SPATIAL AND TEMPORAL PATTERNS OF PHYTOPLANKTON ABUNDANCE AND COMPOSITION IN A WELL-FLUSHED, SUB-TROPICAL ECOSYSTEM

By

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ABSTRACT

SPATIAL AND TEMPORAL PATTERNS OF PHYTOPLANKTON ABUNDANCE AND COMPOSITION IN A WELL-FLUSHED, SUB-TROPICAL ECOSYSTEM

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Anthropogenic activities have resulted in increased eutrophication of many coastal environments throughout the world, heightening concerns over the future integrity and sustainability of impacted ecosystems. The primary objective of this study was to examine trends in phytoplankton biomass and species composition under varying nutrient loads in the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR), a well-flushed sub-tropical estuary located on the northeast coast of Florida. The GTMNERR contains both regions of significant human influence and pristine areas with only modest development, providing an excellent test case for comparing and contrasting phytoplankton community dynamics under varying degrees of nutrient load. Monthly measurements of temperature, rainfall, salinity, Secchi depth, nutrient concentrations and chlorophyll over five years (2005-2009) were examined during this study. Additionally, microscopic analysis of phytoplankton assemblages for the five year study period was performed to examine the structure and dynamics of the phytoplankton community within the GTMNERR. Results of this study indicate that phytoplankton abundance and composition in the GTMNERR is strongly influenced by hydrologic factors, such as flushing and residence times, as well as shifts in climatic conditions. This study provides the first system-wide data on the composition, abundance and dynamics of phytoplankton in the GTMNERR, establishing an important baseline to measure how future changes in the environment will effect primary production and the structure of biological communities.

INTRODUCTION

Increased cultural eutrophication throughout the world has heightened concerns regarding the future integrity of impacted coastal ecosystems (Nixon 1995). Agricultural, industrial and urban pollutants are increasingly entering water bodies, particularly in terms of nutrients which can degrade water quality and precipitate eutrophication (Cloern 2001, Diaz and Rosenburg 2008). As approximately half of the world's population lives within 60 kilometers of the shoreline, coastal waters are particularly vulnerable to anthropogenic nutrient loading. Among the major components of aquatic ecosystems, primary producers such as phytoplankton are often the most directly affected by nutrient enrichment--specifically nitrogen and phosphorus loading. Anthropogenically-driven increases in nutrient concentrations entering coastal ecosystems have been associated with increased occurrence of algal blooms in water bodies throughout the world (NOAA 2003, Hallegraeff 2004, Gilbert and Burkholder 2006, Diaz and Rosenburg 2008). Nutrient loading also increases the potential for hypoxic conditions (Diaz and Rosenburg 2008, Rabalais et al 2010, Howarth et al 2011). Predicting the response of the phytoplankton community to changes in nutrient load is a key watershed management issue; however, defining this relationship is challenging due to the diversity of coastal ecosystems, including variable physical and chemical conditions within estuarine environments. Classic 'single signal, single response' conceptual models, inspired by studies of eutrophication in lakes, are poor predictors of algal production rates in the highly dynamic estuarine environment. For example, annual nutrient loads are higher in San Francisco Bay than in Chesapeake Bay, yet primary production in San Francisco Bay is 20 times lower than in Chesapeake Bay (Cloern 2001). This suggests that additional factors, including morphology and hydrology, should be considered. This new

understanding has led to a categorical approach to ecosystem modeling which recognizes that system-specific attributes may filter and modulate response to changing nutrient loads.

During this study, the effects of different levels of nutrient load on phytoplankton community structure and abundance were examined in one important category of estuary: well-flushed, sub-tropical ecosystems. Well-flushed estuaries, which frequently experience low water residence times and comparatively high salinities, have been characterized by lower phytoplankton biomass and different community structure than more restricted ecosystems (Knoppers et al. 1991, Monbet 1992, Phlips et al. 2004, 2006, Badylak et al. 2007). However, strong exchange of water with the coastal environment can also subject well-flushed ecosystems to incursions of coastal harmful algal blooms (HAB), such as the toxic red tide species *Karenia brevis* (Steidinger 1983). Sub-tropical, well-flushed ecosystems are widespread throughout the world, although they are not as well studied as those in temperate environments. This suggests that further study on the structure and function of such ecosystems is warranted, especially as sub-tropical regions of the world attain higher levels of human development.

Knowledge of the phytoplankton community is crucial to the broader understanding of coastal ecosystems, as phytoplankton form the base of the aquatic food web and serve the nutritional needs of a wide range of animals such as the keystone species *Crassostrea virginica* (eastern oyster). Furthermore, phytoplankton are excellent and widely used indicators of biological integrity and physio-chemical conditions in aquatic ecosystems due to their rapid and predictive response to environmental change (EPA, 2002). Estuaries are irreplaceable natural resources, providing an abundance of biological, recreational and economic value to societies and nations around the world. Consequently, evaluating phytoplankton dynamics is an essential

component of watershed planning and management to help ensure the health and sustainability of vital estuarine ecosystems.

OBJECTIVES

The primary objective of this study was to examine trends in phytoplankton biomass and species composition under varying nutrient loads in a well-flushed sub-tropical estuary--specifically, the Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR) on the northeast coast of Florida (Figure 1). The GTMNERR is an excellent example of a well-flushed sub-tropical estuary. Since the GTMNERR contains both regions of significant human influence and pristine areas with only modest development, it provides a test case for comparing and contrasting phytoplankton structure, abundance and dynamics under varying degrees of nutrient load.

Two principal hypotheses were tested in this study:

1) Differences in phytoplankton standing crop between regions of the GTMNERR are expected to be small by comparison to the differences in estimated nitrogen and phosphorus loads due to the high flushing rates within the system.

2) Phytoplankton communities in the GTMNERR are expected to be dominated by fast growing taxa (i.e. diatoms, small phytoflagellates and picoplanktonic cyanobacteria) due to shorter residence times usually experienced by well-flushed estuaries.

METHODOLOGY

Site Description

The study area focused on the Tolomato River Estuary (TRE) and the Matanzas River Estuary (MRE) associated with the Guana Tolomato Matanzas National Research Reserve (GTMNERR) located on the northeast coast Florida (Figure 1). The GTMNERR, which was designated as a National Research Reserve in 1999, is a system of bar-bounded, estuarine lagoons that is divided into two regions separated by the city of St. Augustine. The TRE is located within the northern component of the GTMNERR, forming a portion of the Intracoastal Waterway before joining Guana River and Matanzas River, ultimately emptying into the Atlantic Ocean via the St. Augustine inlet. The MRE, located partially within the southern component of the GTMNERR, extends approximately 25 km from the inlet at Ft. Matanzas to the inlet at St. Augustine. The GTMNERR experiences a humid, sub-tropical marine climate that is typical of the northeast Florida coastal region. Summers are generally warm and wet while winters are commonly mild and dry. The GTMNERR is also subject to tropical storm activity which can affect water quality conditions (Dix 2008), as well as significantly impact the coastal environment.

Ecology

The region's unique climate and broad range of habitats contribute to the ecological biodiversity of the GTMNERR, represented by the presence of a variety of wildlife. Many rare and protected species have been observed in the GTMNERR, including the roseate spoonbill (*Ajaia ajaja*), the endangered wood stork (*Mycteria americana*), the migratory North Atlantic right whale (*Eubalaena glacialis*), and three species of sea turtles (*Chelonia mydas, Caretta*

caretta, Dermochelys coriaciea). Commercial and recreationally valuable species present at the GTMNERR include oysters, clams, crabs, shrimp and an assortment of finfish--like mullet, snapper, flounder, drum, spotted sea trout, gag grouper and black sea bass.

Primary production throughout the GTMNERR is mostly by phytoplankton. Studies have characterized the GTMNERR as having relatively low phytoplankton biomass compared to other estuaries along the east coast of Florida (Phlips et al. 2004). Primary consumers in the study area include the eastern oyster (*Crassostrea virginica*) which is a dominant suspension feeder in the GTMNERR (Dix 2010). Zooplankton, which can contribute significantly to grazing rates, have not been quantified in the GTMNERR as of the date of this study.

Water Quality Sampling Sites

Pine Island (PI):

Pine Island (Site PI) is the northern most sampling site in the GTMNERR and is located near Pine Island in the Tolomato River Estuary, approximately 16 km north of the city of St. Augustine (Figure 2). The site receives freshwater drainage from several tidal tributaries, and experiences longer water residence times and quick response to salinity due to a tidal node north of the site (Phlips et al. 2004). Land use in the Tolomato River Planning Unit is reported as 81% upland forests, wetlands, and surface waters; 13% urban areas; and 5% agriculture/rangeland (DEP 2008). Estimated watershed input of total nitrogen (TN) and total phosphorus (TP) for this region of the GTMNERR is approximately 9,623 kg/yr and 1,471 kg/yr, respectively (Phlips et al 2004).

San Sebastian (SS):

The San Sebastian sampling site (Site SS) is located in the Matanzas River Estuary at the mouth of the San Sebastian River, a major tributary that receives drainage from the developed St. Augustine region (Figure 2). In addition, Site SS also receives freshwater inflow from overland runoff and nearby creeks. Site SS is tidally influenced by the St. Augustine inlet approximately 4 km to the north, and experiences relatively short residence times (Phlips et al. 2004). Land use in the Matanzas River Planning Unit is reported as 68% upland forests, wetlands, and surface waters; 24% urban areas; and 6% agriculture/rangeland (DEP 2008). Estimated watershed input of total nitrogen (TN) and total phosphorus (TP) for Site SS are approximately 95,528 kg/yr TN and 15,848 kg/yr TP, respectively (Phlips et al 2004).

Ft. Matanzas (FM):

The Ft. Matanzas site (Site FM) is located in the Matanzas River Estuary, approximately 4 km north of the Ft. Matanzas inlet (Figure 2). Site FM is subject to regular tidal exchange with the Atlantic Ocean via the Matanzas inlet; however, the site does not experience major freshwater inflow. Flushing time is shorter at Site FM than Site SS and Site PI (Sheng et al. 2009). The region of the GTMNERR where Site FM is located is characterized as relatively pristine with only moderate urban development compared to Site SS. Estimated watershed input of total nitrogen (TN) and total phosphorus (TP) for Site FM are approximately <10,000 kg/yr TN and <2,000 kg/yr TP, respectively (Phlips et al 2004).

