Plankton Blooms

What regulates the onset, persistence and fate of planktonic algal blooms in Florida Bay?

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About this report

This report draws its material directly from syntheses compiled for the 2001 Florida Bay Science Conference. The Florida Bay Science Program organizes itself around five central research questions. Topical teams associated with each question consist of modelers and researchers working in the Bay and adjacent marine systems. These teams compiled the original synthesis documents.

In preparation for the 2003 Florida Bay Science Conference, the research teams have modified the existing synthesis documents to bring them up to date and implement a more uniform, common format. In some cases, entirely new documents have been drafted, such as the information here on ecosystem history and on nutrient dynamics. The present report compiles these separate documents into one and provides the reader with summary material as a guide to the contents.

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Introduction

From the 1950's to the mid 1980's Florida Bay was characterized by expansive seagrass beds, mangrove islands, and crystal clear water. In the past 16 years, there have been some dramatic changes in the ecology of Florida Bay, with the die-off of large areas of seagrass and the appearance of intense planktonic algae blooms. There is a general consensus in the scientific community that these phenomena are indicative of changes in key environmental conditions within the bay. The shift in primary producers, and the alteration of the photic environment in Florida Bay, has been hypothesized to have major impacts on the flora and fauna of the bay (e.g., Boesch et al., 1993). Many of the changes have recently been reviewed by Fourqurean and Robblee (1999). In this paper we examine the current state of knowledge about the character and causes of planktonic algae blooms in the bay.

In reviewing the scope of our knowledge on algal blooms in Florida Bay it is important to keep in mind that detailed monitoring of water quality in the bay has only been underway for just over a decade. This is a somewhat surprising fact considering the importance of this aquatic resource to Florida and the surrounding waters of the Atlantic Ocean and Gulf of Mexico. One of the factors that triggered the initiation of extensive multi-disciplinary research in the bay was the on set of massive cyanobacterial blooms over large areas of the bay in the early 1990's.

The first quantitative indications of major increases in phytoplankton densities in the interior regions of Florida Bay came from chlorophyll a data collected by Florida International University (Boyer et al. 1997, 1999). The latter research effort, which began in 1988, indicated a significant step increase in chlorophyll levels in 1991/92. The increase in algal biomass within the bay was corroborated by incidental observations by individuals frequenting the bay for other research and recreation activities. In 1993 the monitoring efforts of FIU were joined by a separate research group from the University of Florida that revealed high concentrations of cyanobacteria in the central portion of Florida Bay (Fig. 6.1) (Phlips and Badylak 1996, Phlips et al. 1999). In 1994 the phytoplankton research efforts were further expanded to include the Florida Marine Research Institute. All three research teams observed large cyanobacteria blooms in the central regions of the bay, particularly in the summer and fall (Phlips et al. 1999, Steidinger et al. 2001).

During the same period of time, algal bloom events were also recorded in the western region of the bay (Fig. 6.1). However, the latter blooms were not typically dominated by cyanobacteria, but rather by diatoms (Phlips and Badylak 1996, Phlips et al. 1999, Steidinger et al. 2001). Recent efforts by researchers from the University of Miami focusing on the western bay have provided further support for the importance of diatom blooms in the western region. Analysis of sediment cores from the western side of Florida Bay indicate that diatom blooms along the western margin were a well established feature by 1970, well prior to the increases in cyanobacteria blooms within the Bay's interior (Fig. 6.5; Jurado 2003). Most recently, chemotaxonomic studies of phytoplankton in the Bay have been initiated using of high-performance liquid chromatography analysis with a full spectrum photodiode array detectors (Louda, 2001).

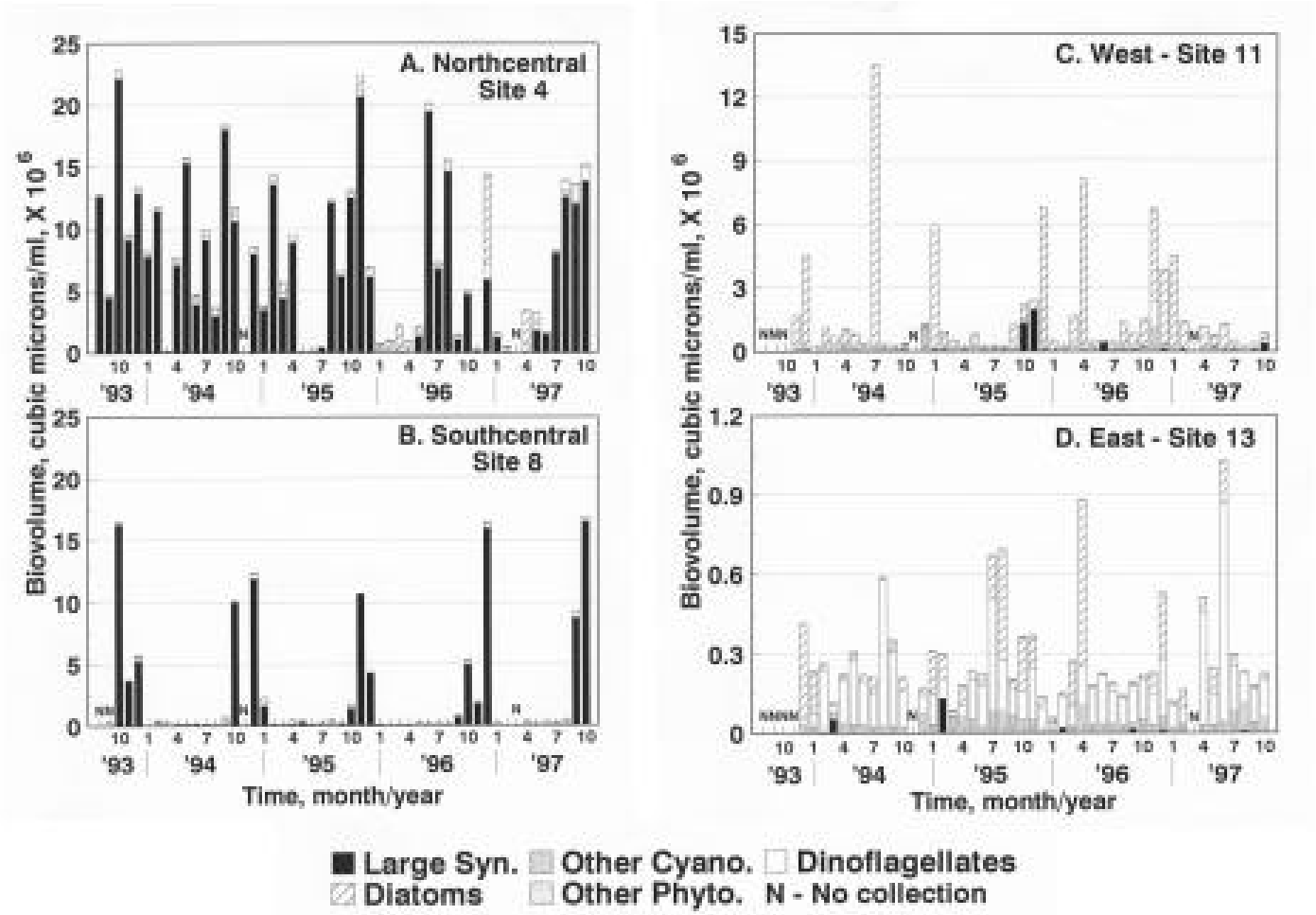


Figure 1. Biovolume of *Synechococcus elongatus* (Large Syn.), other Cyanobacteria, dinoflagellates, diatoms and other phytoplankton at four Sampling sites representative of different regions of Florida Bay (Phlips et al. 1999).

Regional Differences

The observed disparity in the quantity and quality (i.e. composition) of phytoplankton biomass in different parts of the bay manifests the need to view phytoplankton dynamics by ecological zones. In contrast to the phytoplankton blooms encountered in the western and central parts of Florida Bay, the eastern portion of the bay is almost devoid of blooms (Fig. 6.1). There have been several efforts to divide the Florida Bay into ecologically distinct zones. These zonal breakdowns have been based on a variety of parameters, including geology (Prager *et al*., 1996), distributions of benthic plants (Zieman *et al*., 1989), faunal distributions (Thayer and Chester, 1989; Holmquist *et al*., 1989), and water quality characteristics (Phlips et al. 1995, Boyer *et al*. 1997, 1999; Burd and Jackson 2001). These efforts have yielded from 3 to 20 zones with different boundary designations. The lack of consensus on the specific boundaries and number of zones is largely attributable to differences in the choice of parameters used in the discrimination of the regions.

If the focus is limited to the frequency of phytoplankton blooms and the general composition of the blooms, it is possible to define three general regions that roughly follow longitudinal lines of demarcation (Fig. 6.2): (1) The eastern region of the bay, east of 80° 39’ W Long. and west of the Florida Keys, where major phytoplankton blooms are seldom observed, (2) The central region of the bay, between 80° 39’ W Long. and 80° 49’ W Long., where bloom concentrations of cyanobacteria (i.e. greater than 1 million cells per ml) are regularly encountered and (3) The western region of the bay, west of 80° 49’ W Long., which experiences periodic blooms of diatoms. This provides a useful context for discussing both the character of blooms in the bay and the factors that control them.

