

3-25-2005

Seasonal and Spatial Trends of *Karenia brevis* Blooms and Associated Parameters Along the 10-Meter Isobath of the West Florida Shelf

Elizabeth Singh
University of South Florida

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Seasonal and Spatial Trends of *Karenia brevis* Blooms and Associated Parameters Along the 10-Meter
Isobath of the West Florida Shelf

by

Elizabeth Singh

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
College of Marine Science
University of South Florida

Major Professor: Gabriel A. Vargo, Ph.D.
Pamela Hallock Muller, Ph.D.
Karen A. Steidinger, Ph.D.

Date of Approval:
March 25, 2005

Keywords: Red Tides, Harmful Algal Bloom, ECOHAB, Particulate Matter, Inorganic Nutrients

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ACKNOWLEDGEMENTS

It has taken me a long time to get to this point, in fact much longer than I had planned. There are many people I would like to thank for the support over the years. First, I thank my advisor Dr. Gabriel Vargo for his patience with me. I also thank my committee members, Dr. Karen Steidinger, who suggested this project, and Dr. Pamela Hallock Muller. I am fortunate to have two very strong female role models, and they served as calm voices of reason when I needed it. I am deeply grateful to my husband Sean for his unwavering support and confidence in me. I am so blessed to have my daughters, Amy and Erin, who are my motivation for everything. My parents deserve to be mentioned, as they are the ones who first exposed me to the world of marine science.

I am also indebted to Dr. Cynthia Heil, whose help and advice was invaluable. Merrie Beth Neely and the other students in Dr. Vargo's Lab were always willing to drop everything to help me find data or answer yet another question. I am grateful to all of the researchers that took part in the ECOHAB cruises and collected the data presented. Dr. Ted Van Vleet also supported my efforts to complete this project. Thanks to Jennifer Cannizzaro for her editing skills and for teaching me how to use Surfer. Jyotika Virmani and Christina Simoniello also went above and beyond by editing several versions of this manuscript. I am so grateful to my many other friends who would not let me give up.

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Seasonal and Spatial Trends of *Karenia brevis* Blooms and Associated Parameters Along the 10-Meter Isobath Of the West Florida Shelf

Elizabeth Singh

ABSTRACT

Karenia brevis is a toxic marine dinoflagellate species that blooms almost every year in the Gulf of Mexico. These blooms have had devastating effects on local economies, as well as on the fauna of the area. The ECOHAB:Florida project was founded to study the population dynamics and trophic impacts of *K. brevis*. The project included a series of monthly hydrographic offshore research cruises, as well as monthly surveys of a transect along the 10-meter isobath of the West Florida Shelf. This study focused on data from the alongshore transect over a three-year period (1999-2001). Physical parameters (temperature, salinity, and density) and chemical parameters (particulate carbon, nitrogen, and phosphorus; dissolved inorganic nitrogen and phosphorus) of the West Florida Shelf were analyzed. The amount of chlorophyll *a* and the location and amount of *K. brevis* cells present were also examined. Clear spatial, seasonal, and interannual patterns in the hydrographic parameters, particulate matter (C, N, P), dissolved inorganic nutrient (nitrite, nitrate, and phosphate), and chlorophyll *a* concentrations were found. At various times throughout the study, the location of *K. brevis* blooms was influenced by all of these factors except for the amount of dissolved inorganic nutrients. There were differences in particulate matter ratios present in bloom and non-bloom periods. No clear-cut differences in dissolved inorganic nutrients between bloom and non-bloom periods were found. Finally, relationships between the biological indicators of blooms (i.e., chlorophyll *a*) and the aforementioned physical and chemical parameters were found.

1. INTRODUCTION

1.1 Background on *Karenia brevis* Blooms

Coastal communities across the United States have been increasingly impacted by red tides, or harmful algal blooms (HABs) (Anderson 1995). *Karenia brevis* is the dinoflagellate responsible for the majority of Florida's red tide blooms. Originally described as *Gymnodinium breve* (Davis 1948), it was later reclassified as *Karenia brevis* (Daugbjerg et al. 2000). Numerous toxic microalgal species have been identified in the Gulf of Mexico (GOM), but only *K. brevis* has been found to repeatedly cause fish kills and present a health risk through the production of brevetoxins (Steidinger et al. 1998). Incidents of fish kills and discolored water in Florida are not a new phenomenon. The Ft. Myers News Press published the first written reference in 1577 (Karen Steidinger, Fish and Wildlife Conservation Commission, pers. comm.). The first official report was published in 1844 (as cited in Rounsefell and Nelson 1966), although the causative organism was not identified until 1946 (Davis 1948).

