics is distinguishing between the effects of short-term and cyclical (e.g., La Niña/El Niño cycles) patterns versus longer-term changes in state (Beisner et al. 2003; Viaroli et al. 2008).

The growing availability of long-term data sets for coastal ecosystems has provided an opportunity to explore the influences of eutrophication on phytoplankton dynamics within the

context of trends in climatic conditions (Cloern and Jassby 2010; Zingone et al. 2010; O'Neil et al. 2012; Paerl and Paul 2012; Wetz and Yoskowitz 2013). Some of these extended time series provide examples of shifts in phytoplankton composition and abundance related to changes in climatic conditions at various time scales. For example, in Laguna Madre estuary in Texas, an extreme low-temperature period in December of 1989 and associated die-off of aquatic flora and fauna resulted in spikes in ammonia levels precipitating blooms of the brown tide species *Aureoumbra lagunensis*, which persisted for the following 8 years (Buskey et al. 1996, 1997). The dominance of *A. lagunensis* during the extended bloom period was promoted by hypersaline conditions, caused by an extended period of below-average rainfall, which competitively favored this exceptionally euryhaline species (Buskey et al. 1998; Buskey et al. 2001).

Another example of intense algal blooms associated with shifts in climatic conditions is haptophyte blooms in the Baltic Sea. Blooms of the harmful haptophyte *Chrysochromulina* spp. have been associated with periods of above-average water temperatures and reduced salinities related to high rainfall (Skjodal and Dundas 1991; Belgrano et al. 1999; Gjøsæter et al. 2000). The blooms have been designated as major features in apparent regime shifts in plankton communities of the region (Reid et al. 1998). Changes in the character and abundance of plankton linked to shifts in climate have also been documented in other regions of the Atlantic (Frages and Bakum 1993; Beaugrand et al. 2002; Johns et al. 2003; Edwards and Richardson 2004; Lefebvre et al. 2011). On a broader geographic scale, it has been suggested that future increases in carbon dioxide levels and global temperature regimes may lead to increasing dominance of dinoflagellates, cyanobacteria, and certain microflagellate species over diatoms that prefer cooler temperatures (Nehring 1998; Wasmund et al. 1998; Edwards et al. 2001, 2006; Paerl and Paul 2012; O'Neil et al. 2012). Such shifts in phytoplankton communities can have ripple effects on the overall structure and function of affected ecosystems (Edwards and Richards 2004; Wetz and Yoskowitz 2013).

The central objective of this study was to examine correlations between shifts in climatic conditions and other environmental variables and phytoplankton blooms in a chain of connected subtropical lagoons on the central east coast of Florida, i.e., Mosquito Lagoon (ML), northern Indian River Lagoon (NIRL), and Banana River Lagoon (BRL). All three lagoons are subject to long water residence times, but varying levels of anthropogenically enhanced nutrient loads (Sigua and Tweedale 2003; Adkins et al. 2004; Steward and Green 2007; Gao 2009). The results of the study indicate that shifts in the structure and biomass of the phytoplankton community were correlated to climatic variability, which principally changes in rainfall and temperature, as it directly affects salinity, hydrology (e.g., water residence time), and nutrient

availability and indirectly affects other biota, such as grazer and benthic macrophyte populations.

Methods

Site Description

Five sampling sites were the focus of the study, located in the central ML, southern ML, NIRL, northern BRL, and central BRL (Fig. 1). The five sites represent regions of major phytoplankton bloom activity. To explore salinity preferences of key phytoplankton species, data from three additional sites were included in the analyses, sites 6–8 (Fig. 1).

The sampling regions are microtidal and have long water residence times, with estimated mean water half-lives (i.e., 50 % exchange) of 76 days in the ML, 107 days in the NIRL, and 156 days in the BRL (Sheng and Davis 2003; Steward et al. 2005; Reyier et al. 2008; D. Christian, unpublished data). All three regions included in the study are characterized by small watersheds relative to the size of the receiving basins but vary in terms of land use characteristics (Sigua and Tweedale 2003; Adkins et al. 2004; Steward et al. 2005). The NIRL and BRL watersheds have significant urban/residential areas along with some agriculture, light industry, and native wetlands. The ML watershed is ~70 % undeveloped, consisting of natural upland and wetland preserves in the south (mostly within the Canaveral National Seashore and Merritt Island Wildlife Refuge) and some residential and urban land uses in the northern and central regions of the ML.

Field and Laboratory Procedures

Sampling locations and frequencies varied over the study period (i.e., November 1997 to July 2013). The site in the central ML was sampled monthly from November 1997 to October 1999 and December 2007 to July 2013. The sites in the southern ML and northern BRL were sampled twice a month from May 2006 to July 2013. The sites in the NIRL and central BRL were sampled approximately monthly from November 1997 to April 2006, then twice per month from May of 2006 to July 2013. The latter sampling period was designated the "intensive sampling period."

Salinity and temperature were measured with YSI or Hach/Hydrolab environmental multiprobes. 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. Zooplankton samples were preserved on site with Lugol's solution. Bacteria samples were preserved on-site with buffered formalin. Aliquots of water for chlorophyll *a* analysis were filtered

Fig. 1 Location of sampling sites. Five primary sites (1–5) are shown as *filled symbols* in the Mosquito Lagoon (ML), northern Indian River Lagoon (NIRL), and Banana River Lagoon (BRL). Secondary sites (6–8) that are in the Indian River Lagoon are shown as *open symbols*, along with proximity of nearby city
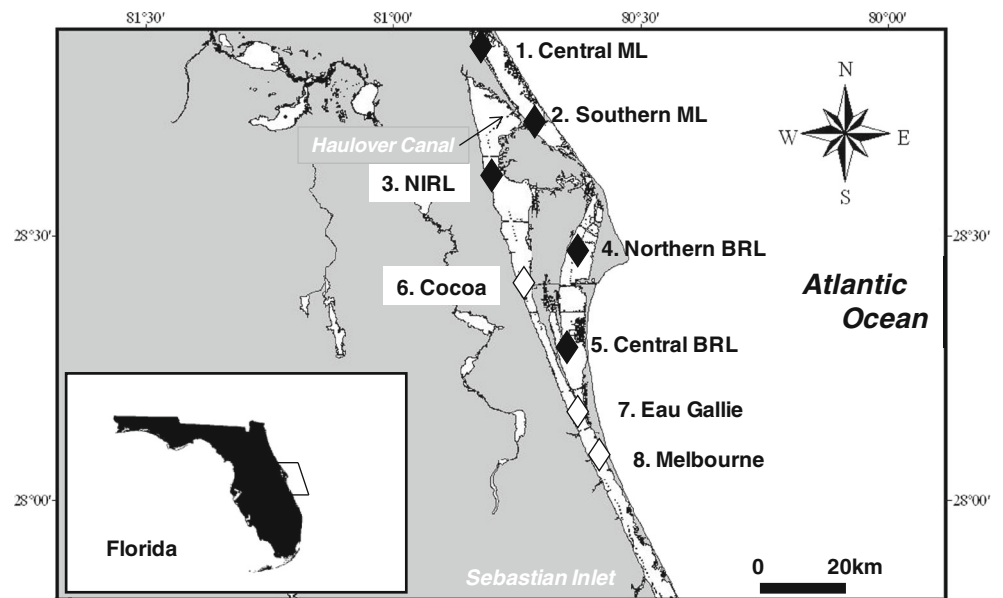
onto 0.7-μm filters (i.e., Whatman GF/F) on-site and stored frozen until analysis, or in some cases due to logistical issues, water was kept cold and filtered within 36 h. Additional aliquots of water were frozen for determination of total nitrogen and total phosphorus (APHA 1998; Parsons et al. 1984).

Climate Data

Rainfall data for the Titusville Meteorological Station, located near the NIRL sampling site, was obtained from the NOAA Climatological Data for Florida Web site (ncdc.noaa.gov). "Deviations from normal" are based on departures from mean values calculated from 1980 to 2012. Doppler rainfall data for the major lagoons (i.e., ML, NIRL, and BRL) were obtained from St. Johns River Water Management District (via contract with Vieux Inc.) at a 1-km^2 spatial resolution. The data were calibrated to continuously recording gauges spaced throughout the region. All grid cells occurring partially or wholly over the lagoons and their watersheds were used in developing daily, area-weighted, mean precipitation for each of the subregions. The multivariate ENSO Index data were obtained from the NOAA Web site (esrl.noaa.gov/psd/enso/mei).

Chemical Analysis

Chlorophyll *a* on filters was extracted with 95 % ethanol (Sartory and Grobbelaar 1984) and measured using a Hitachi dual beam spectrophotometer, according to Standard Methods (APHA 1998). Total nitrogen (TN) and total phosphorus (TP) concentrations were determined using Standard Methods APHA (1998), with some modifications from U.S.E.P.A. methods (1983), in accordance with Phlips Laboratory at the University of Florida NELAP QA/QC approved Certification #E72883.

Plankton 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 were 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 and scanning electron microscopy (Badylak et al. 2004). Scanning and transmission electron microscopy and fluorescence microscopy were used to confirm the taxonomic composition of the 2011 and 2012 blooms, which were dominated by the chlorophyte Pedinophyceae sp., picoplanktonic cyanobacteria, and the pelagophyte *A. lagunensis*. The distinctive size, morphological appearance under phase microscopy, and presence of uniquely shaped single flagella were used to identify Pedinophyceae sp. during cell counts. Similarly, distinct morphological characteristics were used to count *A. lagunensis*. The identity of *A. lagunensis* as the dominant species in the 2012 and 2013 was further confirmed using SEM/TEM (Phlips et al. 2012) and from the results of contemporaneous work using immunological methods of identification by C. Gobler of the State University of New York (Gobler et al. 2013; and personal communications with

C. Gobler) and A. Corcoran of Florida's Fish and Wildlife Research Institute (personal communications).

To explore the potential role of mixotrophic and heterotrophic dinoflagellates in top-down pressure on phytoplankton blooms, numerical abundances were determined for genera containing species known to exhibit these functional attributes, including *Akashiwo sanguinea*, *Ceratium furca*, *Cochlodinium polykrikoides*, *Dinophysis* spp., *Gonyaulax* spp., *Gymnodinium* spp., *Gyrodinium* spp., *Heterocapsa* spp., *Karenia* spp., *Karlodinium veneficum*, *Prorocentrum* spp., and *Scrippsiella* spp. (Burkholder et al. 2008; Joeng et al. 2010).