In the most general terms, phytoplankton standing crops are dictated by factors that control gains and losses of algal biomass (Fig. 6.3). From a gain perspective the most obvious contributor to the increase in phytoplankton biomass is cell growth. Net growth rates are under the control of resource availability, like nutrient and light, as well as factors that affect the rates of photosynthetic and respiratory activity, like temperature, salinity and oxygen levels. Algal biomass can also increase as a consequence of inputs to the water column from the benthos through resuspension or from inflows of water from adjacent environments.

In terms of loss functions one of the most important over-riding considerations is the water residence time. In many coastal ecosystems phytoplankton biomass is limited by the rate of flushing with water of lower phytoplankton content. Flushing rates are generally related to a combination of rainfall inputs, tidal mixing and wind driven circulation. Many environments with long residence times tend to have higher phytoplankton crops than environments with short residence times, assuming similar nutrient and light availability characteristics (Monbet 1992). There are also biological processes that contribute to the loss of biomass in many aquatic ecosystems, like grazing by benthic and planktonic filter-feeding organisms. The rates of loss are closely tied to the structure and abundance of the grazer community and environmental factors that impact the rate of activity, like salinity, temperature and phytoplankton composition (e.g. presence of toxic species).

While most of these gain and loss processes are operating to some extent in all coastal marine ecosystems, the relative magnitude of their impact varies from system to system. This certainly appears to be the case in comparing the three regions of Florida Bay. It is therefore appropriate to examine the character and causes of blooms in the bay on a regional basis.

Summary of Research

Research to date indicates that there are three ecologically distinct regions within the Bay from the standpoint of algal blooms; the Northeast region, Central region and West region. The nature and causes of blooms can be most appropriately summarized within the context of these three regions, Table 6.1.

Northeast Region

- Algal blooms are largely absent from the Northeast region of Florida Bay. The phytoplankton community of the Northeast region is a diverse mixture of cyanobacteria, dinoflagellates, diatoms and microflagellates, none of which form blooms.

- The lack of algal blooms in the Northeast region of Florida Bay is largely attributable to the severe phosphorus limitation characteristic of the region. Despite significant water inflows to the region from the Everglades, the very low phosphorus levels in these inputs combined with the calcium carbonate rich waters of the region result in nutrient-limited conditions.

Central Region

- Large algal blooms have been a common feature of the Central region since at least 1992. The focal point for blooms in the Central region is in the north Central region from Rankin and extending into Whipray basin. The greatest bloom activity is generally in the summer and early fall, although blooms have been observed in other seasons. In the fall and early summer blooms originating in the north Central region are pushed southward by prevailing wind-driven circulation into the south Central region, where they can spread out into the Atlantic reef tract through cuts in the Florida Keys. The dominant bloom-forming alga in the Central region is the picoplanktonic cyanobacterium *Synechococcus elongatus*, although several species of diatom and dinoflagellate do occasionally occur in bloom proportions.

- Nutrient limitation of phytoplankton growth in the Central region appears to switch back and forth from phosphorus to nitrogen. The nature of the sources of nutrients for blooms in the Central region has been a subject of considerable debate, yielding several hypotheses: (1) A significant supply of nutrients for algal production is available from the flocculent muddy sediments within the region, (2) A groundwater source of phosphorus is present within the region that, in combination with nitrogen from the Northeast region, feeds algal blooms, (3) Nutrients from the shelf region west of the Bay are available to blooms in the Central region via tidal water exchange and (4) Atmospheric deposition is a significant source of nutrients (particularly N) for algal primary production. These hypotheses are not mutually exclusive and several mechanisms may be operational at the same time.

- The domination of blooms in the Central region by *Synechococcus elongatus* is attributable to the unique ecophysiological characteristics of this species of cyanobacterium. These characteristics include: (1) Wide tolerance to salinity, (2) Superior ability to compete for phosphorus at low concentrations, (3) Ability to regulate buoyancy and thereby take advantage of nutrients available in the sediments and (4) Lower susceptibility to grazing losses.

West Region

- Algal blooms are also a common feature of the West region of Florida Bay. These are dominated by diatoms, in contrast to the cyanobacterial blooms in the north Central region. The diatom-dominated blooms in the West region are mainly *Rhizosolenia* spp. *Chaetoceros* spp. and pennates are major genera in term of cellular biomass. Diatom blooms in the West region begin in late summer and are advected into the bay from shallow coastal waters off Cape Sable.

- The diatom-dominated blooms in West Florida Bay are mainly limited in their growth by nitrogen, either singly or in combination with phosphorus and/or silicon supply. Temperature, salinity and light do not appear to be important factors in the initiation or maintenance of diatom blooms. Maximum growth rates of the diatom community during bloom initiation in the West region range from 1 to 2 day^{-1} (first-order rate constant), based on increases in netplankton (> 5μm size fraction) chlorophyll a or biogenic silica. The onset of diatom blooms on the western Florida Shelf appears to be associated with enhanced riverine outflow, predominantly from the Shark River. The onset of increased diatom biomass occurs within the riverine, low-salinity plume near Cape Sable.

Table 6.1: Summary of research on plankton blooms by region

	West	Central	East
General Characteristics	Boyer et al. 1997, 1999; Phlips and Badylak 1996; Steidinger et al. 2001; Phlips et al. 1999; Jurado 2003	Boyer et al. 1997, 1999; Phlips and Badylak 1996; Steidinger et al. 2001; Phlips et al. 1999; Phlips et al. 2002	Boyer et al. 1997, 1999; Phlips and Badylak 1996; Steidinger et al. 2001; Phlips et al. 1999
Nutrients		Robblee et al. 1991; Durako 1994; Carlson et al. 1994; Zieman et al. 1994; Lapointe et al. 2001; Lapointe and Barik 2001; Tomas et al. 1999; Brand et al. 2001; Lapointe et al. 1990, 1994; Paul et al. 1995a, 1995b	
Composition and Growth Rates	Jurado 2003; Tomas et al 1999	Richardson et al. 2001	
Grazing and Flushing		Lynch and Phlips 2000; Brenner et al. 2001	

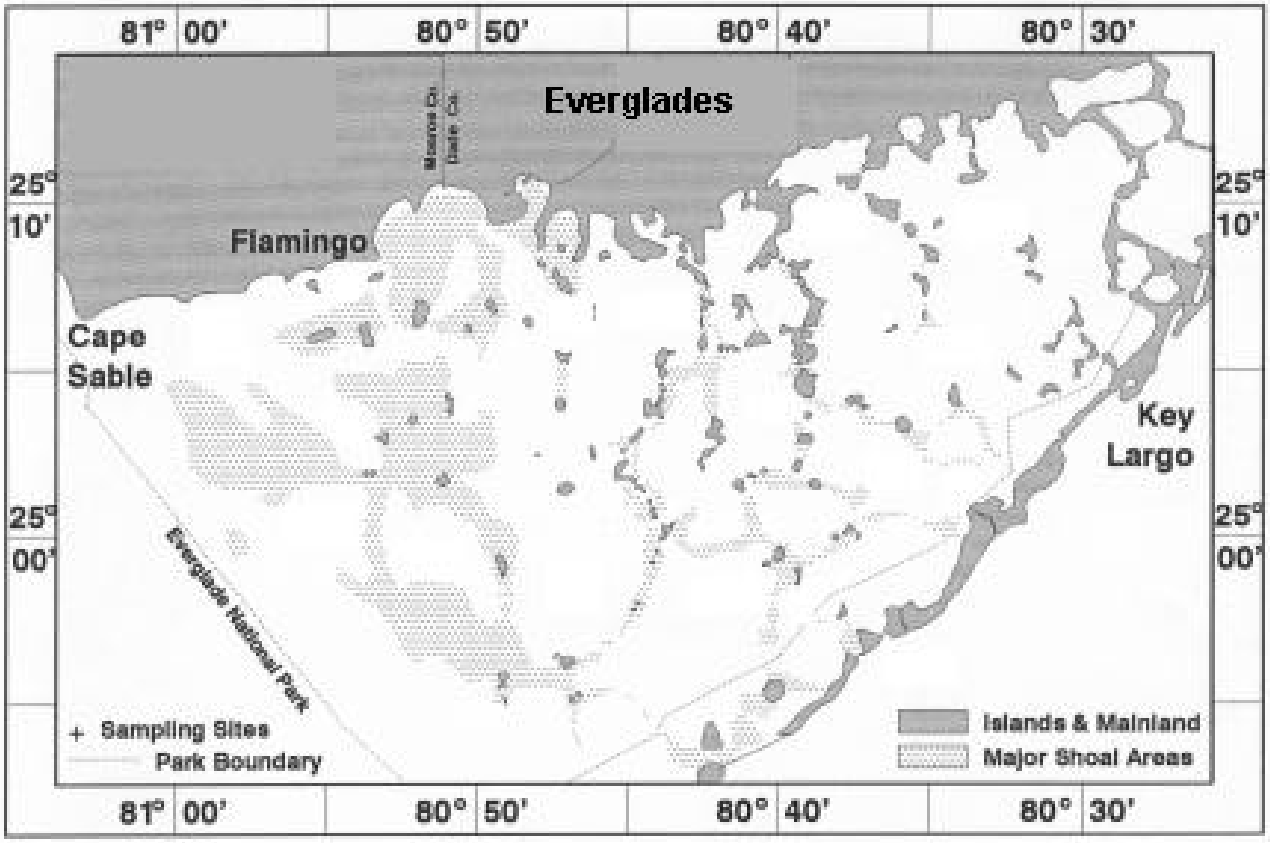


Figure 6.2. Florida Bay basin configurations.