Water Collection and Analyses

Water samples collected on a monthly basis at three sites (Figure 2) for the years 2005-2009 were analyzed during this study. This five-year period was selected because it includes one drought year (2006), one flood year (2009), and one year noted for a major incursion of a toxic red tide (2007). As part of the GTMNERR Monitoring Program, samples were collected by Dr. Phlips at the University of Florida for water chemistry and phytoplankton analysis. Water samples were collected with an integrating sampling tube which captures water from the surface to within 0.1m from the bottom. Samples withdrawn for water chemistry analysis were maintained on ice during return to Dr. Phlips' laboratory at the University of Florida for further processing, in adherence with guidelines set forth by Dr. Phlips' NELAP QAQC Accreditation #E72883. Additionally, aliquots of water withdrawn for picophytoplankton analysis were kept on ice for subsequent analysis using autofluorescence microscopy. Samples for analysis of the rest of the phytoplankton were preserved with Lugols solution and archived at Dr. Phlips' laboratory.

Total nitrogen (TN), Total Phosphorus (TP) and Chlorophyll *a* concentrations were obtained from Dr. Phlips' laboratory, which carried out water chemistry analysis during the course of this study. On-site measurements of water temperature, salinity and secchi depth, as well as results of picophytoplankton analysis were also provided by Dr. Phlips.

Rainfall data was obtained from the Centralized Data Management Office of the National Oceanic and Atmospheric Administration's **(**NOAA**)** National Estuarine Research Reserve System (NERRS). Total Precipitation is measured every fifteen minutes at the Pellicer Creek meteorological station in the GTMNERR as part of the NERRS System-wide Monitoring Program. The sub-tropical region of Florida where the GTMNERR is located is characterized by

a wet season from June through October, which coincides with the tropical storm season, and a dry season from November through May.

It is important to note that certain data was not included for analysis during this study. Phytoplankton samples for the month of July 2005 were not available, as well as picophytoplanktonic data during July 2005, October 2007 and May 2009. Chlorophyll *a* values for January 2005 were not available. Water temperature values during February 2005 were not available. Secchi depth readings were not taken during July 2006, May 2007 and December 2007. Additionally, certain water chemistry data values were removed because they appeared as unrealistically high or low outliers during data analysis. Outliers removed include: Salinity at Site SS during January 2006; TN at Site SS during May 2005; TP at Site FM during May 2005 and April 2006; and TP at Site PI during August 2005 and June 2006.

Phytoplankton Analysis

Microscopic analysis of archived phytoplankton samples was conducted during this study, and general phytoplankton composition was determined using the Utermohl method (Utermöhl 1958). Preserved samples were settled in 19mm inner diameter cylindrical chambers. Phytoplankton cells were identified and counted at 400X and 100X with a Nikon phase contrast inverted microscope. At 400X, a minimum of 100 cells of a single taxa and 30 grids was counted. If 100 cells were not counted within 30 grids, up to a maximum of 100 grids was counted until one hundred cells of a single taxa was reached. At 100X a total bottom count was completed for taxa greater than 30 microns.

Cell biovolumes were estimated by assigning combinations of geometric shapes to fit the characteristics of individual taxa. Specific phytoplankton dimensions were measured for at least

30 randomly- selected cells. Volumes were calculated for each cell type (Smayda 1978). Taxa exhibiting a range of cell sizes, such as occurs with many diatom species, was divided into size classes to provide more accurate estimates of biovolume. The total biovolume per sample was calculated as the sum of the estimated cell volumes for each species.

For the purpose of description and discussion, 'blooms' were defined as phytoplankton biovolumes for individual species which fell within the top 25% of biovolumes observed over the study period for all individual species; i.e. > 1.2×10^6 μm^3 ml^{-1}.

References used most frequently to aid in taxonomic identification of phytoplankton in this study were Tomas (1997) and Prescott (1973). Potentially toxic or problematic species were identified using the guidelines of Steidinger et al (1999) and Steidinger (2008).

RESULTS

Physical-Chemical Parameters

RAINFALL – Monthly rainfall totals ranged from < 1 cm (May 2006) to 45 cm (May 2009) at the Pellicer Creek meteorological station located in the GTMNERR (Figure 3). Rainfall was generally greater from June through October (the wet season) than November through May (the dry season). Annual rainfall total was higher during 2005 (118 cm), 2007 (132 cm) and 2009 (149 cm) than during 2006 (79 cm) and 2008 (103 cm). During 2005, monthly rainfall totals never fell below 5cm, indicating the year was consistently wet.

TEMPERATURE – Surface water temperatures observed at all sites reflected the subtropical climate of the region with an annual range of 12.1° C to 31.1° C (Figure 4). Water temperatures generally exceeded 20° C from April through November during the study period. Lowest temperatures were mostly observed during February.

SALINITY - Over the five year study period, mean salinity values ranged from 28.5 psu at Pine Island (Site PI) to 32.0 psu at San Sebastian (Site SS) (Table 1). The greatest range in salinity, 8.64 – 38.18 psu, was observed at Site PI (Figure 5) where tidal water exchange is much lower than other sites. Salinity was greatest for all sites during spring and summer of 2006 when rainfall amounts were low.

SECCHI DEPTH - Light transmission through the water column, expressed as Secchi depth, was highest at Site SS and lowest at both Ft. Matanzas (Site FM) and Site PI (Figure 6). Mean Secchi depth ranged from 1.1 m at Site PI to 1.3 at Site SS (Table 1). Secchi depth remained relatively low during 2005 and also during the summer of 2008 and summer 2009. However, Secchi depth generally increased during 2006 and 2007, as well as during the winter season of 2009.

CHLOROPHYLL - Mean chlorophyll *a* (Chl *a*) values ranges from 3.9 µg L^{-1} at Site FM to 5.2 µg L^{-1} at Site PI (Table 1) with concentrations up to 16.3 µg L^{-1} observed at the latter site (Figure 7). The highest peaks in Chl *a* were observed in October 2007 at Site FM (22.6 µg L^{-1}) and Site SS (16.5 µg L^{-1}) (Figure 4). All three sites showed a general trend of increasing Chl *a* values for the duration of the study period (Figure 7).

NITROGEN - Mean total nitrogen (TN) concentrations ranged from 0.38 mg L^{-1} at Site FM to 0.56 mg L^{-1} at Site PI (Table 1). Highest TN concentrations (1.18 mg L^{-1}) were observed at Site PI (Figure 8). Nitrogen concentrations appeared to be higher during the summer than winter, correlating to the wet season during which periods of high rainfall generate overland freshwater runoff.

PHOSPHORUS - Mean total phosphorus (TP) concentrations were the same at Site FM and Site SS (0.05 mg L^{-1}) and slightly higher at Site PI (0.07 mg L^{-1}) (Table 1). The greatest range in

TP concentrations (0.04 - 0.13 mg L^{-1}) was observed at Site PI (Figure 9). Phosphorus concentrations generally appeared higher in the summer than the winter; however Site PI demonstrated greater temporal variability than Sites SS and FM.

Phytoplankton Abundance and Composition

Mean biovolume values were the same at Ft. Matanzas (Site FM) and Pine Island (Site PI), at 1.1 10^6 μm^3 ml^{-1}, and just slightly higher at San Sebastian (Site SS) at 1.4 10^6 μm^3 ml^{-1} (Table 2). The highest biovolume peak at each site was observed during wet seasons (Figure 10). In addition, phytoplankton biovolumes were divided into size classes: picoplankton (biovolume < 8 μm^3 ml^{-1}), nanoplankton (biovolume 8 - 8,000 μm^3 ml^{-1}), and microplankton (biovolume 8,000 – 8,000,000 μm^3 ml^{-1}) size classes (Table 2). Percentages of biovolume by size classes were similar for Site FM and Site SS, with the highest percentages of biovolume as nanoplankton. Site PI had the largest percentage of microplankton present.

Several major algal groups, including dinoflagellates, diatoms, cyanobacteria, chlorophytes, cryptophytes, euglenoids, and microflagellates, were represented in the GTMNERR during this study; however, diatoms were the dominant group during most biovolume peaks at all sites (Figure 10). Dinoflagellate presence in the phytoplankton community during the study period was generally more pronounced at Sites SS and FM than Site PI, particularly during October 2007 when dinoflagellates dominated the biovolume peaks at Site FM and Site SS (Figure 10). Cyanobacteria contributed significantly to total biovolume throughout the GTMNERR, but were seldom dominant.

The most frequently observed taxa (present in more than 95% of samples collected), with mean biovolume greater than 50,000 μm^3 ml^{-1}, were the same at all three sites: cryptophytes,

small pennate diatoms (i.e. individual bv < 1000 μm^3 ml^{-1}), small-sized centric diatoms (diameter 05µm-30µm), medium-sized centric diatoms (diameter > 30µm-100µm), and spherical picoplanktonic cyanobacteria (Table 3). In terms of maximum numerical abundance, picoplanktonic cyanobacteria were observed as having the greatest number of cells/ml at all sites during the study. Maximum numerical abundances of spherical picoplanktonic cyanobacteria and the picoplanktonic cyanobacterium *Synechococcus* were greater at Site FM and Site SS than at Site PI (Table 3). While frequently present at all sites, cryptophytes, small pennate diatoms, small-sized centric diatoms and cyanobacteria were not observed at bloom levels (i.e. biovolume > 1.2 x 10^6 μm^3 ml^{-1}) over the course of this study. Maximum biovolumes of individual species are best discussed on a site-specific basis to highlight spatial and temporal variability of bloom forming taxa within the GTMNERR, including potentially toxic or problematic species.