Fluorescence microscopy was used to enumerate picoplanktonic cyanobacteria (i.e., picocyanobacteria) at ×1,000 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 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. Phytoplankton carbon values (as µg carbon ml^{-1}) were estimated by using conversion factors for different taxonomic groups applied to biovolume estimates (expressed as 10^6 µm^3 ml^{-1}), i.e., 0.061×biovolume of diatoms, 0.22×biovolume of cyanobacteria or small picoplanktonic eukaryotes, and 0.16×biovolume of dinoflagellates or other taxa (Ahlgren 1983; Sicko-Goad et al. 1984; Verity et al. 1992; Strathmann 1997; Work et al. 2005).

For the purpose of description and discussion, "blooms" were defined as phytoplankton carbon values for individual species which fell within the top 20 % of total phytoplankton carbon values in all samples examined over the study period, i.e., >1 µg carbon ml^{-1}.

For zooplankton analysis, 3,000-ml aliquots of Lugol's preserved sample water were filtered through a 41-µm pore size mesh filter. The zooplankton on the filter were rinsed into a scintillation vial and adjusted to a final volume of 20 ml. Zooplankton were counted using the Utermöhl method (Utermöhl 1958). Cylindrical chambers with a 19-mm inner diameter were used to settle aliquots of sample. Settling time was a minimum of an hour. Zooplankton and microzooplankton were identified and counted at ×100 magnification with a Leica phase contrast inverted microscope. A minimum of 3 ml was counted. If 100 individuals of a single taxon were not reached after 3 ml was counted, then counting continued until 100 individuals of a single taxon were reached, or the entire 20-ml aliquot was counted, whichever came first. For the purpose of presentation, zooplankton were categorized into four groups, protozoans (e.g., ciliates), arthropods (e.g., copepods, crustacean nauplii), rotifers, and other taxa (e.g., mollusk larvae, echinoderm larvae). Small-celled protozoans (i.e., <41 µm), e.g., *Mesodinium rubrum*, were enumerated during the phytoplankton counts and added to the total zooplankton counts.

Seagrass and Drift Algae Methods

Seagrass fixed transects were monitored in the summer and winter, corresponding to times of annual maximum and minimum biomass abundance, respectively (Virnstein and Morris 1996). Each transect consisted of a graduated line, extending perpendicular from shore out to the deep edge of the grass bed. Every 10 m along the line, various metrics were measured within a 1-m^2 quadrate, centered on the line. Metrics included water depth (corrected to MLW), total transect length (measured from shore to deep edge), seagrass percent cover (density) for each seagrass species, seagrass shoots m^{-2}, drift macroalgae percent cover and biomass, and an estimate of epiphyte biomass, according to methods detailed in Morris et al. (2001). Similarly, the average seagrass percent cover (density) along each transect length was calculated and used to estimate the average seasonal seagrass density for the same area. This same data compilation process was used to estimate the area's seagrass, epiphytes, and drift algae biomass.

Drift macroalgae in deeper water (≥1.5 m and generally outside grass beds) were surveyed using a hydroacoustic methods (Riegl et al. 2005). Hydroacoustically derived biomass data for drift macroalgae were generated along east-west parallel transect lines, generally spaced less than 0.5 km apart, according to field methods and lagoon-specific classification algorithms developed by Riegl et al. (2005) and Riegl (2013). No hydroacoustic surveys were conducted in 2011; therefore, measurements of drift macroalgae biomass outside grass bed margins were unavailable for that year. Estimates for 2011 were calculated for each lagoon by applying trends in the ratios of survey-to-transect biomass of three previous survey years to the 2011 transect biomass.

External Nutrient Load Estimate Methods

External nutrient loads were calculated as the sum of modeled watershed loading, direct atmospheric deposition, and point discharge from wastewater treatment plants that file monthly reports to the Florida Department of Environmental Regulation (FDEP). Modeling of watershed loads was performed using an adaptation of the pollutant load screen model (PLSM; Adamus and Bergman 1995), which was calibrated to loading data collected from watersheds in the central IRL (Green and Steward 2003). For this investigation, the model was modified to predict TN and TP loading from runoff and base flow on a monthly time step. Direct atmospheric

deposition came from Doppler-derived rainfall data with a spatial resolution of 1 km^2 and a daily time step.

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).

Results

Physical, Chemical, and Climatic Characteristics

Water temperatures ranged from 4 to 33 °C over the study period (Fig. 2), with little vertical stratification (i.e., surface versus bottom temperature differences <2 °C, with few exceptions). The subtropical location of the lagoon results in water temperatures that generally exceed 20 °C from March to November and winter minimum water temperatures between 10 and 15 °C. However, in the winter of 2009/2010, water temperatures dipped to well below temperatures encountered during the study period, i.e., 4 °C. The exceptionally low winter water temperatures continued in 2010/2011, returning to more typical values in the winter of 2011/2012.

East-central Florida, where the sampling sites were located, is characterized by a cool dry season extending from November to May and a warm wet season extending from June to October, which includes the tropical storm season that peaks in August–September. Patterns of interannual variation in rainfall often follow the El Niño/La Niña cycle, as exemplified by the El Niño Southern Oscillation Index (ENSO) (Fig. 3a), with the former being characterized by generally higher rainfall than the latter. Superimposed on these interannual patterns
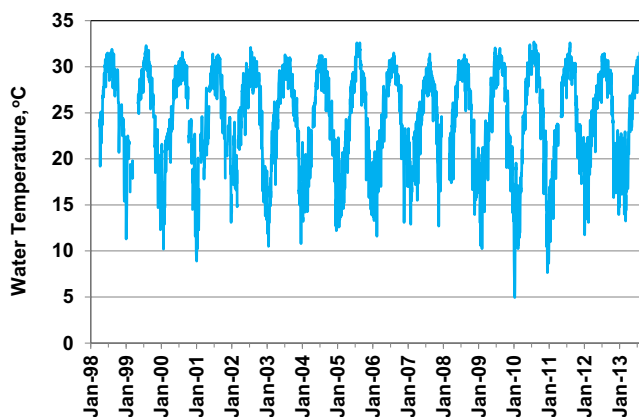
Fig. 3 Multivariate ENSO Index (MEI) over the study period (i.e., positive values indicate El Niño conditions and negative values indicate La Niña conditions) (*top*) and departures from normal rainfall levels (i.e., monthly) at the Titusville Meteorological Station (*bottom*) (US Climate Service, 2013), located near the NIRL site

Fig. 2 Daily average water temperatures in the Haulover Canal, which connects the southern ML and NIRL (temperatures measured at USGS station #02248380, Haulover Canal)
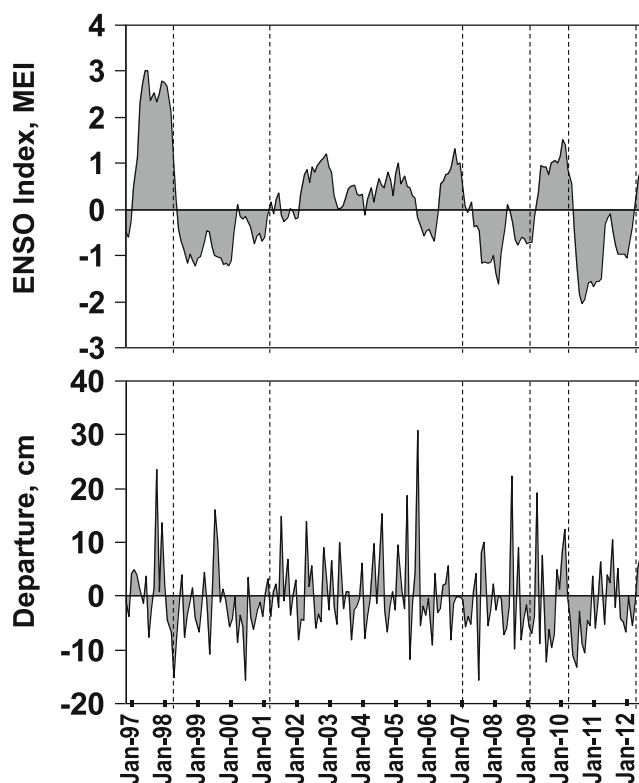
were summer storm events throughout the study period, resulting in shorter-term peaks in rainfall independent of longer-term patterns (e.g., summers of 1999 and 2008) (Fig. 3b).

Salinities ranged from 22.6 to 45.2 psu in the ML, 15 to 39.5 psu in the NIRL, and 10.0 to 39.7 psu in the BRL. Extended periods of high rainfall were associated with depressed or declining salinities, such as the El Niño periods of 1997 and 2001–2005 (Fig. 4). Conversely, extended periods of predominantly below-average rainfall (e.g., 1998–2000, 2010–2012) resulted in elevated salinities, such as 1998–2000 and 2010–2012 (Fig. 4). Vertical stratification of salinity was very limited (i.e., only a handful of differences between surface and bottom salinities greater than 1–2 psu), due to shallow depths (i.e., 1.5–3 m) and lack of major freshwater inflows within close proximity of the sampling sites.

Secchi disk depths ranged from 0.1 to 2.6 m in the ML, 0.3 to 2.6 m in the NIRL, and 0.3 to 2.5 m in the BRL. All three lagoons experienced periods of low-light transmission, with Secchi depth values of 0.4–0.5 m or less, such as during the protracted phytoplankton blooms of 2011, 2012, and 2013 (Fig. 4).