Karenia brevis is commonly found in the GOM at background concentrations of up to 10^3 cells L^{-1} (Steidinger 1975; Geesey and Tester 1993). However, *K. brevis* blooms in west Florida coastal waters often occur at concentrations of 10^6 cells L^{-1} or greater. It is unclear exactly what causes the cells to aggregate and blooms to occur, but it is believed that natural processes such as ocean circulation patterns and meteorological events are contributing factors (Steidinger et al. 1998; Vargo et al. 2001). Once a bloom has developed in offshore waters and has been transported to nearshore waters, it can often be maintained for several months to years (Walsh et al. 2003).

Four distinct stages have been proposed for *K. brevis* blooms: initiation, growth, maintenance, and termination/dissipation (Steidinger and Vargo 1988). It is hypothesized that blooms originate in the mid West Florida Shelf (WFS), approximately 18-74 km offshore (Steidinger and Haddad 1981; Steidinger et al. 1998). The blooms undergo an increase in biomass via normal cell growth of approximately 0.3 divisions per day, or via physical aggregation. The blooms are then transported inshore by a combination of factors such as wind, tidal, and current action, the exact relationships of which are yet to be identified

(Steidinger et al. 1998). Nearshore blooms can be maintained for months to years, probably by nutrients from point and non-point sources, such as agricultural runoff and river runoff (Geesey and Tester 1993; Steidinger et al. 1998). When conditions are no longer favorable, the bloom dissipates.

Laboratory studies have shown that a Florida isolate of *K. brevis* exhibits optimum growth rates at salinities between 27 and 37 ppt and at temperatures between 22 and 28°C (Aldrich and Wilson 1960; Wilson 1966; Eng-Wilmot et al. 1977). Early field studies by Finucane and Dragovich (1959) and Rounsefell and Nelson (1966) generally support those findings. Steidinger and Ingle (1972) reported the occurrence of *K. brevis* in Tampa Bay at a temperature of nearly 38 °C, but this was probably an anomalous event. These temperature and salinity preferences demonstrate that *K. brevis* is a shelf species, not an estuarine species.

1.2 Effects of *K. brevis* Blooms

Karenia brevis blooms are of special concern to the general public for many reasons. When wave and wind action disrupts the cells, the brevetoxins become aerosolized and this can cause respiratory distress in humans (Pierce 1986; Pierce et al. 1990). Swimmers have complained of itching and irritation when swimming in *K. brevis* blooms (Landsberg 2002). Human consumption of shellfish contaminated by brevetoxins has resulted in cases of Neurotoxic Shellfish Poisoning (NSP) (Baden 1989). Symptoms of NSP include nausea, vertigo, abdominal pain, and diarrhea (Landsberg 2002). NSP is of concern not only to consumers who eat shellfish, but also to fishermen whose livelihoods are directly affected when shellfish harvesting areas are closed. Finally, the economic costs of beach cleanups and reduced tourism can be considerable (Habas and Gilbert 1974). This is of particular importance in Florida, where tourism is one of the states' major industries (Steidinger and Vargo 1988). For example, the 1971 red tide bloom on the west coast of Florida was estimated to have economic damages of \$20,000,000 (Habas and Gilbert 1974). The 1995-96 Florida event cost at least twice as much (Solutions To Avoid Red Tide, www.start1.com).

In addition to its negative health effects on people, *K. brevis* blooms have caused illness and death to a variety of wildlife. In 1982, 39 manatees (*Trichechus manatus latirostris*) died from exposure to *K. brevis*, with an additional 149 manatee deaths in 1996 along the west coast of Florida (O'Shea et al. 1991; Bossart et al. 1998). Other organisms such as fish, shellfish, birds, and dogs have also been negatively

impacted by *K. brevis* exposure (Steidinger et al. 1973; Forrester et al. 1977; Steidinger and Vargo 1988; Lipscomb et al. 1994; Landsberg 2002).

1.3 Hydrography

There are distinct seasonal hydrographic changes that characterize the WFS environment. Summer patterns include thermal stratification with strong vertical gradients (Vargo et al. 2001). During the fall transitional period, atmospheric cold fronts penetrate southward and vertical mixing occurs, resulting in a relatively homogenous water column (Yang and Weisberg 1999; Vargo et al. 2001; Vargo et al. in press). Salinity fronts occur as a result of the increased rainfall during the summer and fall rainy season (Vargo et al. 2001). Thermal and salinity fronts can be formed when estuarine water moves into the coastal zone, which can result in horizontal stratification (Vargo et al. in press).