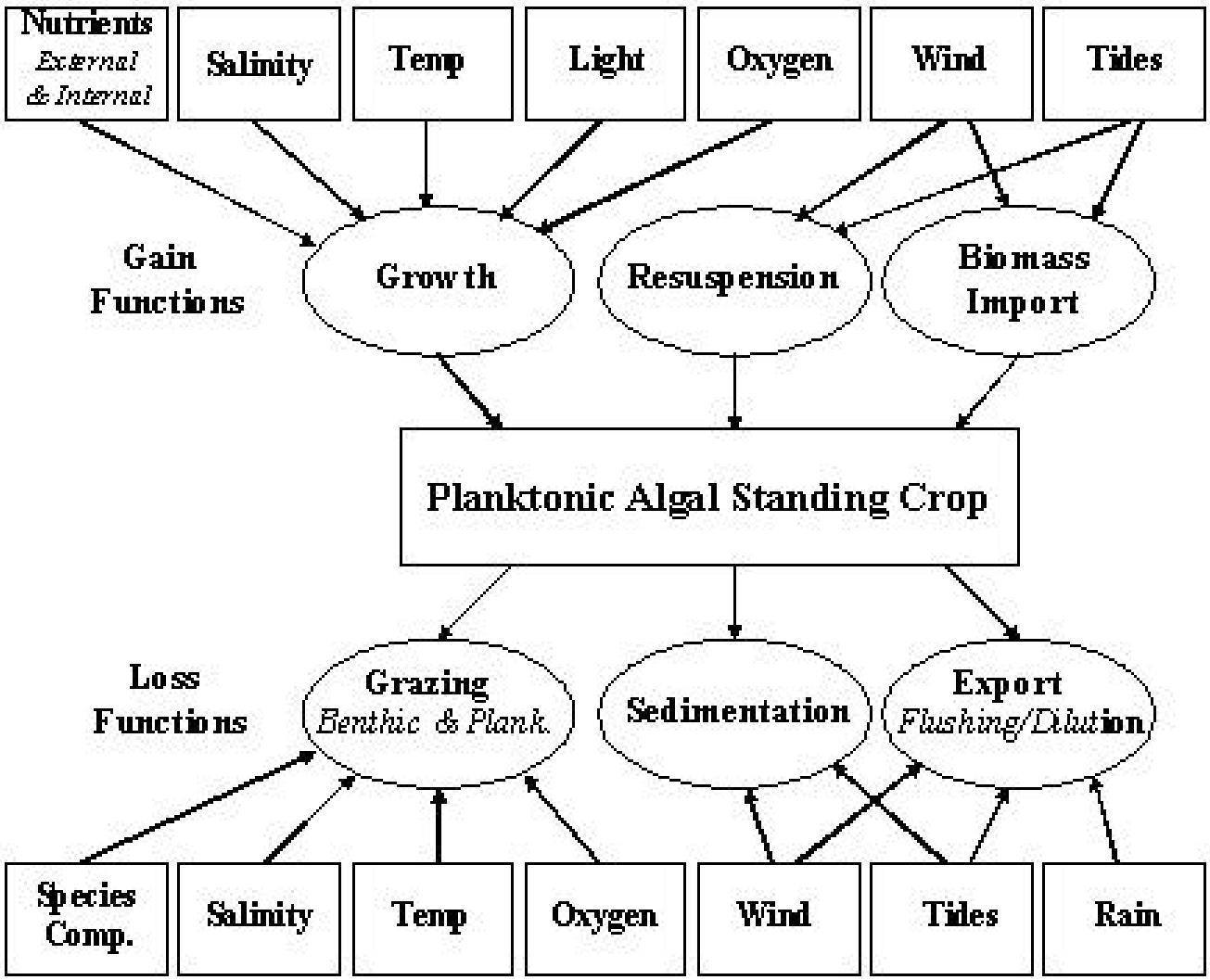


Figure 6.3: Gain versus loss functions for phytoplankton standing crops

Eastern Florida Bay

Phytoplankton abundance in the Eastern Bay is the lowest of the three zones within the bay (Fig. 6.1). Chlorophyll *a* concentrations in the Eastern Bay are typically < 2 mg m^{-3} throughout the year. Phlips *et al*. (1999) report that the maximum chlorophyll *a* concentrations in this region were < than 5 mg m^{-3} between August 1993 and October 1997, with most values < 1 mg m^{-3} (Fig. 6.4). Similarly, Boyer *et al*. (1997, 1999) observed low chlorophyll concentrations in eastern Florida Bay for the period between 1989 and 1997 (i.e. mean = 0.85 mg m^{-3}).
The phytoplankton communities in the Eastern Bay are primarily composed of centric diatoms (e.g., *Thalassiosira* sp.), dinoflagellates (e.g., *Protoperidium* spp. *Ceratium* sp., *Prorocentrum micans*) and small cyanobacteria that constitute the major fraction of cellular biovolume (Phlips and Badylak 1996). Steidinger et al. (2001) of the Florida Marine Research Institute (FMRI) reported that the dominant phytoplankton taxa in the region from fall 1994 to early summer 1995 were dinoflagellates, while cyanobacteria were the most abundant taxa from late 1996 to spring, 1997. Cellular biovolume serves a useful index to phytoplankton biomass that is independent of physiological-induced changes in pigment concentrations such as occurs in chlorophyll *a*. In Eastern Florida Bay, total phytoplankton biovolume is < 1 μm^3 ml^{-1}, a value several-fold less than that in the Western and Central Bay (Fig. 6.1)(Phlips *et al*. 1999).

Two factors result in strong phosphorus limitation of primary production in the region, helping to explain the low phytoplankton concentrations that typify this region of the bay. The eastern region of Florida Bay receives significant freshwater inputs from Taylor Slough and the C-111 canal system. Salinity values in the eastern basins are on average lower than in the Central and Western Bay, with typical values from 20 to 30 ppt (Fig. 6.4) (Phlips *et al*. 1999). The external surface water inputs to eastern Florida Bay are very low in phosphorus (Boyer *et al*., 1999). In addition the high concentrations of calcium in the region tend to bind free phosphate.

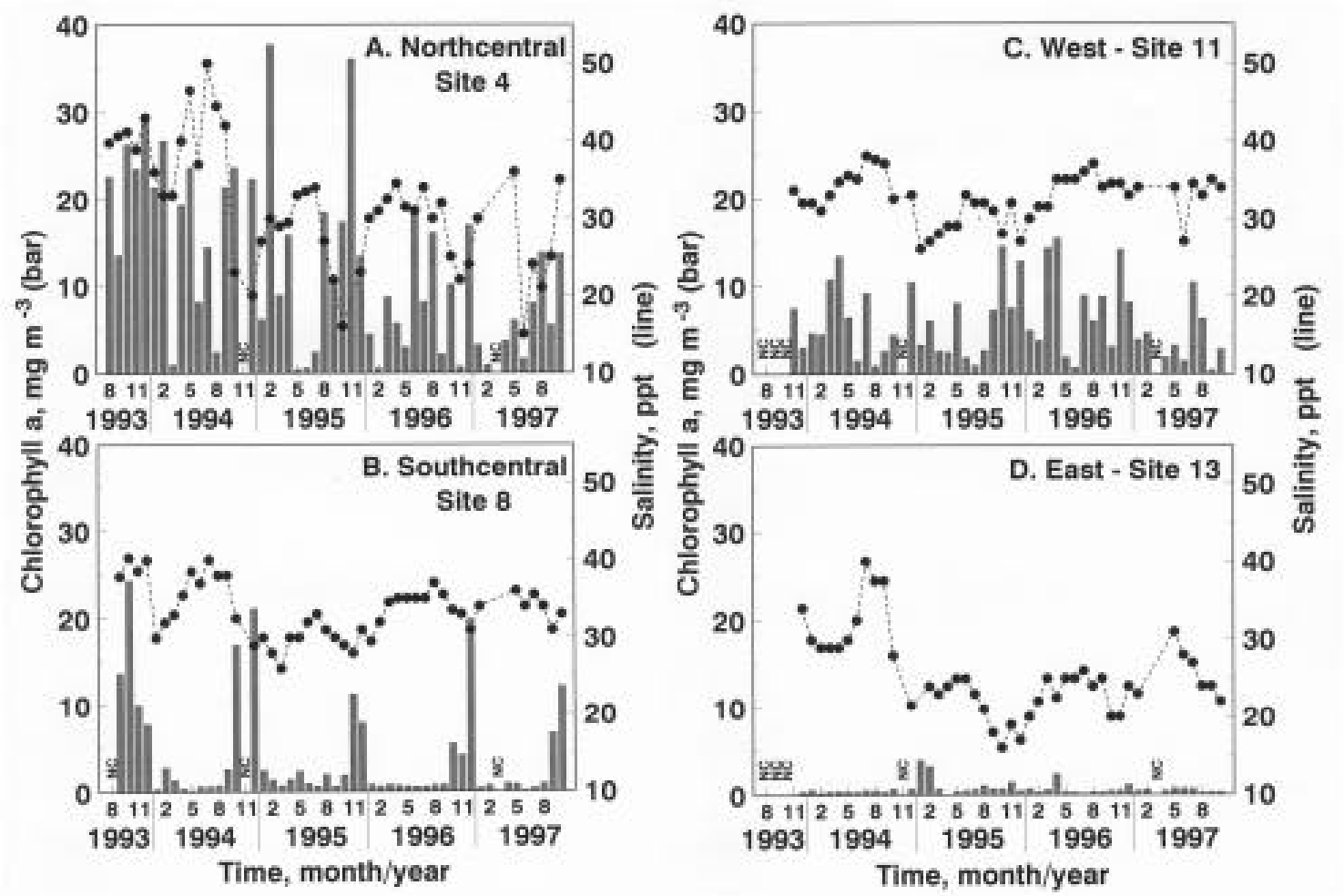


Figure 6.4. Chlorophyll *a* concentrations and salinities at for sampling sites Representative of different regions in Florida Bay (Phlips et al. 1999).