Annual mean TN concentrations ranged from 66 to 116 μmol l^{-1} in the ML, 68 to 122 μmol l^{-1} in the NIRL,
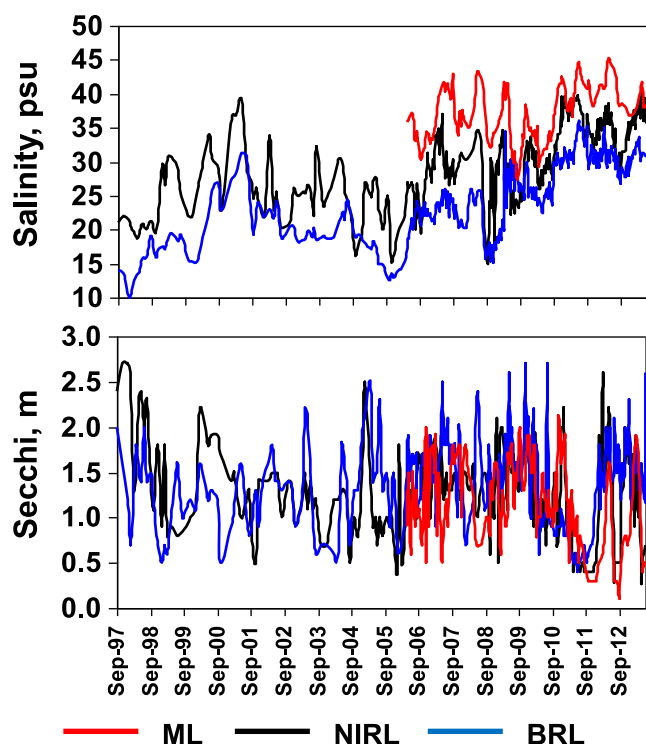
Fig. 4 Surface water salinity (*upper*) and Secchi depth (*lower*) at southern ML site (*red line*), NIRL site (*black line*), and central BRL site (*blue line*)

and 76 to 148 µmol l^{-1} in the BRL (Table 1). During the intensive sampling period (2007–2013), annual mean TN concentrations in the ML were similar from 2007 to 2010, then increased substantially in 2011 and remained elevated in 2012, before declining in 2013 (Fig. 5). Annual mean TN concentrations in the NIRL had a similar pattern as the ML until 2012, when mean concentration declined. In the BRL, annual mean TN concentrations had two peaks, in 2008 and 2011.

Annual mean TP concentrations ranged from 0.77 to 2.19 µmol l^{-1} in the ML, 1.10 to 3.03 µmol l^{-1} in the NIRL, and 1.06 to 3.45 µmol l^{-1} in the BRL (Table 1). During the intensive sampling period (2007–2013), annual mean TP concentrations in the three lagoons remained relatively constant from 2007 to 2009 before increasing in 2010, most notably in the BRL, and reached major peaks in 2011 (Fig. 5). In the

Table 1 Range of annual mean values for total phosphorus (TP), total nitrogen (TN), and chlorophyll *a* (CHL)

Region	TN (µmol l^{-1})	TP (µmol l^{-1})	CHL (µg l^{-1})
ML	66–116 (88)	0.77–2.19 (1.65)	5.2–51.0 (12.9)
NIRL	68–122 (88)	1.10–3.03 (1.65)	4.8–43.5 (12.5)
BRL	76–148 (105)	1.06–3.45 (1.74)	4.0–58.7 (14.8)

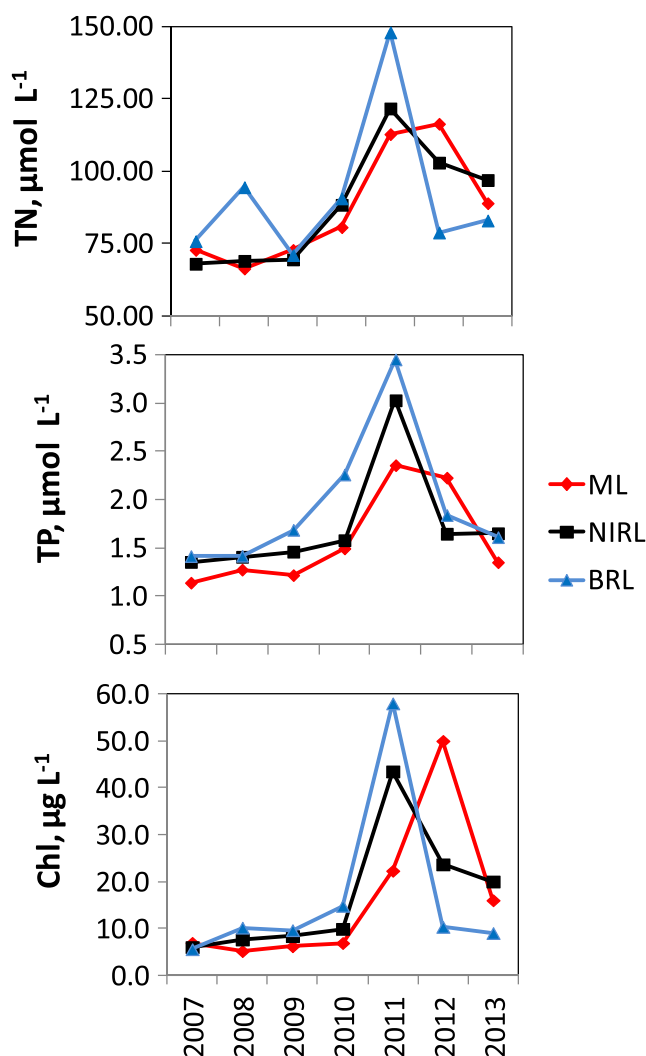Average of mean annual values for the study periods in the three regions are shown in parentheses

Fig. 5 Annual mean total nitrogen (TN) (*upper*), total phosphorus (TP) (*middle*), and chlorophyll *a* (Chl) (*lower*) concentrations at the southern ML site (*red line*), NIRL site (*black line*), and central BRL site (*blue line*) during the intensive sampling period (2007–2012). Standard deviations for mean TN values ranged from 22 to 41 % of the mean at ML, 18 to 39 % of the mean at NIRL, and 20 to 34 % of the mean at BRL. Standard deviations for mean TP values ranged from 35 to 55 % of the mean at ML, 21 to 48 % of the mean at NIRL, and 21 to 38 % of the mean at BRL. Standard deviations for mean Chl values ranged from 53 to 140 % of the mean at ML, 55 to 93 % of the mean at NIRL, and 35 to 107 % of the mean at BRL

BRL and NIRL, annual mean TP concentrations declined in 2012 and 2013 but remained high in the ML in 2012, then declined in 2013.

Phytoplankton Biomass

Annual mean chlorophyll *a* concentrations (CHL) ranged from 5.2 to 51.0 µg l^{-1} in the ML, 4.8 to 43.5 µg l^{-1} in the NIRL, and 4.0 to 58.7 µg l^{-1} in the BRL (Table 1). During the intensive sampling period (2007–2013), annual mean CHL concentrations were similar in all three lagoons from 2007 to

2010 (Fig. 5). In 2011, there was a large increase in annual mean CHL in all three lagoons most prominently in the NIRL and BRL. In 2012, the trends diverged between regions, with a continued increase in ML, but declines in the NIRL and BRL.

Correlations between TN, TP, and CHL varied by region (Table 2). In ML, CHL was correlated to TN and TP. In the NIRL, CHL was most strongly correlated to TP. In the BRL, CHL was only correlated to TP.

Annual median phytoplankton biomass (i.e., in terms of carbon) ranged from 0.106 to 0.534 μg carbon ml^{-1} at the central ML site, 0.202 to 2.377 μg carbon ml^{-1} at the southern ML site, 0.163 to 1.454 μg carbon ml^{-1} at the NIRL site, 0.288 to 2.161 μg carbon ml^{-1} at the northern BRL site, and 0.199 to 2.347 μg carbon ml^{-1} at the central BRL site. For the study period prior to 2011, annual median biomass values were mostly less than 1 μg carbon ml^{-1} at all sites. In 2011, annual median biomass values were greater than 2 μg carbon ml^{-1} in the BRL, and in 2012, annual median biomass values were greater than 2 μg carbon ml^{-1} in the ML. The latter observations highlight the magnitude of the 2011 and 2012 bloom events.

Phytoplankton blooms (i.e., phytoplankton carbon >1 μg ml^{-1}) were observed at all five primary sites over the study period (Fig. 6). After a period of relatively low bloom activity during the predominantly below average rainfall period from the summer of 1998 through the spring of 2001 (La Niña period), there was an increase in the magnitude and frequency of blooms in the BRL and NIRL. From a general seasonal perspective, diatoms frequently dominated blooms during colder months (i.e., November–March) in the NIRL and BRL (e.g., *Dactyliosolen fragilissimus*, *Rhizosolenia setigera*, *Cerataulina pelagica*, *Skeletonema costatum*, and *Pseudo-nitzschia* spp.), while picocyanobacteria and dinoflagellates (i.e., most often *Pyrodinium bahamense*; see Badylak et al. 2004) typically dominated blooms during warmer months (i.e., April–October). The seasonal disparity between diatom and dinoflagellate blooms is illustrated by the relationship between water temperature and biomass levels of centric chain-forming diatoms and the dinoflagellate *P. bahamense* (Fig. 7).

In 2010, the character of phytoplankton blooms began to deviate from prior observations in the central BRL. Exceptionally cold winter water temperatures (Fig. 8) coincided with an uncharacteristically intense diatom bloom, which reoccurred in the spring (Fig. 6). The subsequent summer and fall were characterized by elevated levels of picoplanktonic cyanobacteria (i.e., picocyanobacteria) (Fig. 6), depressed Secchi depths (i.e., <1 m), and above-average salinities (Fig. 8). In the spring of 2011, a major phytoplankton bloom started in the central BRL and spread from the spring through the summer into the northern BRL, NIRL, and ultimately into the southern ML (Fig. 6) (Table 3). The bloom was codominated by picocyanobacteria and a small-celled (i.e., <5 μm) chlorophyte, i.e., Pedinophyceae sp., not previously observed as a bloom component. In 2012 and 2013, the magnitude of blooms further increased, centering on the ML and NIRL, but not including the BRL (Fig. 6). The latter blooms were dominated by another species not previously observed at bloom levels in the study region, i.e., the brown tide species *A. lagunensis*.

