SPRING PHYTOPLANKTON DYNAMICS IN A SHALLOW, TURBID COASTAL SALT MARSH SYSTEM UNDERGOING EXTREME SALINITY VARIATION, SOUTH TEXAS

A Thesis

by

ELIZABETH MICHELE HEBERT

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

May 2004

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

Daniel L. Roelke (Co-Chair of Committee)	James L. Heilman (Co-Chair of Committee)
Frances I. Gelwick (Member)	Kirk O. Winemiller (Member)
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ABSTRACT

Spring Phytoplankton Dynamics in a Shallow, Turbid Coastal Salt Marsh System Undergoing Extreme Salinity Variation, South Texas. (May 2004)

Elizabeth Michele Hebert, B.S., University of Michigan

Co-Chairs of Advisory Committee: Dr. Daniel Roelke
Dr. James Heilman

The contribution of phytoplankton productivity to higher trophic levels in salt marshes is not well understood. My study furthers our understanding of possible mechanisms controlling phytoplankton productivity, abundance, and community composition in salt marshes. Across three consecutive springs (2001 to 2003), I sampled the upper Nueces Delta in south Texas, a shallow, turbid, salt marsh system stressed by low freshwater inflow and wide ranging salinity (<15 to >300 ppt). Water column productivity and respiration were estimated using a light-dark bottle technique, and phytoplankton biovolume and community composition were determined using inverted light microscopy. To determine their effect on the phytoplankton community, zooplankton and bacterioplankton abundance and several physical parameters were also assessed. Meaningful relationships among the numerous variables evaluated in this study were identified using principal component analysis (PCA). Despite high turbidity, phytoplankton productivity and biovolume were substantial. Resuspension appeared to play a major role in phytoplankton dynamics, as indicated by a positive relationship between ash weight and biovolume that explained up to 46% of the variation in the PCA. Negative relationships between zooplankton grazers and pennate diatoms of optimal sizes for these grazers suggested a functional grazing food chain in this system. Salinity also may have been important in phytoplankton dynamics, whereas nutrients appeared to play a minor role. Salinity increases may have been responsible for a decoupling observed between phytoplankton and grazers during late spring. Findings suggest

hypotheses for future studies focused on the role of phytoplankton in salt marshes, particularly those stressed by reduced freshwater inflow and high salinities.

DEDICATION

For my husband, Andy

ACKNOWLEDGMENTS

I would like to thank the following individuals who have supported, facilitated, or contributed to this research:

The project would not have been possible without the invaluable assistance from my field partners: Sara Augustine, Jenny Birnbaum, Yesim Buyukates, Nick Cramer, Allison Fong, George Gable, Andy Hebert, Leah Hurley, and Luz Romero.

My advisor Dan Roelke and my committee members James Heilman, Frances Gelwick, and Kirk Winemiller provided much time and helpful guidance.

My gratitude goes to George and Shirley Sorenson for allowing me access to their private land to sample. Many thanks to Luis Rodriquez for granting me permission and physical access to the property before each sampling trip.

James Dodson, with the Nueces River Authority, answered many questions for me regarding the hydrology of the Nueces Delta area.

I thank my parents for their undying support and their wisdom which they eagerly shared.

Lastly, I thank my husband and best friend Andy, whose existence made the rough times bearable.

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INTRODUCTION

Salt marshes are considered productive systems that export materials and organisms to adjacent estuaries (Teal 1962; Odum 1980; Dame and Allen 1996). Until the mid seventies, the prevailing paradigm in estuarine ecology was that organic detritus, derived mainly from vascular plants, was the major energy source for estuarine food webs. More recent studies using stable isotopes have shown that phytoplankton and benthic algae may have equivalent or greater importance than macrophytes for marsh consumers (Haines 1977; Peterson et al. 1986; Peterson and Howarth 1987; Sullivan and Moncreiff 1990; Deegan and Garritt 1997; Page 1997; Kurata et al. 2001; Moens et al. 2002).

Due to the turbid nature of salt marsh estuaries, early workers in these systems often assumed that phytoplankton production was relatively low compared to that of vascular plants (Haines 1977). These assumptions were largely based on a study by Ragotzkie (1959), that concluded respiration in the tidal Duplin River, Georgia, far exceeded phytoplankton production. This study, however, took place in particularly deep, turbid areas of the Duplin, and results may have been misleading. More recent studies have shown phytoplankton production to be high even in turbid conditions (MacIntyre and Cullen 1996; Pennock et al. 1999) and thus algal production in salt marshes should not be disregarded. Even in systems where algal production is lower than that of vascular plants, it may still contribute a disproportionate amount to the pool of utilizable carbon. Depending on the genera present, algal carbon is often more digestible than plant detritus (Tenore and Hanson 1980; Mann 1986) and can be assimilated more efficiently (Ryther 1969; Mallin and Paerl 1994).

The contribution of phytoplankton to the pool of carbon utilizable by metazoans may also depend largely on the structure and function of the marsh. For example, estuaries with a low tidal range (Deegan and Garritt 1997) and/or high nutrients

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This thesis follows the style and format of *Estuaries*.

(Underwood and Kromkamp 1999) will likely have enhanced phytoplankton production. Similarly, reduced freshwater inflow can raise salinity, thereby reducing macrophyte productivity (Zedler 1980; Zedler 1982), as well as reducing the contribution of upland detritus (Peterson et al. 1986). Significance of algal production can also depend on the proportion of the marsh that has open water (Pomeroy et al. 1981) and on the dominant macrophytes present. For instance, in a hypersaline marsh where the dominant macrophyte was *Salicornia virginica*, phytoplankton contributed a greater proportion of detritus entering the foodweb compared to phytoplankton in marshes dominated by *Spartina* (Page 1997). Detritus from *Salicornia* spp. has been demonstrated to be a generally poor food source (Haines 1977; Williams 1981), and less desirable than *Spartina* detritus (Haines and Hanson 1979).

As the contribution of algae becomes more prominent in marsh and estuarine systems, the significance of algal grazers in food chains leading to higher consumers also increases. Microzooplankton such as copepods and rotifers can serve as a major link between phytoplankton and higher trophic levels such as mollusks and fishes (Day et al. 1989). However, the significance of this link is, in part, a function of the phytoplankton community composition, i.e., the edibility of the algal community (Paerl 1988), which microzooplankton strongly influence through preferential grazing and consumer-driven nutrient recycling (Martin 1970; Ryther and Sanders 1980; Lynch and Shapiro 1981; Elser and Urabe 1999). Complicating this process is the microbial loop, where the activities of bacterioplankton and grazing by microflagellates and ciliates recycle much of the organic matter produced through primary production (Nielsen and Richardson 1989, Legendre and Rassoulzadegan 1995, Mariottini and Pane 2003).

As can be seen from this brief review of the literature, the role of algal productivity in salt marsh systems is not well understood. My goal is to further an understanding of plankton community dynamics and productivity in salt marshes. My study focuses on the upper reaches of the Nueces River Delta, a system stressed by reduced freshwater inflows, and characteristic of salinities ranging from <15 to >300 ppt.

METHODS

Study site and hydrologic characterization

The upper Nueces Delta (27.85°N, 97.55°W) is a salt marsh within the Nueces Estuary in south Texas (Fig. 1). This semi-arid region is characterized by low annual rainfall (75 cm yr^{-1}) that usually occurs during the fall (Lott and Ross 1997; Fig. 2a), high temperatures in summer along with prevailing southeasterly winds, high evaporation, and a low tidal range. The study site was in the upper reaches of the marsh, several miles from Nueces Bay, with only minimal connectivity through a series of narrow channels and ponds. During my study (2001 through 2003), ponds were <1 m deep. The ponds and channels were turbid; little to no submerged macrophytes were present to stabilize the soft sediments. Elevated areas of vegetation were dominated by *Salicornia* and *Borrichia* spp.

Over the past decade, the upper Nueces Delta experienced reduced freshwater inflow due to the construction of dams within the watershed and the channelization of the Nueces River (Bureau of Reclamation 2000). Riverine inflow events were rare, and occurred only when the adjacent Nueces River overtopped its banks following heavy rains. The altered hydrology of the system has greatly changed the natural salinity regime in the marsh. The combination of reduced riverine inflow, low tidal range, and high evaporation in the summer has resulted in extreme hypersaline conditions in the upper reaches of the delta. The delta has been characterized as a reverse estuary during these times (Montagna et al. 2002).

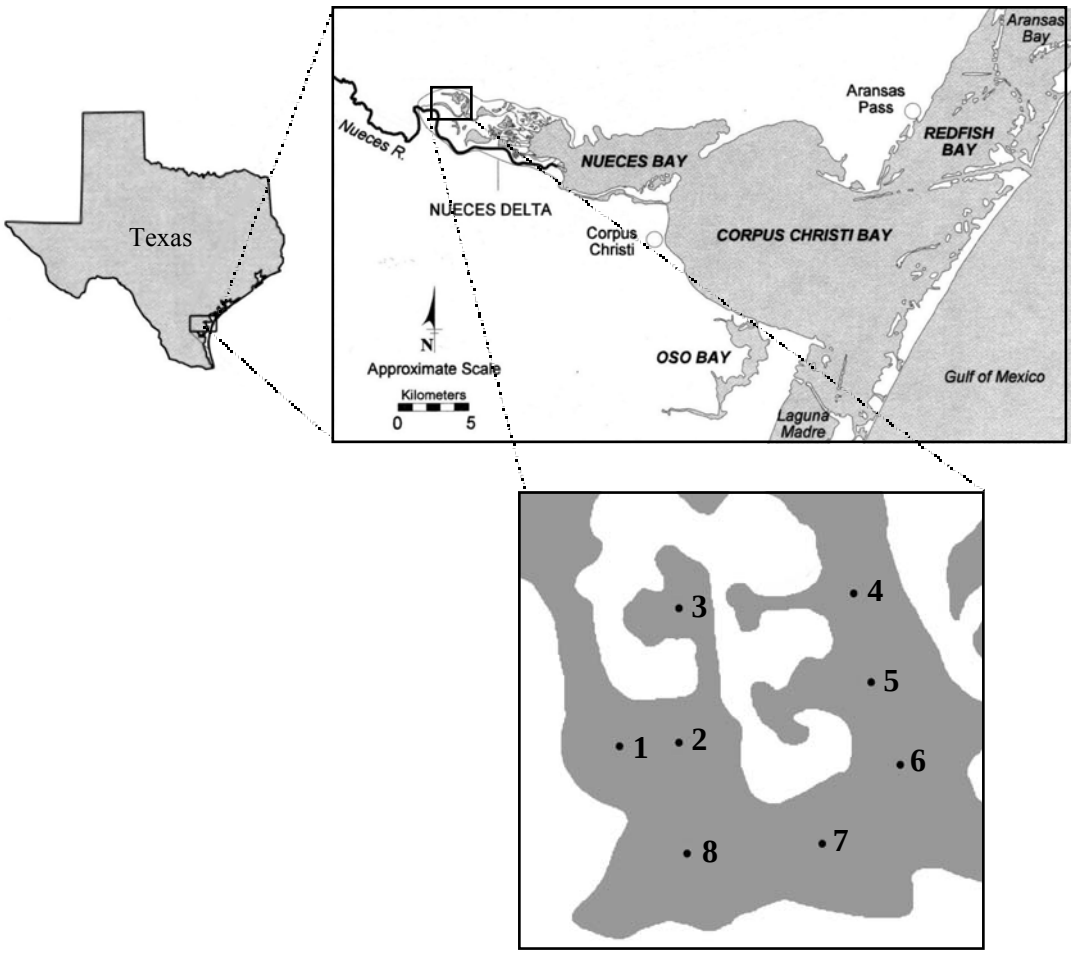

Fig. 1. The study area encompassed 8 stations within the upper Nueces Delta. (Scale is in kilometers).

In fall 2002, however, the Nueces Delta experienced four distinct freshwater flooding events as a result of high precipitation within the watershed and a local hurricane (Fig. 2b). Following each flood event, the area was inundated with freshwater for several weeks. The area had not received flooding of this magnitude in more than a decade.

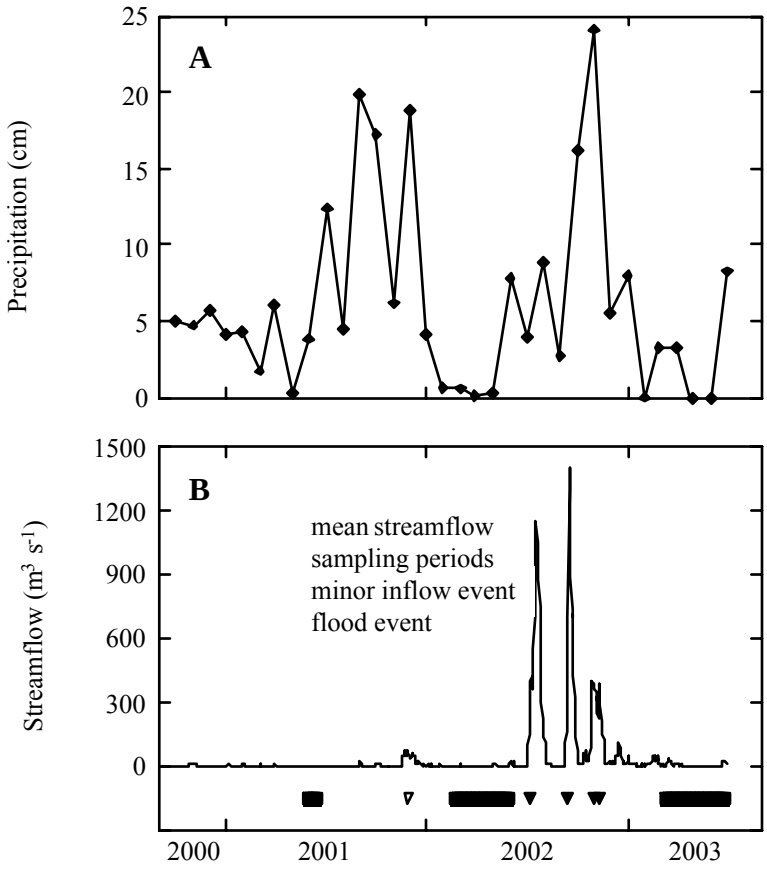

Fig. 2. Hydrology of the Nueces Delta area. A) Total monthly precipitation at Corpus Christi International Airport, about 16 km from the study site (from The Corpus Christi National Weather Service Office). B) The mean daily streamflow of the Nueces River (from the United States Geological Survey). During minor inflow events, the Nueces River temporarily overtopped its bank, inundating the upper Nueces Delta with freshwater for a period of hours. During the flood events, the upper Nueces Delta was inundated for several weeks and completely flushed of saltwater. Water depths roughly tripled.

Overview of data collection

Sampling focused on plankton response to changing physical factors documented approximately 2 weeks apart during the spring season. Three, eight, and nine trips were conducted in 2001, 2002, and 2003, respectively (Table 1). Eight stations, all of which were broadly connected and within 0.5 km of the others (Fig. 1) were sampled during each trip, unless part of the marsh was dry (Table 1).

Water column productivity and respiration

Gross phytoplankton primary productivity was measured using a traditional light-dark bottle technique. The experiments used three 1 l bottles of borosilicate glass, two transparent bottles (light) and one opaque (dark). The dark bottle was wrapped in aluminum foil and two layers of electrical tape to prevent light penetration. The other two bottles were not manipulated and thus should allow full passage of light. Just prior to incubation, the bottles were filled with surface water from each of the sampling sites in a manner that minimized introduction of disturbed sediments. Bottles were capped after their dissolved oxygen concentrations came to equilibrium with the ambient water. Ambient dissolved oxygen was measured (nearest 0.1 mg l^{-1}) at the water's surface with a hand-held YSI Model 95 dissolved oxygen probe. The bottles were then incubated just under the water's surface for 2-4 hours, depending on conditions, but always spanning the noon hour. The dark bottle always faced north, to prevent shading of the light bottles.

TABLE 1. Sampling dates, dry stations, and environmental observations.

Date	Dry stations	Skies	Winds	Salt crust present?	Cyanobacteria mats present?	Crab die-off?
May 30, 2001	none	p/c	moderate	no	no	no
June 6, 2001	none	clear	light	yes	no	no
June 13, 2001	7,8	p/c	moderate - high	yes	no	no
February 22, 2002	none	clear	high	no	no	no
March 15, 2002	none	p/c	light	no	no	no
March 27, 2002	none	p/c	light - moderate	no	no	no
April 5, 2002	none	overcast	moderate	no	no	no
April 18, 2002	none	p/c	high	no	no	no
May 1, 2002	none	clear	high	no	no	no
May 15, 2002	none	p/c	mod	no	yes	yes
May 29, 2002	none	p/c	light	no	yes	no
March 10, 2003	none	p/c	light - moderate	no	no	no
March 21, 2003	none	clear	light - moderate	no	no	no
April 4, 2003	none	p/c	moderate - high	no	no	no
April 18, 2003	none	p/c	moderate - high	no	no	no
May 2, 2003	none	overcast	moderate	no	no	no
May 16, 2003	none	p/c	moderate - high	no	no	no
May 30, 2003	none	clear	light - moderate	no	no	no
June 13, 2003	3,7,8	p/c	moderate - high	no	no	no
June 26, 2003	1,2,3,6,7,8	p/c	light	no	no	yes

When salinity was greater than 80 ppt, dissolved oxygen concentrations measured using the probe were not reliable, but percent saturation was not affected. In this case, dissolved oxygen concentrations were calculated using equations in APHA (1989), which account for the percent oxygen saturation, temperature, and salinity.

As expected, the light bottles usually experienced an increase in oxygen (positive net primary productivity) and the dark bottles a decrease in oxygen (respiration). Gross

primary productivity in terms of dissolved oxygen was determined by adding the oxygen evolved in the light bottles to the oxygen consumed in the dark bottles. Assimilation of carbon was determined using previously reported relationships between O_2 evolved during photosynthesis and incorporation of CO_2 (Wetzel and Likens 1991), which gave values in units of g-C m^3 hr^{-1}. Daily productivity values in units of g-C m^2 day^{-1} were estimated by multiplying by the depth and then multiplying by 12 hours. To compare productivity values among the different sampling dates, from which chlorophyll a concentrations varied, assimilation indices using gross productivity were calculated (mg-C day^{-1} µg-chl a^{-1}).

Plankton abundance and community composition

During a sampling trip, one water sample was collected from each station using a 1 l Nalgene bottle. Immediately after collection, portions were removed from each bottle for later analysis. For phytoplankton enumeration, a 100 ml portion was preserved by adding 5 ml 25% gluteraldehyde. For bacterioplankton counts, a ~10 ml portion was preserved using paraformaldehyde and placed on ice. For chlorophyll a and nutrient samples, 10-50 ml portions were filtered through three 47 mm GF/F glass microfibre filters. Filters were wrapped in aluminum and placed on ice for chlorophyll a analysis, and the filtrate was saved and put on ice for nutrient analysis (see below). All samples placed on ice in the field were transported to a freezer with 12 hours after collection. Microzooplankton were sampled by filtering 3-5 l of water from each station through a 63 µm mesh, and preserved with buffered formaldehyde (5% v/v).