SITE PI (PINE ISLAND) - Several species of diatoms were observed at bloom levels of biovolume at Site PI during the study period (Table 3). During July 2009, large-sized centric diatoms (diameter > 100µm-200µm) and medium-sized centric diatoms (diameter > 30µm-100µm) reached maximum biovolume values of 5 million μm^3 ml^{-1} and 3 million μm^3 ml^{-1}, respectively (Figure 11 and Figure 12). Another large-sized diatom, *Odontella regia* (diameter ~100µm-200µm), reached bloom level of 2 million μm^3 ml^{-1} during August 2009 (Figure 13). The diatom *Skeletonema costatum* c.f. was observed at bloom levels in July 2007, with a maximum biovolume of 1 million μm^3 ml^{-1} (Figure 14). Additionally, potentially toxic or problematic dinoflagellates observed at Site PI during the study period included *Prorocentrum mexicanum, Gonyaulax polygramma* and *Dinophysis caudata*; however, biovolume levels were well below the bloom threshold.

SITE SS (SAN SEBASTIAN) – Bloom levels of several species of diatoms were observed at Site SS during the study period (Table 3). During August 2009, large-sized centric diatoms (diameter > 100µm-200µm) and medium-sized centric diatoms (diameter > 30µm-100µm) each reached maximum biovolume values of 2 million μm^3 ml^{-1} (Figure 11 and Figure 12). Diatom *Guinardia spp.* reached bloom level of biovolume at 3 million μm^3 ml^{-1} during August 2007 (Figure 15). A large bloom of the toxic marine dinoflagellate *Karenia brevis* was observed at Site SS during October 2007 (Table 3, Figure 16). Additionally, potentially toxic or problematic dinoflagellates observed at Site SS during the study period included *Prorocentrum mexicanum* and *Gonyaulax polygramma*; however, biovolumes were well below bloom levels.

SITE FM (FT. MATANZAS) – A bloom of the toxic marine dinoflagellate *Karenia brevis* was observed at Site FM during October 2007, as also observed at Site SS (Table 3, Figure 16). There were no other blooms events observed at Site FM during the study period. Other potentially toxic or problematic dinoflagellates observed at Site FM during the study period included *Prorocentrum mexicanum, Prorocentrum minimum, Gonyaulax polygramma* and *Dinophysis caudata*; however, biovolumes for each of these species were well below the bloom threshold.

DISCUSSION

The primary objective of this study was to examine trends in phytoplankton biomass and species composition under varying nutrient regimes in a well-flushed, sub-tropical estuary. The study focused on three regions within the GTMNERR that represent different combinations of residence times and watershed input of nutrients. Results of the study demonstrate the

importance of hydrodynamic processes, as well as shifts in climatic conditions, in defining the effects of different nutrient regimes on phytoplankton composition and abundance. The impacts of hydrology and climate can be viewed from three perspectives: 1) the role of water residence time; 2) allochthonous inputs to the ecosystem; and 3) the influences of climatic conditions.

Influence of Residence Time on the Phytoplankton Community in the GTMNERR

As expected, the tidally flushed environment and associated low residence times of the GTMNERR limit phytoplankton biomass accumulation. As observed in Monbet's (1992) comparison of biomass in a wide range of macro- and microtidal ecosystems, high rates of flushing restrict biomass potential. This is reflected in the small differences in phytoplankton standing crop between the highly-developed watersheds of the St. Augustine region and the comparatively pristine Matanzas region of the GTMNERR, despite an order of magnitude difference between regions in external nitrogen and phosphorus loading (Phlips et al. 2004). The importance of residence time is further indicated by the higher summer phytoplankton peaks at Site PI than Sites SS and FM. Because of the distance of Site PI from the St. Augustine Inlet, water residence times are estimated to be several times longer than the 2-4 days characteristic of the regions associated with Sites SS and FM (Dix et al. 2012). The importance of this difference is exemplified by the maximum growth rates associated with the type of phytoplankton taxa found in the GTMNERR, which range from 0.5 to 2.5 doublings per day (Stolte and Garcés 2006). Within the context of the various ways phytoplankton biomass can be lost from the GTMNERR, such as grazing by zooplankton and benthic filter-feeding invertebrates (e.g. the extensive oyster beds found in the GTMNERR), tidal flushing rates have been shown to rank high on the list (Dix et al. 2012). Similar observations have been made in other coastal

ecosystems around the world where spatial differences in flushing rates and water residence times play a major role in defining biomass potential (Cloern and Jassby 2010, Zingone et al. 2010), such as the Indian River Lagoon (Phlips et al. 2011), Florida Bay (Phlips et al. 1999) and Tampa Bay (Badylak et al. 2007) in Florida, and the inner shelf coastal lagoons of Brazil (Knoppers et al. 1991, Abreu et al. 2010).

The high flushing rates and short water residence time of the GTMNERR are also reflected in the dominant phytoplankton species observed in the system. The phytoplankton community is dominated by diatoms, small phytoflagellates and picoplanktonic cyanobacteria. These taxa are known for their relatively high growth rates (Stolte and Garcés 2006, Reynolds 2006). Short water residence times favor faster growing phytoplankton groups (Smayda and Reynolds 2001, Murrell and Lores 2004, Reynolds 2006, Quinlan and Phlips 2007), in contrast with severely restricted ecosystems where large-celled dinoflagellates often dominate blooms, such as the inner reaches of the Indian River Lagoon, where water residence times ranges from months to a year (Phlips et al. 2006, 2011). The dominance of diatoms in bloom events in the GTMNERR may also reflect the shallow polymictic character of the system. With the exception of the October 2007 occurrence of *Karenia brevis*, all phytoplankton blooms in the GTMNERR during the study period were diatoms. The tidally-driven, vertically-mixed environment of the GTMNERR favors diatom species, which are less sensitive to turbulence and are potentially biostimulated by motion (Reynolds 2006). These findings support the second hypothesis of this study that the phytoplankton communities in the GTMNERR were expected to be dominated by fast growing taxa due to shorter residence times usually experienced by well-flushed estuaries.

The effect of residence time on phytoplankton composition was further indicated by differences in phytoplankton size distribution between the more restricted Site PI and Sites SS

and FM. Larger phytoplankton were relatively more abundant at Site PI, where residence times are longer and mixing energy is lower than at Sites SS and FM. The existence of a tidal node just north of the Pine Island sampling site contributes to weaker tidal flushing in this region of the GTMNERR compared to sites closer to inlets. Reduced tidal influence at the PI site is supported by the large and prolonged declines in salinity observed at Site PI.

Allochthonous Influence on Phytoplankton Biomass in the GTMNERR

Phytoplankton biomass in the GTMNERR was also influenced by exchange of water with the Atlantic Ocean. Well-flushed ecosystems, like the GTMNERR, are often subject to allochthonous influence. This is reflected in results of this study by the frequent observation of high abundances of picoplanktonic cyanobacteria in the GTMNERR. Picoplanktonic cyanobacteria are common oceanic species and major components of the phytoplankton community in oceans (Reynolds 2006). While present at all sites in the GTMNERR during this study, higher maximum biovolumes of picoplanktonic cyanobacteria were observed at Sites SS and FM than Site PI, due to Sites SS and FM being located within close proximity to inlets.

Well-flushed estuaries can also be subject to periodic incursions of coastal harmful algal blooms (HABs) (Steidinger 1983). During the study period, bloom concentrations of the toxic red tide species *Karenia brevis* were observed in October 2007 at Sites SS and FM. *Karenia brevis* is known to be sensitive to salinities below 25 psu, but the higher salinities experienced at Sites SS and FM due to strong tidal exchange likely facilitated the persistence of high cell densities. *Karenia brevis* was not observed at Site PI, demonstrating the weaker tidal forces at the site.

Influence of Climatic Conditions on Phytoplankton Biomass in the GTMNERR

Phytoplankton biomass peaks in the GTMNERR are correlated to climatic conditions. From a seasonal perspective, mean winter biomass levels (expressed as chlorophyll *a*) are lower than the rest of the year, which has been attributed to reduced temperatures and light fluxes during winter months (Dix et al. 2012). The results of this study show the same trend for phytoplankton biovolume. In addition, chlorophyll *a* and biovolume levels observed in this study generally coincided with periods of relatively low rainfall, providing further support for the hypothesis that hydrologic conditions play a key role in defining biomass potential. Residence time is increased during low rainfall periods because of reduced rates of flushing and increased stabilization of the water column, thus providing a more favorable environment for the accumulation of phytoplankton biomass. Water column stability in estuaries promotes phytoplankton blooms by inhibiting vertical mixing and reducing the grazing opportunity of benthic consumers (Cloern 1991). While all three sites exhibited this trend, biomass peaks were particularly pronounced at Site PI where there is less tidal influence and residence times are longer.

The importance of hydrology in the control of phytoplankton biomass in the GTMNERR results in apparent contradiction in the relationship between nutrient concentrations and biomass. For example, while 2005 was a year of high nutrient levels due to large rainfall-induced inputs from the watershed, it was characterized by relatively low phytoplankton biomass. It is also noteworthy that the apparent trend of increasing phytoplankton biomass observed in the GTMNERR over the study period may be the result of periodic low rainfall periods during 2006-2009, following the consistently rainfall of 2005. These observations highlight the difficulty of

modeling the relationships between nutrient levels and biomass in highly dynamic coastal ecosystems (Cloern 2001).

Broader Impacts

Overall, the well-flushed nature of the GTMNERR appears to provide the system with a degree of resilience to the type of intense algal blooms observed in more restricted ecosystems with nutrient inputs from anthropogenic sources (NOAA 2003, Hallegraeff 2004, Gilbert and Burkholder 2006, Phlips et al. 2011). However, as local human development increases, it can be expected that nutrient loads will increase, which may impact the larger coastal environment of northeast Florida that receives outflows from the GTMNERR. Understanding how estuarine systems respond to nutrient loading is a crucial component of watershed management, helping to ensure the future integrity and sustainability of coastal ecosystems. This study provides the first system-wide data on the composition, abundance and dynamics of phytoplankton in the GTMNERR. The results will assist managers of the reserve, and other state and federal agencies, to evaluate how future changes in the environment, such as land-use in the watershed and changes in hydrodynamic characteristics in the estuary, will effect primary production and the structure of biological communities.