The relationships between external nutrient load and phytoplankton bloom peaks changed from 1998–2009 to 2010–2011 (note that external load data estimates are not yet available for 2012 and 2013). The change is visible by comparing the correlations between major bloom peaks and external loads preceding the peaks (i.e., 2 months before bloom peaks) for two time periods, i.e., 1998–2011 versus 1998–2009 (Table 4). The weaker correlations for the 1998–2011 data set reflect the high phytoplankton biomass peaks relative to low external loads in 2010 and 2011.

Among the major blooms observed over the study period, those involving *P. bahamense*, the Pedinophyceae/picocyanobacteria consortium and pelagophytes (i.e., *A. lagunensis*) are particularly noteworthy because of their magnitude, duration, and/or potential harmful effects. The environmental conditions preceding and during major bloom events of these species were distinct in several key ways, as illustrated by three bloom events, i.e., the *P. bahamense* bloom of 2006 (i.e., red tide), the Pedinophyceae/picocyanobacteria bloom of 2011 (i.e., green tide), and the pelagophyte bloom of 2012 (i.e., brown tide).

Red Tide of 2006

In 2006, bloom levels of *P. bahamense* biomass were first observed in the central BRL (site 5) in June, following a period of elevated rainfall and when water temperatures (i.e., greater than 20 °C for over a month) (Fig. 9). The latter observation reflects the tropical character of the species (Fig. 7). A second larger peak in *P. bahamense* biomass appeared in August, coinciding with a period of elevated rainfall. The rainfall events in the Spring and Summer of 2006 were associated with increases in both TN and TP

Table 2 Pearson correlation coefficients between chlorophyll *a* (CHL) and total nitrogen (TN) and total phosphorus (TP) at the five primary sites

Site	TN	TP
Central ML	**0.46 (<0.0001)**	**0.32 (0.0036)**
Southern ML	**0.25 (0.0038)**	**0.23 (0.0061)**
NIRL	**0.30 (<0.0001)**	**0.65 (<0.0001)**
Northern BRL	0.07 (0.4470)	**0.71 (<0.0001)**
Central BRL	0.04 (0.5680)	**0.48 (<0.0001)**

Significance values are shown in parentheses

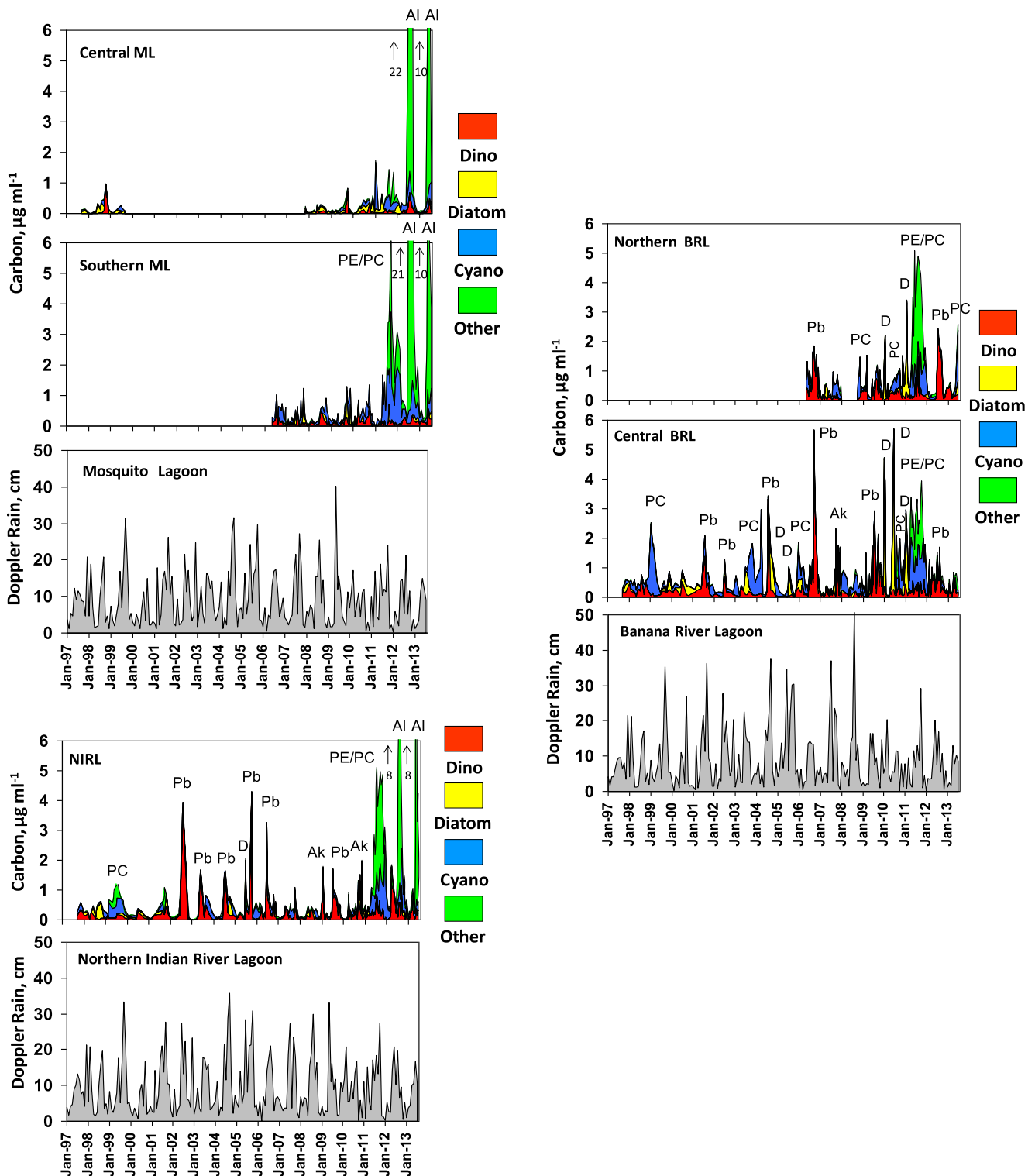Significant correlations ($p<0.05$) are shown in bold

Fig. 6 Phytoplankton biomass (phytoplankton carbon) subdivided into four groupings, i.e., dinoflagellates (*Dino*), diatoms (*Diatom*), cyanobacteria (*Cyano*), and all other taxa (*Other*). The dominant species associated with major peaks are shown: *Ak Akashiwo sanguinea*, *Al* *Aureoumbra lagunensis*, *D* centric diatoms, *Pb Pyrodinium bahamense*, *PC* Picocynaobacteria, *PE/PC* Pedinophyceae sp./Picocyanobacteria. Doppler rainfall patterns in each subregion of the study are presented below the biomass time series for each subregion (i.e., monthly totals)

concentrations (Fig. 9). The positive relationship between annual peaks in *P. bahamense* biomass and rainfall levels prior

to the blooms was also evident over the entire study period (Fig. 10). In a broader sense, the latter relationship is also
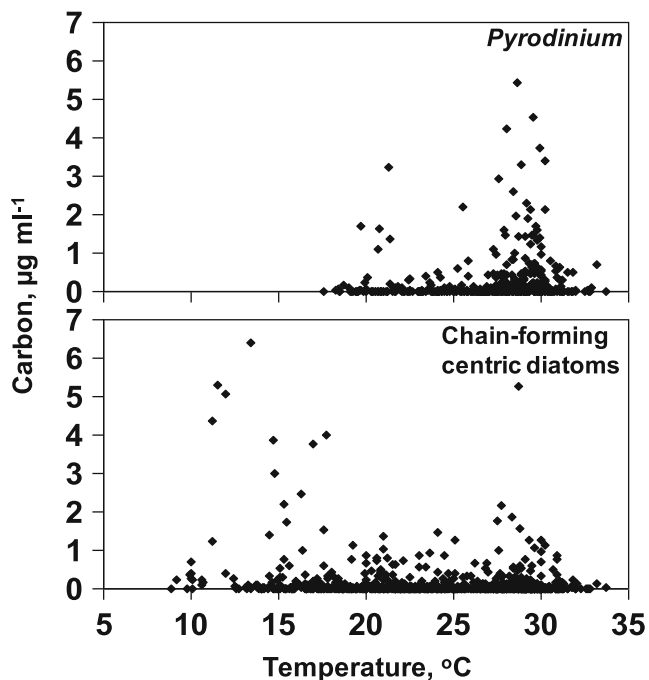
Fig. 7 Distribution of *Pyrodinium bahamense* and chain-forming centric diatom biomass versus surface water temperature, including all eight sampling sites

manifested in the positive relationship between *P. bahamense* biomass and El Niño periods (Fig. 11), which are often associated with elevated rainfall levels in east-central Florida (Fig. 3).