Upwelling is of major importance in the WFS area. Upwelling may be generated by interactions between currents or by current-landmass interactions (Haddad and Carder 1979). Wind also plays a major role in the coastal upwelling and downwelling in this area (Weisberg et al. 2000). Along-shelf water flow is primarily a result of the along-shelf component of wind stress (Yang and Weisberg 1999). The across-shelf transports also lead to coastal upwelling and downwelling, and may greatly impact the distributions of important continental marine materials (Yang and Weisberg 1999). The shelf circulation responds rapidly to the wind changes (Yang et al. 1999), therefore the southward flow of the Loop Current along the upper slope/outer shelf can be a source of upwelled water to the WFS (Haddad and Carder 1979).

The hydrography and associated features of the water column of the WFS affects the distribution of *K. brevis* cells and the initiation of blooms. *K. brevis* blooms have been associated with the vertically homogenous water column that often occurs just after breakdown of vertical stratification (Vargo et al. 2001). The formation of thermal and salinity fronts is often associated with elevated *K. brevis* populations, as they act as both barriers and a means of transport (Vargo et al. 2001). Upwelling could influence the onshore and offshore movements of *K. brevis* blooms (Haddad and Carder 1979).

1.4 *K. brevis* and Nutrients

Karenia brevis can utilize a variety of nutrients, both organic and inorganic, in order to form and maintain blooms (Vargo and Shanley 1985; Steidinger and Vargo 1988; Bronk et al. in press).

Consequently, the oligotrophic environment of the Gulf of Mexico is favorable to *K. brevis* blooms (Steidinger et al. 1998). In fact, the blooms can contribute a significant amount of the annual primary productivity in this area (Vargo et al. 1987).

The specific sources of major nutrients (i.e., nitrogen and phosphorus) required to maintain long lasting blooms have not been positively identified (Steidinger et al. 1998, Vargo et al. 2001), although internal recycling of nutrients in surface waters is a major factor in oligotrophic waters (Harris 1986). Adequate nutrient sources must be available to support offshore bloom initiation. Offshore nutrient sources could include upwelling/downwelling events, the direct input of ammonia from rain (Steidinger et al. 1998), and regeneration via the grazing activity of heterotrophic flagellates on bacteria (Caron and Goldman 1990; Carlsson and Graneli 1998). Another source of offshore nutrients, particularly nitrogen, could come from the excretion of NH_3 and dissolved organic nitrogen (DON) amino acids, including excretion from the diazotroph *Trichodesmium* spp. (Lenes et al. 2001; Walsh and Steidinger 2001).

Nutrients in the nearshore environment on the WFS come from a variety of point and non-point sources (Steidinger et al. 1998). Nearshore nutrients could be provided by atmospheric deposition, although it can supply only a small fraction of the nutrients needed for *K. brevis* bloom maintenance (Heil et al. 2001; Vargo et al. 2001; Vargo et al. in review). Nearshore nutrients could also be derived from resuspended sediments and/or near-bottom phytoplankton populations (Heil et al. 2001; Vargo et al. 2001), through regeneration via excretion following grazing activity (Caron and Goldman 1990), macrozooplankton and microzooplankton excretion, or the remineralization of dead and decaying fish killed during blooms (Walsh et al. in review).

Another possible source of both organic and inorganic nearshore nutrients (especially phosphorus) is estuarine influx, particularly during the wet season and when trapped by near-shore fronts (Vargo et al. 2001; Vargo et al. in press). Vargo et al. (in press) demonstrated that estuarine transport could supply from 5 to 20% of the nitrogen required and 4 to 90% of the required phosphorus to support the daily growth needs of a *K. brevis* bloom of 3×10^5 cells L^{-1} . However, these nutrients are restricted to a relatively small

area just offshore, except during periods of high river flow such as during the rainy season (Vargo et al. in review). Therefore, estuarine transport could only be a source of nutrients for bloom maintenance, and could not be the sole nutrient source.

1.5 Nutrient Stoichiometry

Hodgkiss and Ho (1997) stated, “Nutrient ratios can be...important regulators, particularly in terms of species selection.” Eutrophication of coastal waters alters nutrient ratios, and is an important factor in the increased blooming of some species as well as in species changes (Smayda 1990; Hodgkiss and Ho 1997). This is not a local issue applicable only to the *K. brevis* populations in the WFS, it is a worldwide concern (Hodgkiss and Ho 1997).