Central Florida Bay

Over the past twelve years the central region of Florida Bay has been the site of intense and prolonged algal blooms. In contrast to the eastern region of the bay, where biovolumes of phytoplankton seldom exceeded 1 million μm^{-1}/ml, biovolumes in the central bay have regularly exceeded 10 million μm^{-1}/ml (Phlips et al. 1999). The intensity of blooms in the central bay is somewhat masked by the fact that chlorophyll content of phytoplankton in the region is relatively low by comparison to the western bay and some other coastal ecosystems in Florida (Phlips et al. 1999, Phlips et al. 2002). It has been hypothesized that this is partially attributable to the very shallow depth in the central region of the bay (i.e. generally less than 2m), resulting in high light availability and sun adaptation by algal cells (Phlips et al. 1999). It is also possible that the domination of the plankton community by the cyanobacterium *Synechococcus elongates* cf. and nutrient limitation contributes to the low ratio. Irrespective of the causes for the low ratios, it is important to consider the ratio when evaluating the intensity of blooms in the bay. For example, peak chlorophyll concentrations in the St. Johns River in northeast Florida are 3-4 times those in central Florida Bay but the peak biovolumes of phytoplankton are very similar (Phlips et al. 2000). These considerations manifest the fact that the 20-40 mg m^{-3} chlorophyll levels commonly encountered in central Florida Bay are representative of serious bloom conditions, whereas similar chlorophyll levels in other ecosystems might be viewed as moderate bloom levels.

Over the twelve years since the initiation of major phytoplankton blooms in central Florida Bay the most intense blooms have occurred during the summer and early fall, except during 1993 and 1994 when high phytoplankton standing crops persisted throughout the year. Three of the past ten years (1993, 1994, and 1998) exhibited particularly intense blooms. Phytoplankton blooms in the central region of Florida Bay originate in the northern part of the region. For most of the peak bloom season, i.e. May-September, phytoplankton populations in the south central region are relatively low. However, in the fall and early winter passing cold fronts, along with the concomitant shift in wind direction to the north, displaces phytoplankton-rich water southward. This recurring pattern is apparent from the appearance of bloom concentrations of phytoplankton as far south as the Florida Keys reef.

Cause of Blooms in the Central Region

The apparent rise of planktonic algae blooms in the central region of Florida Bay in the early 1990's raises two fundamental questions: (1) What changes occurred in the region that facilitated the onset of the blooms and (2) What are the nutrient sources that have sustained blooms since that time? In relation to the first question, the onset of blooms indicates one of two possibilities, (a) more nutrients were made available for phytoplankton production either through redirection of internal reserves and/or increases in external loading and/or (b) biomass loss terms were dramatically reduced. The presence of a thick organic sediment layer in the north-central region of Florida Bay indicates that this region of the bay has historically been productive. Prior to the 1990's the dominant primary producers in the central bay were most probably seagrasses. Even after 1990 seagrasses were still present in the region, although not as prominently as in previous years.

One of the principal hypotheses about the cause of phytoplankton blooms in the central bay focuses on the role of seagrass die-off in making available internal nutrient reserves for planktonic production (Robblee et al., 1991; Durako, 1994; Carlson et al., 1994; Zieman et al., 1994). There are a number of ways that reductions in seagrass populations could enhance nutrient availability for planktonic production, including: (1) Through the addition of recyclable nutrients from dead seagrass, (2) By increasing access to sediment bound nutrients via increased resuspension and diffusion and (3) By reducing competition for nutrient between phytoplankton and epiphytic/benthic algae living in seagrass communities. In addition to increasing nutrient availability, the reduction in seagrass communities can impact phytoplankton loss processes. The populations of filter-feeding organisms associated with seagrasses can influence phytoplankton densities, particularly in very shallow environments like Florida Bay. The physical presence of dense seagrass beds also increases the sedimentation of algae by reducing the potential for resuspension of algae and sediments.

The importance of seagrass die-off in the stimulation of phytoplankton blooms is not a universally accepted concept. Some researchers have suggested that this line of reasoning is backwards, namely that increases in planktonic production actually led to the demise of seagrasses (Lapointe et al. 2001, Lapointe and Barile 2001). The authors of this hypothesis cite as evidence observations of increases in turbidity by local users of the bay prior to the seagrass die-off in the late 1980's (DeMaria 1996, Lapointe and Barile 2001) However these observations are primarily restricted to the western region of the bay and therefore do not provide substantial insight into what occurred in the central bay during the 1980's. There is also insufficient information available to establish the specific mechanisms by which increases in phytoplankton concentrations in the central region of Florida Bay might cause seagrass mortality. The most common rationale for such an effect is related to light limitation of seagrass production. However, the north central region of the bay is very shallow (i.e. generally less than 2m. in depth) and it remains to be demonstrated whether blooms could cause the demise of seagrass populations based on decreased light availability. It is possible that such an argument might be more tenable in the western bay and shelf environment, where average depths are greater.

Residence time of water in the bay has been estimated on the order of 1 to 2 months (Jackson and Burd, 1999; Top et al., 2001). Given the repeated observations of the algal bloom in north central Florida Bay being driven to the south every winter by cold fronts plus the flushing of the bay by Hurricane Georges in 1998, it is doubtful that the nutrients from decomposed seagrasses 13 years ago have not been flushed out and are instead continuing to fuel the bloom. This is particularly true in the deep channel south of Cape Sable where tidal currents flow in and out daily and there was no significant seagrass dieoff; and yet there is persistently high phosphorus and algal blooms.

Seagrass dieoff and the resulting biomass decomposition and sediment resuspension also cannot explain the spatial distribution of the algal blooms or nutrients in Florida Bay. It is well established that the general flow of water is from the northwest (around Cape Sable) to the southeast through the passes between the Florida Keys (Smith, 1994; Wang et al, 1994; Lee et al., 2002). The nutrients and algal blooms should be at the same place or downstream of the seagrass dieoff locations. A comparison of the distribution of average chlorophyll concentrations from 1996 to 2000 (Brand 2002; Fig. 13.2) with the distribution of seagrass dieoff

in 1987 (Brand 2002; Fig. 13.4) indicates that much of the algal bloom area is upstream, not downstream of the seagrass dieoff areas. Furthermore, a comparison of the inorganic nitrogen (N) and total phosphorus (P) spatial distributions (Brand 2002; Figs. 13.5 and 13.6, respectively) with seagrass dieoff areas reveals that the highest concentrations of nutrients are neither downstream nor at the same location as much of the seagrass dieoff. While there is some overlap of high N and high P areas in northcentral Florida Bay where some of the seagrass died, seagrass decomposition could not generate a nutrient pattern with P upstream to the northwest and N to the northeast of the seagrass dieoff area, with currents flowing to the southeast.

Irrespective of which came first the seagrass die-off or the algae bloom, the central questions remain the same, what are the sources of nutrients for phytoplankton blooms and has the trophic state of the central bay increased over the past few decades. It is important to consider the possibility that the overall pool of nutrients may have remained stable but that the distribution has changed, along with changes in loss terms. This argument falls within the concept of 'alternative stable states'. Under this scenario a major environmental disruption that resulted in seagrass die-off could have ushered in environmental conditions conducive to the persistence of phytoplankton blooms. Such disruptive events could include major storms, prolonged drought or flood periods or even a major shift in nutrient loading.

The first step in addressing these questions is to identify what nutrients actually limit the production potential of phytoplankton in the central bay. There is little doubt that primary production in the eastern region of the bay is strongly phosphorus limited, as previously reviewed. There is also a significant body of evidence to suggest that the western region of the bay and adjacent shelf environment are most commonly limited by nitrogen, suggesting an excess supply of phosphorus to this region. The nutrient limitation status of the central bay is more ambiguous. A number of biogeochemical indicators, like ratios of total N: total P and inorganic N: inorganic, indicate that phosphorus should be the most limiting nutrient (Fourqurean et al. 1993, Boyer et al. 1997, 1999). However, it is well known that many organic N molecules are not readily available to phytoplankton, while many organic P molecules are bioavailable, due to the activity of phosphatase enzymes (Vitousek and Howarth, 1991). The results of nutrient enrichment bioassays in the central region of the bay suggest that the limiting status can alternate between phosphorus and nitrogen (Tomas et al. 1999). This observation implies that at different times changes in the loading rate of either nutrient could stimulate increases in phytoplankton production. A number of hypotheses have been forwarded regarding potential sources of phosphorus and nitrogen for phytoplankton blooms in the central region of Florida Bay. Most of these concepts deal specifically with the north central region of the bay where blooms appear to originate. It is important to recognize that these hypotheses are not mutually exclusive. It is likely that various pathways of nutrient supply operate simultaneously, even though the relative importance of each varies over time and space.