Phytoplankton and zooplankton were enumerated using inverted light microscopy (Utermöhl 1958). The volume settled, and thus the resolution of the counts, depended on the turbidity of the sample and the plankton abundance. The goal was to maximize the volume settled without interference from detritus, sediment, or other organisms.

In the plankton enumeration using whole water, phytoplankton cells or units (filaments, colonies, etc.) between 5 and 25 µm were counted at 400x, and cells or units

greater than 25 μm were counted at 200x. At least 100 cells were counted at each magnification and thus more than 200 cells were counted per sample. Ciliates and rotifers smaller than 75 μm were counted along with the phytoplankton, using the whole water samples at 200x or 40x. Random fields of view were counted that were distributed fairly evenly across the settled area (pseudo-random).

In the plankton enumeration using the concentrated water samples (objects larger than 63 μm), adult copepods and cladocerans were counted at 40x for the entire settled area. Other zooplankton greater than 75 μm were counted at 200x. At least 100 individuals were counted at 200x per sample. In cases where large phytoplankton greater than 75 μm were not abundant and thus not seen in the whole water samples, these cells were enumerated along with the microzooplankton at 200x or 400x, using the concentrated water. When it was not practical to count the entire settled area, pseudo-random fields of view were counted that were distributed across the settled area.

Phytoplankton were identified to the lowest taxonomic level feasible using the inverted microscopy method. For analysis, data were then organized into five main groups: diatoms, cyanobacteria filaments, autotrophic flagellates, unknown flagellates (autotrophic *or* heterotrophic), and other algae. Components of these five groups that made up more than 5% of the total biovolume were further analyzed and displayed in graphs. In order to determine size-selective grazing, I focused on the pennate diatoms because they dominated the phytoplankton on most sampling dates and they are generally considered edible and palatable to grazers. Diatoms were divided into three size classes according to established optimal predator-prey size ratios (Hansen et al. 1994). Small diatoms (2-20 μm) were considered the optimal size for grazing by rotifers, nauplii, and ciliates, and medium diatoms (21-75 μm) were considered optimal for grazing by copepods. The large diatoms (>75 μm) were considered too large to be grazed upon.

Zooplankton were placed into the following groups: adult copepod, copepod nauplii, rotifers, polychaete larvae, ciliates, and nematodes, and rotifers were identified to genus level when possible. For analysis, the zooplankton were grouped together based

on size and ecology. The grazers (adult copepods, rotifers, copepod nauplii, and ciliates) were placed into two size categories, with copepods comprising the larger category. Many of the ciliates observed in this study were large bodied, i.e., 100 µm in length, and when prevalent they were considered to feed on the same size prey as rotifers. The detritivores were comprised of polychaete larvae, nematodes, and bacterioplankton, and were divided into two size categories.

Bacterioplankton samples were stained with acridine orange, filtered through 0.2 µm black filters (Poretics) and counted directly using epifluorescent microscopy. At least 200 cells were counted per sample, and the fields of view examined were evenly distributed throughout the settled area.

As an analog to biomass, phytoplankton biovolume was determined using the microscopy methods of Wetzel and Likens (1991). Dimensions were determined for each cell counted, and the shape of each cell was compared to a familiar geometric shape for which the biovolume calculation is known. We also measured chlorophyll a concentrations as an indicator of biomass following the methods of the U. S. Environmental Protection Agency (EPA; 1992). As an indicator of grazing levels, phaeophytin concentrations were determined (EPA 1992).

Physical parameters

To asses their impact on the plankton community, physical parameters including salinity, temperature, nutrients, total inorganic suspended solids, and water depth were determined. Water depth can generally be assumed to be independent of time of day due to minimum influence of daily tides in this upland area. Salinity was measured using a standard refractometer. When salinities exceeded 100 ppt, triplicate 1:9 dilutions of marsh water to deionized water were conducted. The frozen filtrate was thawed and analyzed for nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), urea, soluble reactive phosphorus (SRP), and silicate (SiO_3) using an autoanalyzer (Grasshoff et al. 1983). For total phosphorous, an unfiltered water sample was used. Concentrations were determined using a persulfate oxidizing digestion technique (Wetzel and Likens 1991). Total

inorganic suspended solids were determined through the measurement of ash weight of whole water samples preserved in gluteraldehyde, following the techniques of the American Public Health Association (APHA; 1989). In addition to measured physical parameters, observational data of environmental conditions were also recorded, such as wind speed, weather, and the presence of benthic cyanobacterial mats.

To determine if nutrient concentrations were constraining phytoplankton growth, relative growth rates (μ_{rel}) according to varying concentrations of DIN, SRP, and silica were calculated for diatoms, flagellates and cyanobacteria for each sampling date. Relative growth rates were determined using the Monod equation, and thus μ_{rel} was calculated as

$$\mu_{rel} = \frac{S}{K_{\mu} + S}$$

where S was the nutrient concentration and K_{μ} was the half saturation constant for growth. Typical values for half saturation growth constants (K_{μ}) for diatoms, flagellates and cyanobacteria were obtained from Eppley and Thomas (1969), Jorgensen (1979), Tilman et al. (1982), Sommer (1986), and Matsuda et al. (1999).

Statistics

To identify meaningful relationships among the numerous variables evaluated in this study, a principal component analysis (PCA) was applied using programming and packaged matrix functions (The Math Works, Inc. 1992). Most, but not all, of the parameters discussed in the text were included in the PCA (Appendix A).

RESULTS

When considering which years to include in the PCA analysis, two problems were identified when combining data from 2001 with data from 2002 and 2003. The first problem was that, due to later initiation of sampling in 2001 than other years, these shorter-term data (three samples) were more like a snapshot in time than a series, as compared to the longer-term data (eight and nine samples) in later years. A second problem was the extreme conditions that were unique to 2001, such that relationships established under more normal ambient conditions in later years might not have existed.

When comparing PCA results for 2002 and 2003 data only (PCA1) to results for all three years (PCA2) most of the relationships appeared qualitatively similar. Relationships that were different included those between grazers and phytoplankton size classes, and between plankton groups and salinity. Below, I focus mostly on results from PCA1. I discussed results from PCA1 and PCA2, however, when comparisons with and without extreme salinities were considered.

Physical parameters and general observations

During the three periods of sampling, the upper Nueces Delta experienced a wide range of salinities, temperatures, and suspended sediment levels (Fig. 3a, b, and c). The range of recorded salinity values was quite extreme, varying from brackish conditions (11 ppt) in 2003 to near saturation levels (300 ppt) in 2001. During each sampling period, salinities ranged 110 ppt, 126 ppt, and 80 ppt in 2001, 2002, and 2003, respectively. Water temperature tended to correlate with the progression of spring and ranged from 17.6 °C in late winter, 2002, to 35.7 °C in late spring, 2001. Fluctuations in water column ash weight indicated numerous sediment resuspension events, with a particularly large event in 2003. Fluctuations in water depth (Fig. 3d) were indicative of evaporation and possibly yearly tidal influence. The daily tidal range at this elevated and nearly isolated site was at most 1 cm (Heilman, unpublished data), and thus had little effect on depth on a daily scale.

On most sampling days, winds were very dynamic, and changed frequently in speed (Table 1) and direction. Generally, winds would be calm in the early morning then would increase in intensity until mid-afternoon. High winds were prevalent throughout the months of sampling each year (Fig. 4). At the end of 2001, when salinities were very extreme, the bottom of the marsh ponds were covered with a hard crust layer most likely due to the precipitation of various elements (Table 1). At the end of 2002, when salinities were also quite high, thick cyanobacterial mats, composed mostly of *Lyngbya* sp., covered the bottom of the ponds.

Throughout most of the 2002 and 2003 sampling, before salinities reached extreme levels, benthic organisms, fish, and wildlife within the study site were abundant and thriving. Blue crabs (*Callinectes sapidus*), many with body sizes greater than 13 cm, were numerous, as well as shrimp, other crustaceans, and small fish. Large (>25 cm) red drum (*Sciaenops ocellatus*) were observed on a few occasions in 2003, most likely taking advantage of the shallow, turbid waters to feed. Birds were numerous and diverse, and included the American avocet (*Recurvirostra americana*), roseate spoonbill (*Ajaia ajaja*), pelicans, and several others I did not identify. There was usually an abundance of bird guano along the shore.

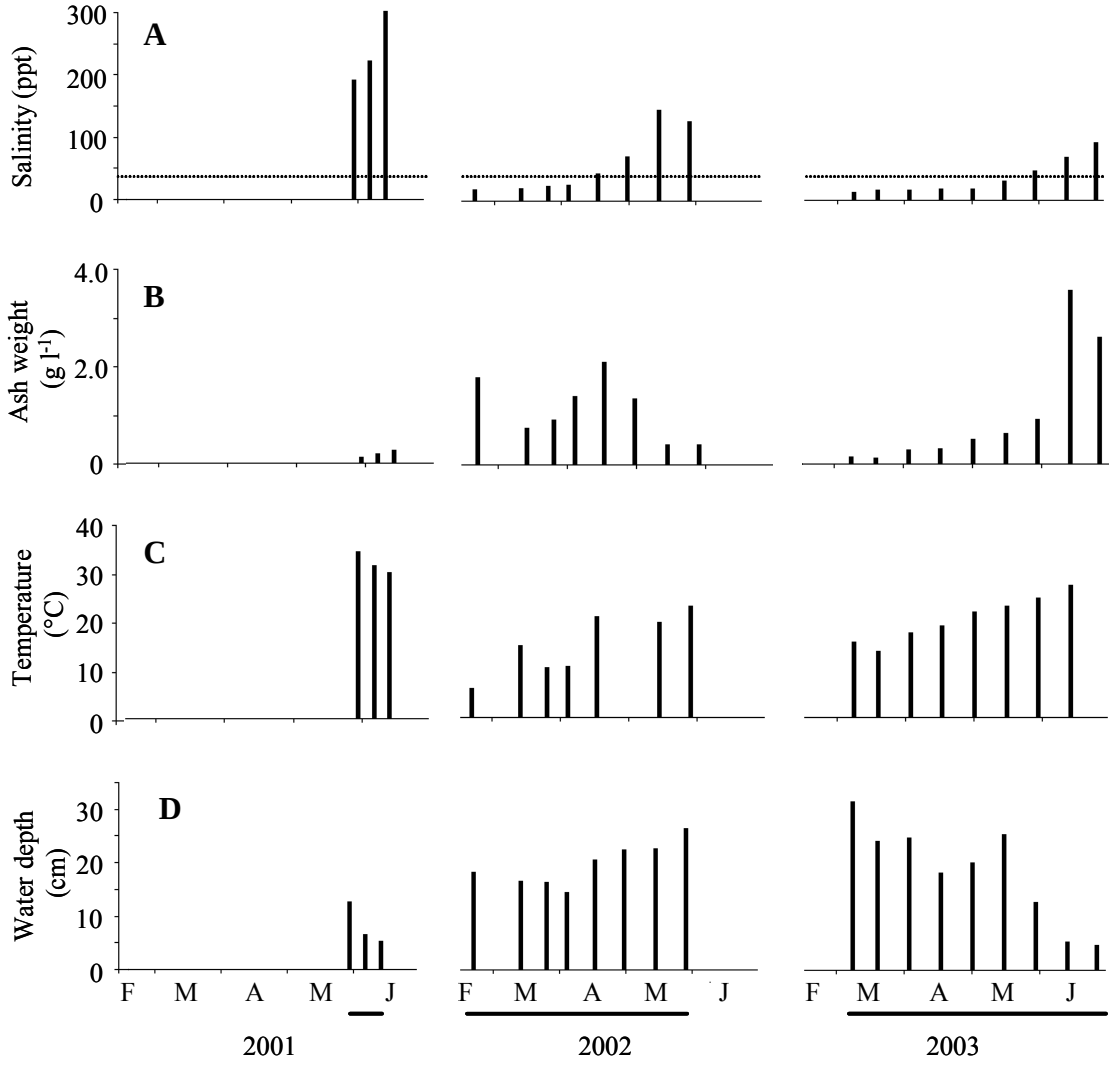

Fig. 3. Water column physical parameters. Bottom bars indicate the sampling periods. A) Salinity. The thin line indicates the salinity of seawater (35 ppt). B) Ash weight. This was used as an analog of suspended sediments. C) Temperature at the start of bottle incubations. D) Depth. Data are averages for all 8 stations except for salinity, which was only measured at station 2.

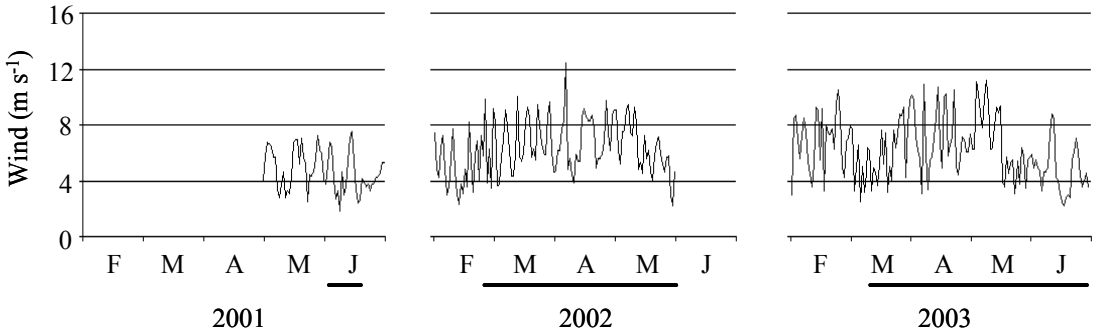

Fig. 4. Average daily wind speeds at the Corpus Christi International Airport, about 16 km from the study site (from The Corpus Christi National Weather Service Office). Bottom bars indicate the sampling periods.

Extreme salinities and temperatures appeared to have a negative effect on these animals, however. In 2001, a large fish kill occurred before the 6 June sampling, when thousands of small fish (~2.5 cm) lined the entire marsh shoreline. On 15 May 2002 and 26 June, 2003, massive crab die-offs had recently occurred (Table 1), and there were several dead crabs per square meter in the water column, sediment, and along the shoreline. In general the air and water had a strong crab-like odor. Both crab die-offs occurred after the salinity had reached about 70 ppt. Birds were generally less abundant late in the spring, potentially indicating a dwindling food source.

Phytoplankton biovolume and community composition

Biovolume measurements of phytoplankton are not frequently reported in the literature, probably due to the high time requirements of microscopy. Some reports of phytoplankton biovolume from a coastal lagoon (Gilabert 2001) and a hypersaline coastal saltern system (Pedrós-Alió et al. 2000) ranged an order of magnitude from 10^8 to 10^9 $\mu m^3 l^{-1}$. My values, which fluctuated greatly through time (Fig. 5a) and space (see Appendix C for standard deviations), only fell within this range 65% of the time. Seven of the twenty sampling occasions the mean biovolume was on the order of 10^{10} $\mu m^3 l^{-1}$, with our highest value (9.92×10^{10} $\mu m^3 l^{-1}$) occurring in 2003. Interestingly, this peak corresponded with the peak in ash weight (mentioned above). In addition, a strong relationship between biovolume and ash weight was indicated on the first principal component of PCA1 (which includes data from 2002 and 2003 only; Appendix A), which represented ~26% of the total variability, in which higher ash weights, mostly from the second year of sampling, corresponded to higher biovolumes.

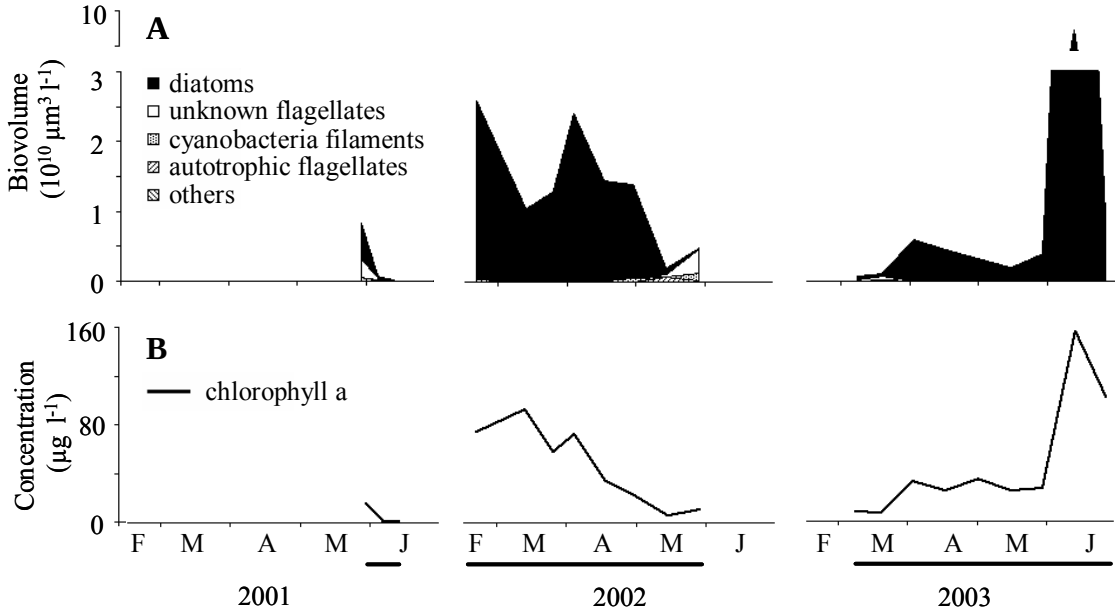

Fig. 5. Spring phytoplankton biovolume. Data are average values for all 8 stations. Bottom bars indicate the sampling periods. A) Phytoplankton biovolume categorized as five groups, which made up 100% of the phytoplankton biovolume. B) Water column chlorophyll a.