Phytoplankton growth is frequently nutrient limited, and the uptake of nutrients often follows the Redfield ratio (Smayda 1989). The Redfield ratio is a relatively constant stoichiometric ratio at which organisms fix carbon, nitrogen, and phosphorus, and is typically around 106:16:1 (C:N:P) (Redfield 1958; Redfield et al. 1963). Heil (1986) found typical particulate molar ratios for cultures of *K. brevis* in seawater-based medium to be: C:N = 6-11; C:P = 90-107; N:P = 9-19. Shanley and Vargo (1993) reported C:N values of 7.7-11.5. Heil et al. (2001) found an average *in situ* N:P ratio of a *K. brevis* bloom of 39.3. These results vary from Redfield ratios. Klausmeier et al. (2004) found that the Redfield ratio (in particular N:P) is an average of species specific ratios, as opposed to a universally accepted number, and that could explain some of these variations.

According to Hecky and Kilham (1988), “deviations from mean dissolved nutrient concentrations are the rule.” However, it is important to know not only the concentration of the nutrient, but also the pool size and the rate of turnover (Harris 1986). Deviations in these factors often lead to nutrient limitation, although it is essential to note that only one nutrient can be limiting at any given time (Droop 1974; Rhee 1978; Kilham and Kilham 1984). In fact, Hecky and Kilham (1988) state that every phytoplankton population is, or soon will become, limited by something.

No single factor has been found to limit the accumulation of *K. brevis* blooms on a consistent basis, rather it is a combination of physical and chemical environmental parameters, including nutrient

availability (Steidinger et al. 1998). However, *K. brevis* blooms have occurred in waters where the concentrations of inorganic nitrogen and phosphorus were potentially limiting (Heil et al. 2001). Vargo et al. (in press) demonstrated that particulate N:P ratios have indicated that some *K. brevis* blooms were P-limited, while N-limitation occurred in others. According to Harris (1986), the amount of total nitrogen stock and the flux of dissolved inorganic nitrogen (DIN) are necessary to determine the limiting nutrient. The limiting nutrient may depend on the stage of the bloom (Vargo et al. in press), and on the relative turnover times of the nutrient pools, rather than on their concentrations (Harris 1986).

Nutrient:chlorophyll *a* ratios are also important factors in phytoplankton growth. The C:Chl ratio is of particular importance as specific growth rate is determined by the amount of photosynthesis (normalized to chlorophyll *a*) divided by the C:Chl ratio (Cullen et al. 1992). Typical C:Chl, N:Chl, and P:Chl weight ratios for *K. brevis* cultures are: C:Chl = 241-516; N:Chl = 21-79; P:Chl = 6-15 (Heil 1986). Shanley (1985) reported values of C:Chl ratios of 59-124, while Goldman (1980) reported values of 100-150 at low proportions of maximum growth rates and 25-50 at high proportions of maximum growth rates.

1.6 Study Background

HABs across the world occur in many diverse and variable forms, and their effects on people and wildlife are just as variable (Anderson 1995). While our knowledge of the toxicology and ecology of these algal species has increased dramatically over the past few decades, there is still much to be learned. To address this need, the National Science Foundation (NSF) and the National Oceanic and Atmospheric Administration (NOAA) co-sponsored a workshop in 1994 on the Ecology and Oceanography of Harmful Algal Blooms (ECOHAB) (Anderson 1995).

While the ECOHAB workshop encompassed a variety of national issues, each region of the United States clearly faced varying and complex issues that were unique to the area and the harmful algal bloom species present. The regional ECOHAB programs were formed as a result of this workshop, including the Gulf of Mexico regional ECOHAB program, ECOHAB:Florida. Seasonal outbreaks of HABs (specifically *Karenia brevis*) are recurrent phenomena in Florida, and they have captured the attention of both the general public and scientists for more than half a century (Kusek 1998). Through

studies initiated by the ECOHAB:Florida programs, and the work to understand the population dynamics and trophic impacts of Florida HABs continues today.

The principle objectives of the ECOHAB:Florida program included:

1. modelling the initiation, maintenance, and export of *K. brevis* red tides on the WFS on different temporal and spatial scales to predict landfall,
2. identifying the physical parameters that affect movement and concentration of *K. brevis*, and
3. determining the nutrient sources that allow growth and persistence of large *K. brevis* populations in coastal waters (Steidinger et al. 2004).

In support of these goals, the ECOHAB:Florida program included a series of monthly hydrographic cruises on the WFS from June 1998 through August 2002. These cruises consisted of three onshore-offshore transects from Tampa Bay to Charlotte Harbor which defined the ECOHAB:Florida “control volume”, an area with known boundaries (for modeling purposes) in the region of West Central Florida where *K. brevis* blooms commonly occur.

In addition to these monthly ECOHAB:Florida transects, a monthly alongshore transect of 13 stations was supported with funds from the state of Florida. This transect went from Tampa Bay to Charlotte Harbor along the 10-meter isobath, and allowed for sampling of nearshore blooms and the examination of the physical conditions and nutrient status of these blooms.