Hypothesis 1: Internal supply of nutrients

There are a number of potential internal sources of both nitrogen and phosphorus for phytoplankton production. The thick layer of flocculent organic sediments found in the north central region of the bay represents a potential pool of bioavailable nitrogen and phosphorus. The recent die-off of seagrasses in the region have made this pool more accessible, through enhanced diffusion and resuspension processes. There has been considerable debate within the

scientific community whether the size of this pool and the rate of supply from the sediments are sufficient to sustain the blooms observed over the past decade. This is certainly an issue that warrants future attention. The current information available is insufficient to either accept or reject this hypothesis.

There are a number of biological processes that impact the internal supply rate of bioavailable nutrients. Nitrogen fixation by autotrophic and heterotrophic bacteria and cyanobacteria is a potential source of nitrogen. In some aquatic ecosystems nitrogen fixation can represent a major source of nitrogen. Conversely denitrification processes can result in a loss of bioavailable nitrogen. Very little is known about the magnitude of either process in north central Florida Bay.

Another key element of internal supply of nutrients for phytoplankton production is the rate of recycling, permanent sedimentation/binding and export of nutrients within the north central region. Due to the severe restriction of tidal exchange of water between the north central region and the waters of the Gulf of Mexico and the Atlantic Ocean residence times for water are long. The restriction should provide more time for recycling and less opportunity for wash out of nutrients. As in the case of the aforementioned processes very little is known about the actual rate constants for recycling, sedimentation or export of nutrients.

Hypothesis 2: Groundwater Sources of Phosphorous

Phosphorite deposits were created in the Miocene in northeast Florida and subsequently transported south into South Florida by Appalachian erosion resulting in the high phosphorus observed in geological formations in certain areas of South Florida (Brand, 1996; Brand et al., 2001). Groundwater outflows from these formations can contain high phosphorus levels (Brand 2002). The distribution of water column P correlates well with the phosphorite deposits (Brand 2002). There has been an effort to discover direct phosphorus–rich groundwater inputs within the north central region of Florida Bay, without success to date. In a less direct manner, phosphate mining in central Florida may have increased the input of phosphorus into southwest Florida coastal waters, possibly reaching the interior of Florida Bay via south-flowing coastal currents and then tidal or wind-driven water exchange.

It has been hypothesized that the phosphorite deposits are a persistent source of P that has not changed significantly over the past few thousand years (Brand et al. 2001, Brand 2002). Actually, phosphate mining over the past century may have increased the input of P into coastal waters, but there is no evidence that it has increased substantially in the past two decades. Indeed, phosphate inputs have probably declined over the time period that the algal blooms increased in Florida Bay.

Hypothesis 3: External Loading of Nutrients

Current information on geographical gradients of critical nutrient elements in and around Florida Bay indicates that the most likely external surface water sources of bioavailable nitrogen are from the eastern half of the bay (Fig. 6.5a). Conversely, phosphorus gradients in the region indicate that the most likely source of bioavailable phosphorus is from west of the bay (Fig. 6.5b). A number of researchers have proposed that the blooms in the north central part of the bay are sustained by nitrogen inputs from the east combined with phosphorus inputs from the west. The proponents of this concept suggest that phytoplankton blooms in the north central

region of the bay are a result of increases in nitrogen loading related to recent changes in water management practices in southeast Florida. They also suggest that phosphorus loading to the north central region of the bay from the western shelf has remained constant over the same period of time.

Examination of the ratio of inorganic N : total P indicates ratios greater than the Redfield ratio in eastern Florida Bay and ratios less than the Redfield ratio in western Florida Bay. This suggests the potential for P limitation in the east and N limitation in the west. The results of around 1000 nutrient bioassays conducted over a year and a half indeed show mostly P limitation in the east and N limitation in the west, with a spatial distribution similar to the inorganic N : total P ratios (Brand 2002). Lavrentyev et al. (1998) and Tomas et al. (1999) have also observed P limitation in eastern Florida Bay and N limitation in western Florida Bay. The largest algal blooms are in central Florida Bay where high P from the west meets high N from the east, and the inorganic N : total P ratio is close to the Redfield ratio (Brand 2002).

Everglades N

The following scenario is envisioned for explaining the increase in N load to Florida Bay. In the early 1980's agricultural runoff from the Everglades Agricultural Area (EAA) was diverted south via the South Dade Conveyance System (Fig. 6.6), which was designed to enhance the flow of water from the Everglades canal system into eastern Florida Bay (Light and Dineen, 1994; South Florida Water Management District, 1992).

This engineering was successful and more water was injected into Florida Bay, beginning around 1980 (South Florida Water Management District, 1992). It is hypothesized that this led to the injection of not only more freshwater into Florida Bay, but also more N (Brand 2002). N and P are scavenged from the water as it moves south from the Everglades Agricultural Area to Florida Bay, but approximately 60 mM N remains, as it is not scavenged by the limestone and vegetation as efficiently as P (c.f. analysis by Brand 2002). The C111 Interim Plan implemented in the early 1990s increased flow into northeast Florida Bay even more (Ley, 1995). The C111 canal was altered so that more water would flow to Taylor Slough further to the west and less water would flow to the east. This had the effect of injecting N-rich water closer to the area of high P in western Florida Bay. There are no significant algal blooms at the mouth of Taylor Slough because of the lack of P.

Unfortunately, there do not appear to be any good N concentration data in Florida Bay before the beginning of the large regional monitoring program in 1989. Upstream, however, Walker (1991) found nitrate and phosphate inputs increased between 1983 and 1989 in Taylor Slough and between 1977 and 1989 in the Shark River. Walker (1991) observed a 20%/year increase in nitrate in water flowing through the C111 canal into Florida Bay between 1983 and 1989 and a 11%/year increase at the S12A station where water flows into the Shark River system.

A comparison of chlorophyll concentrations over time at 4 stations in northcentral Florida Bay where the major bloom occurs, with the flow of the N-rich water into Florida Bay through the Taylor Slough system shows a general correlation, with highest chlorophyll concentrations in 1994 and 1995, when water flow was highest (Brand 2002). The same correlation appears when the data are examined on a monthly basis. There appears to be a 1 to 2 month lag between when

the water is pumped into the bay and when the algal bloom appears to the west of the input site. This is to be expected, as the N-rich, P-poor water from Taylor Slough entering Florida Bay in the east will not generate an algal bloom until it mixes with the P-rich water to the west. A comparison of the spatial extent of the bloom during the dry season when there is little input of N-rich water from Taylor Slough and during the rainy season when there is a large input of N-rich water from Taylor Slough also demonstrates how input of the N-rich water from the agricultural areas through Taylor Slough helps generate the algal blooms.

The scenario does however depend on several assumptions for which the evidence is currently lacking or insufficient. The primary assumption is that there is sufficient water exchange between the western shelf, the putative source of phosphorus, and the north central bay to sustain blooms. Current hydrodynamic data is insufficient to establish this rate of exchange. There is also a need to more carefully examine the nutrient limitation status of phytoplankton in the central bay. As mentioned above, chemical data indicates the north central region should be phosphorus-limited, while bioassay data indicates a mixed limitation status.

Hypothesis 4: Sewage As A Source Of Nutrients

Another potential source of nutrients is sewage and other nutrient-rich freshwater runoff from land in nearby areas of high human activity. In the case of Florida Bay, this would be primarily the heavily populated Florida Keys. Considerable amounts of N and P are estimated to be generated by human activities in the Florida Keys (EPA, 1992) and some fraction of this is clearly entering the local waters (Lapointe et al., 1990, 1994; Shinn et al., 1994; Paul et al., 1995a, 1995b). The problem with this hypothesis is that the source of the nutrients is downstream of the algal blooms, not upstream. Sewage may be causing local eutrophication and leading to algal overgrowth of the coral reefs downstream, but cannot be the source of the nutrients generating the algal blooms upstream to the northwest. Concentrations of nitrogen, phosphorus and chlorophyll all decrease, not increase, along transects from northern Florida Bay to the Florida Keys. The algal blooms in Florida Bay are, in fact, the furthest away from the Florida Keys and the human population.

Hypothesis 5: Atmospheric Inputs

Until recently, the potential role of atmospheric deposition of bioavailable nutrients in supporting algal blooms in Florida Bay was largely discounted. However, recent information indicates that such inputs may indeed be an important element to the broader nutrient budget of the bay (Rudnick et al. 1999).