FIGURES AND TABLES

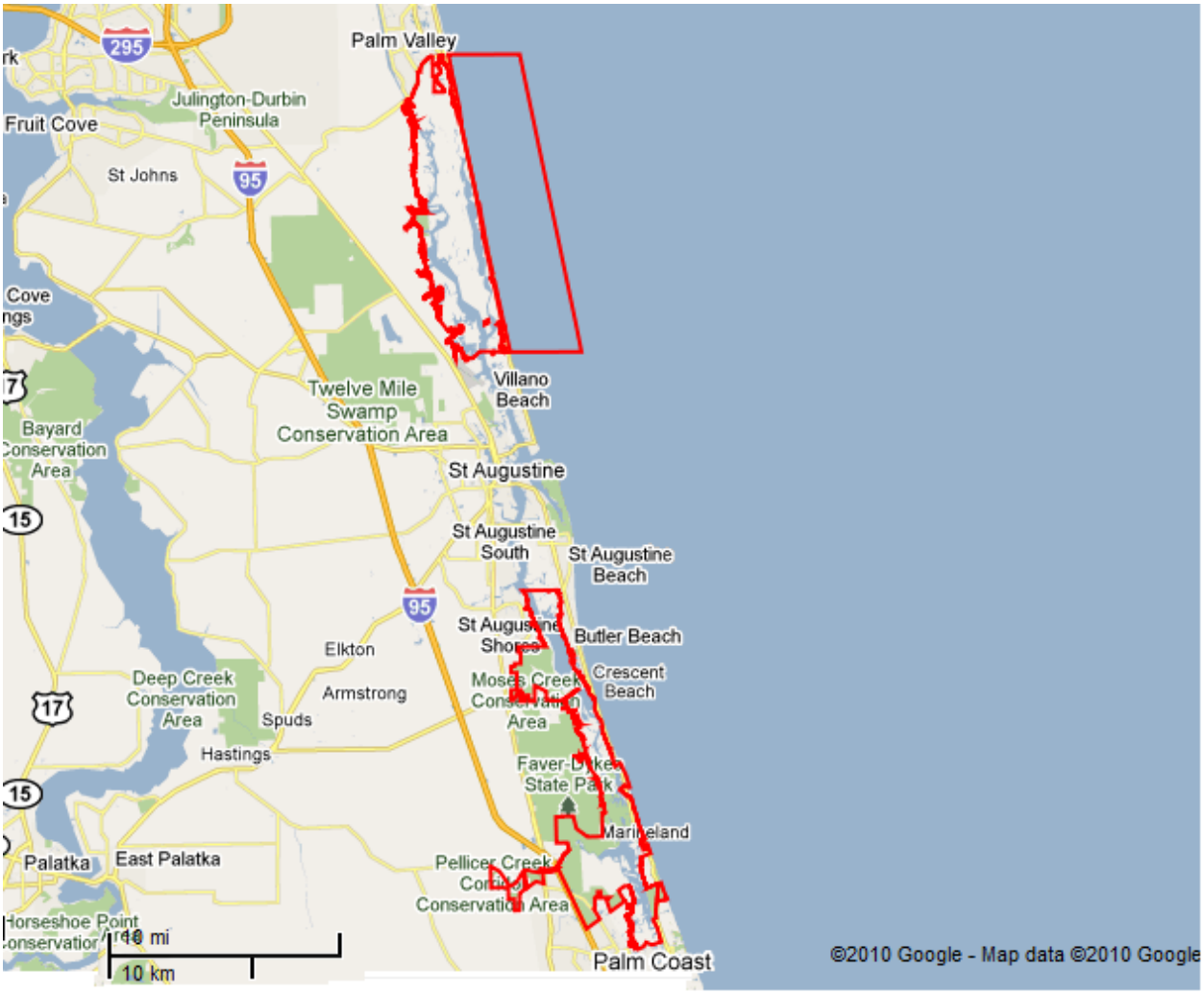

Figure 1. Location Map of the GTMNERR.

(Source: NOAA, National Estuarine Research Reserve System)

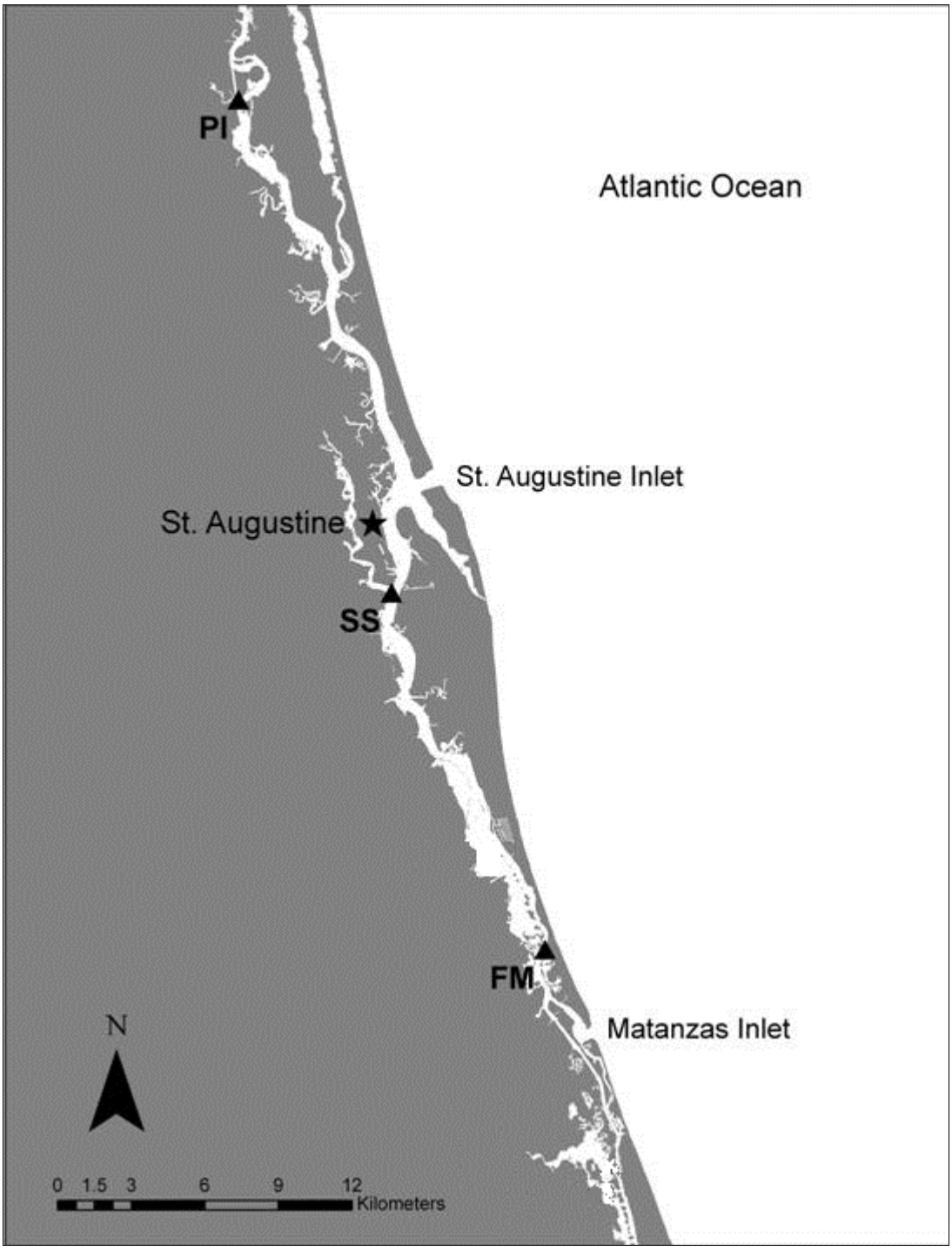

Figure 2. Sampling Site Locations within the GTMNERR.
Sampling sites: Pine Island (PI), St. Augustine (SS), Fort Matanzas (FM).