1.7 Study Objectives

The current study focuses on the even-numbered stations of the alongshore transect of the monthly research cruises over a three-year period (1999-2001). The following hypotheses will be examined:

1. The surface distribution of *K. brevis* populations varies seasonally and spatially in relation to estuarine derived density fields.
2. Particulate matter (C, N, and P) and their ratios vary seasonally, spatially, and interannually.
3. There are differences in particulate matter ratios between bloom and non-bloom periods.
4. Dissolved nutrient concentrations vary seasonally, spatially, and interannually.

5. The dissolved nutrient concentrations differ between bloom and non-bloom periods.
6. Relationships exist between biological indicators of blooms (i.e., chlorophyll *a*) and physical and chemical parameters.

2. METHODS

As part of the multidisciplinary ECOHAB:Florida program, monthly hydrographic cruises were conducted on board one of two research vessels, R/V Suncoaster or R/V Bellows, operated by the Florida Institute of Oceanography (FIO). Over the three-year course of the monthly synoptic ECOHAB cruises, approximately 72 stations were sampled (Fig. 1). These stations were chosen to obtain a representative sample of the physical, chemical and biological descriptors of this area of the WFS ecosystem. My study will focus on three years (1999, 2000, 2001) of data from seven of those stations (70, 72, 74, 76, 78, 80, 82) (Table 1) that followed an alongshore transect at the 10-meter isobath from Tampa Bay to Fort Myers. Those stations were chosen because significant *K. brevis* blooms were found in these nearshore waters during the three years included in this study (Fig. 2D). In this study, a “bloom” is defined as an accumulation of *K. brevis* cells with a concentration of 5000 cells L⁻¹ or higher. This value was chosen because it is the minimum concentration level at which a shellfish harvesting ban is enforced in Florida (Earnest Truby, Fish and Wildlife Conservation Commission, pers. comm.).

A seawater pump connected to a reservoir containing a Falmouth Scientific CTD (conductivity, temperature, and density), a SeaPoint chlorophyll *a* fluorometer, and a Wetlabs C Star transmissometer was used for constant underway collection of surface data. All stations were sampled quasi-synoptically within a 48 hour period. A vertical CTD profile, using a Seabird CTD, was conducted at each station. At even-numbered stations, water samples were collected at 0 and 5 m during the CTD cast with a rosette sampler and 8 L Niskin bottles. Water from both depths was collected for determination of chlorophyll *a*, inorganic nutrients (NO₃₊₂, PO₄) and *K. brevis* concentrations. Additionally, water samples from 0.5 m were processed for total dissolved phosphorus (TDP), total dissolved nitrogen (TDN), particulate phosphate (PP), particulate nitrogen (PN), and particulate carbon (PC).

Water samples collected for determination of TDP concentrations were processed according to the methods of Solórzano and Sharp (1980). Briefly, water samples were passed through precombusted (2 hours, 450°C) GF/F filters (25 mm), 0.2 ml of 0.17 M MgSO₄ was added, and the samples were frozen on

board the ship. All samples were taken back to the University of South Florida (USF) College of Marine Science where they were dried and then baked at 450-500°C for 2 hours. After adding 3 ml of 0.75 M HCl, the samples were heated at 80°C in a drying oven. Deionized water and 1 ml of mixed reagent was added to each sample, and the samples were analyzed with a Beckman Spectrophotometer Model DU550. Dissolved organic phosphorus (DOP) was determined by subtracting inorganic PO₄ values from TDP concentrations.

Samples collected to determine particulate phosphate were processed according to the methods of Solórzano and Sharp (1980). Water samples were passed through precombusted (2 hours, 450°C) GF/F filters (25 mm), and filters were washed twice with 2 ml aliquots of Na₂SO₄. After adding 2 ml of 0.017 M MgSO₄ to each sample, the filters were frozen in precombusted (2 hours, 450°C) scintillation vials. All samples were taken back to USF College of Marine Science and analyzed with a Beckman Spectrophotometer Model DU550.

Duplicate particulate carbon and nitrogen samples were collected on precombusted (2 hours, 450°C) GF/F filters (13 mm). The filters were rinsed with 0.1N HCl in filtered (0.7µm) seawater to remove inorganic carbonate, followed by a filtered seawater rinse to remove the acid. The samples were frozen in precombusted (2 hours, 450°C) aluminum foil on board the ship and taken back to USF College of Marine Science. The samples were then lyophilized for 24 hours, frozen and stored in darkness, and analyzed using a Carlo Erba Elemental Analyzer Model 1106 (Heil et al. 2001).