Domination by Cyanobacteria

One outstanding feature of algal blooms in the central region of Florida Bay is the domination of the cyanobacterium *Synechococcus elongates*. A study of algal blooms in the region from 1993-1997 showed that *Synechococcus elongates* represented over 90% of total phytoplankton biovolume in most instances when total phytoplankton biovolume exceeded 5 million μm^3/ml (Phlips et al. 1999). Although cyanobacteria are the most abundant phytoplankton in central Florida Bay, other taxonomic groups can play important roles (Phlips et al. 1999, Steidinger et al. 2001). For example, between May 1994 and April 1995, the diatoms *Cyclotella choctawatcheeana* and *Chaetoceros* cf. *salsugineus* were frequently important elements of

phytoplankton biomass (Steidinger et al. 2001). Again in July 1995, March 1996, and January 1997 diatoms were numerous.

Based on empirical observations and experimental studies a number of hypotheses have been forwarded to explain the domination of *Synechococcus elongates* in the central region of Florida Bay. Several of these hypotheses are based on some of the unique ecophysiological characteristics of this cyanobacterium. Several research groups have demonstrated the broad range of salinities over which *S. elongates* can sustain high growth rates, i.e. 5-50ppt (Phlips and Badylak 1996, Richardson 2001). Because of the isolation of central Florida Bay from tidal mixing and the proximity of the north central bay to the adjoining Everglades this region is subject to wide swings in salinity. For example, salinities exceeded 40ppt during the drought period of 1992-94, but dropped to as low as 11 ppt during subsequent flood periods, like 1995 and 1997 (Fig. 6.4) (Phlips et al. 1999, Boyer et al. 1999). The euryhaline character of *S. elongates* most probably provides it with an advantage in terms of long-term prominence. However, it does not fully explain the fact that intense blooms of *S. elongates* have been observed during time periods when salinities have remained in a moderate range, i.e. 25-35 ppt.

Another factor that may contribute to the success of *S. elongates* is its ability to compete for nutrients at low concentrations (Richardson 2001). As a picoplanktonic species, one might expect *S. elongates* cf. to have low half-saturation constants for nutrient uptake, strictly from surface area to biovolume considerations. Experimental studies have provided support for this hypothesis. In a study of the kinetics of phosphorus (PO_4-P) dependent growth a comparison was made of four important phytoplankton species found in the bay, the cyanobacterium *Synechococcus elongatus*, an unidentified spherical picoplanktonic cyanobacterium, and the diatoms *Chaetoceros* cf. *salsugineus*, and *Cyclotella choctawhatcheeana* (Richardson et al. 2001). The results for growth tests revealed maximal growth rates for *S. elongatus*, the spherical cyanobacterium, *C. cf. salsugineus* and *C. choctawhatcheeana* of 1.38, 1.37, 2.48 and 3.37 divisions day^{-1}, respectively. The half-saturation constant for growth, K_u, was determined to be 0.005 - 0.05 μmoles liter^{-1} for the latter three species. The K_u for *S. elongatus* could not be determined as the growth rate was still maximal at the lowest test concentration of phosphate. A test of phytoplankton resource-based competition using Equilibrium Resource Competition (ERC-theory) predicts that *S. elongatus* is the superior competitor under P-limitation over the range of salinities examined (15 to 50 ppt). The superior competitive ranking of S. *elongatus* can be attributed to the exceptionally low K_i values. The model ranked the spherical cyanobacterium second in terms of phosphate competition, with the diatoms last. In competition experiments under steady and varying P-limitation, *S. elongatus* also dominated in terms of biovolume at the end of all experiments at all salinities. Thus, with sufficient time *S. elongatus* should competitively displace all the other species under P-limited conditions. Competition experiments further revealed that under nitrogen-limiting conditions the two cyanobacteria species usually co-dominated in terms of biovolume under steady and non-steady state conditions. In summary, under both steady state and non-steady state conditions the cyanobacteria *S. elongatus* is the superior competitor for orthophosphate and can frequently out-compete diatoms under N limiting conditions.

Related to the question of nutrient competition is the ability of *S. elongates* to regulate it's buoyancy by altering the presence of gas vesicles (Phlips and Bledsoe, unpublished data). Under

phosphorus-limited conditions the presence of gas vesicles diminish and *S. elongates* cells loose buoyancy. It has been suggested that with the loss in buoyancy nutrient-depleted cells can sink to the sediment/water interface, where they can take advantage of higher nutrient availability (Phlips et al. 1999).

Beside the characteristics that may enhance the competitive advantage of *S. elongates* in acquiring resources for growth, there may also be ways this species is favored by lower magnitude of certain loss terms. It has been proposed the *S. elongates* are responsible for the observed demise of sponges in Florida Bay (Butler et. al. 1995), due to their adverse effects on the filtration apparatus of sponges. While there is evidence that sponges can effectively filter-out *S. elongates* from the water column (Lynch and Phlips 2000), the long-term affects of filtering the mucilage producing cyanobacterium are not known. Irrespective of the direct effects of *S. elongates* on sponge health, it is clear that the diminishing sponge populations in the bay result in reduced grazing pressure on phytoplankton and thereby increase the potential for blooms (Lynch and Phlips 2000).

As in the case of sponges, the relationship between *S. elongates* and other grazers, both benthic (e.g. bivalves) and planktonic (e.g. zooplankton), are not well defined. There is evidence that zooplankton grazing rates are periodically high enough to impact phytoplankton population dynamics (Brenner et al. 2001). In grazing experiments daily metabolic C demand of the net zooplankton community ranged from <2% to >100% of the phytoplankton C stock. Microphytoplankton growth rates ranged from 0.08 to 2.33 d^{-1} at 50% available light. Diatoms, dinoflagellates, and the cyanobacterium *Synechococcus* typically dominated the microphytoplankton community, though chlorophytes and prasinophytes were occasionally major constituents. Microzooplankton grazing rates ranged from 0.00 to 5.28 d^{-1}, and their average ingestion rates ranged from 0.67 to 3.42 mg C m^{-3} d^{-1}. These ingestion rates correspond to a daily ingestion demand ranging from < 1 % to >300 % of the initially available carbon, indicating that microzooplankton are capable of exerting a controlling influence on the phytoplankton community. Despite the observed grazing rates, the frequency of cyanobacterial blooms in the north central region of the bay demonstrate that grazing activity is frequently not sufficient to prevent blooms, although it may play a role in their ultimate demise. There is no information on whether the domination of *S. elongates* in the north central region is in any way related to selective avoidance by grazers, benthic or planktonic.

Western Florida Bay

The highest phytoplankton biovolume in Western Florida Bay generally occurs in the late summer to winter when the annual diatom bloom reaches its seasonal peak. Phytoplankton composition in the Western Bay is distinct from the Central Bay in that a higher proportion of total biovolume occurs in diatoms. Phlips and Badylak (1996) were the first to identify the species composition of bloom components in western Florida Bay. They found that centric (predominantly *Rhizosolenia*) and pennate (*Cocconeis*, *Navicula*, *Surirella*) diatoms were dominant species in terms of cell abundance in December 1993. Steidinger et al. (2001) subsequently reported that other taxa, especially cyanobacteria, may also account for a large fraction of total biovolume in western Florida Bay, and potentially equal the biovolume attributed to diatoms. In 2000 and 2001 Jurado (2003) conducted a study of netplankton (diatom) silica demand at Carl Ross Key in western Florida Bay. She found centric diatoms, predominantly *Rhizosolenia* and *Chaetoceros* spp, and *Thalassiosira nitzschiodes*, as well as pennate diatoms (*Nistchia*, *Navicula*, *Gyrosigma* spp.) dominated the netphytoplankton fractions (> 5 ìm). These observations are in general agreement with Phlips and Badylak (1996). Peak concentrations of chlorophyll *a* (2 – 9 mg m^{-3}), were higher than that observed in the eastern Bay, but less than that in the north central basins. Netplankton chlorophyll *a* accounted for > 50% of total pigment biomass.

While relatively few, if any, observations of phytoplankton community composition exist prior to 1990 in western Florida Bay, biogenic silica in the sedimentary record from Carl Ross Key suggest that an increase in the abundance of diatoms has occurred since 1960 (Figure 6.5). Biogenic silica is a distinct marker for the presence of diatoms. Although only two values exist from the sedimentary record before 1960, the vertical profile suggests that biogenic silica concentrations have increased from < 1 to > 1 mg Si (g sediment)$^{-1}$ sometime after 1950, although values in the last decade have been highly variable. This trend suggests that enhanced diatom biomass in Western Florida Bay has developed within the past four or five decades.

Cellular division rates determine the success of a species in the natural environment. Net growth rates equal the difference between the cellular division rate and the sum of all processes that represent losses, including grazing, sinking, advection, and death. Net increases in phytoplankton communities of as little as 0.1 day^{-1} result in an increase of <1 to > 20 mg m^{-3} chlorophyll *a* in less than a month. Although we have no direct measures of net phytoplankton growth rates in western Florida Bay, community growth rates for netplankton have been estimated from increases in chlorophyll a and biogenic silica in dilution gradient experiments. This method, principally developed by Landry et al., (1985) and colleagues, provides a measure of maximum growth. In March 2001, when phytoplankton abundance was low, netplankton chlorophyll *a* exhibited growth rates of 1.5 day^{-1}, increasing to 2.9 day^{-1} in May, July and September, as netplankton biomass increased. By November 2001 netplankton biomass had reached a ‘stationary phase, and maximum growth rates were again ca. 1 day^{-1}. Grazing losses ranged from 0.6 to 1.75 day^{-1} in these experiments, yielding net growth rates of 0.5 (November) to > 1.3 day^{-1} in May and September. Although these experiments represent only the potential for diatom growth in situ, they suggest that conditions in summer-fall provide diatoms with a setting for growth rates than exceed the sum of losses.