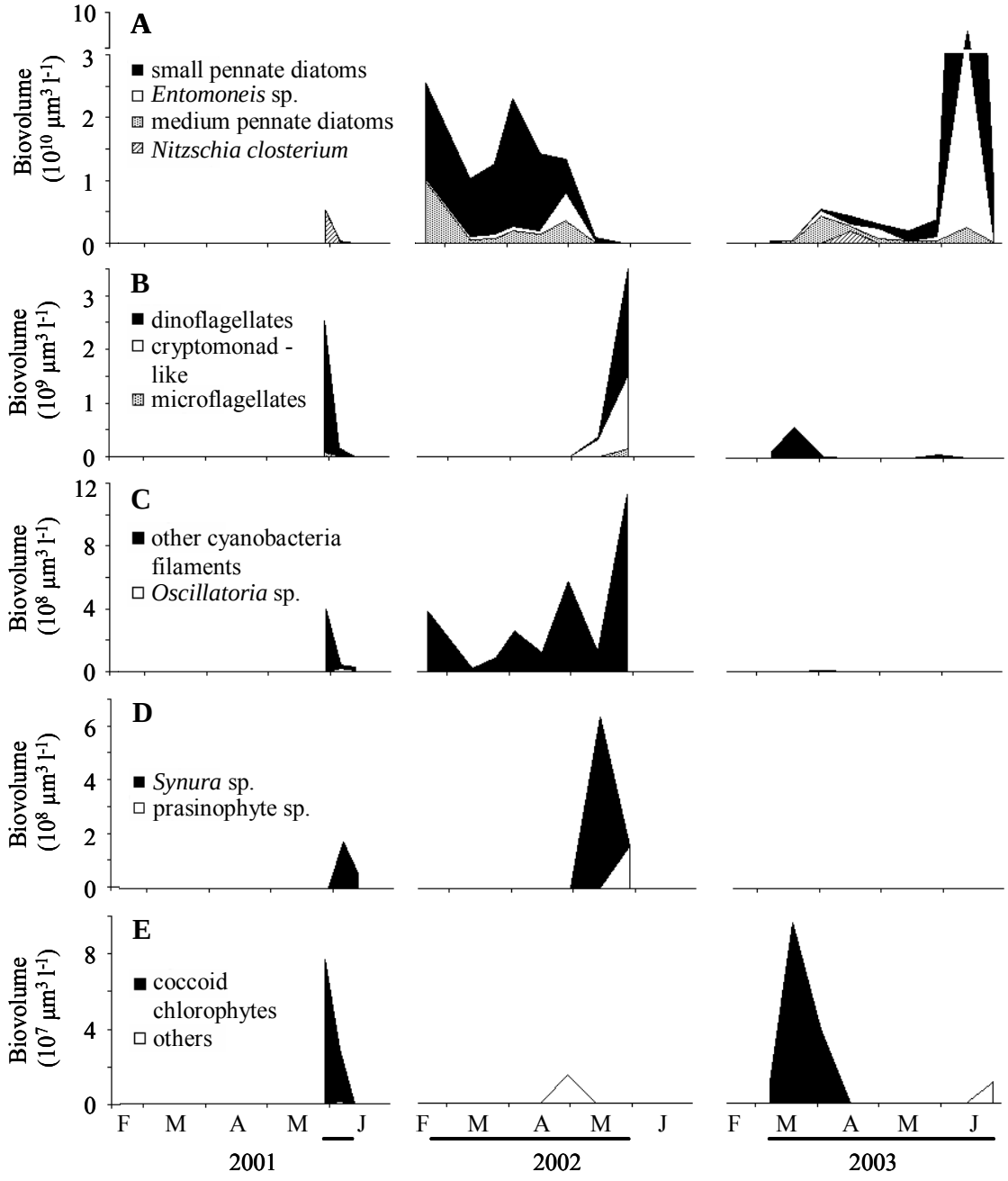

Fig. 6. Spring phytoplankton biovolume. Represented taxa made up at least 5% of the biovolume during at least one sampling. Data are average values for all 8 stations. Bottom bars indicate the sampling periods. A) Diatoms. B) Unknown flagellates (autotrophic or heterotrophic flagellates). C) Cyanobacteria filaments. D) Autotrophic flagellates. E) Other phytoplankton.

Chlorophyll a concentrations, which ranged from <1 - 156 μg l^{-1} (Fig. 5b), were high, but comparable to previous concentrations reported from the Nueces Delta area (Bureau of Reclamation 2000). Changes in chlorophyll a were generally correlated with changes in biovolume (Fig. 5a and b), and this observation was supported in PCA1 (Appendix A) along the first principal component. Chlorophyll a was lowest (<2 μg l^{-1}) at the end of 2001 when the salinity was extremely high. Indeed, PCA1 showed a negative relationship (although weak) between chlorophyll a and salinity along the second principal component (~23% of the total variability). PCA2 (which includes data from all years) indicated a strong relationship along the first component (~26% of the total variability).

Throughout most of the sampling, the phytoplankton community composition was dominated by small- and medium-size pennate diatoms as well as the large (>75μm) diatoms *Entomoneis* sp. and *Nitzschia closterium* (Figs. 5a and 6; see Appendix B for a full list of observed taxa). PCA1 (Appendix A) indicated a strong positive relationship between percent of small diatoms and ash weight along the first principal component, which is consistent with the observation that small diatoms comprised a high percent of the total biovolume. The other phytoplankton categories showed either no relationship (cyanobacteria) or a negative relationship (all other categories) with ash weight along the first principal component. The correlation of small pennates with ash weight indicates that these diatoms are likely associated with the sediments. The large peak in biovolume on 13 June, 2003, which correlated highly with ash weight, was composed mostly of small pennates (~72%) and *Entomoneis* (~24%) (Fig. 6a), further supporting that the small pennates, as well as possibly *Entomoneis*, are associated with the sediments.

Several genera of phytoplankton exhibited a remarkable halotolerance and euryhalinity during this study. *Entomoneis* was found in moderate concentrations (10^8 μm^3 l^{-1}) at salinities ranging from 16 to 142 ppt (Fig. 6a). *Nitzschia closterium* reached an average abundance of 8.29×10^9 μm^3 l^{-1} and was the dominant phytoplankter present at a salinity of 190 ppt at the beginning of 2001. The autotrophic flagellate *Synura*, which is actually considered a freshwater genus (Graham and Wilcox 2000), appeared to thrive

in salinities over 100 ppt, and was quite conspicuous in settled samples during the 2001 and 2002.

Upon examination of all phytoplankton groups (Fig. 6), there appeared to be two types of communities present, one high biovolume community dominated by diatoms, and another relatively low biovolume community where dominance was shared by flagellates, coccoid green algae, cyanobacteria filaments, and diatoms. The low biovolume community appeared to correspond with high salinity, as in the end of 2001 and 2002, but not always, as in the beginning of 2003. The first principal component of PCA1 (Appendix A) supported this observation and indicated that the biovolume percentages of flagellates and "other algae", which included coccoid green algae, were negatively related to ash weight and biovolume. With the inclusion of 2001 in the PCA analysis, this relationship is stronger and includes the cyanobacteria. There also was a strong negative relationship between these algal groups and salinity.

Water column productivity and respiration

Like phytoplankton biovolume, mean water column gross and net productivity fluctuated greatly through time (Fig. 7a) and space (see Appendix C for standard deviations). Previous estimates of net phytoplankton primary production in estuarine systems range from <0 g-C m^{-2} day^{-1} to ~2.5 g-C m^{-2} day^{-1} (see Day et al. 1989). Our estimates in the upper Nueces Delta ranged from -0.11 to 2.4 g-C m^{-2} day^{-1}, and thus fell within the range of previous reports. The first principal component of PCA1 (Appendix A) showed a positive relationship between productivity and phytoplankton biovolume, but higher productivity did not always coincide with higher biovolume. For example, the fourth principal component of PCA1 (~8% of total variation) showed a strong negative relationship between the two. A strong negative relationship between productivity and ash weight was also shown on the fourth principal component.

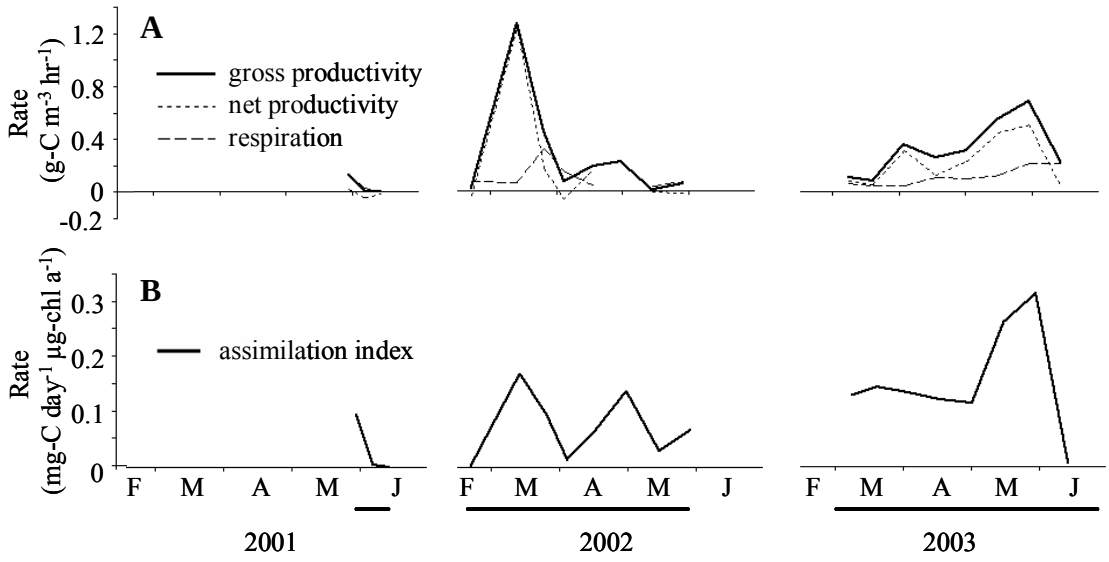

Fig. 7. Spring phytoplankton productivity and respiration. Data are average values for all 8 stations. Bottom bars indicate the sampling periods. A) Phytoplankton gross and net productivity, and respiration. B) Phytoplankton assimilation index (gross productivity per unit of chlorophyll a).

Plankton respiration values from coastal systems in the summer range in the literature from 6.42 to 286 µg-O_2 l^{-1} hr^{-1} (Jensen et al. 1990; Sampou and Kemp 1994; Iriarte et al. 1996; Fourqurean et al. 1997). Several values, which ranged from 0.003 to 0.323 g-C m^{-3} hr^{-1} (8.24 to 862 µg-O_2 l^{-1} hr^{-1}; Fig. 7a), were high comparatively, but still allowed for positive net productivity in the water column. Surprisingly, PCA1 indicated no relationship between respiration and bacteria or ciliates on any axis (Appendix A). Also unexpectedly, respiration did not correlate with water temperature ($R^2 \approx 0$). Instead, the first principal component indicated that respiration was positively related to unknown flagellates, productivity, phytoplankton biovolume, copepods, and polychaetes.

The assimilation indices, or the phytoplankton primary productivity normalized to chlorophyll a (Fig. 7b), were quite variable, indicating that factors other than phytoplankton abundance were affecting productivity. Peaks in the assimilation indices appear to correlate to troughs in biovolume in 2002 (Figs. 5a and 7a). This relationship was also supported in PCA1 (Appendix A), where the assimilation index was negatively related to biovolume on the first principal component. The assimilation index was also negatively related to ash weight on the first component, and negatively related to salinity on the second component.

Nutrients

In 2001, ammonium, SRP, and silica increased markedly over an only 2-week period of sampling (Fig. 8a, b, and c). When these nutrients peaked in 2001, DIN and SRP were at their highest concentrations for the entire three years of sampling. Phytoplankton biovolume, however, was at its lowest magnitude for the entire 3 years (Fig. 5a). Decreasing concentrations of urea, SRP, and silica were apparent at the end of 2002, with a concurrent spike in ammonium on 15 May. Decreasing concentrations of nutrients in 2002 appeared to be correlated to a decrease in phytoplankton biovolume and a switch to a less diatom-dominated plankton community (Fig. 5a). The spike in ammonium was concurrent with a massive crab die-off that had recently occurred before sampling on 15 May (Table 1). At the end of 2003 we saw an increase in urea, which was also concurrent with a second crab die-off that occurred that year.

Concentrations of TP (Fig. 8d) were quite large throughout sampling with a 2002 peak of 47.6 μM and a peak in 2003 of 64.4 μM. Peaks in TP concentrations appeared to be correlated with peaks in ash weight in both years (Figs. 3b and 8d). PCA1 (Appendix A) supported this observation indicating a strong positive relationship among TP and ash weight on the first principal component.

Throughout most of the sampling, the ratio of DIN:SRP was below 16, indicating potentially N-limiting conditions. Accordingly, nitrogen was usually the nutrient constraining growth ($\mu rel < 0.8$) for diatoms, flagellates, and cyanobacteria (Fig. 9a, b,

and c) but sometimes phosphorous was responsible for growth constraint as well, particularly in 2002, and silica constrained growth for diatoms at the end of 2002. Throughout all three years, the phytoplankton community was generally growth constrained by some nutrient.

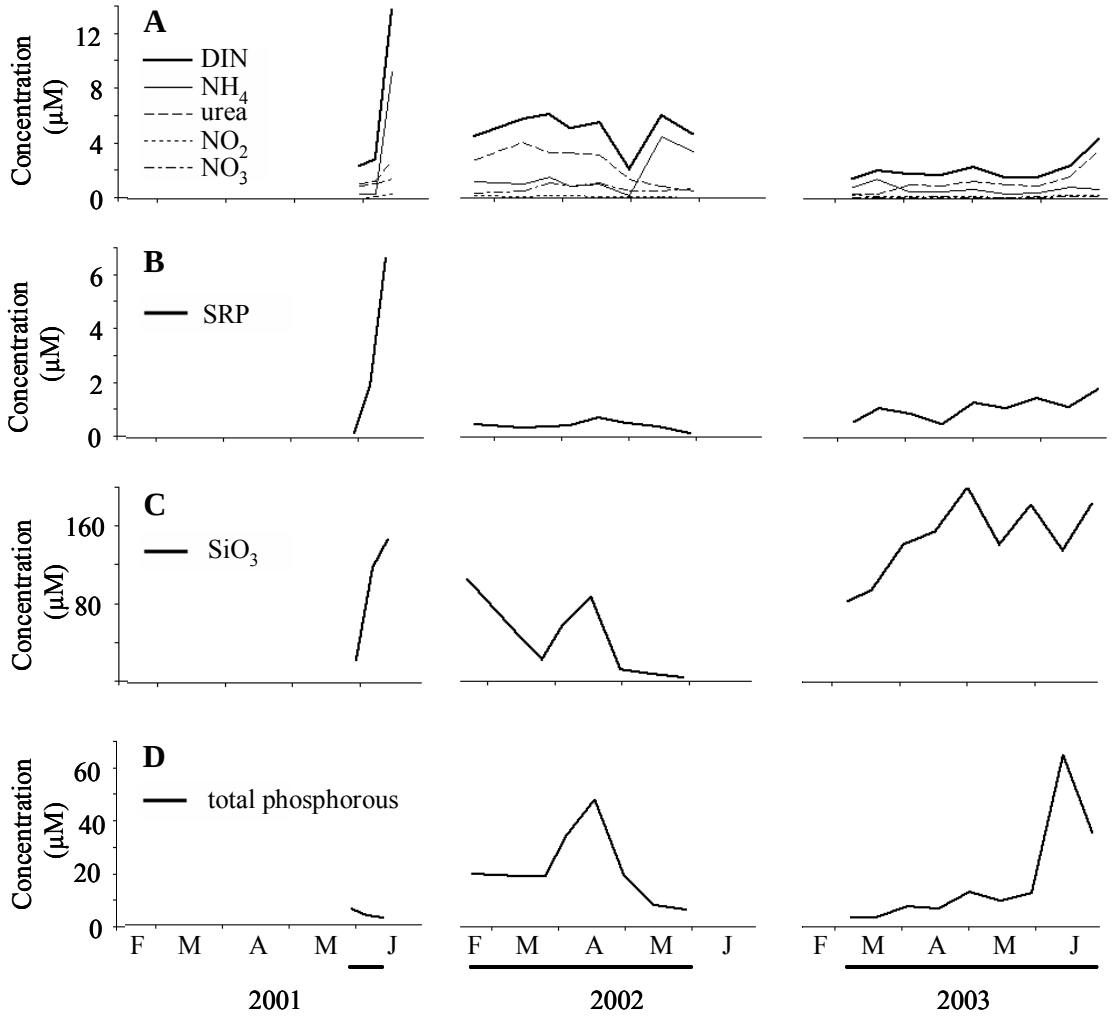

Fig. 8. Water column inorganic nutrients. Data are average values for all 8 stations. Bottom bars indicate the sampling periods. A) Four species of nitrogen and dissolved inorganic nitrogen. B) Soluble reactive phosphorous. C) Silica. D) Total phosphorous.

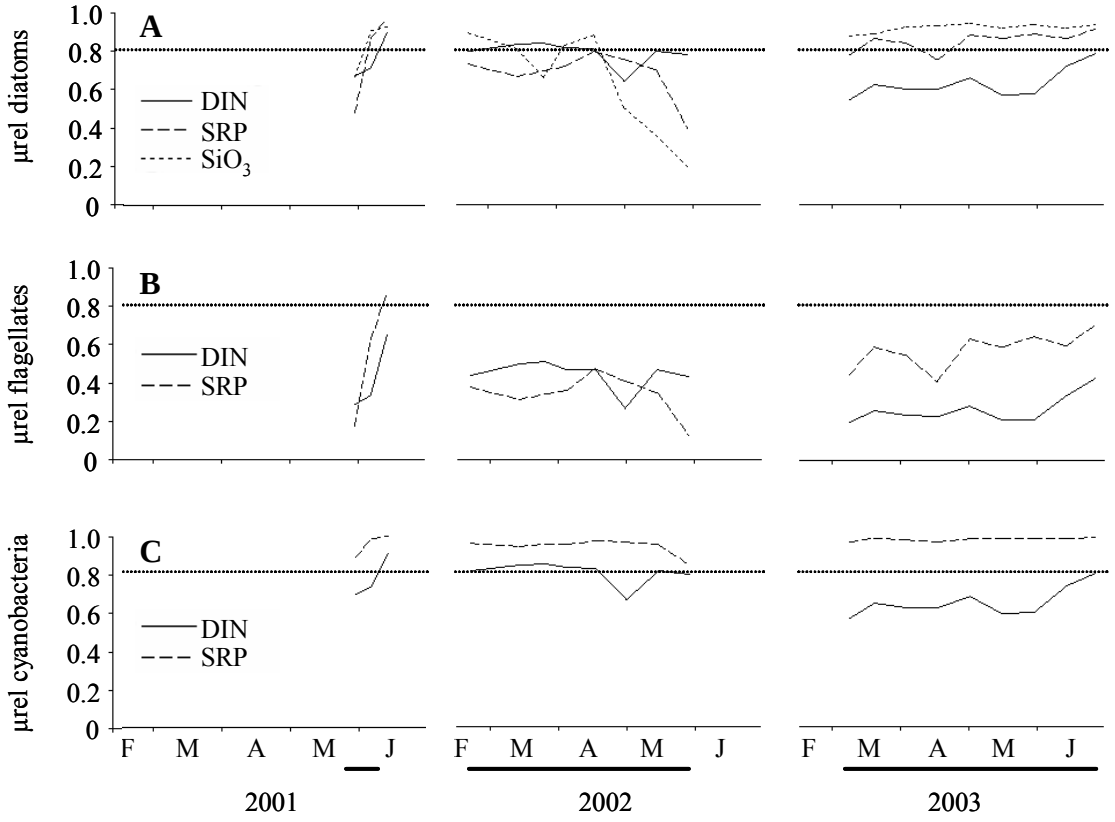

Fig. 9. Relative growth rates of the phytoplankton predicted only from the concentrations of dissolved inorganic nitrogen, soluble reactive phosphorous, and silica. Relative growth rates were calculated from the Monod equation and estimated half saturation growth constants given in the literature. The straight dotted lines indicate 0.8, below which growth rates were considered constrained. Data are average values for all 8 stations for each sampling trip during the 2001, 2002, and 2003 sampling periods. Bottom bars indicate the sampling periods. A) Diatoms. B) Flagellates. C) Cyanobacteria.