To determine inorganic nutrients (PO₄⁻, NO₂, NO₃⁻+NO₂), unfiltered seawater samples from discrete depths were collected from the CTD Niskin bottles in 30 mL HDPE bottles and frozen upright at -20°C. These samples were analyzed on shore following the methods of Gordon et al. (1993), using either an Astoria Analyzer using continuous flow analysis with colorimetric detection or an Alpkem RFA III segmented-flow nutrient analyzer.

Chlorophyll *a* samples were analyzed using the Holm-Hansen and Reimann (1978) protocol. Duplicate water samples were filtered through GF/F filters (25 mm), which were immediately placed in 10 ml methanol in polycarbonate tubes, capped, and mixed on a vortex mixer. Samples were wrapped in

aluminum foil and stored at 0°C until analysis. All samples were taken back to USF College of Marine Science where they were analyzed within one week of collection using a Turner Design 10AU fluorometer.

Samples to determine live *K. brevis* concentration were collected from the Niskin bottles directly into 15 ml scintillation vials. Samples were counted on the ship within 2 hours of collection using a Zeiss dissecting microscope. Values reported are the average of five replicate counts of *K. brevis* in 0.2 ml of surface water according to the methods of Heil et al. (2001). The samples were then preserved with Lugol's Iodine (Tomas 1997).

3. RESULTS

3.1 Hydrography

3.1.1 Temperature

Throughout the three-year study period, the average water temperature reached a maximum of nearly 31°C in August and September, and was at a minimum in January (Fig. 3A, Table 2). The annual average water temperature at all stations combined was similar in 1999 and 2000 (24.34°C and 24.98°C, respectively), but was a degree lower in 2001 (23.38°C) (Fig. 4A). Along the cruise track, average water temperatures were slightly lower at the northern stations, and increased slightly along the sampling path in the southern direction in 1999 and 2000 (Fig. 5A). However, in 2001 the temperature was essentially the same at the northern and southern stations with a peak at station 78. There was minimal vertical and horizontal thermal stratification at all sites in all years (Fig. 2A, Fig. 6).

3.1.2 Salinity

The average salinity typically decreased to minimum values in the late summer and fall, during the rainy season (defined as June through October) (Fig. 3B, Table 2). Horizontal stratification was evident, especially during this period in 1999 and 2001 (Fig. 2B). Strong vertical salinity stratification occurred in these months of all three years as well (Fig. 7). The annual average salinity at all stations combined was similar in 2000 and 2001 (36.28 and 35.89 ppt, respectively), and more than 1 ppt lower in 1999 (34.78 ppt) (Fig. 4B). Along the cruise track, salinity was somewhat lower near the northern and southern ends of the transect, probably due to riverine input from Tampa Bay (northern stations) and Charlotte Harbor (southern stations) (Fig. 5B). Salinity was slightly higher at the middle stations, with the maximum salinity being reached at station 76. In 2001, however, this pattern changed and showed a slight decrease at station 76, with an increase in salinity at the three southern stations.

3.1.3 Density

Average water density decreased in the late summer and fall due to inputs of less dense water from increased tropical storm activity, increased rainfall, and increased river runoff (Fig. 3C, Table 2, Appendices A and B). Both vertical and horizontal density stratification was evident for most months of the year in this study period (Fig. 8, Fig. 2C). The annual average density at all stations combined was very similar in 2000 and 2001 (24.22 and 24.33 kg/m³ respectively), and lower in 1999 (23.28 kg/m³) (Fig. 4C). There was some evident annual density pattern along the cruise track in 1999 and 2000 (Fig. 5C). Lower values were found at the northern and southern locations with the mid stations generally exhibiting slightly elevated values.

3.1.4 Hydrography and *K. brevis* Blooms

All of the *K. brevis* blooms occurred at salinities that fell well within the reported ranges previously mentioned (Aldrich and Wilson 1960; Rounsefell and Nelson 1966; Wilson 1966; Eng-Wilmot et al. 1977) (Table 2). However, there were a few months where blooms occurred outside the reported temperature ranges. Of note are the January 1999 bloom, where the average water temperature was well below the previous reports, and the September 2001 bloom, where the average water temperature was above the earlier reports.

The surface *K. brevis* blooms that occurred in this study area all did so in the fall and winter months (Fig. 2D). Their locations varied, with the majority of the larger and more dense blooms found at the northern and middle stations. *K. brevis* concentrations also varied throughout this study, with surface cell counts ranging from 0 to 5.27x10⁶ cells L⁻¹ (Table 3).

In this study area, *K. brevis* blooms occurred in a wide range of temperatures (16-31 °C) and salinities (32-37 ppt) (Table 2, Fig. 9A and B). The average water density also varied during bloom months (20-26 kg m⁻³) (Fig. 9C).