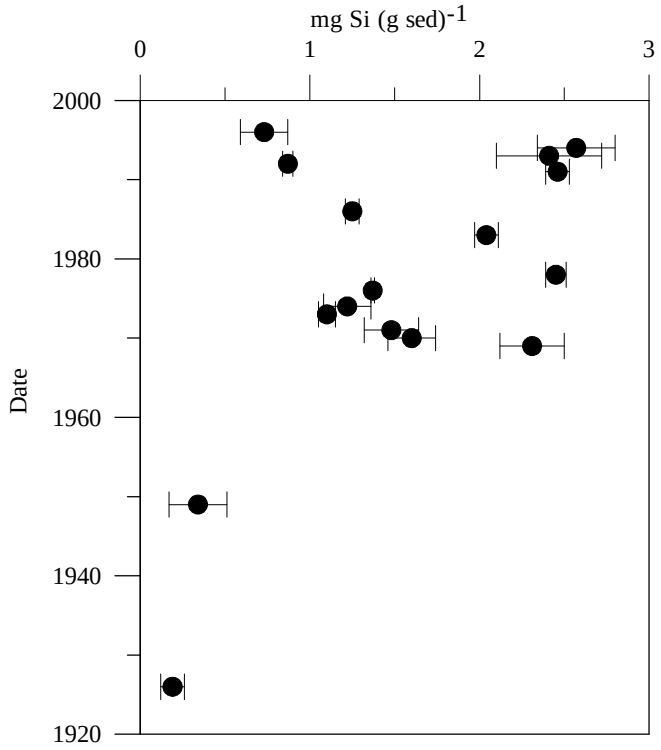


Figure 6.5: Vertical profile of biogenic silica in a sediment core from Carl Ross Key. The sediment samples with corresponding dates were kindly provided by Dr. J. Trefrey, Florida Institute of Technology (Jurado 2003).

Exchange of surface waters in Western Florida Bay with the West Florida Shelf is evident in the nature of the phytoplankton community and property distributions. Salinity values in Western Florida Bay exhibit less temporal variability than the Central or Eastern basins. On average, basins in the Western Bay have a higher average salinity (x = 35.2), lower average TN (30.5 ì mol kg^{-1}) and DIN (< 2 ì mol kg^{-1}), than those in the Eastern or Central Bay (Boyer et al., 1999). Chlorophyll *a* concentrations from the long-term FIU monitoring program averaged 1.9 mg m^{-3} which, as suggested by Phlips et al. (2000), is less that the average values in the Central Bay, but higher than the Eastern Bay.

Ratios of TN: TP (x = 55.6) and DIN: SRP (x = 51.8) in the Western Bay are higher than Redfield values, but lower than that in either the Eastern or Central basins. These characteristics suggest that the Western Bay is strongly influenced by the surface waters of the West Florida Shelf that exchange along the boundary of Everglades National Park. The influence of coastal processes is evident in tidal exchange, which is much greater in the Western Bay than in the interior or eastern basins, due to the fact that the amplitude of the tides is damped from west-to-east across the Bay (Wang et al., 1994).

Bioassays at two locations along the western margin of Florida Bay (Sprigger Bank and Sandy Key) indicate that nitrogen is a primary nutrient that limits phytoplankton growth (Tomas *et al*., 1999). In > 70% of the bioassays between March 1994 and May 1997, Tomas found that nitrogen in combination with silica stimulated growth as compared to single additions of phosphorus or silica. When individual nutrients were excluded from otherwise complete enrichments (all nutrients - N, or all nutrients - P), the lack of nitrogen yielded a final biomass that was similar to controls. Phosphorus limitation of phytoplankton growth rates was detected in about 20% of all experiments, while iron was less frequently identified as a nutrient potentially limiting growth.

The responses to N and Si enrichments are consistent with the marine waters that flow into the western margin of Florida Bay, and the fact that diatoms frequently dominate these waters. The observations of Tomas et al. were confirmed by Jurado (2003) who also found that nitrogen was the principal nutrient limiting both total phytoplankton and netplankton (diatom) growth in western Florida Bay during the 2000 – 2001 diatom bloom, Figure 6.6. Additions of nitrate-nitrogen enhanced growth, as measured by increase of chlorophyll *a* relative to unenriched controls, in 24-hour incubations. Bioassays were made in September and November 2000 as diatom abundance increased, and January and March 2001, when diatom biomass declined. The results consistently show that enrichments with nitrogen, and secondarily silica or phosphorus, stimulated growth of natural populations incubated under simulated in situ conditions. An assessment of temperature and irradiance during the course of the year suggest these two parameters did not effectively limit the growth of diatoms in western Florida Bay. Thus nutrient supply may be the main factor that accounts for the enhanced growth of diatoms in summer and fall in western Florida Bay.

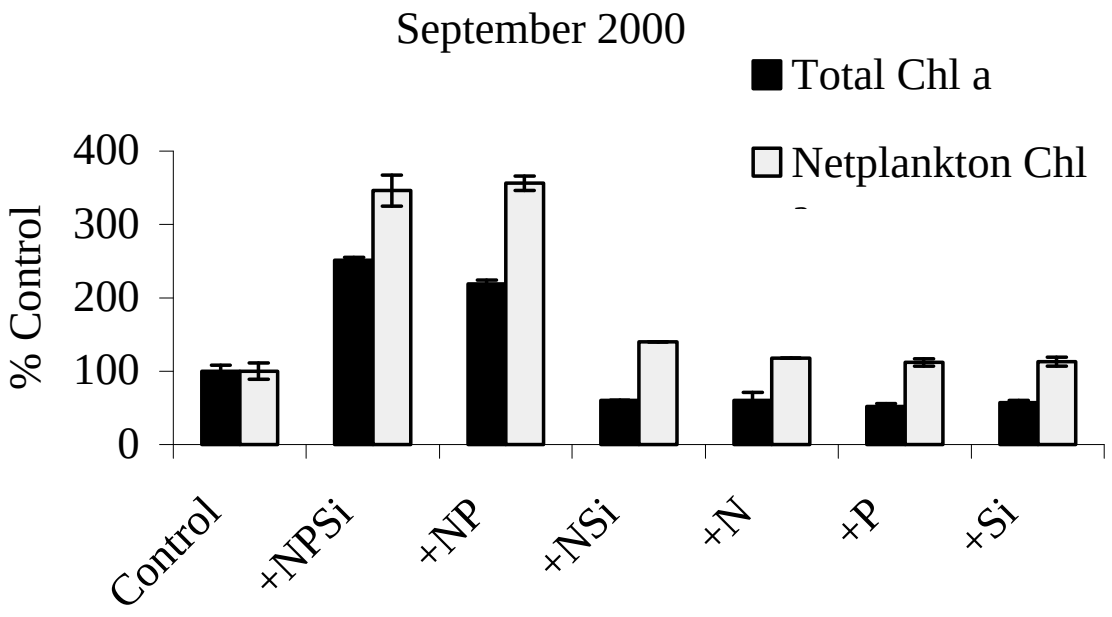


Figure 6.6. Bioassay results from September 2000 at Carl Ross Key (Jurado, 2003). Values correspond to increases in chlorophyll a biomass relative to a control in an incubation of 24 hours. The total phytoplankton community was filtered on Whatman GF/F filter, and the netplankton fraction on a 5 ì m Nuclepore filter. The combination of nitrogen plus phosphorus or silicon typically results in the greatest stimulation of phytoplankton growth.

Seasonal distributions of salinity, nutrients, chlorophyll *a* and biogenic silica on the West Florida inner shelf, south from the Ten Thousand Islands to the western boundary of Everglades National Park, indicate that diatom blooms observed in Western Florida Bay originate in coastal waters off the southwest Florida Shelf. These features develop in the shallow coastal waters west of Cape Sable, and are associated with the low salinity plume emanating from the Shark River and other riverine sources on the southwest Florida coast. A chlorophyll a 'plume' spreads south from Cape Sable to the western margin of Western Florida Bay during the fall (Figure 6.7). Bimonthly cruises of the NOAA SFERPM Program between 1998 and 2003 have mapped surface properties (salinity, nutrient, chlorophyll a, particulate matter) in this region. Spatial distributions indicate that the Shark River is a major source of nutrients, especially silicate, to the region of diatom bloom development. Concentrations of dissolved inorganic nutrients in the Shark River plume at bimonthly intervals indicate that average concentrations of silicon, inorganic nitrogen, and phosphorus in the plume of the Shark River indicate excess silicate relative to inorganic N and P. Little seasonal variation exists in nutrient concentrations, so the volume freshwater flow appears to be the primary determinant of nutrient flux to the inner shelf.