There were a few indications that nutrients influenced the phytoplankton community composition at the time of sampling. In general, dinoflagellates had the lowest relative growth rates, and accordingly were not often seen in the phytoplankton

(Fig. 5a). Furthermore, when the decrease in silica in 2002 lowered the relative growth rate for diatoms, the proportion of diatoms in the phytoplankton greatly decreased. There were also several indications, however, that community shifts were being controlled by factors other than nutrients. For example, in the beginning 2002, despite being unconstrained by nutrients and having the highest relative growth rates, cyanobacteria were not apparent in the phytoplankton (Fig. 5a). Furthermore, flagellates made up a high percentage of the biovolume in 2001 and the end of 2002 (Fig. 5d and e) despite having the lowest relative growth rates.

PCA1 (Appendix A) indicated a strong positive relationship between the assimilation index and silica, SRP, and nitrite on both principal components. This relationship was strongest at the beginning and middle of 2003. A positive relationship, though weak, was also present on the first principal component between the assimilation index and ammonium. Negative relationships existed on the first component between biovolume and all nutrients except for nitrate. These relationships may indicate that high concentrations of nutrients stimulate productivity for diatoms and the rest of the phytoplankton community. PCA1 also illuminated evidence of grazer contributions to nutrient cycling. Urea, for example, was positively correlated with copepod abundance on the first principal component. Urea is a primary form of nitrogen excretion for many invertebrates.

Grazers

During 2001, concentrations of copepods, rotifers, and nauplii were very low (Fig. 10a and b). In 2002 for copepods, and in both 2002 and 2003 for rotifers and nauplii, concentrations started out very high and then decreased to very low numbers or to zero later in the sampling period. Copepod concentrations, which included mostly calanoid copepods and some harpacticoids, were within the range of previously reported values from coastal systems of <1 ind l^{-1} (Hirst et al. 1999) to >3000 ind l^{-1} (Gilabert 2001). Concentrations of rotifers and nauplii also generally were within the range of reported literature values, i.e., from 0 - >2000 ind l^{-1} in coastal systems (Holst et al. 1998, for rotifers; Dagg and Whitledge 1991; Gilabert 2001, for nauplii).

Reports of ciliate concentrations from coastal systems were all on the order of 10^4 ind l^{-1} (Holst et al. 1998; DeLorenzo et al. 2001; Gilabert 2001). Our values, which ranged from 0 to 10^5 ind l^{-1} (Fig. 10c), were thus reasonable. Ciliate concentrations, community composition, and size varied considerably throughout the sampling. Ciliate taxa included both tintinnids and nonloricate ciliates. Ciliate size was large, and usually ranged from 20 µm to 120 µm. One group of ciliates, however, the only group present in 2002, was comprised of individuals as large as 168 µm.

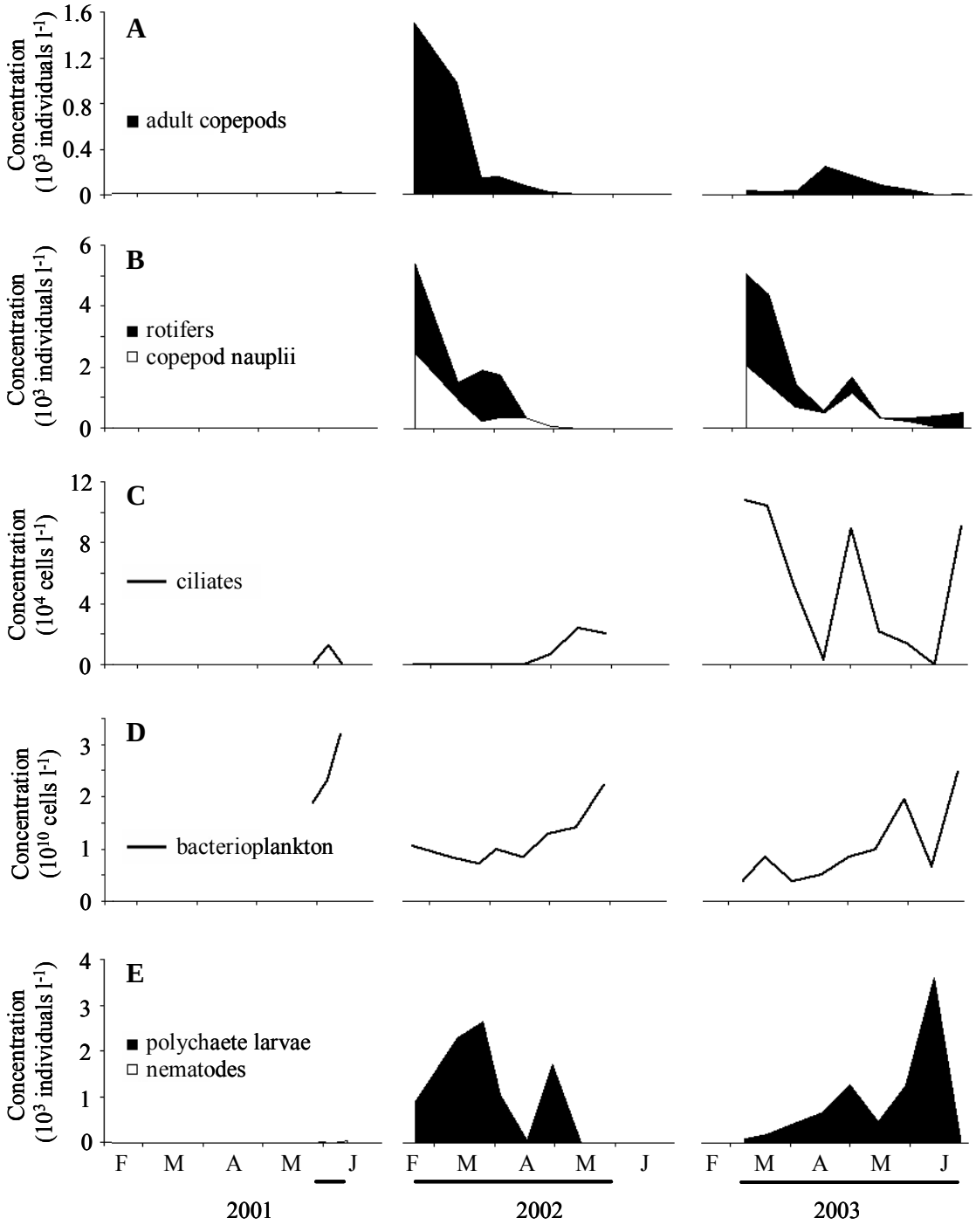

Fig. 10. Heterotrophic plankton. Data are average values for all 8 stations. Bottom bars indicate the sampling periods. A) Adult copepods. B) Rotifers and copepod nauplii. C) Ciliates. D) Bacterioplankton. E) Polychaete larvae and nematodes.

As mentioned earlier, due to their large size, the ciliates in this system were not likely to be feeding on bacterioplankton. Concurrent with this speculation, there was no relationship between ciliates and bacterioplankton on the first or second components of PCA1 (Appendix A). Rather, PCA1 indicated negative relationships between rotifers, nauplii and ciliates with small diatoms on the first principal component, suggesting selective grazing among these plankton groups. A negative relationship between copepods and medium pennate diatoms also occurred on the first component, giving further evidence for selective grazing. Multivariate statistics were needed to observe these associations, for correlations between small diatoms and rotifers ($R^2 = .02$) or nauplii ($R^2 = .07$) or ciliates ($R^2 = .13$) as well as between medium diatoms and copepods ($R^2 = .01$) were not apparent using linear regression. When including data from 2001 in the PCA analyses, the size dependent relationships between diatoms and copepods, rotifers or nauplii do not appear on any axis.

Due to the decreasing concentrations of most grazers each year as spring progressed (Fig. 10a and b), PCA1 (Appendix A) indicated a negative relationship between nauplii and rotifers with salinity. The relationship between the grazers and salinity became more apparent when 2001 was included in the PCA analysis. PCA2 indicated a stronger relationship among rotifers, nauplii, and salinity along the second principal component, as well as a strong negative relationship between copepods and salinity on the first principal component.

Detritivores

Previous reports of bacterioplankton concentrations ranged several orders of magnitude from 10^8 to 10^{10} cells l^{-1} in estuaries (Holst et al. 1998; DeLorenzo et al. 2001) to as high as 10^{11} cells l^{-1} in a hypersaline coastal saltern (Pedrós-Alió et al. 2000). My values for bacterioplankton, which ranged in order of magnitude from 10^9 to 10^{10} cells l^{-1} (Fig. 10d), fell within this range. Bacterioplankton concentrations were highest in the late spring. Accordingly, PCA1 (Appendix A) showed a strong positive relationship between bacteria and salinity along the second principal component, and

PCA2 showed a strong positive relationship between bacteria and salinity along both components. Interestingly, PCA1 showed a strong positive relationship between bacteria and unknown flagellates along the second principal component, as well as a positive relationship between bacteria and ammonium.

Polychaete larvae were generally present at high concentrations (Fig. 10e), though they were not present at all during the 2001 sampling or at the end of 2002. A weak negative relationship existed between polychaetes and bacteria on the second component of PCA1 (Appendix A). Nematodes were also present in the plankton (Fig. 10e), though in relatively low numbers. The highest concentrations of nematodes were observed in 2001.

DISCUSSION

Importance of phytoplankton production in the upper Nueces Delta

The abundance of wildlife and benthic invertebrates in the upper Nueces Delta during spring of 2002 and 2003 indicated that the marsh was highly productive. Data and general observations produced from this study imply that the phytoplankton were important contributors of labile organic carbon to the system in the spring, and thus may have been supporting higher trophic levels.

Despite high turbidity, net phytoplankton production was at least moderate in the marsh. Our daily net productivity estimates, which averaged 0.48 g-C m^{-2} day^{-1}, were comparable to spring and summer values for several estuaries reviewed by Day et al. (1989), including some deeper, less turbid estuaries such as the St. Lawrence, Canada, and Chesapeake Bay. Supporting these productivity values were high phytoplankton biovolume and chlorophyll a concentrations, several of which were higher than those found in many estuarine and coastal systems (Pedrós-Alió et al. 2000; Gilabert 2001, for biovolume; Day et al. 1989, for chlorophyll a). It is possible that the very shallow nature of the marsh increased the time that phytoplankton spent in the photic zone relative to deeper estuaries, thus allowing comparable productivity despite high turbidity. Cole et al. (1992) suggested that in turbid systems, shallow depths may offset respiration and result in net production. MacIntyre and Cullen (1996) observed high water column productivity in a shallow, turbid Texas estuary, and concluded that it was due to a high photosynthetic capacity of the suspended microalgae.

The dominant vascular plants in the system during sampling were *Borrichia* sp. in 2001 and *Salicornia* sp. in 2002 and 2003. Antlfinger and Dunn (1979) determined summer productivity values of *Salicornia virginica* and *Borrichia frutescens* in a Georgia salt marsh to be 1.5 and 2.2 g-C m^{-2} day^{-1}, respectively. Although values from the higher range of our daily productivity estimates were comparable to these rates, the average of all values for the spring was only 32% and 22% of this estimated plant

production. This implies, theoretically, that contribution of fixed carbon from phytoplankton may not be as important as the contribution from plants.

It is important to note that, due to potential errors in my methodology, approximations of daily productivity may include both underestimates and overestimates. For example, in turbid conditions, Madden and Day (1992) discussed potential problems of measuring productivity from bottle incubations when particles are allowed to settle in the bottles. They found that at high ambient light levels productivity actually decreased in the bottles relative to the water column due to artificially increased light penetration and resultant photoinhibition. MacIntyre and Cullen (1996) also suggested that the reduction of turbidity in high light environments could reduce photosynthetic capacity.

Other sources of potential error involved extrapolating total daily productivity from one incubation that spanned a few hours in the afternoon. The clear conditions in 2001 and the end of 2002 probably allowed for a more accurate measurement of productivity compared to turbid conditions. But during midday, water column phytoplankton were probably photoinhibited, which would affect estimates of daily productivity. Under turbid conditions, phytoplankton were not likely to be photoinhibited, but due to high irradiance during midday, daily rates of productivity may have been overestimated. 110 successful incubations were conducted during or around spring during the 3 years of sampling. By averaging all values, for the purposes of comparison with other systems, I hoped to rule out much of this uncertainty.

Assuming that phytoplankton production was low compared to the marsh plants, the contribution of phytoplankton to the pool of utilizable carbon was still likely to be relatively important. This is due to the types of plants present and spring-time conditions in the marsh. As mentioned earlier, detritus produced by *Salicornia* has been demonstrated to be a poor food resource (Haines 1977; Williams 1981). Accordingly, in a marsh dominated by *Salicornia virginica*, Page (1997) showed that the isotopic composition of macroinvertebrates indicated the incorporation of algal carbon more so than carbon from *Salicornia*. In addition, without substantial rainfall and freshwater

inflow, detritus from vascular plants will not be transported as easily from the elevated areas into the ponds to be incorporated into the food web.

Other characteristics of the Nueces Delta may have increased the relative importance of phytoplankton. Reduced freshwater inflow will decrease the amounts of allochthonous organic material into the system, thus reducing the relative contribution to the pool of labile carbon. The low tidal range and freshwater inflow also reduces flushing and allows the accumulation of phytoplankton. In addition, ponds and tidal creeks are extensive. Though the proportion of open water has not been measured, aerial surveys suggest that it is comparable to upland areas, which would also increase the total contribution of phytoplankton carbon in the marsh.

This study emphasized the importance of phytoplankton in the spring. One could speculate that plant production may be more important than phytoplankton production at other times of the year, particularly autumn and winter. The marsh is likely to stay turbid all year, and phytoplankton production probably decreases largely with reduced total irradiance. *Salicornia*, an annual, would die off in the fall, producing a pulse of detritus. Increased rainfall and freshwater inflow would facilitate the transport of plant detritus, introduce allochthonous organic matter, and flush out the phytoplankton.

Spring, however, is a time when many species, several of which are economically important, are dependent on estuaries (Day et al. 1989). In the Gulf of Mexico, species such as menhaden (*Brevoortia* spp.), three species of shrimp [brown (*Penaeus aztecus*), white (*Penaeus setiferus*), and pink (*Penaeus duoraram*)], and blue crabs spawn in coastal waters, then move into the estuaries during late winter or early spring to seek food and shelter. Over the next few months they grow to be adults, then from mid-summer to early winter they migrate back out to coastal waters.

Several factors shaping phytoplankton productivity, abundance, and community composition were examined in this study. For the purposes of discussion each parameter was divided into sections, though there was considerable overlap because all factors were interconnected and directly or indirectly affected the phytoplankton community.

Resuspension and turbidity

Sediment resuspension and turbidity were important factors shaping the phytoplankton community. The strong positive relationship between ash weight and biovolume indicated that benthic microphytobenthos were being entrained along with sediments into the water column and thus contributed to total phytoplankton biovolume. Several studies have observed resuspension of microphytobenthos and its subsequent contribution to water column chlorophyll a by tidal currents (Roman and Tenore 1978; Baillie and Welsh 1980) and wind waves (Demers et al. 1987). Dejonge and Vanbeusekom (1992) observed that microphytobenthos in the upper reaches of the Ems Estuary, Netherlands, was approximately 60% of total phytoplankton, and Shaffer and Sullivan (1988) maintained that 74% of water column diatoms in a shallow estuary were represented by benthic diatom taxa.

The positive relationship between biovolume and productivity indicates that the suspended benthic algae were viable and contributed to water column productivity. This has been observed in several studies (Roman and Tenore 1978; Shaffer and Sullivan 1988). Resuspended particles, however, may have also been inhibiting productivity by increasing light attenuation in the water column. This was indicated by the negative relationship between biovolume and the assimilation index on the first principal component of PCA1, and the strong negative relationship between productivity and biovolume on the 4^{th} principal component (Appendix A). Demers et al. (1987) observed an increase in water column chlorophyll due to resuspended microphytobenthos, but because of the increased turbidity, there was no net change in water column productivity.

Phytoplankton community composition appeared to be greatly altered by resuspension events, largely by the displacement of benthic taxa. Small diatoms, the large diatom *Entomoneis*, and cyanobacteria, the latter being mostly filamentous, may have been normally associated with the sediments and resuspended during windy times. The negative relationship between the flagellates and medium diatoms with ash weight indicates that these groups were normally associated with the plankton.

Throughout the beginning of 2002 and most of 2003, diatoms dominated the phytoplankton despite having lower or similar predicted relative growth rates compared to cyanobacteria. This could simply be due to the possibility that diatoms are resuspended more easily than cyanobacteria. It is also possible that high turbidity and turbulence were having an effect on competition between diatoms and cyanobacteria that overruled the effects of nutrients. Light regime has been observed to affect the outcome of succession, whereby sustained periods of low light favored both diatoms and cyanobacteria (Flöder et al. 2002). Rehbehn et al. (1993), however, showed that the diatom *Actinocyclus* sp. was well adapted to rapidly changing light conditions, and thus was adapted to estuaries with high vertical mixing. Diatoms may also be biophysically stimulated by motion from turbulence (Schöne 1970), giving a competitive advantage under these conditions.

Ash weight was lowest in 2001, the end of spring 2002, and the beginning of spring 2003. In 2001 and 2002, this was most likely due to formation of benthic algal mats and salt crusts, which stabilized sediments, and also due to the flocculation of sediments as a result of high salinity. During these times, the phytoplankton community was co-dominated by flagellates, cyanobacteria, coccoid green algae, and diatoms. It is important to note that the flagellates did not just increase in relative abundance due to the settling of diatoms, but actually increased in concentration during these times. The cyanobacteria, however, appeared to be a baseline community that increased in proportion when the diatoms were out of suspension. An exception is the last trip in 2002, when cyanobacterial abundance more than doubled, probably due to some resuspension of mat filaments.

The flagellates increased during less turbid times despite predictions of low relative growth rates. Turbulence is known to negatively affect dinoflagellates through physical damage, physiological impairment, and behavioral modifications (Smayda 1997). The decreased sediment suspension, however, was not likely due to decreased turbulence, because winds remained strong throughout the sampling (Fig. 4). Rather, it is possible that the flagellates were better competitors under conditions of increased

irradiance. Smayda (1997) asserted that dinoflagellates and flagellates tend to thrive under conditions of high irradiance, long daylength, and reduced water column turbidity, conditions present at the times when their density was high. Compared to diatoms, dinoflagellates also may be better able to adapt to increased light intensities after periods of low irradiance (Smayda 1997).

Salinity

Hypersaline environments, such as the Nueces Delta in the late spring, are often not permanently hypersaline, but rather fluctuate on a seasonal scale due to flooding and evaporation (Ridd and Stieglitz 2002; Newton and Mudge 2003). Laboratory studies have shown that some diatom species from hypersaline environments were able to survive and remain productive over extremely broad salinity ranges (Admiraal 1977, Clavero et al. 2000), which is most likely an adaptation to changing environments (Carpelan 1978). In general, during the three years of sampling in this study, diatoms dominated the phytoplankton community up to salinities of 100 ppt. As mentioned earlier, specific genera of diatoms were present at moderate concentrations throughout very broad salinity ranges, including *Entomoneis* and *Nitzschia closterium*. If diatoms are adapted to changing salinities, they may have had a competitive advantage in the Nueces Delta.