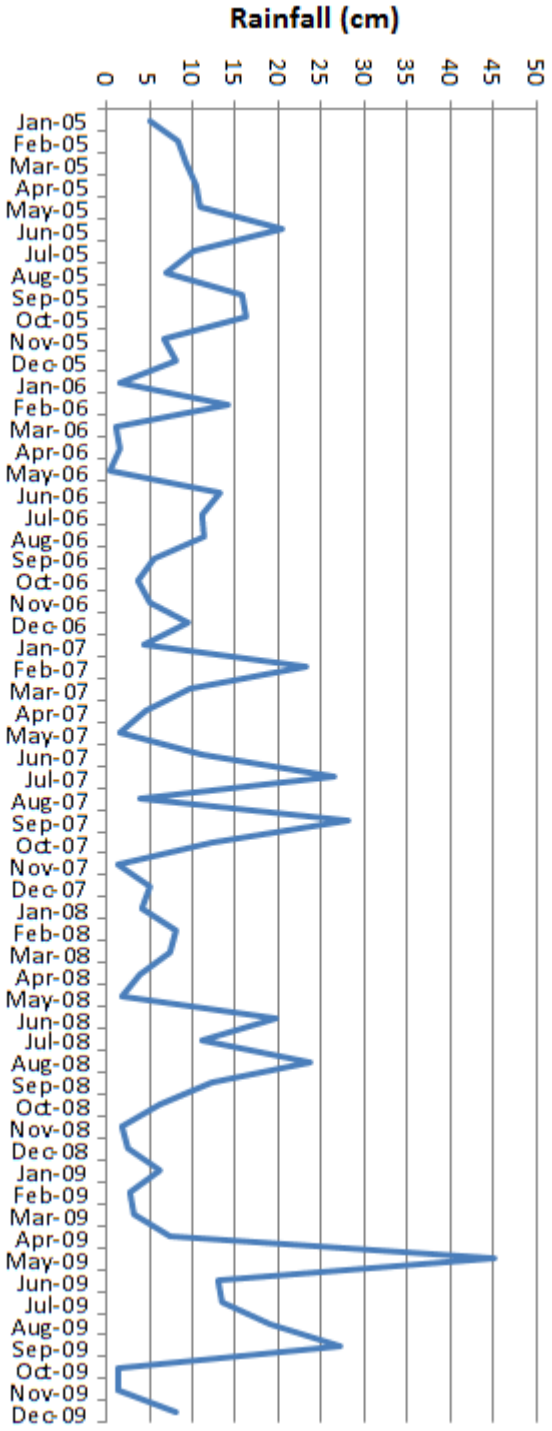

Figure 3. Monthly Rainfall Totals

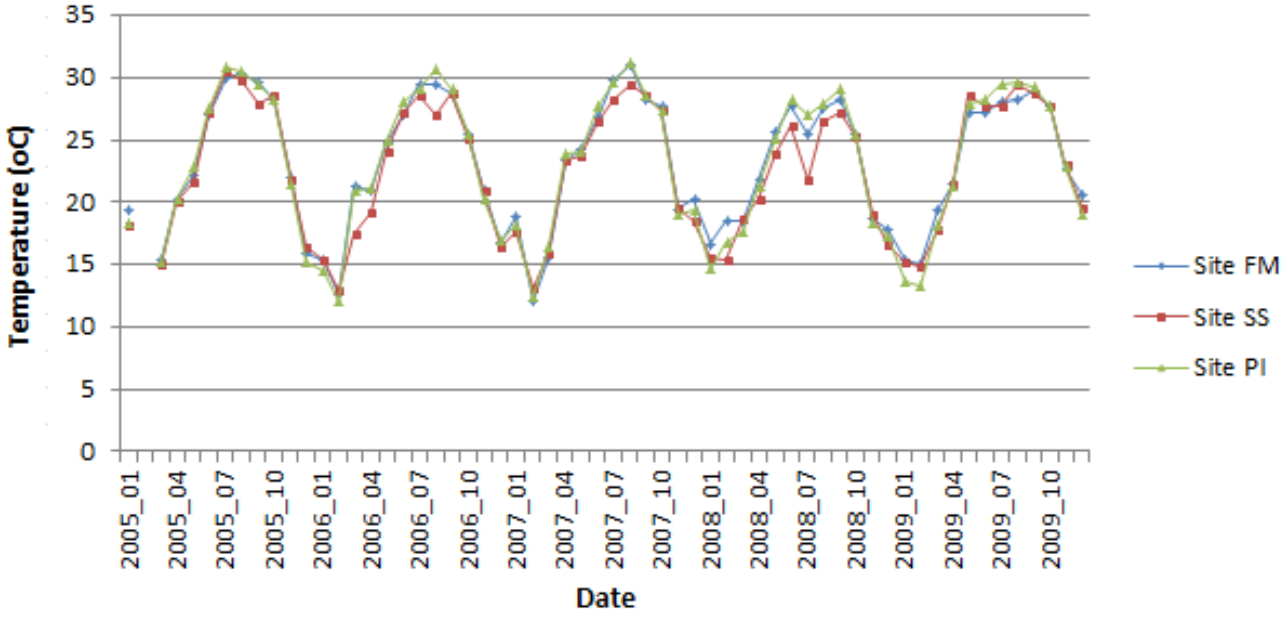

Figure 4. Surface Water Temperature

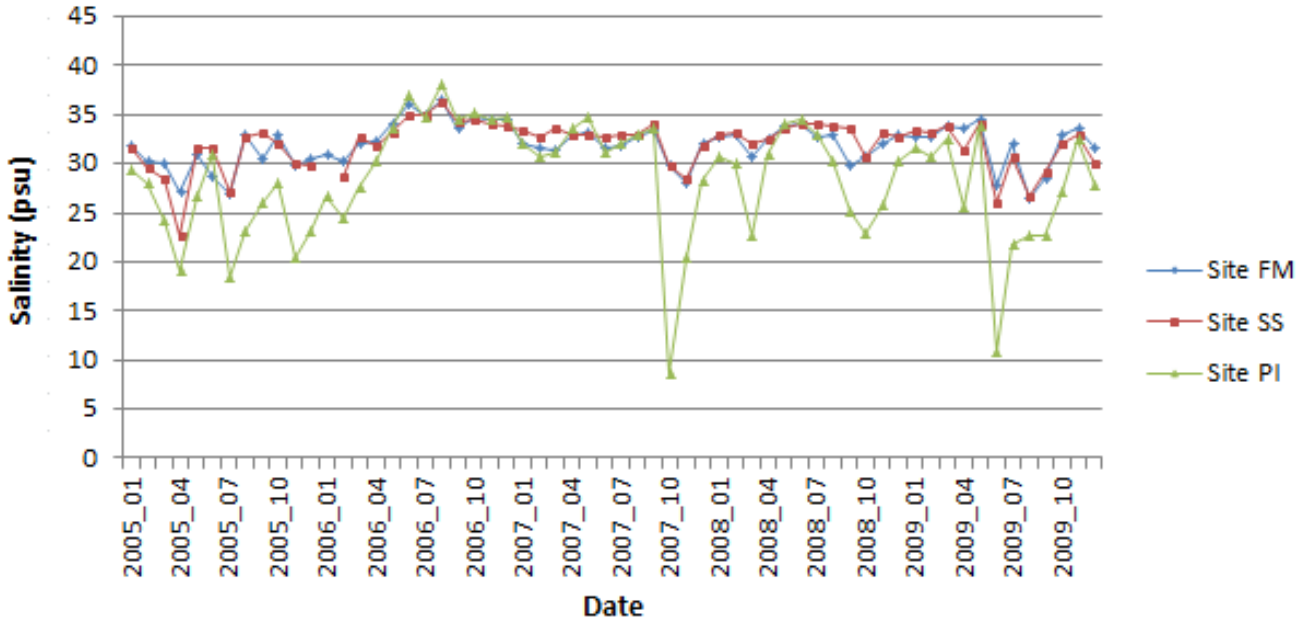

Figure 5. Salinity

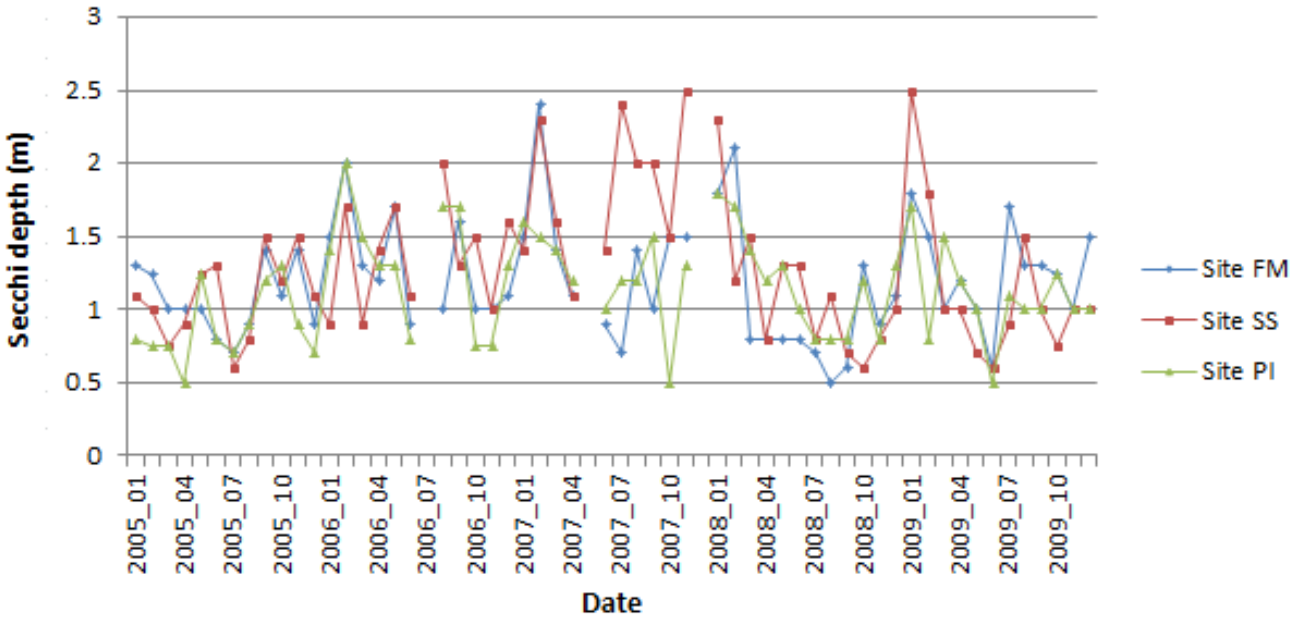

Figure 6. Secchi depth

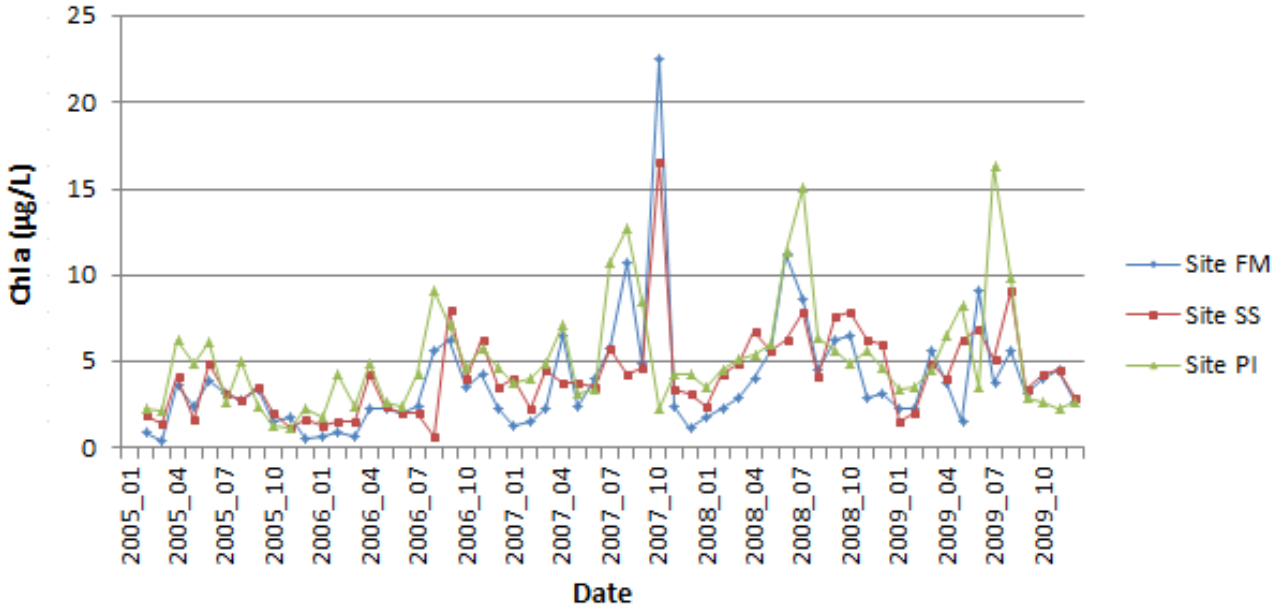