On the Southwest Florida Shelf, exogenous nutrients that support diatom growth are derived from the Shark River and alongshore flow. Increased freshwater flow often occurs in June with the onset of the rainy season, providing an exogenous silicate source to the inner-shelf from riverine sources that contributes to development of the diatom bloom. Between 1998 and 2000 the diatom-dominated bloom on the inner shelf began between August and October. Estimates of the fluxes of nitrate, phosphate and silicate from alongshore advection (based on bimonthly nutrient measurements and alongshore currents from ADCP currents made by T. Lee and colleagues) and that from the Shark River (derived from river discharge and bimonthly nutrient measurements) have been made for the period of bloom inception in 1999 (Jurado, 2003). This is the latest year in which Shark River flow data was available at the time the estimates were made. The resulting flux estimates suggest that during bloom inception, exogenous nutrient sources that support diatom bloom development are largely met by the southerly flow along the SW Florida Shelf (Figure 6.8). When the bloom is at its maximum, after the onset of the rainy season, the Shark River is a major source of nitrate plus nitrite and phosphate. Alongshore advection of silicate appears to be the primary source of this essential nutrient for diatoms, at least in that year.

In summary, diatom blooms in the western basins of Florida Bay are a seasonal extension of blooms that initiate on the southwest Florida Shelf. Various species of *Rhizosolenia* and *Chaetoceros* are the dominant members of this assemblage, in combination with pennates that are likely resuspended from the bottom. Diatoms begin net growth (that is, growth rates exceed losses) with the onset of the rainy season. Bioassays suggest that nitrogen, often in combination with phosphorus and/or silica, potentially 'limit' growth. Nutrients that support diatom growth are derived from riverine sources, principally the Shark River, and alongshelf (southerly) advection. The relative contribution of inorganic nitrogen, phosphorus, and silicon varies with the stage of the bloom, and in other years likely varies with river discharge as well as alongshore flow.

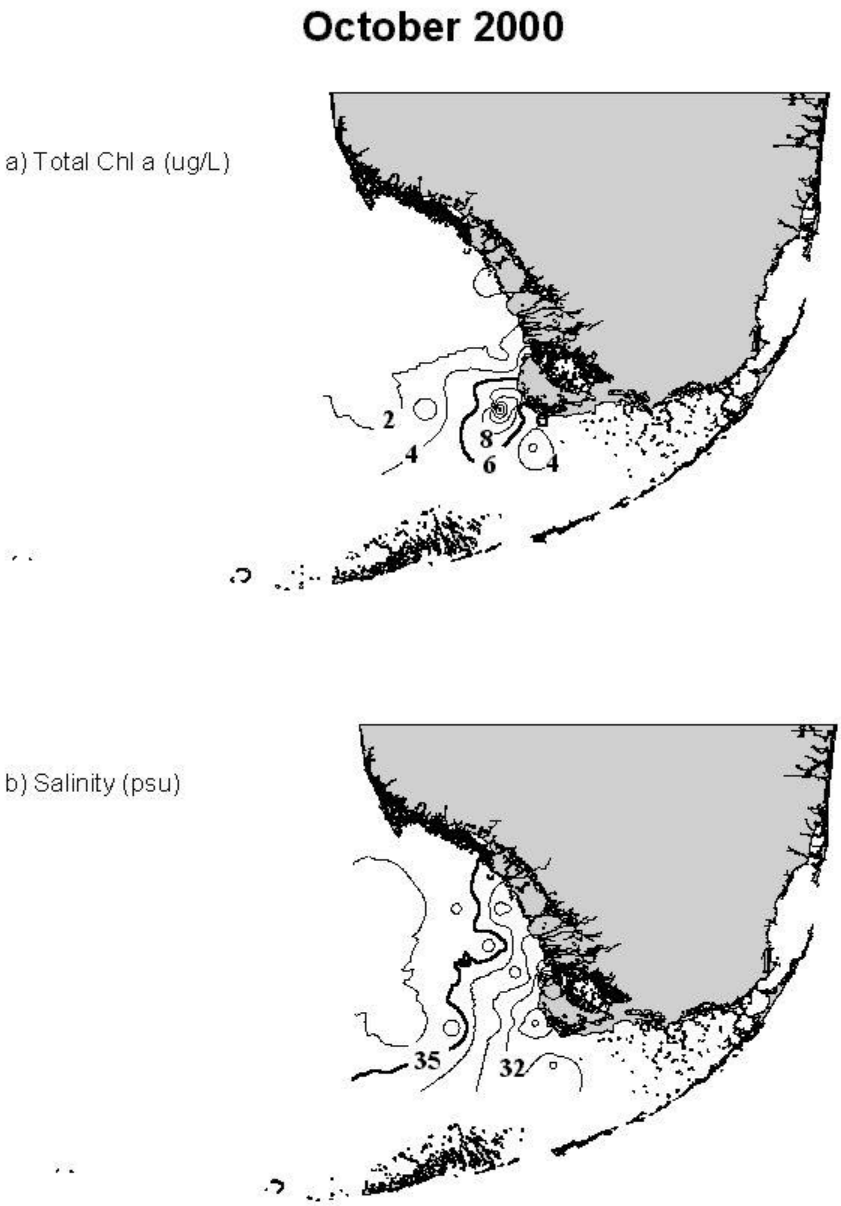
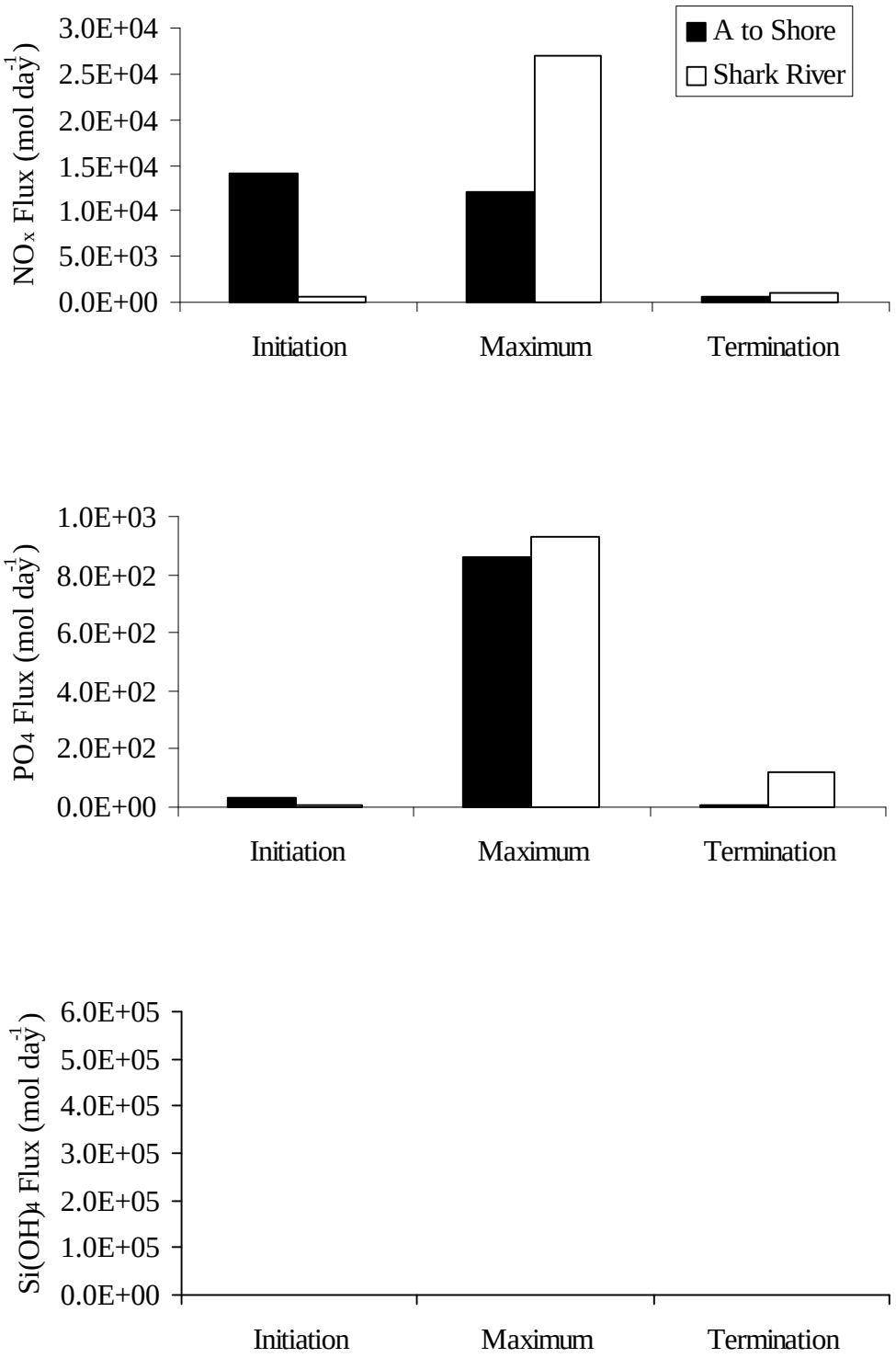


Figure 6.7. Contours of total Chlorophyll *a* concentrations (top) and surface salinity (bottom) in October 2000 during the peak of the annual diatom bloom. Maximum chlorophyll *a* concentration was 17 mg l^{-1} off Middle Cape Sable (Jurado 2003).

Figure 6.8. Comparison of inorganic nutrient fluxes from alongshore advection and Shark River during three phases of the 1999 diatom bloom on the southwest Florida Shelf near Cape Sable. Alongshore flow is based on currents from ADCP A that is located nearshore, just north of the Shark River (Jurado 2003).



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