At salinities greater than 100 ppt, the community switched from domination by diatoms to co-domination by diatoms and flagellates. In descriptive studies of phytoplankton in extremely hypersaline environments, the common groups present were diatoms, cyanobacteria, and the green algal flagellate *Dunaliella* (Davis 1978; Montoya and Olivera 1993; Pedrós-Alió et al. 2000). Dinoflagellates and cryptomonads were rarely seen above 100 ppt, and *Synura* apparently has never been reported from these environments. Thus, an increase in these flagellates at extremely high salinities should not result from salinity alone.

Most likely, salinity affected community composition at extreme salinities through multiple indirect mechanisms. After the first sampling trip in 2001, salinity

promoted the flocculation of sediments as well as the formation of a benthic salt crust, both of which stabilized sediments and increased light penetration in the water column. As mentioned earlier, the resulting high irradiance in this shallow system may have allowed a flagellate community to gain a competitive advantage. The planktonic diatom *Nitzschia closterium* still comprised most of the biovolume at the beginning of 2001, however. This diatom has been observed previously in hypersaline environments (Gilabert 2001).

At the end of 2002, high salinities again encouraged the flocculation of sediments, as well as the formation of benthic microbial mats. Benthic mats are common in shallow, hypersaline environments all over the world (Zedler 1980; Pinckney et al. 1995; Ehrlich and Dor 1985). Just as in 2001, sediments were stabilized and the water was clear, possibly favoring flagellates. Upon examination, mats were composed mostly of diatoms and filamentous cyanobacteria. Occasionally, these groups continued to be resuspended, and thus were still represented to some extent in the water column as well.

Concerning algal processes at high salinities, productivity and respiration have been found to decrease with increasing salinities because more resources are devoted towards osmoregulation (Kirst 1989). In laboratory studies of several diatom genera, a large number of strains ceased to grow above salinities of 75 ppt, and no strains showed net growth above 150 ppt (Clavero et al. 2000). Using a mesocosm approach in a saline lake, Herbst and Blinn (1998) showed that productivity of benthic diatoms was reduced at salinities over 75 ppt. When algae are adapted to hypersaline conditions, effects of osmotic stress may not become apparent until establishment of fairly high salinities (~75 ppt). In this study, PCA1 and PCA2 (Appendix A) showed negative relationships between assimilation indices and salinity, indicating that salinity may have had a negative effect on productivity. This relationship was strongest in 2001 and at the end of 2002, when salinities were greater than 75 ppt. It can not be concluded, however, that this relationship was a direct effect of salinity. Other factors at these times may have affected productivity, such as the change in phytoplankton community composition and/or photoinhibition.

The first principal component of PCA2 (Appendix A) also indicated a strong negative relationship between biovolume and salinity. As with productivity, biovolume was at its lowest when salinities were most extreme. Some studies have shown decreased chlorophyll a concentrations at very high salinities (Pedrós-Alió et al. 2000), likely due to salt stress. But again, due to additional changes in resuspension, irradiance, and grazing in the Nueces Delta at extreme salinities, it is difficult to conclude whether the decrease in phytoplankton biovolume was directly related to salinity stress, or a combination of many additional factors. Late in spring 2002, the bulk of the algal biovolume seemed to switch from the water column to the benthos.

Grazers

This study provided some indication of a functional grazing food chain within this shallow salt marsh system at lower salinities. First, the dominant algal group was small pennate diatoms, which were an optimal size for grazing and lacked surface features than could deter grazing (Sterner 1989). Second, all grazer groups were in moderate to high abundance compared to previously reported values of these groups from coastal systems. Third, the first principal component of PCA1 (Appendix A) showed a negative relationship between each grazer group and pennate diatoms of their optimal size range for feeding. This indicated that the zooplankton might be controlling the size distribution of the phytoplankton through selective grazing, which has often been reported in the literature (Martin 1970; Ryther and Sanders 1980).

Relationships indicating selective grazing were strongest near the beginning of 2002 and 2003 when salinities were lower, and appeared to be weak at the end of 2002. In addition, the relationships were not present at all when including 2001 in the PCA analysis (Appendix A). During 2001 and the end of 2002 and 2003, factors other than grazing, such as salinity and increased irradiance, were likely having the greatest effect on the phytoplankton community. Consequently, at these times both grazers and pennate diatoms were reduced in concentration relative to other times, which reduced the

strength of the negative relationship between these two functional units in the PCA results.

It is important to note that zooplankton feeding efficiency may be reduced in these extremely turbid conditions, wherein most particles in the water were probably non-living. Although filter feeders, calanoid copepods have been shown to engage in selective feeding (DeMott 1988; Tackx et al. 2003), in which phytoplankton particles are assimilated in disproportion to their numerical abundance. *Asplanchna* sp., the dominant rotifer throughout most of the sampling, are carnivorous feeders and also selective (Pennak 1989). Some studies have indicated that SPM loads near 1 g l^{-1} may hinder selective feeding (Gasparini et al. 1999; Tackx et al. 2003). Several times during the study, however, inorganic particles in the water column were close to or higher than 1 g l^{-1}. It is possible that selective feeding of copepods by the small fish in the marsh may also have been affected.

Most of the grazers, including the copepods, rotifers and nauplii, either disappeared or decreased to very low numbers as salinity increased. This could have been due to a few factors, including reduced phytoplankton biovolume, and a reduction in edibility of the phytoplankton community at the highest salinities. The edibility theory is unlikely, however, as two of the main algal groups present at the highest salinities, small pennate diatoms and cryptomonads, should be edible for zooplankton (Sterner 1989). The third group, dinoflagellates, are potentially highly edible (Burkill et al. 1987), but some genera are not and could actually be harmful (Smayda and Shimizu 1993).

Because the decreases seen were so dramatic and similar in both 2002 and 2003, they were most likely due to the extreme salinities and the osmotic stress placed on the animals. It has been shown in saline lakes that zooplankton may be sensitive to salinity changes. Full mortality of copepods occurred above 60 ppt in Lake Fletcher, Antarctica (Eslake et al. 1991), and rotifers disappeared above salinities of 80 ppt in Mono Lake, California (Jellison et al. 2001). In laboratory cultures, increases in salinity can negatively affect copepod (Dexter 1993) and rotifer (Bosque et al. 2001) reproduction. Most studies of the plankton of extreme hypersaline environments (>100 ppt) report

copepods, rotifers, and nauplii in very low numbers (Davis 1978) or not at all (Pedrós-Alió et al. 2000).

Unlike other grazers, ciliates were still present in moderate concentrations on 6 June, 2001 and at the end of 2002. A strong negative relationship between ciliates and small diatoms was shown on the first principal component of PCA1 (Appendix A). Despite ciliates being well represented at high salinities, this relationship was still strongest at the beginning of 2002 and 2003, and when adding 2001 to the analysis, the relationship was still present, but weaker. Again, factors other than grazing may be more important in controlling the phytoplankton community at highest salinities, masking or decoupling relationships between ciliates and phytoplankton seen at lower salinities. Depletion of grazers, reduction in phytoplankton biovolume, and the breakdown of relationships between grazers and their optimal feeding size classes could indicate a collapse of the grazing food chain at higher salinities.

Microbial loop

Bacteria did not appear to contribute much to community respiration in the water column. The PCA1 results (Appendix A) did not indicate a positive relationship between respiration and bacteria, ciliates, or flagellates. There was a positive relationship between copepods and respiration, but merozooplankton, despite their size, generally contribute a small portion to community respiration (Williams 1981). There was, however, a strong positive relationship between productivity, phytoplankton biovolume, and respiration on the first principal component of PCA1. Fourqurean et al. (1997) found similar results in Tomales Bay, California, and concluded that water column respiration was most likely due to the phytoplankton.

Bacterial production did not seem to be directly dependent on phytoplankton carbon, even though this has been frequently observed in past studies (Sampou and Kemp 1994; Iriarte et al. 1996). PCA1 results (Appendix A) did not indicate a positive relationship between bacteria and phytoplankton biovolume or productivity, and thus bacteria may not have been utilizing phytoplankton exudates. Bacterial numbers were

high throughout the sampling period, so if production was not dependent on phytoplankton carbon, there must have been another source. It is likely that bacterial biomass was being largely supported by additions of organic material to the system from birds, which were abundant. During 2001 and the end of 2002, bacteria numbers greatly increased while phytoplankton biovolume decreased. It is possible that, during these times, bacteria were utilizing a pulse from dying phytoplankton, as well as dying fish and crustaceans.

Bacteria numbers were high during 2001 and the end of 2002 and 2003, so it is odd that community respiration was not higher. Pedrós-Alió et al. (2000) found that, at very high salinities in saltern ponds, bacterial biomass was high but activity (incorporation of leucine) was low. The authors postulated that the bacterial community was near its carrying capacity due to low bacterivory in this extreme environment. During this study, unknown flagellates, which included dinoflagellates, cryptomonads, and microflagellates, were the most likely bacterivores in the system. In 2001 and the end of 2002, however, concentrations of these flagellates also were high. It is possible that these flagellates were not particulate feeding, or that their numbers were not high enough to limit bacterial biomass, allowing the bacteria to reach carrying capacity and slowing down bacterial activity.

Nutrients

Salt ponds of the upper Nueces Delta were probably reliant on nutrient recycling, because both tidal influence and freshwater inflow were low. Accordingly, most of the nitrogen was in the form of ammonium, the regenerated form of nitrogen, and nitrate concentrations were relatively low. The system was not completely closed as birds likely contributed substantial amounts of organic matter. The sediments, which were often suspended in high amounts, may have been a source of regenerated nutrients. In particular, total phosphorous was highly correlated to water column ash weight, and silica was loosely correlated in 2002 ($R^2 = 0.49$).

Because the system was essentially closed, we can conclude that nutrient dynamics were a function of changes within the system rather than allochthonous inputs. For example, the dramatic increase in nutrients in 2001 was most likely due to a pulse of DOM from dying phytoplankton, rather than a local precipitation or inflow event. The decrease in silica at the end of 2002 was likely due to uptake by diatoms, and spikes of DIN at the end of 2002 and 2003 may have been due to crab die-offs that occurred around this time. Fluctuations in silica in this shallow system were probably due to algal uptake and silica dissolution.

As discussed earlier, the phytoplankton community did not appear to be controlled by nutrients throughout most of the sampling. This was despite the fact that nutrient concentrations were probably growth constraining. Nutrient concentrations may have influenced phytoplankton production, as evidenced by positive relationships between nutrients and the phytoplankton assimilation index on the first and second components of PCA1 (Appendix A). In addition, nutrients may have occasionally had an effect on phytoplankton community composition. At the end of 2002, for example, the decrease in silica may have played a role in the reduction of diatoms.

CONCLUSIONS AND DIRECTION OF FUTURE RESEARCH

Results for the upper Nueces Delta indicate that phytoplankton are important contributors to productivity in the spring, as evidenced by substantial water column productivity and phytoplankton biovolume despite high turbidity. Negative relationships between grazers and optimal-size pennate diatoms indicated a functional grazer-driven food chain. Resuspension of sediments appeared to play a major role in phytoplankton productivity, abundance, and community composition, as indicated by a positive relationship between ash weight and biovolume that explained up to 46% of the variability in the data. Salinity may have also been important, while nutrients appeared to have played a minor role. Salinity increases may have been responsible for an apparent decoupling of phytoplankton and their grazers late in spring.

Most parameters appeared to have both direct and indirect relationships with the phytoplankton community, and several factors probably masked or confounded the effects of others. Thus, in many cases, observed relationships were uncertain. In addition, the first two components of the PCA analysis explained less than 50% of the variability in the data, indicating that additional factors, not included in this study, may also have influenced the phytoplankton community. Additional data need to be collected as a supplement, to test postulated relationships, and account for the extra variability.

Few studies have been conducted in succulent-dominated, hypersaline salt marshes similar to that of the Nueces Delta, despite their importance in supporting taxa at higher trophic levels, and their economic importance. Future studies in this salt marsh estuary and similar systems, focusing particularly on the phytoplankton, will be very valuable in understanding the mechanisms that drive lower food web dynamics and their importance to higher trophic levels.

To better understand the importance of phytoplankton as a food source in the Nueces Delta and similar systems, multiple stable isotope analyses may be quite useful, as well as measurements of macrophyte productivity. Additional experiments, such as nutrient bioassays, multiple daily productivity measurements, determination of bacterial

activity, and measurements of surface irradiance could aid in our understanding of phytoplankton dynamics. A thorough examination of benthic microphytobenthos should be conducted along with each sampling event. Seasonal sampling should be conducted to document changing food sources with varying freshwater inflow, precipitation, irradiance, and salinity. Sampling should also occur along a larger longitudinal transect of the estuary.

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APPENDIX A

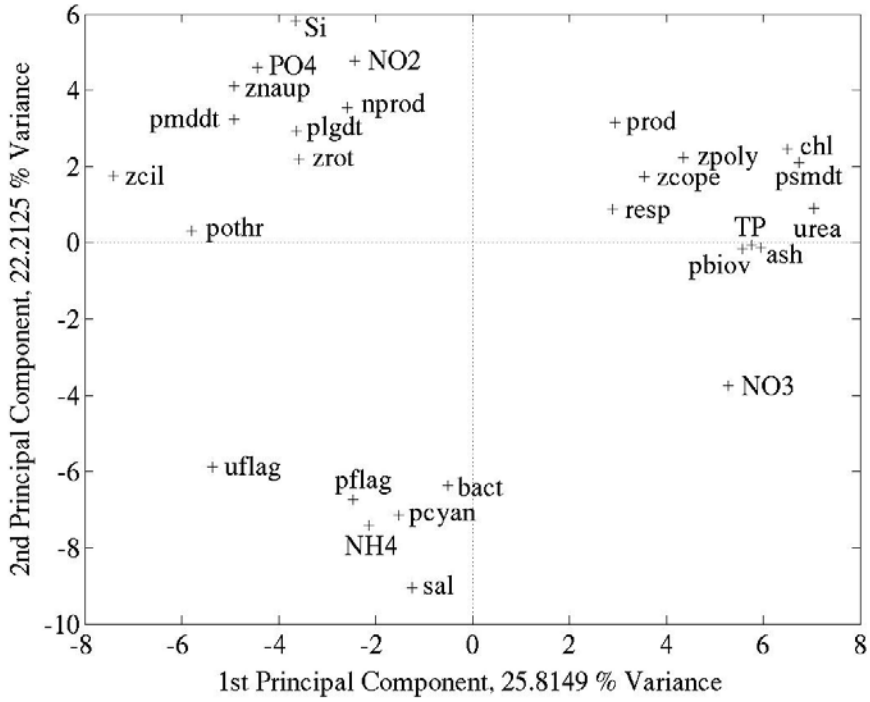
RESULTS FROM THE PCA ANALYSES

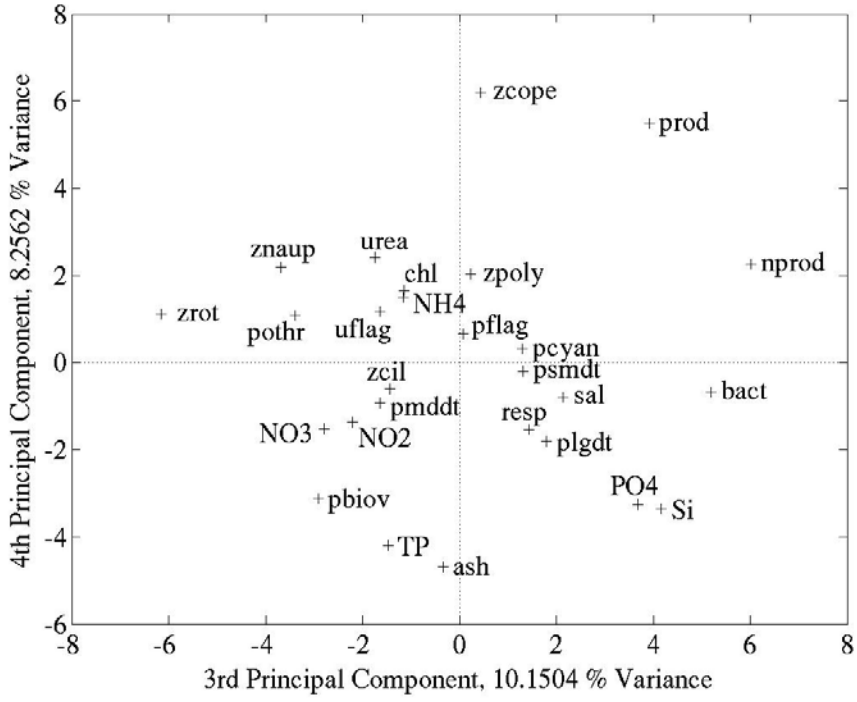
The following appendix contains results from the PCA analyses on the first four principal components for PCA1 (2002 and 2003 only) and PCA2 (2001, 2002, and 2003). The significance of the first four components temporally and spatially is also shown. Parameters included in the analyses and their designations are shown below.

Parameters included in the PCA analyses and their designations.

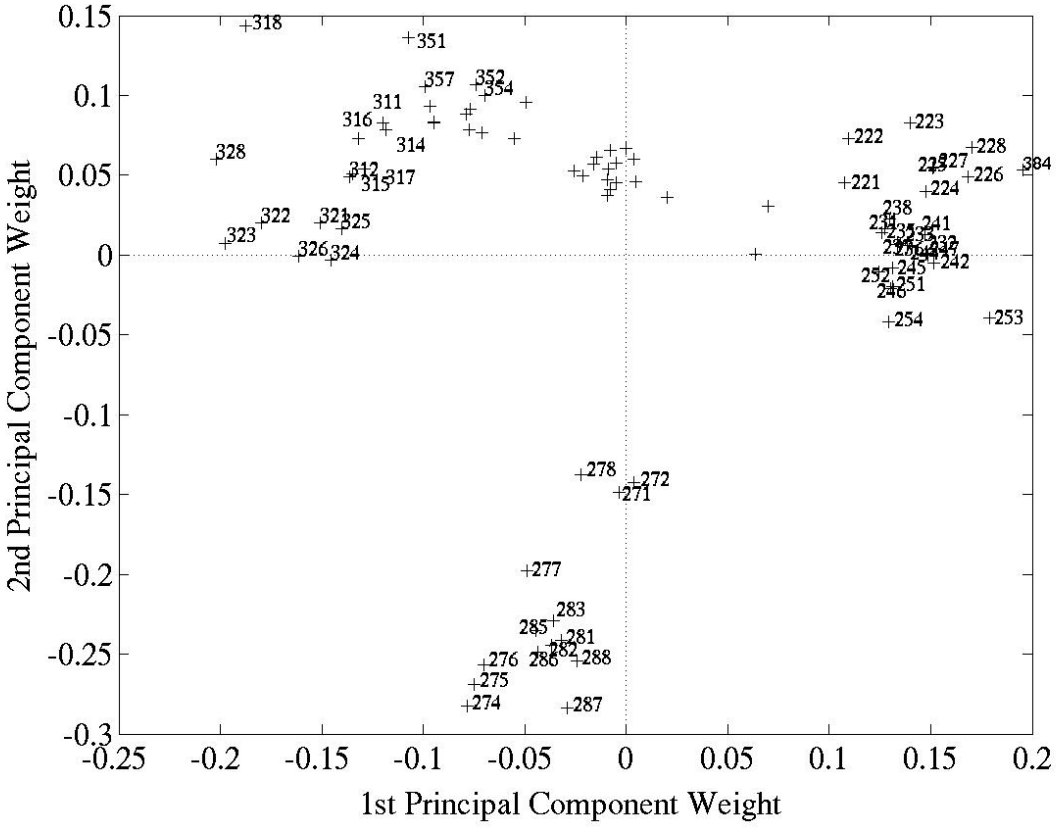
Parameter	Name
salinity	sal
ash weight	ash
total phytoplankton biovolume	pbiov
chlorophyll a	chl
gross productivity	prod
respiration	resp
assimilation index	nprod
small pennate diatoms (% biovolume)	psmdt
medium pennate diatoms (% biovolume)	pmddt
large pennate diatoms (% biovolume)	plgdt
cyanobacteria (% biovlume)	pcyan
autotrophic flagellates (% biovolume)	pflag
unknown flagellates (% biovolume)	uflag
other phytoplankton (% biovolume)	pothr
adult copepods	zcope
copepod nauplii	znaup
rotifers	zrot
ciliates	zcil
bacterioplankton	bact
polychaetes	zpoly
NH_4	NH4
NO_3	NO3
NO_2	NO2
urea	urea
SRP	PO4
total phosphorous	TP
SiO_3	Si

Parameter representation on the first four principal components for PCA1.