Green Tide of 2011

In 2011, the intense and prolonged Pedinophyceae sp./picocyanobacteria bloom was associated with uncharacteristic environmental conditions in the BRL. The Pedinophyceae/picocyanobacteria bloom was preceded by exceptionally cold water temperatures in December of 2010 and January of 2011
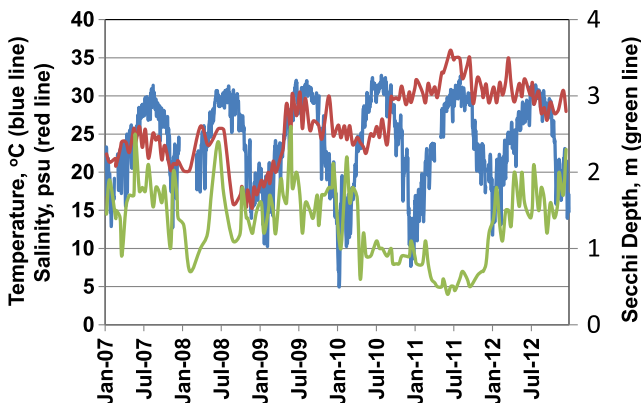

Fig. 8 Variations in surface water temperature, salinity, and Secchi depth from January 2007 to December 2012 in the central BRL

and a diatom bloom in January (Figs. 8 and 12). Bloom levels of Pedinophyceae/picocyanobacteria were first observed on March 15 in the central BRL. Unlike the *P. bahamense* bloom periods of 2004 and 2006, the initiation of the 2011 bloom was not associated with high external loads of TN or TP, even though TP concentrations, and to a lesser extent TN, were well above average (Tables 1 and 3), suggesting the presence of internal sources of nutrients. Rainfall totals associated with the 2004 and 2006 *P. bahamense* bloom periods (i.e., period defined as 1 month prior to the bloom plus the first 3 months of the bloom) were 92 and 55 cm, respectively, compared to 13.7 cm for a similar time frame during the 2011 Pedinophyceae/picocyanobacteria bloom. Estimated external (point source+nonpoint source inputs) TN loads in the central BRL basin were over 59,877 and 25,469 kg during the 2004 and 2006 *P. bahamense* bloom periods, respectively, compared to 10,217 kg during a similar period of the 2011 bloom. Estimated external (point source+nonpoint source inputs) TP loads were 6,742 and 1,752 kg during the 2004 and 2006 bloom periods compared to 517 kg during the 2011 bloom period. Despite the larger external nutrient loads associated with in the 2004 and 2006 blooms than the 2011 bloom period, mean TN and TP concentrations were higher during the 2011 bloom, and in the case of TP, over twice as high.

From 2010 to 2011, there were major declines in biomass of benthic primary producers (i.e., seagrasses, epiphytes, and drift macroalgae) compared to preceding years.

The pattern of decline is illustrated by changes in seagrass densities from 2009 to the summer of 2013 (Fig. 13). Densities declined from the summer of 2009 to the winter of 2009/2010 but recovered in the summer of 2010, similar to the pattern observed in previous years (Personal communication, St. Johns River Water Management District). Densities declined again in the winter of 2010/2011 but did not recover by the summer and remained well below historical values through the summer of 2013. Seagrass biomass in the NIRL and BRL declined from 2,500 t of dry weight in the summer of 2010 to 1,500 t of dry weight in the summer of 2011 (Fig. 14). Epiphyte biomass associated with seagrasses declined from 500 to 250 t dry weight (Fig. 14). Drift algae biomass declined from 9,500 to an estimated 500 t outside of the seagrass canopy and from 1,200 to 43 t within the seagrass canopy (Fig. 14). In total, benthic primary producer biomass declined by 11,450 t. By the summer of 2012, there was a partial recovery of the seagrass and drift algae communities in the NIRL and BRL.

In terms of potential planktonic grazers, densities of all major zooplankton species declined and were low during the initiation of the bloom in March (Fig. 12). Abundances of potential mixotrophic and heterotrophic dinoflagellate species peaked in January during a diatom bloom then declined in February prior to the green tide (Fig. 12). Later in the bloom period, densities of small protozoans (e.g., small ciliates),

Table 3 Total rainfall, estimated total nitrogen (TN) load, estimated total phosphorus (TP) load, mean TN concentration, and mean TP concentration during (i.e., 1 month before and the first 3 months of the bloom period) three bloom events in 2004, 2006, and 2011 in the central BRL

	Rain cm	TN load kg	TP load kg	Mean TN μmol l^{-1} (standard deviation)	Mean TP μmol l^{-1} (standard deviation)
2004 bloom	91.9	59,877	6,742	102.5 (27.3)	1.67 (0.26)
2006 bloom	42.8	25,469	1,752	59.5 (6.1)	1.48 (0.26)
2011 bloom	13.7	10,217	517	120.3 (15.9)	3.74 (0.68)

mixotrophic and heterotrophic dinoflagellates and rotifers showed multiple peaks, but arthropod densities remained low.

Brown Tide of 2012

The brown tide event of 2012 was first observed in June in the southern ML (Fig. 15). Biomass levels peaked in August at 21 μg carbon ml^{-1} (i.e., over 3 million cells ml^{-1}) then declined in September following the passage of a tropical storm, dropping below bloom levels by October. The brown tide event followed a rainfall event in June, which was associated with an increase in TN and TP concentrations (Fig. 15). Salinities in the regions of the bloom exceeded 40 psu through most of the event, peaking at 45 psu in the ML in May, just prior to the bloom (Fig. 15).

Zooplankton densities were low up to June (Fig. 15). Protozoan abundances increased dramatically in July to over 12,000 individuals l^{-1}, just prior to the peak of the brown tide (Fig. 15). After July, protozoan densities declined to near 2,000 individuals l^{-1} in September. Arthropod densities increased from less than 100 individuals l^{-1} to near 300 individuals l^{-1} in June, then declined again to 100 individuals l^{-1} in July before increasing to 300 individuals l^{-1} in August and September. Abundances of potential mixotrophic and heterotrophic dinoflagellates increased at the same time as increases in brown tide biomass and remained elevated after the collapse of the bloom.

There is less information on the dynamics of benthic primary producer communities in the ML than for the IRL and BRL.

Table 4 Pearson correlation coefficients for the relationship between peak bloom biomass levels (i.e., in terms of carbon) and external nutrient load estimates for total phosphorus (TP) and total nitrogen (TN) for the 2-month period prior to the bloom peaks

| Site	Element	Data for 1998–2011	Data for 1998–2009
C. BRL	TP	0.394 (0.0631)	**0.476 (0.0253)**
	TN	**0.592 (0.0029)**	**0.693 (0.0004)**
NIRL	TP	−0.146 (0.4957)	**0.562 (0.0152)**
	TN	−0.116 (0.5890)	0.375 (0.1255)

Values for the NIRL and central BRL sites are shown

Significance values are shown in parentheses, and values at the 0.05 significance level are bolded

Benthic macroalgae populations in the ML showed a major decline in biomass from 2011 to 2013 (Fig. 16). Prior to 2012, benthic algae biomass increased in the spring before declining in the midsummer and fall, but in 2012 and 2013, no spring or summer increases in macroalgae biomass were observed.

Discussion

As observed in other flow-restricted estuaries (Monbet 1992; Knoppers et al. 1991; Phlips 2002; Reynolds 2006), one of the primary driving factors responsible for frequent blooms in the
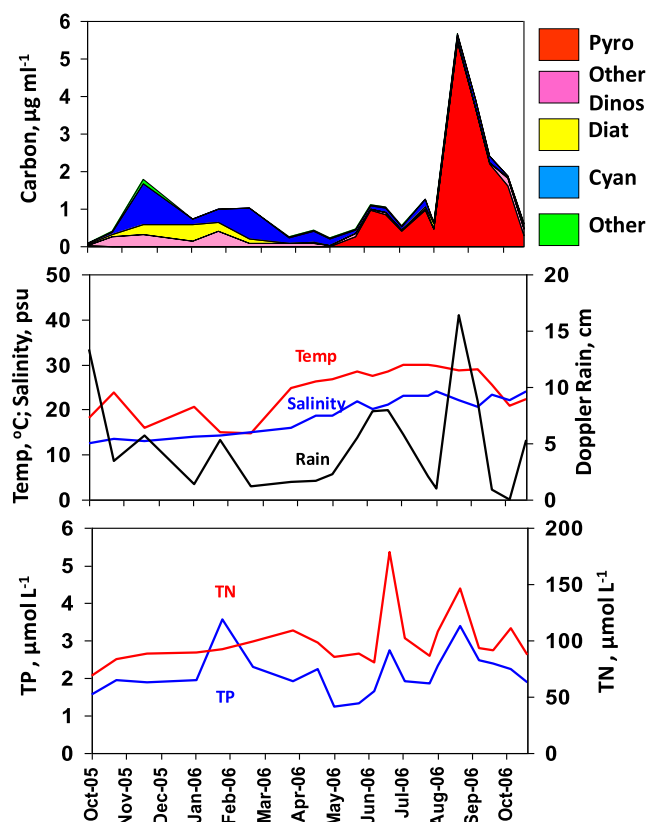
Fig. 9 Phytoplankton biomass divided into five major groups (**a**), i.e., *Pyrodinium bahamense* (*Pyro*), other dinoflagellates (*Other Dinos*), diatoms (*Diat*), cyanobacteria (*Cyan*), and other taxa; surface temperature, salinity and doppler rainfall (**b**); total nitrogen and total phosphorus concentrations (**c**); during the fall 2005 to fall 2006 time period at the central BRL site
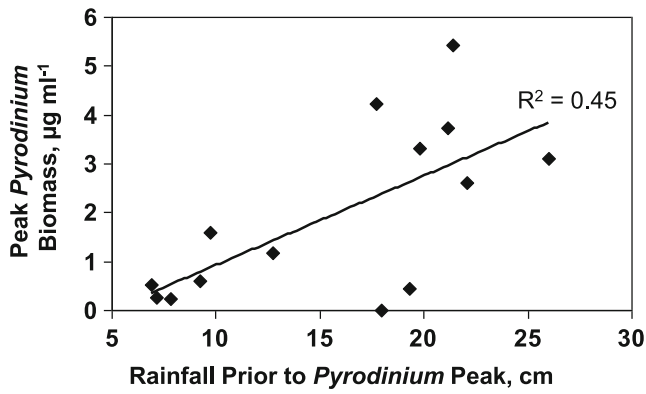
Fig. 10 Relationship between annual peaks in *Pyrodinium bahamense* biomass (i.e., expressed as carbon) and rainfall total prior to the peak (i.e., 2 months prior)