Fig. 2 shows the location and concentration of *K. brevis* blooms as they relate to hydrographic factors in the study area. The large *K. brevis* bloom in late 1999 is clearly associated with the salinity and density fronts that occurred during this period. The highest cell counts occur north of the areas of low

salinity and density. The bloom that occurred in late 2001 began in an area of low density, which also corresponded with decreasing salinity. This was also just north of an area of higher surface temperature. The bloom appeared to spread over the cruise transect as surface density and salinity decreased. It appears that the area of low salinity in November and December of 2001 at station 82 resulted in lower cell counts in this area.

3.2 Chlorophyll *a*

The average chlorophyll concentration varied annually (Fig. 10). It was similar in 1999 and 2001 (2.37 and 2.07 $\mu\text{g L}^{-1}$ respectively), and lowest in 2000 (1.22 $\mu\text{g L}^{-1}$). Along the cruise track, the average chlorophyll values showed an overall increase from north to south (Fig. 11) in 2000 and 2001. However, in 1999, the values for the northern and middle stations were much higher than the southern stations. The monthly average chlorophyll values were relatively low (mostly $<2 \mu\text{g L}^{-1}$) throughout the three year sampling period, with the exception of October 1999 and 2001 (Figs. 12 and 13). These chlorophyll peaks coincide with the presence of very dense blooms of *K. brevis* seen in Figure 2.

3.3 Particulate Matter

Average total molar particulate carbon values were lower in 1999 and 2000 (34.68 and 39.28 respectively), and were much greater in 2001 (49.67) (Fig. 14A). Along the cruise track, the average total particulate carbon was slightly higher at the end stations (Fig. 15A). The observed trend may be correlated with estuarine input in the south from Charlotte Harbor. This pattern did not hold true in 2001, when the average total particulate carbon value increased at station 80. The amount of total particulate carbon fluctuated monthly, and did not appear to follow any annual pattern consistently over the three year study period (Fig. 16A).

The highest average total particulate nitrogen value was measured in 1999 (11.07; Fig. 14B), while the average values in 2000 and 2001 were lower (5.65 and 7.01 respectively). The average total particulate nitrogen values were relatively constant along the cruise track in 2000 and 2001 (Fig. 15B). However, in 1999, stations 72 and 82 had annual average molar nitrogen values that were more than twice as high as those stations in the other years (17.58 and 14.68 respectively). Total particulate nitrogen levels

were mostly <10 throughout the three-year sampling period, with few exceptions (Fig. 16B). There was a large increase in particulate nitrogen during the summer and early fall of 1999, where values were more than triple what they were in the other years.

The highest annual average molar particulate phosphate value was in 2001 (0.238) (Fig. 14C). The average values in 1999 and 2000 were similar (0.176 and 0.156 respectively). In 1999 and 2001, the annual average particulate phosphate was higher at the end stations and lowest at the mid stations (Fig. 15C). The exception to this is in 2000, where the lowest values were at the northern stations. The amount of particulate phosphate in the water fluctuated monthly, and did not appear to follow any consistent pattern over the entire year (Fig. 16C). However, there were peaks in March and October of 1999 (0.283 and 0.315 respectively) and 2001 (0.488 and 0.291 respectively).

3.4 Dissolved Nutrients

Average nitrite (NO_2) values were similar in all three years of this study (Fig. 17A). However, the values in 2000 showed the greatest variability. Along the cruise track, the average NO_2 fluctuated somewhat throughout the three years (Fig. 18A). There was a large increase in NO_2 at station 74 in 2000. The amount of NO_2 fluctuated monthly, and did not appear to follow any annual pattern consistently over the three year study period (Fig. 19A).

Average nitrate (NO_3) values fluctuated throughout this study (Fig. 17B). The values were lowest in 1999 (0.03 μM), and were similar in 2000 and 2001 (0.19 and 0.15 μM , respectively). The values in 2000 showed the greatest variability. Along the cruise track the average NO_3 fluctuated somewhat throughout the three years, and did not appear to follow any consistent pattern (Fig. 18B). There was a large increase in NO_3 at station 74 in 2000. The amount of NO_3 was relatively constant on a monthly basis, with the exceptions of July 2000 and June 2001 (Fig. 19B).

Average inorganic phosphorus (PO_4) values fluctuated throughout this study (Fig. 17C). The values were greatest in 1999 (0.25 μM), and lowest in 2001 (0.10 μM). The values in all three years showed great variability. Along the cruise track the average PO_4 fluctuated somewhat throughout the three years, and did not appear to follow any consistent pattern (Fig. 18C). The amount of PO_4 also fluctuated on a monthly basis (Fig. 19C).