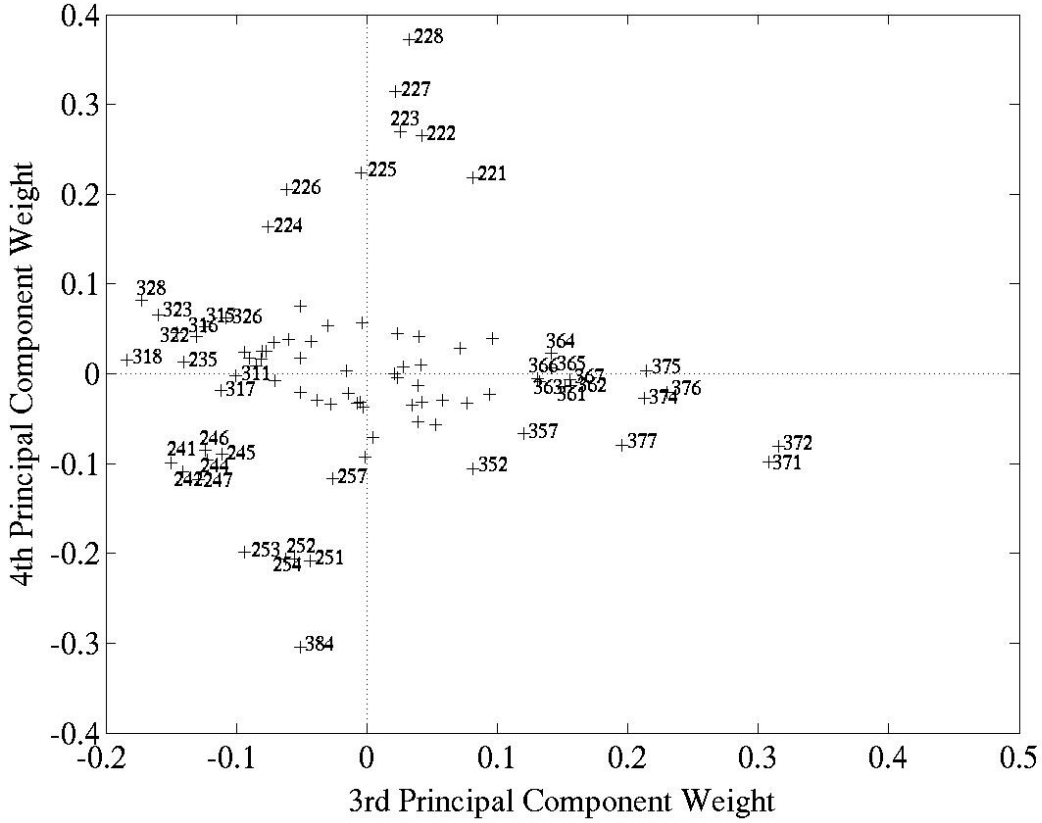




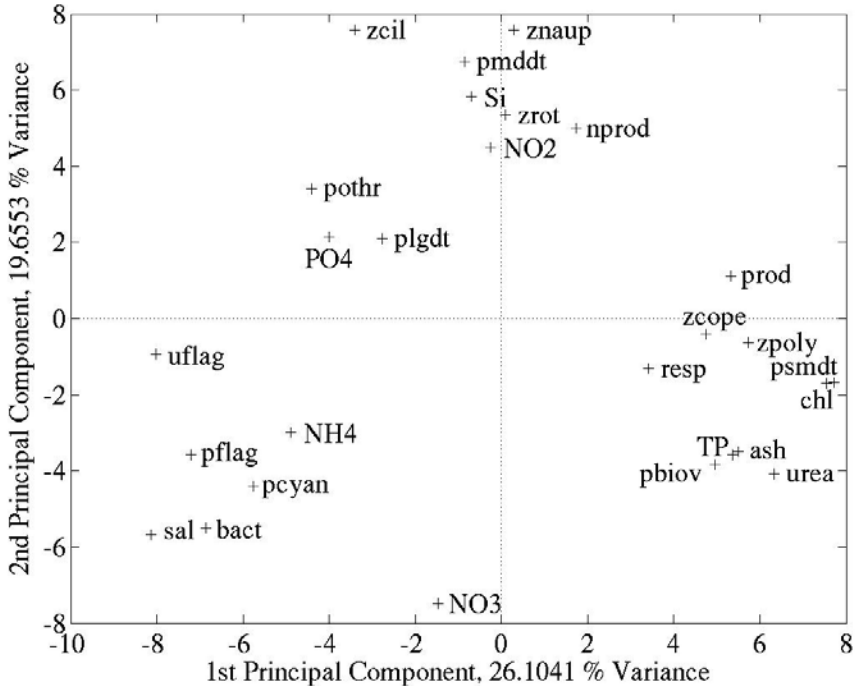
The significance of the first and second principal components of PCA1 at the time and location of each sampling event. Time and location are represented by three numbers. The first number, ranging from 1 to 3, designates the year of sampling (2001 to 2003, respectively). The second number, ranging from 1 to 8, designates the sampling trip for that year (the first trip to the eighth trip, respectively). The third number, ranging from 1 to 8, designates the station number.

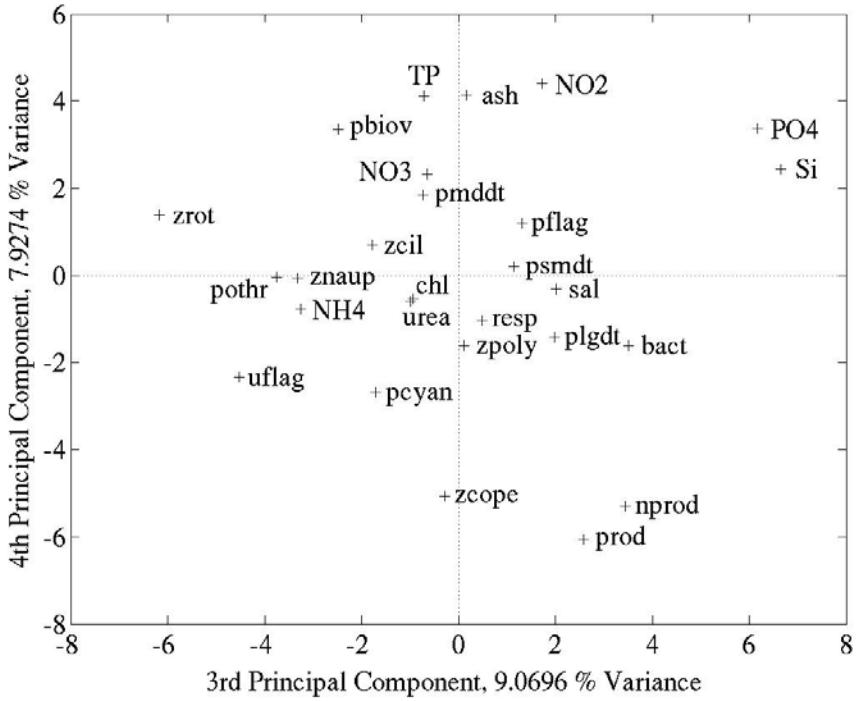


The significance of the third and fourth principal components of PCA1 at the time and location of each sampling event. Time and location are represented by three numbers. The first number, ranging from 1 to 3, designates the year of sampling (2001 to 2003, respectively). The second number, ranging from 1 to 8, designates the sampling trip for that year (the first trip to the eighth trip, respectively). The third number, ranging from 1 to 8, designates the station number.

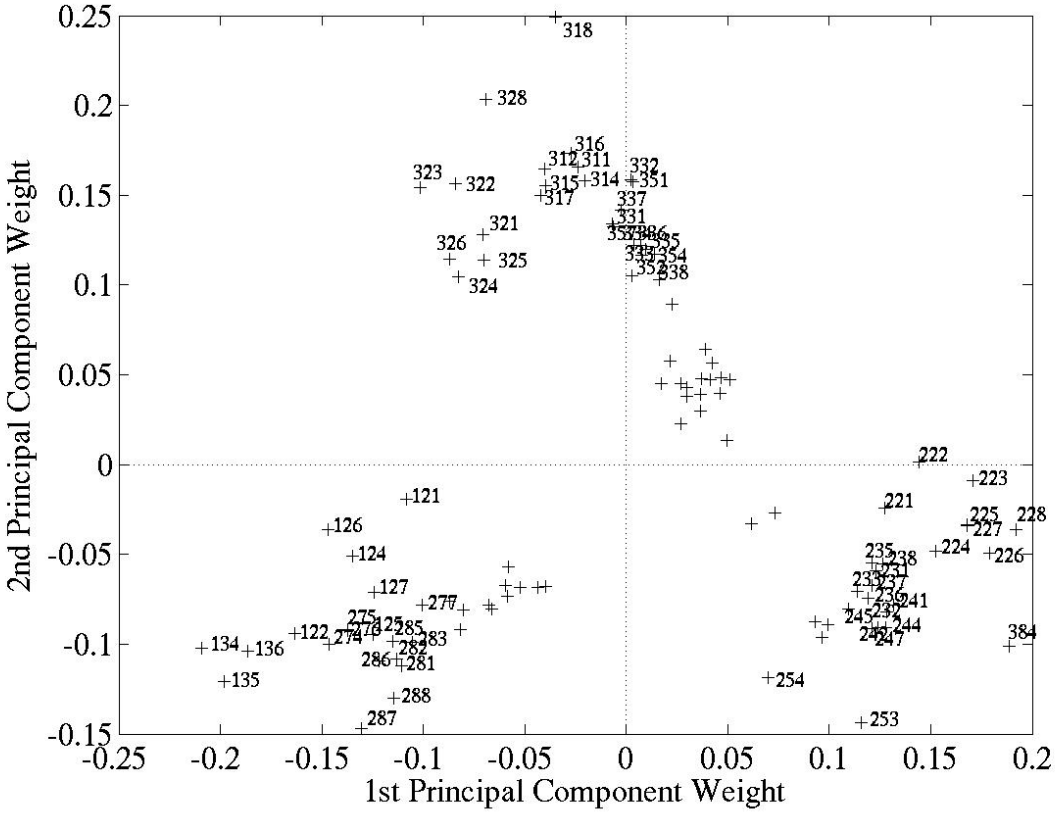


Parameter representation on the first four principal components for PCA2.

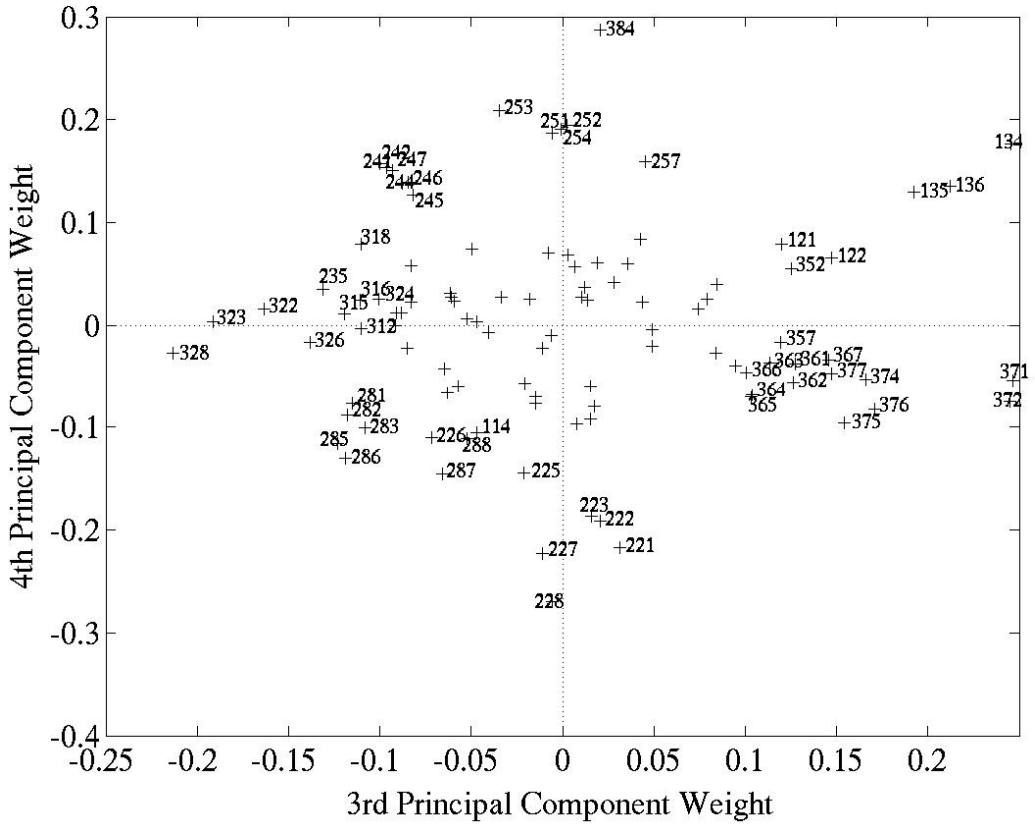




The significance of the first and second principal components of PCA2 at the time and location of each sampling event. Time and location are represented by three numbers. The first number, ranging from 1 to 3, designates the year of sampling (2001 to 2003, respectively). The second number, ranging from 1 to 8, designates the sampling trip for that year (the first trip to the eighth trip, respectively). The third number, ranging from 1 to 8, designates the station number.



The significance of the third and fourth principal components of PCA2 at the time and location of each sampling event. Time and location are represented by three numbers. The first number, ranging from 1 to 3, designates the year of sampling (2001 to 2003, respectively). The second number, ranging from 1 to 8, designates the sampling trip for that year (the first trip to the eighth trip, respectively). The third number, ranging from 1 to 8, designates the station number.



APPENDIX B

IDENTIFIED TAXA AND AVERAGE DATA FOR ALL MEASURED PARAMETERS IN 2001, 2002, AND 2003

Biovolume averages for all phytoplankton taxa in 2001.

Taxa	Sampling date		
	5/30/01	6/6/01	6/13/01
cyanobacteria ($\mu m^3\ l^{-1}$)			
Anabaena sp.	bd	bd	bd
Chroococcus sp.	bd	bd	bd
filament sp.	$3.95x10^8$	$2.61x10^7$	$2.28x10^7$
Lyngbya sp.	bd	bd	bd
Oscillatoria sp.	bd	$1.92x10^7$	$7.83x10^6$
diatoms ($\mu m^3\ l^{-1}$)			
Campylodiscus sp.	$1.10x10^5$	$2.55x10^5$	$2.59x10^5$
centric diatom sp.	bd	$3.98x10^5$	$8.89x10^4$
Entomoneis sp.	$1.36x10^6$	$5.27x10^6$	$7.84x10^5$
Gyrosigma sp.	$1.21x10^4$	bd	$1.52x10^4$
Melosira sp.	bd	bd	bd
Nitzschia closterium	$5.28x10^9$	$1.97x10^8$	$5.82x10^6$
small pennate sp.	$2.21x10^6$	$6.70x10^6$	$1.87x10^7$
medium pennate sp.	$9.70x10^6$	$1.13x10^8$	$1.28x10^7$
large pennate sp.	$6.24x10^4$	$2.08x10^4$	$1.68x10^7$
Surirella sp.	bd	bd	$2.32x10^5$
Synedra sp.	bd	bd	bd
Tabellaria sp.	bd	bd	bd

bd = below detection

Taxa	Sampling date		
	5/30/01	6/6/01	6/13/01
green algae ($\mu m^3\ l^{-1}$)			
coccoid sp.	$6.89x10^7$	$2.46x10^7$	bd
filament sp.	bd	$9.51x10^5$	bd
prasinophycean sp.	bd	bd	bd
others ($\mu m^3\ l^{-1}$)			
cryptomonad - like	bd	bd	$2.99x10^5$
dinoflagellate sp.	$2.45x10^9$	$1.52x10^8$	bd
Euglena sp.	bd	bd	bd
microflagellate sp.	$8.02x10^7$	$2.64x10^7$	$2.78x10^7$
Synura sp.	bd	$1.74x10^8$	$5.49x10^7$
total biovolume ($\mu m^3\ l^{-1}$)	$8.29x10^9$	$7.46x10^8$	$1.69x10^8$

Biovolume averages for all phytoplankton taxa in 2002.