BRL and NIRL is long mean water residence times, i.e., 50 % water exchange rates of 156 and 107 days (Steward et al. 2005), providing ample time for the accumulation of phytoplankton biomass (Phlips et al. 2004, 2010, 2011). Another prerequisite for blooms is the availability of sufficient nutrients. Over the past century, anthropogenic sources of nutrients have enhanced the potential for phytoplankton blooms in many ecosystems around the world (Cloern 2001; Glibert and Burkholder 2006; Anderson et al. 2008; Heisler et al. 2008). The watersheds associated with the BRL and IRL
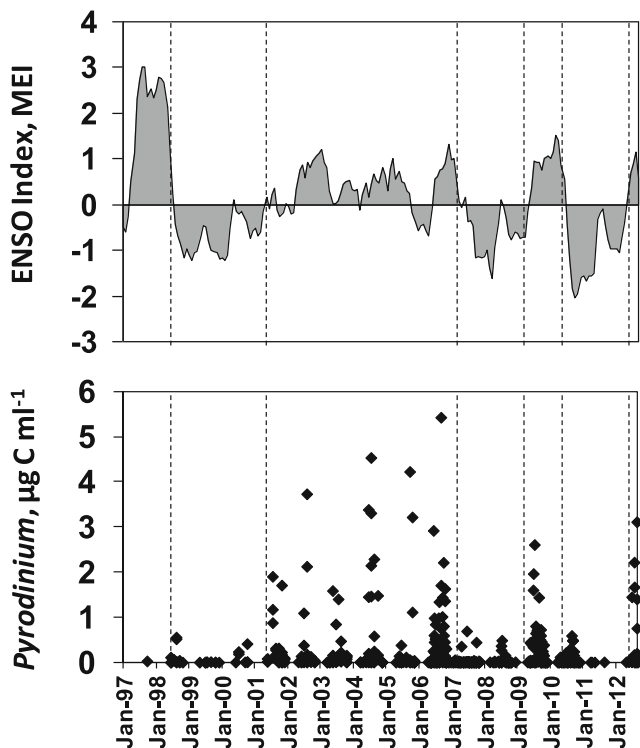

Fig. 11 Relationship between Multivariate ENSO Index (MEI) (*top*) and *Pyrodinium bahamense* biomass (*bottom*) from winter of 1997/1998 to summer of 2012 at all eight sampling sites
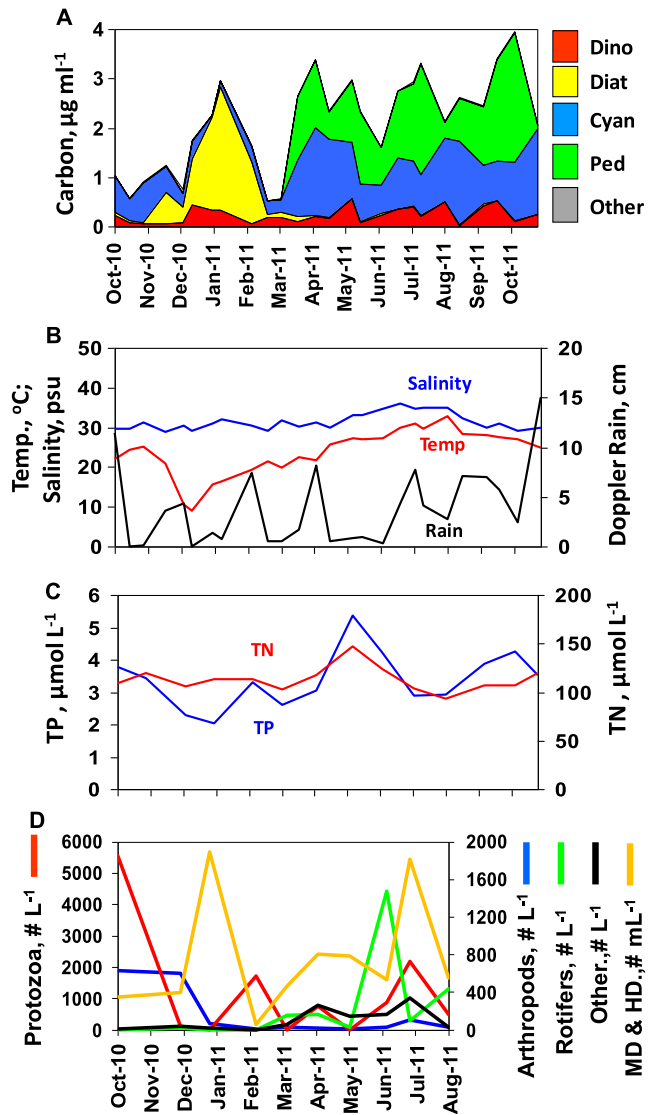

Fig. 12 Phytoplankton biomass divided into five major groups (**a**), i.e., dinoflagellates (*Dino*), diatoms (*Diat*), cyanobacteria (*Cyan*), Pedinophyceae sp. (*Ped*), and other taxa; surface water temperature, salinity, and local doppler rainfall (**b**); total nitrogen and total phosphorus concentrations (**c**); potential grazers of phytoplankton were divided into five groups: protozoa, arthropods (e.g., copepods), rotifers, other zooplankton taxa, and potential mixotrophic, MD, and heterotrophic, HD, dinoflagellates (**d**); during the fall 2010 to fall 2011 time period at the central BRL site

include significant human land uses which enrich nutrient loads (Atkins et al. 2004; Steward et al. 2005). The importance of external loads in supporting blooms in the BRL and NIRL is supported by the observation that up until 2010, phytoplankton biomass peaks were correlated to external nutrient loads prior to the peaks. By contrast, the watersheds of the central and southern ML contain a large proportion of undeveloped land (i.e., 70 %) (Atkins et al. 2004; Steward et al. 2005), and for much of the study period, the ML was characterized by comparatively low phytoplankton biomass, until
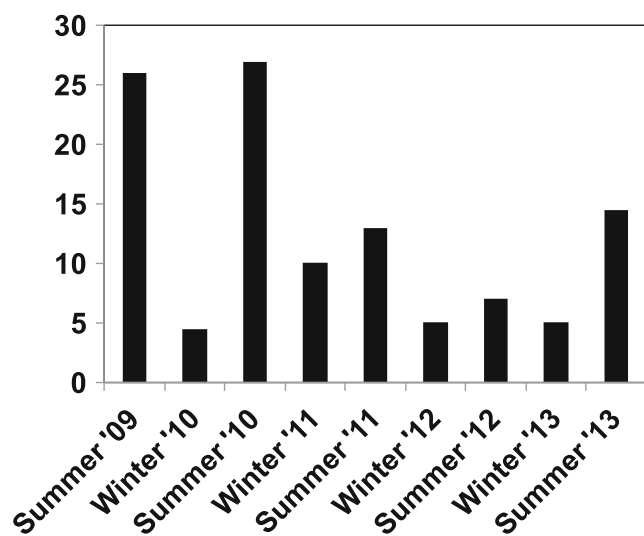
Fig. 13 Average seagrass densities in the NIRL and BRL in midwinter (December to February) and summer (June to August) as percent cover

the major blooms of 2011, 2012, and 2013, which were uncharacteristically dominated by small-celled (i.e., <5 μm) phytoplankton, including chlorophytes, picocyanobacteria, and pelagophytes. A comparison of climatic, physical, chemical, and biological conditions during the major bloom periods of 2006, 2011, and 2012 provides insights into potential drivers responsible for the observed shifts in bloom characteristics from red tides in the NIRL and BLR prior to 2010, green tides in the BRL, NIRL, and ML in 2011, and brown tides in the ML and NIRL in 2012 and 2013. Key traits of the dominant species involved in the red, green, and brown tides help to explain their success, such as nutrient utilization, morphology, susceptibility to grazing, toxin production, and
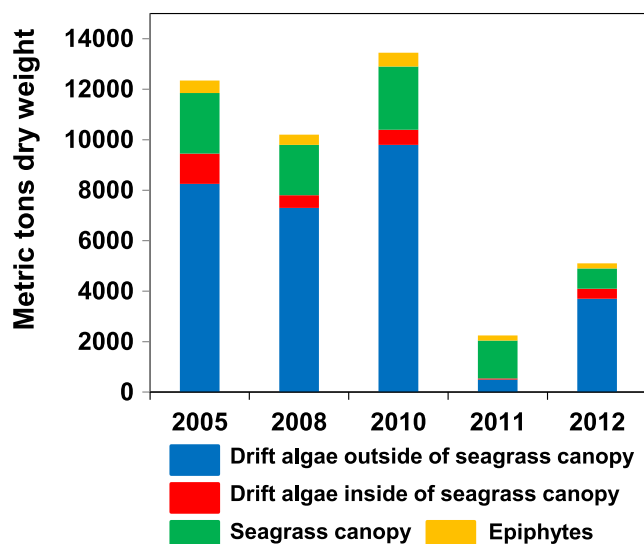