Figure 7. Chlorophyll *a*

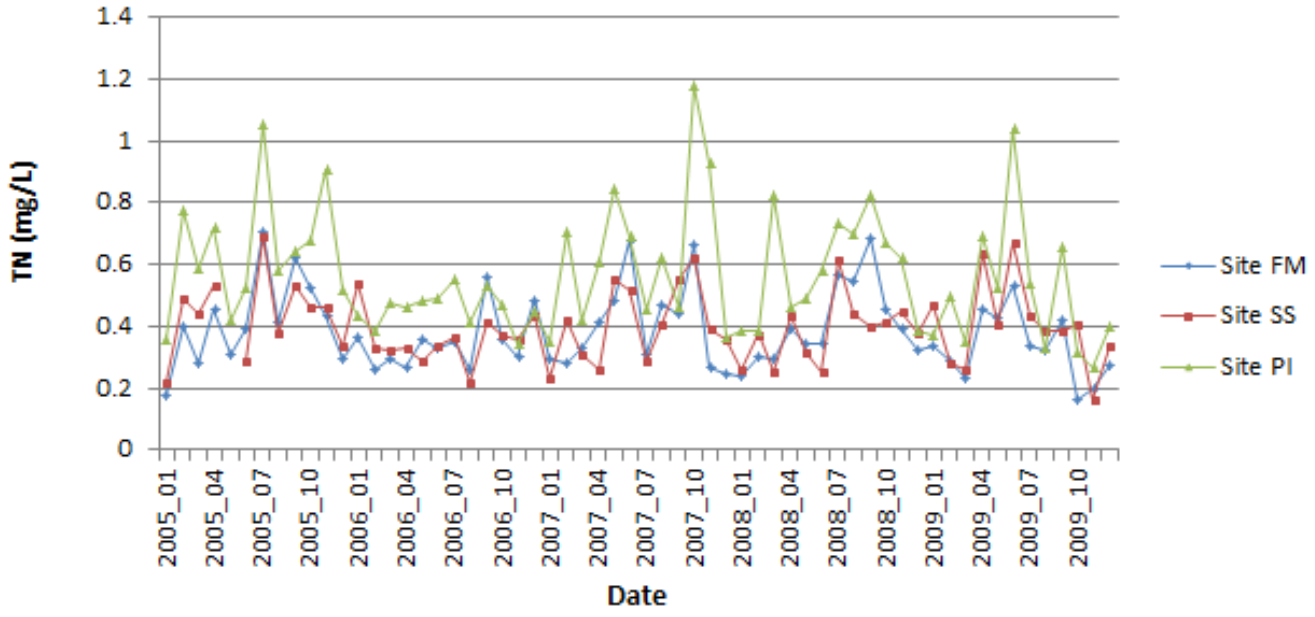

Figure 8. Total Nitrogen

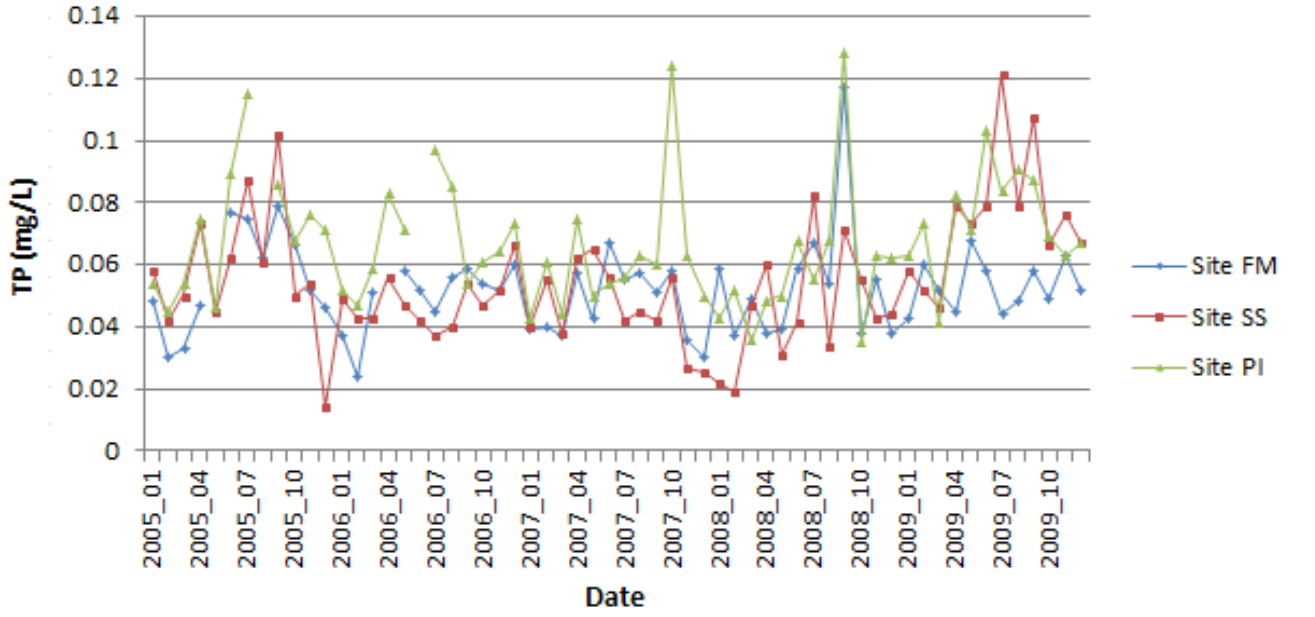

Figure 9. Total Phosphorus

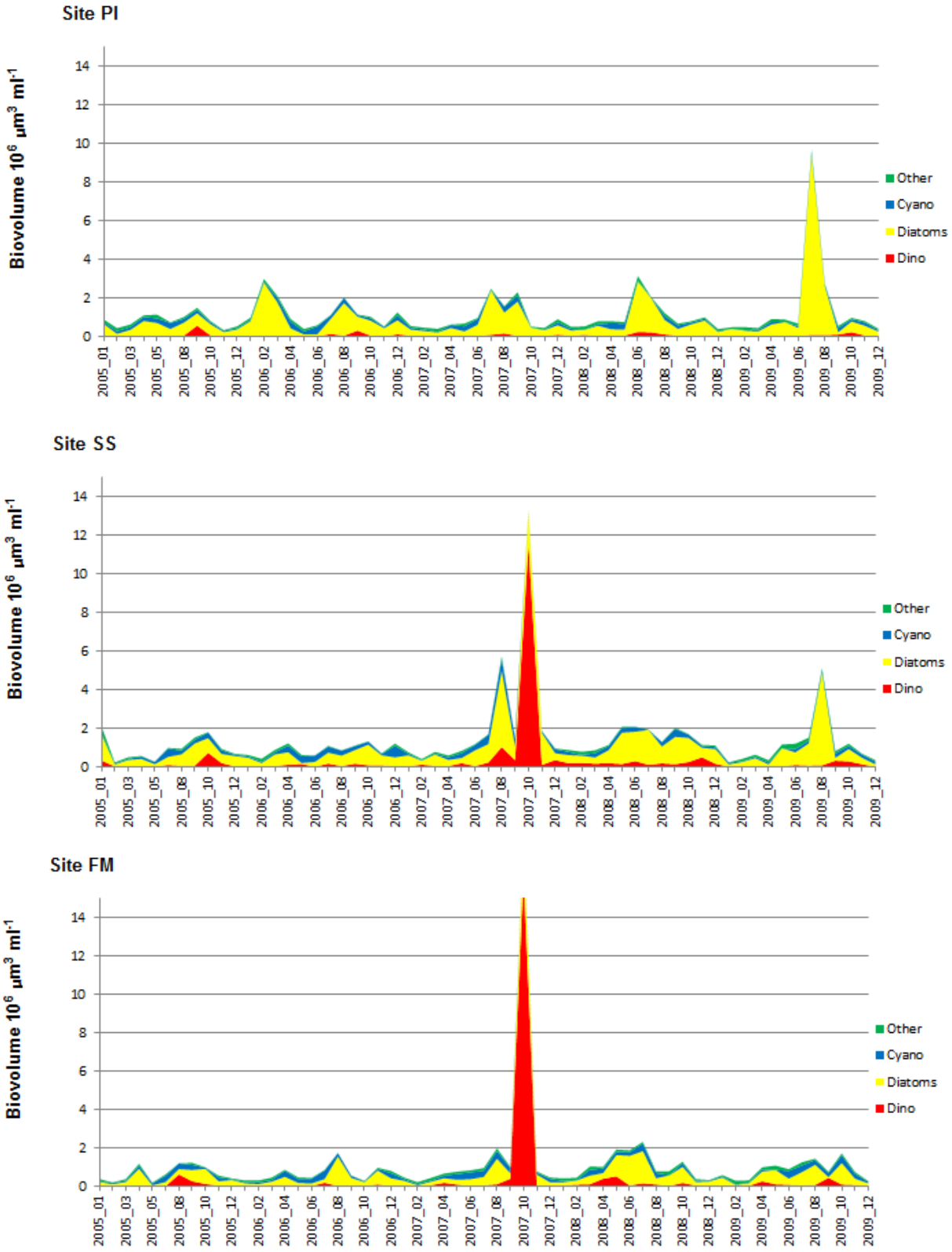

Figure 10. Biovolume by Phytoplankton Division

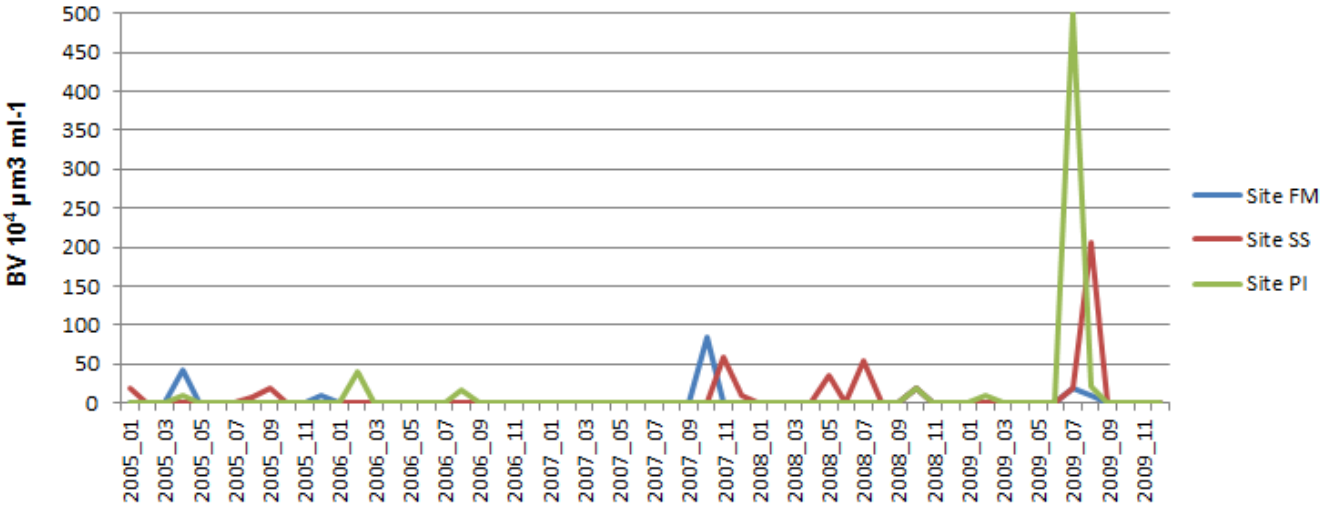

Figure 11. Centric Diatoms 100-200 µm