Taxa	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
cyanobacteria ($\mu m^3 l^{-1}$)								
Anabaena sp.	bd	bd	bd	bd	bd	$2.11x10^8$	$1.14x10^8$	$9.47x10^6$
Chroococcus sp.	bd	bd	bd	bd	bd	$1.53x10^7$	bd	bd
filament sp.	$3.02x10^7$	$1.21x10^7$	$6.34x10^6$	bd	$1.47x10^7$	$6.48x10^5$	$1.11x10^7$	$1.12x10^9$
Lyngbya sp.	$3.51x10^8$	$7.27x10^6$	$8.74x10^7$	$2.63x10^8$	$1.05x10^8$	$3.59x10^8$	bd	bd
Oscillatoria sp.	bd	bd	bd	bd	bd	bd	bd	bd
diatoms ($\mu m^3 l^{-1}$)								
Campylodiscus sp.	$6.75x10^7$	$5.70x10^7$	$5.74x10^7$	$4.59x10^8$	$1.79x10^8$	$2.01x10^7$	bd	bd
centric diatom sp.	bd	bd	bd	bd	bd	bd	bd	bd
Entomoneis sp.	$4.60x10^8$	$5.01x10^8$	$6.28x10^8$	$6.94x10^8$	$5.90x10^8$	$4.47x10^9$	$2.69x10^8$	bd
Gyrosigma sp.	$1.41x10^7$	$1.08x10^6$	bd	bd	bd	bd	bd	bd
Melosira sp.	bd	bd	bd	bd	bd	$2.12x10^7$	bd	bd
Nitzschia closterium	bd	bd	bd	bd	bd	bd	$6.37x10^5$	$4.19x10^7$
small pennate sp.	$1.53x10^{10}$	$9.20x10^9$	$1.12x10^{10}$	$2.03x10^{10}$	$1.22x10^{10}$	$5.29x10^9$	$5.43x10^8$	$5.34x10^5$
medium pennate sp.	$9.71x10^9$	$6.01x10^8$	$7.57x10^8$	$1.96x10^9$	$1.48x10^9$	$3.52x10^9$	$1.01x10^8$	$1.84x10^6$
large pennate sp.	bd	$1.30x10^7$	$1.13x10^8$	$2.86x10^8$	$1.31x10^4$	bd	bd	$1.07x10^7$
Surirella sp.	bd	$7.40x10^5$	$1.48x10^8$	$1.95x10^7$	bd	bd	bd	bd
Synedra sp.	bd	$2.22x10^5$	$3.04x10^5$	$1.16x10^6$	$5.74x10^4$	bd	bd	bd
Tabellaria sp.	bd	bd	bd	bd	bd	bd	bd	bd

bd = below detection

Biovolume averages for all phytoplankton taxa in 2002. Continued.

Taxa	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
green algae ($\mu m^3 l^{-1}$)								
coccoid sp.	bd	bd	bd	bd	bd	bd	bd	bd
filament sp.	bd	bd	bd	bd	bd	bd	bd	bd
prasinophycean sp.	bd	bd	bd	bd	bd	bd	bd	$1.54x10^8$
others ($\mu m^3 l^{-1}$)								
cryptomonad - like	bd	bd	bd	bd	bd	bd	$3.27x10^8$	$1.37x10^9$
dinoflagellate sp.	bd	bd	bd	bd	bd	bd	$4.97x10^7$	$1.98x10^9$
Euglena sp.	bd	bd	bd	bd	bd	bd	bd	bd
microflagellate sp.	bd	bd	bd	bd	bd	bd	$9.79x10^6$	$1.46x10^8$
Synura sp.	bd	bd	bd	bd	bd	bd	$6.38x10^8$	bd
total biovolume ($\mu m^3 l^{-1}$)	$2.59x10^{10}$	$1.04x10^{10}$	$1.30x10^{10}$	$2.40x10^{10}$	$1.45x10^{10}$	$1.39x10^{10}$	$2.06x10^9$	$4.84x10^9$

bd = below detection

Biovolume averages for all phytoplankton taxa in 2003.

Taxa	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
cyanobacteria ($\mu m^3\ l^{-1}$)									
Anabaena sp.	bd	bd	$1.03x10^7$	$1.40x10^6$	bd	bd	bd	bd	bd
Chroococcus sp.	bd	bd	bd	bd	bd	bd	bd	bd	$1.12x10^7$
filament sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
Lyngbya sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
Oscillatoria sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
diatoms ($\mu m^3\ l^{-1}$)									
Campylodiscus sp.	$5.13x10^7$	$1.88x10^7$	$1.16x10^8$	$2.18x10^7$	$5.16x10^6$	bd	bd	bd	bd
centric diatom sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
Entomoneis sp.	$1.81x10^5$	$6.68x10^6$	$9.09x10^8$	$2.96x10^8$	$1.76x10^9$	$8.25x10^7$	$7.18x10^8$	$3.12x10^{10}$	$7.19x10^8$
Gyrosigma sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
Melosira sp.	$1.03x10^7$	$4.90x10^6$	$7.48x10^7$	$1.27x10^8$	$5.13x10^7$	$2.25x10^7$	bd	bd	bd
Nitzschia closterium	$1.19x10^6$	$1.87x10^5$	$1.58x10^7$	$1.95x10^9$	$8.12x10^7$	$8.60x10^6$	bd	bd	bd
small pennate sp.	$8.00x10^7$	$3.66x10^7$	$1.85x10^8$	$1.28x10^9$	$6.08x10^8$	$1.64x10^9$	$2.86x10^9$	6.4810^{10}	$8.51x10^9$
medium pennate sp.	$1.95x10^8$	$3.01x10^8$	$4.37x10^9$	$8.25x10^8$	$5.97x10^8$	$2.86x10^8$	$3.05x10^8$	$2.46x10^9$	$1.33x10^8$
large pennate sp.	$7.29x10^7$	$2.96x10^7$	$8.24x10^7$	$6.98x10^7$	$1.39x10^8$	$2.44x10^6$	$5.34x10^6$	$4.71x10^8$	bd
Surirella sp.	$1.03x10^8$	$3.25x10^7$	$4.71x10^7$	$7.07x10^6$	$3.50x10^7$	bd	$8.08x10^6$	$2.97x10^8$	bd
Synedra sp.	$2.26x10^7$	$3.66x10^6$	$2.20x10^7$	$1.27x10^7$	$6.98x10^6$	bd	bd	$2.44x10^7$	bd
Tabellaria sp.	$1.06x10^5$	$6.90x10^5$	$7.01x10^5$	bd	bd	bd	bd	bd	bd

bd = below detection

Biovolume averages for all phytoplankton taxa in 2003. Continued.

Taxa	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
green algae ($\mu m^3 l^{-1}$)									
coccoid sp.	$1.11x10^7$	$9.62x10^7$	$3.94x10^7$	bd	bd	bd	bd	bd	bd
filament sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
prasinophycean sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
others ($\mu m^3 l^{-1}$)									
cryptomonad - like	$3.16x10^6$	$7.91x10^6$	$6.73x10^6$	bd	bd	bd	bd	bd	bd
dinoflagellate sp.	$9.58x10^7$	$5.53x10^8$	$2.33x10^7$	bd	bd	bd	$5.77x10^7$	bd	bd
Euglena sp.	bd	$2.76x10^7$	bd	$2.06x10^6$	bd	bd	bd	bd	bd
microflagellate sp.	$1.73x10^6$	$1.22x10^7$	bd	bd	bd	bd	$1.16x10^7$	bd	bd
Synura sp.	bd	bd	bd	bd	bd	bd	bd	bd	bd
total biovolume ($\mu m^3 l^{-1}$)	$6.48x10^8$	$1.13x10^9$	$5.90x10^9$	$4.59x10^9$	$3.28x10^9$	$2.04x10^9$	$3.97x10^9$	$9.92x10^{10}$	$9.37x10^9$

bd = below detection

Average concentrations for all zooplankton and bacterioplankton taxa in 2001.

Taxa	Sampling date		
	5/30/01	6/6/01	6/13/01
bacterioplankton (cells l^{-1})	$1.88x10^{10}$	$2.30x10^{10}$	$3.19x10^{10}$
Bosmina sp. (ind l^{-1})	$1.72x10^{-1}$	bd	bd
ciliates (cells l^{-1})	$4.70x10^{2}$	$1.26x10^{4}$	$6.39x10^{1}$
copepod adults (ind l^{-1})	$1.60x10^{0}$	$2.21x10^{0}$	$5.58x10^{0}$
copepod nauplii (ind l^{-1})	$1.03x10^{0}$	$9.28x10^{-1}$	$1.38x10^{0}$
nematodes (ind l^{-1})	$1.66x10^{1}$	$8.14x10^{0}$	$4.48x10^{1}$
polychaete larvae (ind l^{-1})	bd	bd	bd
rotifers (ind l^{-1})			
Asplanchna sp.	bd	bd	bd
Brachionus sp.	bd	bd	bd
Keratella sp.	$3.44x10^{-1}$	bd	bd
rotifer sp.	$1.44x10^{0}$	$6.56x10^{-1}$	bd

bd = below detection

Average concentrations for all zooplankton and bacterioplankton taxa in 2002.

Taxa	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
bacterioplankton (cells l^{-1})	$1.06x10^{10}$	$8.23x10^{9}$	$7.11x10^{9}$	$9.97x10^{9}$	$8.42x10^{9}$	$1.30x10^{10}$	$1.42x10^{10}$	$2.22x10^{10}$
Bosmina sp. (ind l^{-1})	bd	bd	bd	bd	bd	bd	bd	bd
ciliates (cells l^{-1})	bd	bd	bd	bd	$5.78x10^{0}$	$6.54x10^{3}$	$2.42x10^{4}$	$2.00x10^{4}$
copepod adults (ind l^{-1})	$1.50x10^{3}$	$9.77x10^{2}$	$1.49x10^{2}$	$1.55x10^{2}$	$8.09x10^{1}$	$2.37x10^{1}$	bd	$3.44x10^{-1}$
copepod nauplii (ind l^{-1})	$2.46x10^{3}$	$9.48x10^{2}$	$2.38x10^{2}$	$3.46x10^{2}$	$3.50x10^{2}$	$6.38x10^{1}$	bd	bd
nematodes (ind l^{-1})	bd	bd	bd	bd	$7.23x10^{-1}$	bd	$2.75x10^{-1}$	bd
polychaete larvae (ind l^{-1})	$8.80x10^{2}$	$2.32x10^{3}$	$2.65x10^{3}$	$1.03x10^{3}$	$4.91x10^{1}$	$1.72x10^{3}$	bd	bd
rotifers (ind l^{-1})								
Asplanchna sp.	$2.71x10^{3}$	$5.02x10^{2}$	$1.49x10^{3}$	$1.38x10^{3}$	bd	bd	bd	bd
Brachionus sp.	$1.10x10^{2}$	$6.60x10^{1}$	$1.28x10^{2}$	$5.97x10^{1}$	bd	bd	bd	bd
Keratella sp.	bd	bd	bd	bd	bd	bd	bd	bd
rotifer sp.	$1.10x10^{2}$	$6.02x10^{0}$	$6.16x10^{1}$	$3.61x10^{0}$	bd	bd	bd	bd

bd = below detection

Average concentrations for all zooplankton and bacterioplankton taxa in 2003.

Taxa	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
bacterioplankton (cells l^{-1})	$3.81x10^{9}$	$8.37x10^{9}$	$3.71x10^{9}$	$5.09x10^{9}$	$8.45x10^{9}$	$9.82x10^{9}$	$1.94x10^{10}$	$6.52x10^{9}$	$2.47x10^{10}$
Bosmina sp. (ind l^{-1})	$5.50x10^{-1}$	bd	bd	bd	bd	bd	bd	bd	bd
ciliates (cells l^{-1})	$1.08x10^{5}$	$1.04x10^{5}$	$5.02x10^{4}$	$3.02x10^{3}$	$8.93x10^{4}$	$2.14x10^{4}$	$1.35x10^{4}$	bd	$9.01x10^{4}$
copepod adults (ind l^{-1})	$3.44x10^{1}$	$2.56x10^{1}$	$3.71x10^{1}$	$2.47x10^{2}$	$1.78x10^{2}$	$8.25x10^{1}$	$4.50x10^{1}$	bd	$6.11x10^{0}$
copepod nauplii (ind l^{-1})	$2.05x10^{3}$	$1.44x10^{3}$	$6.70x10^{2}$	$4.90x10^{2}$	$1.16x10^{3}$	$3.33x10^{2}$	$2.20x10^{2}$	$2.29x10^{1}$	bd
nematodes (ind l^{-1})	bd	bd	bd	bd	bd	bd	bd	$2.29x10^{1}$	bd
polychaete larvae (ind l^{-1})	$8.58x10^{1}$	$1.97x10^{2}$	$4.41x10^{2}$	$6.82x10^{2}$	$1.28x10^{3}$	$4.67x10^{2}$	$1.25x10^{3}$	$3.59x10^{3}$	$8.56x10^{1}$
rotifers (ind l^{-1})									
Asplanchna sp.	$5.61x10^{2}$	$1.75x10^{3}$	$5.86x10^{2}$	$7.37x10^{1}$	$4.82x10^{2}$	$4.82x10^{0}$	$2.48x10^{1}$	bd	bd
Brachionus sp.	$1.02x10^{2}$	$1.29x10^{2}$	$4.76x10^{1}$	$1.20x10^{0}$	$1.07x10^{1}$	bd	bd	bd	bd
Keratella sp.	$1.66x10^{2}$	$1.28x10^{1}$	bd	$1.81x10^{0}$	bd	bd	bd	bd	bd
rotifer sp.	$2.18x10^{3}$	$1.09x10^{3}$	$1.50x10^{2}$	$1.81x10^{0}$	$2.14x10^{1}$	$1.83x10^{0}$	$6.33x10^{1}$	$3.83x10^{2}$	$5.19x10^{2}$

bd = below detection

Averages of remaining data in 2001.

Parameter	Sampling date		
	5/30/01	6/6/01	6/13/01
ash weight (g l^{-1})	0.103	0.179	0.249
chlorophyll a (µg l^{-1})	15.291	1.230	0.961
gross productivity (mg-C m^{-3} hr^{-1})	122.900	0.469	0.000
net productivity (mg-C m^{-3} hr^{-1})	18.350	-37.689	-14.852
nutrients (µM)			
NO_2	0.036	0.150	0.346
NO_3	0.890	1.068	1.380
NH_4	0.294	0.340	8.901
Urea	1.025	1.225	2.580
SRP	0.151	1.825	6.460
total phosphorous	6.077	3.359	2.700
$HSiO_3$	23.329	117.299	145.720
phaeophytin a (µg l^{-1})	0.231	0.492	1.034
respiration (mg-C m^{-3} hr^{-1})	125.460	34.157	3.090
salinity (ppt)	190.000	220.000	300.000
water depth (cm)	12.500	6.313	5.143
water temperature (^{0}C)	35.675	33.550	32.367

Averages of remaining data in 2002.

Parameter	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
ash weight (g l^{-1})	1.750	0.712	0.892	1.383	2.075	1.333	0.379	0.385
chlorophyll a (µg l^{-1})	74.466	92.936	58.155	72.643	35.102	21.904	5.953	10.323
gross productivity (mg-C m^{-3} hr^{-1})	18.190	1265.322	441.247	74.202	187.777	222.263	15.227	57.002
net productivity (mg-C m^{-3} hr^{-1})	-35.632	1227.705	171.509	-56.320	165.646	*	-4.320	-10.916
nutrients (µM)								
NO_2	0.188	0.117	0.146	0.133	0.122	0.075	0.086	0.023
NO_3	0.319	0.525	1.080	0.823	1.096	0.497	0.507	0.623
NH_4	1.160	1.005	1.494	0.815	0.989	0.123	4.342	3.268
Urea	2.670	3.885	3.169	3.147	3.046	1.276	0.813	0.529
SRP	0.440	0.329	0.379	0.412	0.675	0.500	0.386	0.105
total phosphorous	19.793	19.002	18.986	33.555	47.574	19.274	7.941	6.269
$HSiO_3$	104.396	50.780	22.184	55.659	86.581	11.828	6.944	3.299
phaeophytin a (µg l^{-1})	30.293	2.342	3.991	18.110	12.825	0.938	0.126	0.242
respiration (mg-C m^{-3} hr^{-1})	69.894	68.101	323.303	149.309	45.544	*	39.570	74.245
salinity (ppt)	16.000	18.000	21.000	24.000	41.000	69.000	142.000	125.000
water depth (cm)	19.750	17.750	17.563	15.625	22.188	24.188	24.438	28.663
water temperature (^{0}C)	14.400	21.100	17.600	17.750	25.625	*	24.633	27.100

* = instrumentation problem, data lost

Averages of remaining data in 2003.

Parameter	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
ash weight (g l^{-1})	0.125	0.095	0.268	0.293	0.484	0.594	0.883	3.533	2.575
chlorophyll a (µg l^{-1})	7.906	7.057	33.028	25.197	34.599	24.873	26.669	155.890	102.000
gross productivity (mg-C m^{-3} hr^{-1})	105.784	86.421	356.029	260.085	315.567	549.220	687.057	225.586	~
net productivity (mg-C m^{-3} hr^{-1})	79.329	55.506	313.352	126.052	233.331	445.417	505.279	47.852	~
nutrients (µM)									
NO_2	0.217	0.150	0.151	0.108	0.188	0.112	0.132	0.270	0.238
NO_3	0.089	0.089	0.089	0.139	0.111	0.089	0.089	0.178	0.178
NH_4	0.815	1.394	0.471	0.489	0.684	0.323	0.379	0.844	0.667
Urea	0.302	0.354	0.982	0.917	1.193	0.967	0.884	1.551	3.442
SRP	0.587	1.046	0.873	0.508	1.248	1.046	1.411	1.082	1.745
total phosphorous	3.573	3.511	7.690	6.711	13.259	9.759	12.547	64.420	35.226
$HSiO_3$	83.679	95.237	142.504	155.039	200.435	141.292	181.617	135.027	182.788
phaeophytin a (µg l^{-1})	4.495	1.742	1.680	2.351	8.323	4.889	8.091	44.323	36.832
respiration (mg-C m^{-3} hr^{-1})	64.318	44.266	51.212	113.417	98.683	124.564	218.133	213.281	~
salinity (ppt)	11.000	14.000	15.000	17.000	16.000	29.000	46.000	67.000	91.000
water depth (cm)	31.250	23.750	24.375	17.859	19.857	25.162	12.361	5.154	4.445
water temperature (^{0}C)	21.625	20.181	23.080	24.154	26.326	27.177	28.363	30.350	~

~ = too shallow to collect data

APPENDIX C

STANDARD DEVIATIONS FOR ALL AVERAGE DATA IN 2001, 2002, AND 2003

Standard deviations of average phytoplankton biovolume in 2001.

Taxa	Sampling date		
	5/30/01	6/6/01	6/13/01
cyanobacteria ($\mu m^3 l^{-1}$)			
Anabaena sp.	-	-	-
Chroococcus sp.	-	-	-
filament sp.	$3.11x10^8$	$1.87x10^7$	$1.09x10^7$
Lyngbya sp.	-	-	-
Oscillatoria sp.	-	$3.70x10^7$	$1.92x10^7$
diatoms ($\mu m^3 l^{-1}$)			
Campylodiscus sp.	$1.92x10^5$	$6.78x10^5$	$4.71x10^5$
centric diatom sp.	-	$1.13x10^6$	$2.18x10^5$
Entomoneis sp.	$2.57x10^6$	$1.44x10^7$	$1.03x10^6$
Gyrosigma sp.	$3.42x10^4$	-	$2.91x10^4$
Melosira sp.	-	-	-
Nitzschia closterium	$1.89x10^9$	$1.73x10^8$	$8.74x10^6$
small pennate sp.	$6.26x10^6$	$1.18x10^7$	$2.93x10^7$
medium pennate sp.	$1.81x10^7$	$1.69x10^8$	$1.77x10^7$
large pennate sp.	$1.74x10^5$	$4.97x10^4$	$4.09x10^7$
Surirella sp.	-	-	$5.69x10^5$
Synedra sp.	-	-	-
Tabellaria sp.	-	-	-

Taxa	Sampling date		
	5/30/01	6/6/01	6/13/01
green algae ($\mu m^3 l^{-1}$)			
coccoid sp.	$1.14x10^8$	$4.36x10^7$	-
filament sp.	-	$2.69x10^6$	-
prasinophycean sp.	-	-	-
others ($\mu m^3 l^{-1}$)			
cryptomonad - like	-	-	$7.32x10^5$
dinoflagellate sp.	$8.07x10^8$	$1.74x10^8$	-
Euglena sp.	-	-	-
microflagellate sp.	$2.68x10^7$	$2.68x10^7$	$3.85x10^7$
Synura sp.	-	$9.32x10^7$	$6.41x10^7$
total biovolume ($\mu m^3 l^{-1}$)	$1.85x10^9$	$5.29x10^8$	$1.12x10^8$

- = no standard deviation

Standard deviations of average phytoplankton biovolume in 2002.