Fig. 14 Changes in biomass (as metric tons dry weight) of major components of benthic primary production in the northern IRL and Banana River from 2005 to 2012, during the summer season (i.e., June–August)
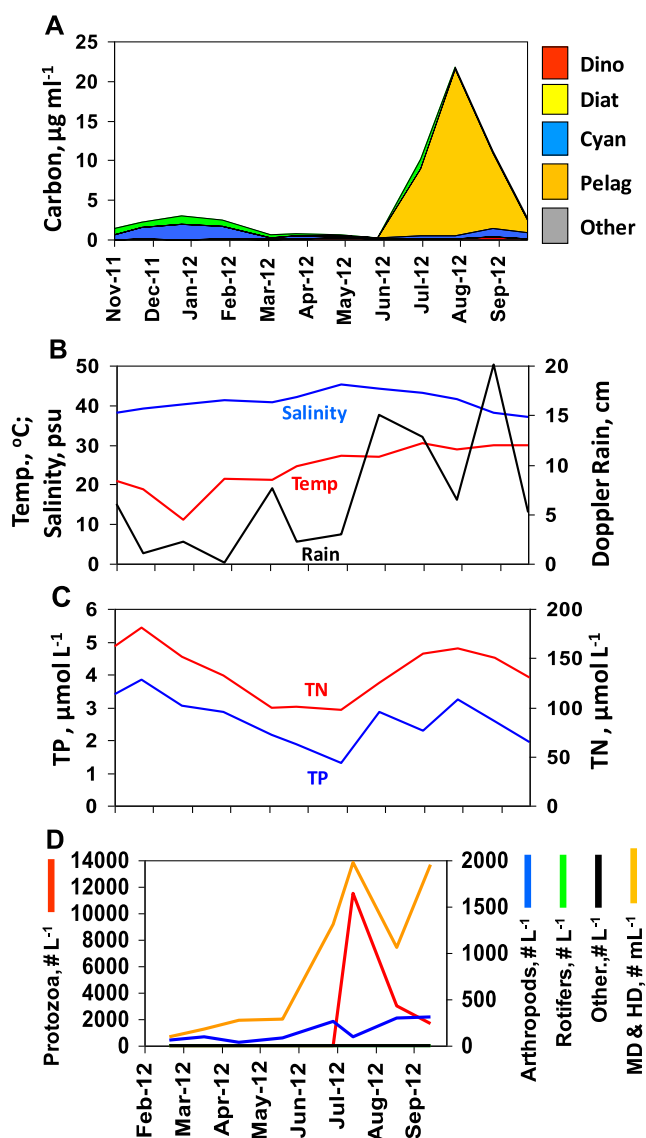
Fig. 15 Phytoplankton biomass divided into five major groups (*top*), i.e., dinoflagellates (*Dino*), diatoms (*Diat*), cyanobacteria (*Cyan*), Pelagophytes (*Pelag*), and other taxa (**a**); surface water temperature, salinity, and local doppler rainfall (**b**); total nitrogen and total phosphorus concentrations (**b**); potential grazers of phytoplankton were divided into five groups, i.e., protozoa, arthropods (e.g., copepods), rotifers, other zooplankton taxa, and potential mixotrophic, MD, and heterotrophic, HD, dinoflagellates; during the 2012 time period at the central ML site

adaptability to variations in physical-chemical conditions, such as temperature, salinity, and light availability.

Red Tides

Over the first 14 years of the study period, blooms of *P. bahamense* were most commonly associated with a similar combination of environmental conditions. Because of its tropical nature, blooms of *P. bahamense* were restricted to warmer months of the year from April to October, when temperatures

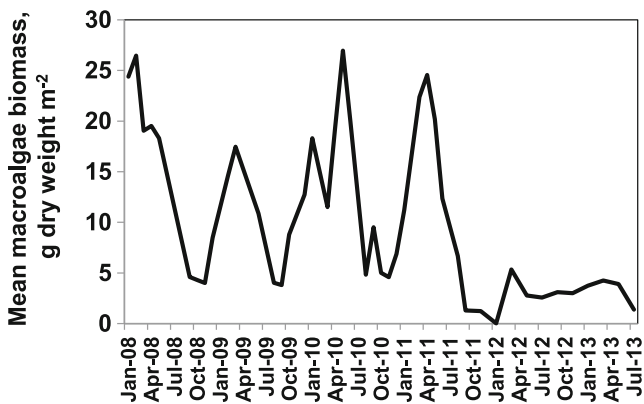**Fig. 16** Mean macroalgae biomass in the Mosquito Lagoon from January 2008 to July 2013

exceeded 20 °C. The most intense blooms coincided with periods of above-average rainfall in 2002–2006, the spring of 2009 and summer of 2012, reflecting the influence of elevated external loads of growth-limiting nutrients associated with elevated rainfall levels. The importance of external nutrient loads for *P. bahamense* blooms is supported by the positive relationship observed between the magnitude of annual peaks in *P. bahamense* biomass and rainfall prior to the events. The relationship between nutrient levels and phytoplankton biomass is further suggested by the strong positive correlation between TP and CHL in the NIRL and BRL. The fact that high winter/spring rainfall levels in central Florida are often correlated to El Niño periods helps to explain the apparent correlation between *P. bahamense* blooms and El Niño. It has been hypothesized that the relationship between *P. bahamense* blooms and periods of elevated external nutrient load is in part attributable to the high nutrient requirements of the species (Phlips et al. 2006; Usup et al. 2012). Extended periods of high rainfall are also associated with variable and depressed salinities which selectively favor euryhaline species (Lewitus et al. 2008; Kreble 2013; Strom et al. 2013), such as *P. bahamense*, which has been observed at bloom levels at salinities near 13 to 35 psu (Phlips et al. 2006).

Given sufficient nutrient availability, the toxic nature (Landsberg et al. 2006; Abbott et al. 2009) and large size of *P. bahamense* may also contribute to bloom formation by reducing top-down pressure on biomass accumulation (Phlips et al. 2006). As recently proposed by several researchers, change in top-down pressure on phytoplankton communities influences both bloom formation and community structure, as it relates to relative susceptibility of different species to grazing (Mitra and Flynn 2006; Sunda et al. 2006; Sunda and Shertzer 2012). The results of a recent study of *P. bahamense* blooms in Tampa Bay in Florida showed that the abundance of certain elements of the zooplankton community declined during peaks in bloom biomass (Badylak and Phlips 2008), as has been noted for other toxic phytoplankton species (Smayda 2008; Turner 2006).

Green Tide

The Pedinophyceae/picocyanobacteria bloom of 2011 was the first major bloom observed over the 16-year study period involving a small-celled (i.e., <5 μm) flagellated eukaryote, other than dinoflagellates. The nature of the bloom is also noteworthy because pedinophytes have not been previously identified as major bloom species on any HAB lists (e.g., IOC; www.marinespecies.org/hab/). The green tide began during a period of comparatively low external nutrient loads, raising questions about the conditions that precipitated the event. The answer may lie in the combined effects of changes in several factors, including exceptionally low winter water temperatures in 2009/2010 and 2010/2011 and higher than average salinities (i.e., due to predominantly below-average rainfall conditions in 2010 and early 2011), low zooplankton abundances, and shallow Secchi depths (i.e., <1 m). The changes likely enhanced bloom potential by increasing internal nutrient loads from dying benthic biomass and reducing top-down pressure on bloom initiation. The changes in physical and chemical conditions may also have competitively favored the small-celled phytoplankton species observed in 2011–2013, such as low-light availability, high salinity, and altered nutrient characteristics.

Due to shallow depths, the NIRL, BRL, and ML are normally characterized by significant benthic primary producer biomass, including seagrasses, drift macroalgae, and epiphytes (Steward et al. 2005, 2007), as observed in many other shallow estuaries in the region (Murrell et al. 2009). Benthic primary producer biomass in the study region declined substantially from 2010 to 2011, representing a potentially large internal nutrient source. The role of low winter temperatures experienced during 2009/2010 and 2010/2011 on this decline is in part attributable to the prominent presence of tropical species in benthic primary producer biomass, such as the seagrass species *Syringodium filiforme*, *Halodule beaudettei* (i.e., *Halodule wrightii*), and *Thalassia testudinum* and drift macroalgae, such as *Gracilaria tikvahiae* and *Hypnea cervicornis* (Virnstein and Carbonara 1985; Riegl et al. 2005), all of which have been shown to be negatively impacted by temperatures below 20 °C (Phillips 1960; Lapointe and Ryther 1978; Ding et al. 2013).

The importance of declines in benthic primary producers in supplying nutrients for the 2011 bloom is supported by a comparison of the loss in benthic biomass from 2010 to 2011 and the gain in phytoplankton biomass. Within the area of the lagoon affected by the bloom, an estimated 11,450 t of benthic primary producer biomass was lost between 2010 and 2011, while approximately 6,600 t of phytoplankton was present at the peak of the bloom in the summer of 2011. The relative similarity of the loss and gain estimates provides further evidence of the potential role of internal nutrient loads in support of the 2011 bloom. The drought conditions and

exceptionally low temperatures that characterized the winters of 2009/2010 and 2010/2011 may not only have had negative effects on benthic aquatic biomass but also increased accumulation of organic matter in local terrestrial watersheds, subsequently released into the lagoon during rainfall-induced runoff.

In addition to the binding up of nutrients in benthic biota, drift macroalgae, seagrass, and epiphytic algae are potential competitors with planktonic primary producers for water column nutrients (MacIntyre et al. 2004; Sunda et al. 2006). Therefore, declines in the biomass of these benthic primary producers have the dual effects of freeing up bound nutrients and reducing competition with phytoplankton for nutrients in the water column, an effect enhanced by shallow depth. The great longevity of the 2011 bloom may in part be attributable to the reduction of competition for external nutrient loads entering the lagoons during the wet season.

In terms of light availability, the months leading up to the green tide were characterized by shallow Secchi depths (i.e., <1 m), which declined even further to below 0.5 m during the bloom period. Persistently, low Secchi depths (i.e., <1 m) would likely be detrimental for seagrass communities given that mean depths in the BRL and NIRL are near 2 m (Duarte 1991; Tomasko et al. 2001; Steward et al. 2005), helping to explain the observed losses in seagrass biomass from 2010 to 2011. A similar argument for light limitation can be made for the observed declines in drift macroalgae.