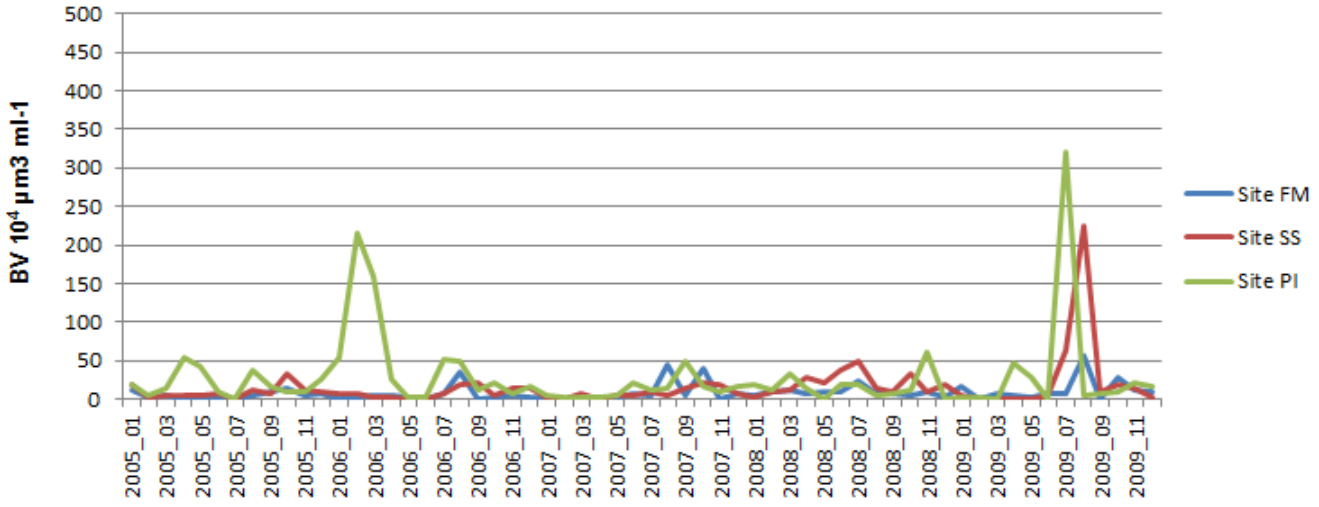

Figure 12. Centric Diatoms 30-100 µm

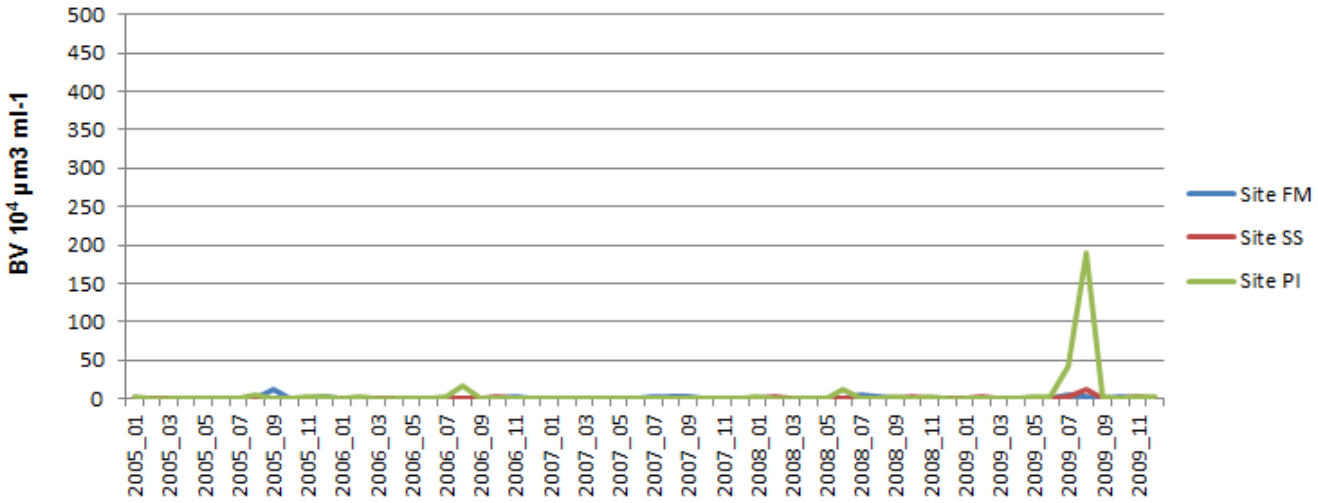

Figure 13. ***Odontella regia***

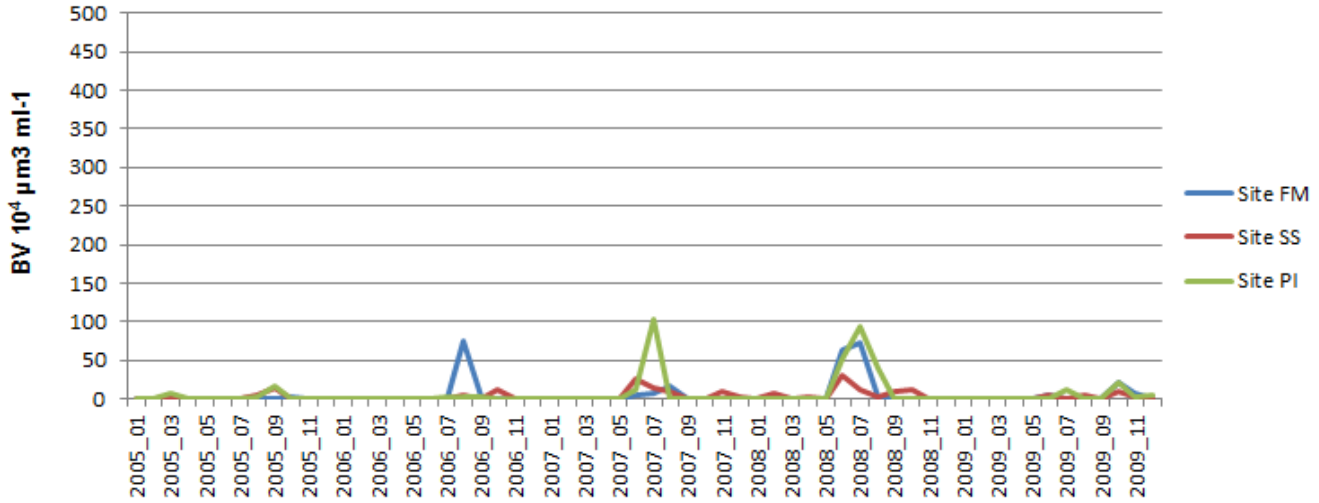

Figure 14. ***Skeletonema costatum***

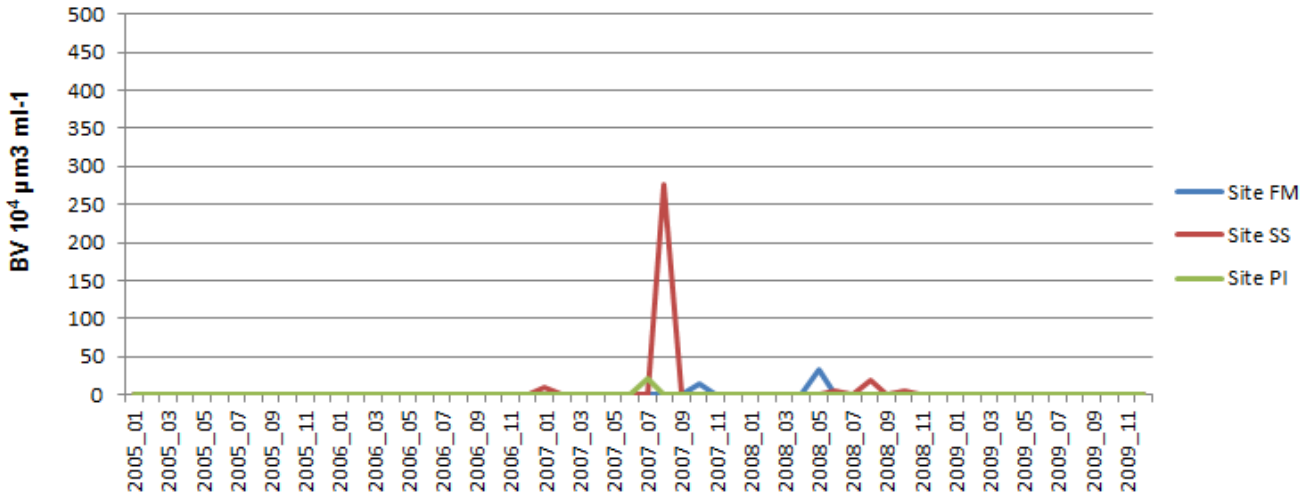

Figure 15. *Guinardia* spp.