Taxa	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
cyanobacteria ($\mu m^3 l^{-1}$)								
Anabaena sp.	-	-	-	-	-	4.02×10^8	1.57×10^8	2.68×10^7
Chroococcus sp.	-	-	-	-	-	4.34×10^7	-	-
filament sp.	6.03×10^7	2.18×10^7	7.70×10^6	-	2.17×10^7	1.35×10^6	1.71×10^7	3.38×10^8
Lyngbya sp.	1.29×10^8	1.25×10^7	1.40×10^8	3.90×10^8	1.29×10^8	5.61×10^8	-	-
Oscillatoria sp.	-	-	-	-	-	-	-	-
diatoms ($\mu m^3 l^{-1}$)								
Campylodiscus sp.	1.35×10^8	4.85×10^7	4.65×10^7	3.60×10^8	2.66×10^8	3.99×10^7	-	-
centric diatom sp.	-	-	-	-	-	-	-	-
Entomoneis sp.	9.21×10^8	6.58×10^8	5.11×10^8	8.11×10^8	6.23×10^8	4.03×10^9	4.83×10^8	-
Gyrosigma sp.	2.81×10^7	3.06×10^6	-	-	-	-	-	-
Melosira sp.	-	-	-	-	-	5.99×10^7	-	-
Nitzschia closterium	-	-	-	-	-	-	1.19×10^6	3.52×10^7
small pennate sp.	4.62×10^9	4.72×10^9	6.44×10^9	7.44×10^9	5.98×10^9	2.13×10^9	4.59×10^8	1.51×10^6
medium pennate sp.	1.41×10^9	2.37×10^8	3.14×10^8	1.41×10^9	9.57×10^8	2.99×10^9	1.03×10^8	5.21×10^6
large pennate sp.	-	2.94×10^7	1.20×10^8	3.42×10^8	3.72×10^4	-	-	3.04×10^7
Surirella sp.	-	1.45×10^6	2.19×10^8	5.45×10^7	-	-	-	-
Synedra sp.	-	3.75×10^5	4.42×10^5	8.65×10^5	8.10×10^4	-	-	-
Tabellaria sp.	-	-	-	-	-	-	-	-

- = no standard deviation

Standard deviations of average phytoplankton biovolume in 2002. Continued.

Taxa	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
green algae ($\mu m^3 l^{-1}$)								
coccoid sp.	-	-	-	-	-	-	-	-
filament sp.	-	-	-	-	-	-	-	-
prasinophycean sp.	-	-	-	-	-	-	-	$1.18x10^8$
others ($\mu m^3 l^{-1}$)								
cryptomonad - like	-	-	-	-	-	-	$1.13x10^8$	$9.53x10^8$
dinoflagellate sp.	-	-	-	-	-	-	$4.69x10^7$	$1.50x10^9$
Euglena sp.	-	-	-	-	-	-	-	-
microflagellate sp.	-	-	-	-	-	-	$7.69x10^6$	$7.88x10^7$
Synura sp.	-	-	-	-	-	-	$4.25x10^8$	-
total biovolume ($\mu m^3 l^{-1}$)	$4.55x10^9$	$4.56x10^9$	$7.10x10^9$	$9.51x10^9$	$6.49x10^9$	$7.86x10^9$	$6.41x10^8$	$2.37x10^9$

- = no standard deviation

Standard deviations of average phytoplankton biovolume in 2003.

Taxa	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
cyanobacteria ($\mu m^3\ l^{-1}$)									
Anabaena sp.	-	-	$6.58x10^6$	$3.22x10^6$	-	-	-	-	-
Chroococcus sp.	-	-	-	-	-	-	-	-	$1.59x10^7$
filament sp.	-	-	-	-	-	-	-	-	-
Lyngbya sp.	-	-	-	-	-	-	-	-	-
Oscillatoria sp.	-	-	-	-	-	-	-	-	-
diatoms ($\mu m^3\ l^{-1}$)									
Campylodiscus sp.	$4.09x10^7$	$1.40x10^7$	$9.43x10^7$	$2.09x10^7$	$1.46x10^7$	-	-	-	-
centric diatom sp.	-	-	-	-	-	-	-	-	-
Entomoneis sp.	$5.12x10^5$	$1.89x10^7$	$1.28x10^9$	$2.63x10^8$	$4.93x10^8$	$1.12x10^8$	$4.28x10^8$	$4.11x10^{10}$	$3.21x10^8$
Gyrosigma sp.	-	-	-	-	-	-	-	-	-
Melosira sp.	$2.43x10^7$	$4.05x10^6$	$5.26x10^7$	$8.04x10^7$	$8.31x10^7$	$3.55x10^7$	-	-	-
Nitzschia closterium	$3.38x10^6$	$3.46x10^5$	$6.39x10^6$	$4.55x10^8$	$4.07x10^7$	$6.29x10^6$	-	-	-
small pennate sp.	$2.65x10^7$	$1.52x10^7$	$6.61x10^7$	$3.98x10^8$	$2.18x10^8$	$3.31x10^8$	$7.54x10^8$	$3.84x10^{10}$	$4.04x10^7$
medium pennate sp.	$1.42x10^8$	$8.79x10^7$	$2.02x10^9$	$3.39x10^8$	$2.74x10^8$	$1.64x10^8$	$2.15x10^8$	$2.07x10^9$	$2.45x10^7$
large pennate sp.	$1.13x10^8$	$5.11x10^7$	$9.50x10^7$	$9.99x10^7$	$1.61x10^8$	$6.91x10^6$	$1.41x10^7$	$5.00x10^8$	-
Surirella sp.	$1.05x10^8$	$8.12x10^7$	$3.34x10^7$	$2.00x10^7$	$5.17x10^7$	-	$2.14x10^7$	$6.65x10^8$	-
Synedra sp.	$1.14x10^7$	$3.16x10^6$	$1.57x10^7$	$9.19x10^6$	$9.07x10^6$	-	-	$3.35x10^7$	-
Tabellaria sp.	$2.99x10^5$	$1.95x10^6$	$7.29x10^5$	-	-	-	-	-	-

- = no standard deviation

Standard deviations of average phytoplankton biovolume in 2003. Continued.

Taxa	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
green algae ($\mu m^3 l^{-1}$)									
coccoid sp.	$1.37x10^7$	$4.71x10^7$	$4.11x10^7$	-	-	-	-	-	-
filament sp.	-	-	-	-	-	-	-	-	-
prasinophycean sp.	-	-	-	-	-	-	-	-	-
others ($\mu m^3 l^{-1}$)									
cryptomonad - like	$7.13x10^6$	$8.50x10^6$	$1.32x10^7$	-	-	-	-	-	-
dinoflagellate sp.	$7.35x10^7$	$2.88x10^8$	$2.52x10^7$	-	-	-	$7.30x10^7$	-	-
Euglena sp.	-	$3.14x10^7$	-	$3.91x10^6$	-	-	-	-	-
microflagellate sp.	$4.89x10^6$	$1.36x10^7$	-	-	-	-	$1.55x10^7$	-	-
Synura sp.	-	-	-	-	-	-	-	-	-
total biovolume ($\mu m^3 l^{-1}$)	$3.20x10^8$	$3.91x10^8$	$2.02x10^9$	$5.64x10^8$	$6.66x10^8$	$3.75x10^8$	$7.85x10^8$	$7.80x10^{10}$	$2.72x10^8$

- = no standard deviation

Standard deviations for zooplankton and bacterioplankton concentrations in 2001.

Taxa	Sampling date		
	5/30/01	6/6/01	6/13/01
bacterioplankton (cells l^{-1})	4.04×10^{9}	4.96×10^{9}	5.82×10^{9}
Bosmina sp. (ind l^{-1})	4.86×10^{-1}	-	-
ciliates (cells l^{-1})	3.98×10^{2}	8.55×10^{3}	8.76×10^{1}
copepod adults (ind l^{-1})	2.38×10^{0}	2.83×10^{0}	7.21×10^{0}
copepod nauplii (ind l^{-1})	2.41×10^{0}	1.35×10^{0}	2.30×10^{0}
nematodes (ind l^{-1})	1.61×10^{1}	8.54×10^{0}	2.89×10^{1}
polychaete larvae (ind l^{-1})	-	-	-
rotifers (ind l^{-1})			
Asplanchna sp.	-	-	-
Brachionus sp.	-	-	-
Keratella sp.	9.72×10^{-1}	-	-
rotifer sp.	3.02×10^{0}	1.86×10^{0}	-

- = no standard deviation

Standard deviations for zooplankton and bacterioplankton concentrations in 2002.

Taxa	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
bacterioplankton (cells l^{-1})	$1.78x10^{9}$	$9.82x10^{8}$	$9.82x10^{8}$	$9.85x10^{8}$	$1.11x10^{9}$	$4.21x10^{9}$	$3.02x10^{9}$	$1.63x10^{9}$
Bosmina sp. (ind l^{-1})	-	-	-	-	-	-	-	-
ciliates (cells l^{-1})	-	-	-	-	$7.57x10^{0}$	$2.60x10^{3}$	$5.78x10^{3}$	$1.42x10^{4}$
copepod adults (ind l^{-1})	-	$3.65x10^{2}$	$1.55x10^{2}$	$8.63x10^{1}$	$2.75x10^{1}$	$2.21x10^{1}$	-	$9.72x10^{-1}$
copepod nauplii (ind l^{-1})	-	$3.19x10^{2}$	$1.33x10^{2}$	$1.38x10^{2}$	$8.28x10^{1}$	$6.00x10^{1}$	-	-
nematodes (ind l^{-1})	-	-	-	-	$2.04x10^{0}$	-	$7.78x10^{-1}$	-
polychaete larvae (ind l^{-1})	-	$9.89x10^{2}$	$1.37x10^{3}$	$8.08x10^{2}$	$3.01x10^{1}$	$7.31x10^{2}$	-	-
rotifers (ind l^{-1})								
Asplanchna sp.	-	$2.55x10^{2}$	$8.63x10^{2}$	$4.84x10^{2}$	-	-	-	-
Brachionus sp.	-	$9.10x10^{1}$	$8.97x10^{1}$	$4.53x10^{1}$	-	-	-	-
Keratella sp.	-	-	-	-	-	-	-	-
rotifer sp.	-	$1.70x10^{1}$	$3.80x10^{1}$	$1.02x10^{1}$	-	-	-	-

- = no standard deviation

Standard deviations for zooplankton and bacterioplankton concentrations in 2003.

Taxa	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
bacterioplankton (cells l^{-1})	$1.01x10^{9}$	$1.22x10^{9}$	$8.79x10^{8}$	$2.05x10^{9}$	$1.22x10^{9}$	$1.90x10^{9}$	$6.30x10^{9}$	$4.57x10^{8}$	$4.58x10^{8}$
Bosmina sp. (ind l^{-1})	$1.02x10^{0}$	-	-	-	-	-	-	-	-
ciliates (cells l^{-1})	$5.78x10^{4}$	$1.65x10^{5}$	$1.73x10^{4}$	$8.76x10^{2}$	$2.53x10^{4}$	$8.17x10^{3}$	$1.42x10^{4}$	-	$3.90x10^{4}$
copepod adults (ind l^{-1})	$1.52x10^{1}$	$2.22x10^{1}$	$1.90x10^{1}$	$1.12x10^{2}$	$7.56x10^{1}$	$5.00x10^{1}$	$3.37x10^{1}$	-	$8.64x10^{0}$
copepod nauplii (ind l^{-1})	$9.72x10^{2}$	$3.27x10^{2}$	$2.39x10^{2}$	$2.07x10^{2}$	$3.60x10^{2}$	$1.55x10^{2}$	$6.28x10^{1}$	$3.24x10^{1}$	-
nematodes (ind l^{-1})	-	-	-	-	-	-	-	$3.24x10^{1}$	-
polychaete larvae (ind l^{-1})	$8.73x10^{1}$	$6.16x10^{1}$	$2.19x10^{2}$	$2.46x10^{2}$	$2.85x10^{2}$	$2.64x10^{2}$	$4.40x10^{2}$	$9.23x10^{2}$	$3.46x10^{1}$
rotifers (ind l^{-1})									
Asplanchna sp.	$4.21x10^{2}$	$1.24x10^{3}$	$2.10x10^{2}$	$5.00x10^{1}$	$2.52x10^{2}$	$8.92x10^{0}$	$4.27x10^{1}$	-	-
Brachionus sp.	$1.21x10^{2}$	$8.36x10^{1}$	$1.91x10^{1}$	$3.41x10^{0}$	$2.62x10^{1}$	-	-	-	-
Keratella sp.	$1.52x10^{2}$	$1.94x10^{1}$	-	$5.11x10^{0}$	-	-	-	-	-
rotifer sp.	$1.72x10^{3}$	$4.16x10^{2}$	$2.34x10^{2}$	$5.11x10^{0}$	$2.62x10^{1}$	$3.39x10^{0}$	$6.26x10^{1}$	$4.12x10^{2}$	$3.37x10^{2}$

- = no standard deviation

Standard deviations for remaining data in 2001.

Parameter	Sampling date		
	5/30/01	6/6/01	6/13/01
ash weight (g l^{-1})	0.067	0.087	0.166
chlorophyll a (µg l^{-1})	2.089	0.516	0.829
gross productivity (mg-C m^{-3} hr^{-1})	47.650	1.149	0.000
net productivity (mg-C m^{-3} hr^{-1})	43.527	23.758	8.811
nutrients (µM)			
NO_2	0.013	0.032	0.101
NO_3	0.000	0.000	0.216
NH_4	0.097	0.155	6.732
Urea	0.000	0.317	1.574
HPO_4	0.000	1.518	3.716
total phosphorous	1.522	3.073	1.208
$HSiO_3$	3.349	29.049	15.043
phaeophytin a (µg l^{-1})	0.480	0.388	0.378
respiration (mg-C m^{-3} hr^{-1})	54.109	22.707	2.687
salinity (ppt)	-	-	-
water depth (cm)	2.563	2.329	2.738
water temperature (^{0}C)	0.806	1.923	0.451

- = no standard deviation

Standard deviations for remaining data in 2002.

Parameter	Sampling date							
	2/22/02	3/15/02	3/27/02	4/5/02	4/18/02	5/1/02	5/15/02	5/29/02
ash weight (g l^{-1})	0.234	0.114	0.154	0.471	0.315	0.267	0.387	0.442
chlorophyll a (µg l^{-1})	10.685	14.962	11.672	4.531	3.332	6.723	1.774	1.790
gross productivity (mg-C m^{-3} hr^{-1})	18.852	409.850	81.399	65.235	38.967	55.379	13.399	20.279
net productivity (mg-C m^{-3} hr^{-1})	46.410	451.625	57.693	64.981	84.843	-	40.822	36.601
nutrients (µM)								
NO_2	0.146	0.036	0.033	0.029	0.072	0.016	0.034	0.009
NO_3	0.165	0.062	0.331	0.092	0.697	0.087	0.159	0.000
NH_4	0.185	0.184	0.719	0.067	0.955	0.079	3.573	1.806
Urea	0.280	0.622	0.367	0.143	1.459	0.183	0.020	0.312
HPO_4	0.030	0.046	0.052	0.015	0.149	0.049	0.058	0.000
total phosphorous	3.630	4.744	8.603	13.939	16.934	4.160	1.754	0.893
$HSiO_3$	16.428	12.256	1.937	3.186	5.740	1.936	3.019	2.810
phaeophytin a (µg l^{-1})	4.797	3.399	3.911	3.879	6.059	1.128	0.196	0.396
respiration (mg-C m^{-3} hr^{-1})	33.732	49.439	63.015	44.893	37.322	-	39.007	27.239
salinity (ppt)								
water depth (cm)	2.500	5.175	4.982	4.868	4.869	5.707	5.741	7.202
water temperature (^{0}C)	0.770	0.183	0.535	0.311	0.320	-	0.493	0.294

- = no standard deviation

Standard deviations for remaining data in 2003.

Parameter	Sampling date								
	3/10/03	3/21/03	4/4/03	4/18/03	5/2/03	5/16/03	5/30/03	6/13/03	6/26/03
ash weight (g l^{-1})	0.024	0.009	0.035	0.057	0.075	0.036	0.073	0.560	0.130
chlorophyll a (µg l^{-1})	1.217	1.033	7.614	2.238	7.580	3.216	2.412	32.701	5.770
gross productivity (mg-C m^{-3} hr^{-1})	65.285	36.109	66.394	64.180	114.560	52.215	133.252	-	-
net productivity (mg-C m^{-3} hr^{-1})	31.752	41.720	53.631	73.830	117.556	34.259	234.754	-	-
nutrients (µM)									
NO_2	0.117	0.015	0.019	0.021	0.059	0.047	0.014	0.097	0.081
NO_3	0.000	0.000	0.000	0.056	0.038	0.000	0.000	0.000	0.000
NH_4	0.528	0.771	0.317	0.092	0.374	0.192	0.069	0.415	-
Urea	0.124	0.084	0.221	0.115	0.191	0.315	0.102	0.316	1.765
HPO_4	0.071	0.065	0.071	0.064	0.114	0.157	0.491	0.275	0.179
total phosphorous	0.668	0.365	1.496	0.935	2.425	1.746	3.317	13.057	6.227
$HSiO_3$	8.389	1.495	9.990	8.542	8.024	18.189	30.437	7.087	0.884
phaeophytin a (µg l^{-1})	4.863	0.293	1.347	2.037	1.901	0.775	1.008	6.821	2.395
respiration (mg-C m^{-3} hr^{-1})	52.126	73.826	42.952	61.966	22.208	58.553	146.163	-	-
salinity (ppt)									
water depth (cm)	6.453	5.120	6.116	5.561	6.694	7.079	5.790	3.334	0.898
water temperature (^{0}C)	1.164	1.079	0.592	0.505	0.473	0.381	0.471	0.212	-

- = no standard deviation

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Education

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Professional Experience

2000-present	Graduate Assistant-Research at Texas A&M University
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Publication

Fejes, E. M., J. Birnbaum, F. Gelwick, and D. L. Roelke. 2003. Vertical distribution of herbivorous zooplankton in a well-mixed lake system in which the main predator is a non-selective filter-feeding fish. *The Journal of Freshwater Ecology* 18:333-336.

Selected Scientific Talk (1 of 7)

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