A number of physiological features shared by some picocyanobacteria and small-celled eukaryotes may also have contributed to the success of these species in taking advantage of recycled nutrients emanating from internal sources. Small cell size and high surface area to volume ratios can provide a selective advantage in competition for growth-limiting nutrients over larger species (Reynolds 2006; Behrenfeld et al. 2008). It is noteworthy that soluble reactive phosphorus and nitrate concentrations in the study region were generally low during the 2011 bloom (SJRWMD, unpublished data), accentuating the importance of nutrient uptake capacity as a factor in competition between phytoplankton species, such as through the expression of alkaline phosphatase activity during periods of low soluble reactive phosphorus but elevated organic phosphorus availability (Dyhrman and Ruttenberg 2006; Kathuria and Martiny 2011; Liu et al. 2001; Moore et al. 2005; Muhlstein and Villareal 2007; Sun et al. 2012). In addition, some species of picocyanobacteria and small-celled eukaryotes have demonstrated the ability to effectively use organic forms of nitrogen and phosphorus as nutrient sources, which can be abundant in systems subject to decomposition of organic matter or significant recycling of nutrients by grazer communities (Wheeler 1983; Paerl et al. 1999; Berg et al. 2002; Mulholland et al. 2002; Berman and Bronk 2003; Burkholder et al. 2008; Lindehoff et al. 2011; Sun et al. 2012; Yuan et al. 2012). Bacterial decomposition and

remineralization of dead benthic biomass can result in internal loading of ammonium and organic forms of nitrogen, phosphorus, and carbon in the water column (Lomas et al. 2004), which can favor the growth of microflagellates, pelagophytes, and picoplanktonic cyanobacteria capable of efficiently utilizing these nutrient sources (Burkholder et al. 2008; Gobler and Sunda 2012; DeYoe et al. 2007; Sun et al. 2012).

In addition to bottom-up issues associated with the 2011 bloom, there is evidence that low grazing pressure contributed to the initiation of the bloom. The exceptionally cold temperatures in December 2010 and January 2011 were accompanied by declines in abundances of zooplankton and potential mixotrophic/heterotrophic dinoflagellates, likely contributing to reduced grazing pressure during the initiation of the Pedinophyceae/picocyanobacteria bloom. The uncharacteristically cold temperatures may also have negatively impacted benthic grazer communities (e.g., filter-feeding macroinvertebrates), but there is insufficient information to evaluate that potential. During the remainder of the 2011 bloom, there were periodic peaks in protozoans, mixotrophic/heterotrophic dinoflagellates, and rotifer abundance. However, the stability and longevity of the bloom suggest that grazing rates on the small-celled species that dominated the bloom were insufficient to restrict the longevity of the bloom and may even have contributed to recycling of nutrients for further phytoplankton production (Nugraha et al. 2010). Similar indications that certain small-celled phytoplankton species are subject to relatively low grazing losses relative to their growth rates have been reported in other ecosystems (Buskey 2008; Smayda 2008; Sunda and Shertzer 2012).

Brown Tides

In a continuation of unexpected events, the major bloom in the ML and NIRL in 2012 was the first recorded major event involving brown tide species (i.e., *A. lagunensis*) in the study region (Phlips and Badylak 2012; Gobler et al. 2013). As in the 2011 green tide event, there are indications that both internal and external nutrient loads contributed to the bloom. An earlier study of ML showed periods of nutrient limitation, which alternated between phosphorus, nitrogen, and nitrogen-phosphorus colimitation (Phlips et al. 2002). In 2011 and 2012, annual mean TN and TP levels in ML were well above average, indicating the presence of previously undefined sources of nutrients for phytoplankton production. Estimates of external nutrient loads for ML are not currently available; therefore, it is necessary to speculate on the sources for these high concentrations. There are indications that declines in drift algae biomass, which began in the late spring of 2011 and extended through the summer of 2013, may have contributed to the availability of nutrients for phytoplankton. The exceptionally high salinity levels (i.e., up to 45 psu) in 2011 and 2012 may have negatively impacted benthic flora and fauna in

the ML. Some of the main benthic primary producer species in the ML, such as the seagrass *S. filiforme* and the drift macroalgae *G. tikvahiae* and *H. cervicornis*, have been shown to be sensitive to salinities in excess of 40 psu (McMillan and Moseley 1967; Bird et al. 1979; Ding et al. 2013). By contrast, hypersaline conditions have been shown to play a role in enhancing the potential for *A. lagunensis* blooms in Texas, during which salinities reached up to 70 psu (Buskey et al. 1998). It is also likely that the low Secchi (i.e., <0.5 m) depths experienced in the ML during the summer to fall of 2011 contributed to declines in macroalgae biomass, as observed in the BRL and NIRL.

In addition, the brown tide of 2012 followed peaks in rainfall associated with increases in both nitrogen and phosphorus concentrations. The mean total dissolved nitrogen/total dissolved phosphorus ratios (molecular) during the 2012 brown tide in the ML were relatively high, i.e., 148 (Phlips & SJRWMD, unpublished data), which are known to enhance the potential for *A. lagunensis* blooms (Liu et al. 2001; DeYoe et al. 2007). The presence of high levels of ammonia, which is known to stimulate blooms of *A. lagunensis* (Liu et al. 2001; DeYoe et al. 2007), could not be evaluated due to a lack of data on ammonia. It is possible to hypothesize that ammonia levels were elevated due to recycling of benthic biomass.

In terms of the potential role of top-down control of the brown tide, zooplankton densities prior to the bloom were relatively low, contributing to the initiation of the event. Densities of protozoa and potential mixotrophic/heterotrophic dinoflagellates increased substantially during the bloom, but the brown tide still attained exceptionally high biomass, suggesting that grazing rates were outstripped by growth rates of the pelagophyte. Previous reports indicate that *A. lagunensis* is resistant to grazing by both planktonic and benthic species, which contribute to the formation brown tides (Buskey et al. 1997; Liu and Buskey 2000; Gobler et al. 2013).

Conclusion—Climatic Variability and State Shifts

Ecosystems often exhibit recurring successional patterns in phytoplankton composition and abundance that can extend over many years (Smayda 1980; Reynolds 2006). From 1997 to 2009 in the NIRL and BRL, this trend is exemplified by recurring blooms of the dinoflagellate *P. bahamense* associated with periods of elevated rainfall levels, during which external nutrient loads are enhanced and salinities are depressed, favoring this euryhaline species (Phlips et al. 2006, 2011). The development and persistence of *Pyrodinium* blooms may also be enhanced by low grazing losses and reintroduction of recruits from reserves of resting cells (i.e., cysts) in the sediments (Badylak and Phlips 2008; Phlips et al. 2006; Usup et al. 2012).

In contrast to the latter pattern of reoccurring *Pyrodinium* bloom, in 2011, there was an unexpected shift in the character of blooms in the NIRL and BRL toward domination by picocyanobacteria and small-celled eukaryotes (i.e., <5 μm), representing a possible state shift (Beisner et al. 2003; Viaroli et al. 2008). The shift appears to have been driven by a combination of uncharacteristic climatic conditions, including exceptionally cold winter water temperatures in 2009/2010 and 2010/2011 and below-average rainfall levels in 2010 and early 2011. These conditions contributed to significant increases in salinity and important changes in key biological communities, including extensive losses in benthic primary producer biomass and alterations in grazer community structure and abundance. The location of central Florida in the biogeographical transition zone between tropical and temperate clines (Webb 1990) can increase sensitivity of biological communities to low-temperature excursions due to the prominent presence of large numbers of subtropical and tropical flora and fauna, such as tropical seagrasses, macroalgae, and plankton (e.g., *P. bahamense*).

The central tipping point in the state shift appears to have been the loss in benthic primary producer biomass, resulting in a shift in internal nutrient pools from the benthos to the water column. The shift appears to have started in the BRL in 2010 with the advent of an intense diatom bloom which coincided with exceptionally low winter water temperatures, followed by picocyanobacteria blooms in the late summer and fall, which decreased light availability for benthic primary producers. Major phytoplankton blooms continued in the winter and spring of 2011, spreading into the NIRL and ultimately the southern ML in the summer of 2011.

In a continuation of unexpected events, 2012 saw a major brown tide in the ML, a region characterized by relatively undeveloped watersheds and little prior bloom activity. Several of the conditions in the ML during 2012 were similar to those observed in the NIRL and BRL in 2011, including reduced benthic primary producer biomass, elevated salinities, and low planktonic grazer abundances during the initiation of the bloom. In both 2011 and 2012, the high nutrient levels that supported exceptionally high phytoplankton biomass in the ML appeared to emanate in part from redistribution of internal nutrient pools (i.e., from declining benthic primary producers), in addition to external loads, which were largely directed into phytoplankton biomass, rather than being shared by benthic primary producers.

The 2011, 2012, and 2013 blooms of small-celled phytoplankton in ML, NIRL, and BRL share some of the antecedent conditions associated with prominent blooms of small-celled phytoplankton in other ecosystems, such as the brown tide events involving *Aureoumbra* in Texas (Buskey et al. 2001) and picocyanobacteria blooms in Florida Bay (Phlips et al. 1999). As observed in this study, blooms in these systems occurred in shallow restricted estuaries with long water

residence times (i.e., multiple months), during periods of well above-average salinity and high-light attenuation caused by persistently high phytoplankton biomass, both of which contributed to the declines in benthic primary producer biomass.

The shifting character of phytoplankton blooms in the ML, NIRL, and BRL provides some insights into future management challenges. The NIRL and BRL have a history of bloom activity facilitated by long water residence times and enhanced by anthropogenically enriched external nutrient loads (Sigua and Tweedale 2003; Adkins et al. 2004; Steward et al. 2005; Steward and Green 2007; Gao 2009; Phlips et al. 2010, 2011). Correlations between rainfall levels, external nutrient loads, and bloom activity support the hypothesis that reductions in anthropogenic sources of nutrients have the potential to reduce the frequency and intensity of blooms. In terms of the unexpected intense blooms of small-celled eukaryotic phytoplankton in 2011, 2012, and 2013, the return of more typical temperature and rainfall conditions may lead to a recovery of benthic primary producer communities. Such a recovery may help to drive a shift back to more typical phytoplankton composition and dynamics by enhancing competition between planktonic and benthic primary producers for nutrients entering the lagoon from external sources and stabilizing sediments which can be a source of internal nutrients and light absorbing tripton through wind resuspension. There are preliminary indications that there is a recovery underway to more typical conditions, as reflected in the observed modest increases in benthic primary producer biomass in the NIRL and BRL in 2013, along with declines in small-celled phytoplankton biomass and nutrient levels relative to 2011. However, the results also show that even temporary extremes in climate can result in rapid and dramatic changes in ecosystem structure, including phytoplankton communities.

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