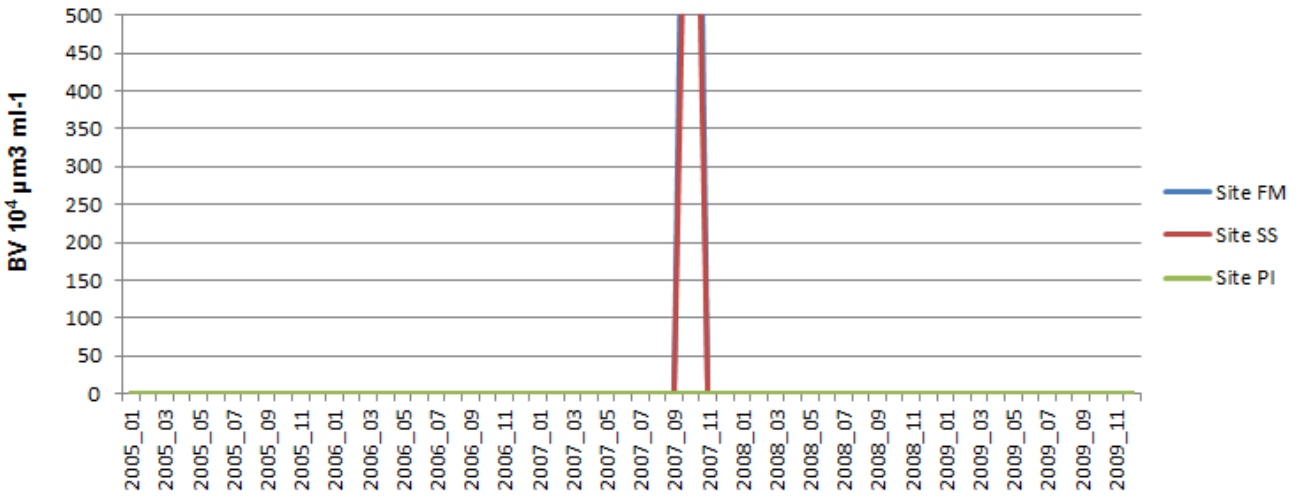

Figure 16. *Karenia brevis*
(* Biovolume values: FM = 1530 and Site SS = 1118)

Table 1. Means and Standard Deviations of Water Quality Parameters

Site		Salinity (psu)	Temp (°C)	Secchi (m)	Chl *a* (µg/L)	TN (mg/L)	TP (mg/L)
FM	Mean	31.9	23.1	1.2	3.9	0.38	0.05
	Std	2.2	5.2	0.4	3.4	0.13	0.01
SS	Mean	32.0	22.5	1.3	4.2	0.40	0.05
	Std	2.5	5.2	0.5	2.6	0.12	0.02
PI	Mean	28.5	23.1	1.1	5.2	0.56	0.07
	Std	5.9	5.7	0.4	3.2	0.20	0.02

Table 2. Mean Total Biovolumes and Size Distributions

Site	Mean BV (10^6 µm^3 / ml)	Chl *a*/BV ratio	Pico	Nano	Micro
FM	1.1	3.5	16%	61%	23%
SS	1.4	3.0	13%	53%	34%
PI	1.1	4.5	12%	36%	51%

Table 3. Species observed with mean biovolume >10,000 µm^3 ml^{-1}

(red=toxic or potentially harmful species)

Site FM	10^3 µm^3 ml^{-1}	# months present	10^3 µm^3 ml^{-1}		
Species Description	Mean BV	Total observations	Max bv observed	Max bv date	Max cells/ml
Karenia brevis	259.39	1	15304	2007_10	3476.2
spherical picoplanktonic cyanobacteria	164.33	57	398	2008_07	497261.5
Centric diatom >30-100µ	81.64	54	555	2009_08	9.0
Cryptophyte	76.48	59	169	2009_02	3597.1
Pennate diatom bv <1000	53.26	59	204	2009_07	1571.8
Centric diatom 05-30µ	52.15	59	240	2009_10	659.9
Skeletonema costatum c.f.	47.28	16	744	2006_08	1169.8
Pennate diatom bv 1000-8000	35.55	50	230	2008_07	181.6
Centric diatom >100-200µ	30.57	6	837	2007_10	0.4
Protoperidinium spp <30µ	25.34	5	528	2005_08	36.3
Pleurosigma/Gyrosigma	22.83	46	199	2006_11	3.4
Gyrodinium spirale c.f.	18.02	27	249	2007_10	3.8
Pennate diatom bv 8000-36000	17.51	34	324	2007_10	17.4
Cerataulina pelagica	15.74	5	250	2008_05	90.7
Navicula spp apical axis <50µ	14.88	12	240	2005_04	45.3
Dactyliosolen fragilissimus	13.54	10	315	2005_10	72.5
Rhizosolenia setigera >7000bv	13.21	17	271	2007_10	30.6
synechococcus picoplanktonic cyanobacteri	12.61	28	193	2006_07	69027.6
Chaetoceros spp	11.46	8	454	2009_05	1753.2
unidentified spherical flagellate <15µ	10.95	58	198	2009_05	3687.8
Thalassionema nitzschioides	10.51	17	124	2008_06	151.1

Table 3 cont. Species observed with mean biovolume >10,000 μm^3 ml^{-1}
(red=toxic or potentially harmful species)

Site SS	10^3 µm³ ml⁻¹	# months present	10^3 µm³ ml⁻¹		
Species Description	Mean BV	Total observations	Max bv observed	Max bv date	Max cells/ml
Karenia brevis	189.47	1	11179	2007_10	2539.1
spherical picoplanktonic cyanobacteria	172.05	57	617	2007_08	771308.4
Centric diatom >30-100µ	151.80	58	2250	2009_08	11.6
Centric diatom >100-200µ	74.80	10	2055	2009_08	3.4
Centric diatom 05-30µ	69.03	58	250	2008_07	698.3
Cryptophyte	62.70	59	149	2008_02	3113.5
Pennate diatom bv <1000	60.81	59	231	2005_09	4715.5
Guinardia	52.65	5	2755	2007_08	570.0
Navicula spp apical axis <50µ	40.84	22	512	2008_09	96.7
Pleurosigma/Gyrosigma	40.29	51	278	2007_07	8.4
Pennate diatom bv 1000-8000	40.27	50	241	2006_09	182.6
Skeletonema costatum c.f.	32.13	23	300	2008_06	471.6
Gyrodinium spirale c.f.	30.97	32	192	2005_10	2.4
Dactyliosolen fragilissimus	29.95	26	271	2007_11	163.2
Pennate diatom bv 8000-36000	28.69	45	1024	2007_10	34.0
Thalassionema nitzschioides	28.59	35	281	2008_09	519.9
Paralia sulcata	21.46	38	616	2005_01	90.7
Odontella aurita	15.82	7	570	2009_05	60.5
Protoperidinium spp <30µ	15.59	2	755	2007_08	51.8
synechococcus picoplanktonic cyanobacte	15.22	28	244	2006_12	87034.8
Prorocentrum mexicanum	13.66	33	99	2006_05	5.6
Gyrodinium pinque c.f.	13.41	13	136	2008_11	56.7
Cerataulina pelagica	13.25	8	187	2009_03	68.0
Rhizosolenia setigera	12.69	19	211	2008_05	326.5
Prorocentrum micans	11.54	19	260	2005_10	9.4
Protoperidinium sp. >30µ	11.01	28	127	2007_12	3.2
Leptocylindrus danicus	10.05	3	349	2006_03	103.6

Site 21	10^3 µm³ ml⁻¹	# months present	10^3 µm³ ml⁻¹		
Species Description	Mean BV	Total observations	Max bv observed	Max bv date	Max cells/ml
Centric diatom >30-100µ	281.09	59	3216	2009_07	58
spherical picoplanktonic cyanobacteria	135.09	57	408	2006_06	510204
Centric diatom >100-200µ	103.97	7	5016	2009_07	9
Cryptophyte	86.07	59	190	2005_05	4534
Centric diatom 05-30µ	71.29	59	474	2007_09	1028
Skeletonema costatum c.f.	62.81	17	1029	2007_07	1617
Pennate diatom bv <1000	51.83	59	143	2007_09	1224
Odontella regia	48.25	18	1898	2009_08	31
Pleurosigma/Gyrosigma	28.41	50	223	2007_07	8
Thalassionema nitzschioides	27.07	27	221	2007_09	223
Rhizosolenia setigera >7000bv	22.93	28	268	2008_06	19
Pennate diatom bv 1000-8000	22.58	39	215	2007_09	181
Gyrodinium spirale c.f.	18.97	24	168	2009_10	3
Pennate diatom bv 8000-36000	17.87	24	365	2007_08	13
Navicula spp apical axis <50µ	14.94	12	349	2009_06	66
Odontella moblilienis	13.00	29	294	2009_08	13
Rhizosolenia setigera	11.49	10	426	2008_06	280
Protoperidinium spp <30µ	10.08	2	330	2005_09	23
Dactyliosolen fragilissimus	10.04	11	137	2009_07	82

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