3.5 Nutrient Stoichiometry

The nutrient stoichiometry of particulate matter varied greatly (Table 4). Average particulate molar C:N values were similar in 2000 and 2001 (9.66 and 8.97, respectively), and were lower in 1999 (7.46) (Fig. 20A). The molar C:N ratio fluctuated monthly, and did not appear to follow any annual pattern consistently over the three year study period (Fig. 21A). Along the cruise track the molar C:N ratio fluctuated somewhat throughout the three years (Fig. 22A).

Average particulate molar C:P values were similar in 1999 and 2001 (238.39 and 234.10, respectively), and were higher in 2000 (280.43) (Fig. 20B). The molar C:P ratio fluctuated monthly, and did not appear to follow any consistent annual pattern (Fig. 21B). The molar C:P ratio along the cruise track fluctuated somewhat throughout the three years (Fig. 22B).

Average particulate molar N:P values were highest in 1999 (48.61), and lowest in 2001 (31.89) (Fig. 20C). The values were the most variable in 1999. The molar N:P ratio fluctuated monthly, although most values were below 40 (Fig. 21C). Along the cruise track the molar N:P ratio fluctuated somewhat throughout the three years (Fig. 22C). In 2000 and 2001, some evidence of estuarine effects could be seen, as the values at the northern and southern stations were lower than that at the middle stations.

4. DISCUSSION

4.1 *K. brevis* and Hydrography

HYPOTHESIS: The surface distribution of *K. brevis* populations varies seasonally and spatially in relation to estuarine derived density fields.

Knowledge of hydrographic factors is vital in understanding the distribution of *K. brevis* blooms. Temperature (Eppley 1972; Goldman and Ryther 1976) and salinity fronts and the resultant density fronts, as well as other factors such as wind direction and coastal currents, are key to bloom growth, development, and movement (Steidinger et al. 2001).

The WFS exhibited definite seasonal and spatial hydrographical patterns (Fig. 2A, B, C). The average water temperatures were higher in the summer and early fall months and cooler in the winter months (Fig. 3A), which corresponded with the local air temperature patterns (Wooten 1985). The average salinity and density decreased in the late summer and fall (Fig. 3B and C, Table 2, Appendices A and B, Fig. 7), because of increased precipitation from local convectional and tropical storms (Schmidt et al. 2001). Salinity and density were lower at the end stations in 1999 and 2000, probably due to input of riverine water from Tampa Bay and Charlotte Harbor.

According to Vargo et al. (2001), the waters of the WFS typically show strong vertical stratification in the summer months. The salinity and density data for this study area corroborate this (Fig. 7, Fig. 8). Atmospheric cold fronts, vertical mixing, and upwelling due to wind lead to the breakdown of stratification, and result in a relatively homogenous water column in the fall and winter (Wiseman and Sturges 1999; Weisberg et al. 2000; Vargo et al. 2001). Most *K. brevis* blooms on the WFS occur after the breakdown of vertical stratification (Vargo et al. in press). Horizontal stratification, and therefore the development of thermal, salinity, and density fronts, often occurs when precipitation within the Tampa Bay and Charlotte Harbor watersheds leads to an increased flux of estuarine water moving into the coastal zone (Wiseman and Sturges 1999; Vargo et al. in press). These coastal fronts are key factors in bloom movement, and can contain *K. brevis* blooms nearshore (Lester et al. 2001; Steidinger et al. 2001). In fact, the longest lasting and densest *K. brevis* blooms occurred in conjunction with the periods of lowest surface

density (Fig. 2C, D). The cores of the blooms often appear to be on the higher salinity and density side of surface fronts (Fig. 2B, C, D) (Haddad 1982).

Since the *K. brevis* blooms occurred in the cooler fall and winter months, one would expect the average water temperature during the bloom months to be lower than during the non-bloom months. However, the average temperature during the non-bloom months is slightly lower than that during the bloom months (Table 5). This could be because the hydrographic data for some of the warmer months was not obtained. Also, when blooms occurred, they often did so in the years with warmer water temperatures in that specific month (Table 2). For example, blooms occurred in January 1999 and 2000, but not in January 2001, and the water temperature was much lower in January 2001 than in the previous two years.

Hurricanes and tropical storms are major weather phenomena in Florida and can have a great influence over the hydrography of the broad shallow shelves that are characteristic of the WFS (Wiseman and Sturges 1999). The Atlantic hurricane season lasts from June 1-November 30 (NOAA/National Weather Service- National Hurricane Center data). These storms, as well as the associated rainfall (Appendix B), could easily affect water temperature, salinity, density, and movement. Three major storms occurred off the west coast of Florida during this study period. Tropical Storm Harvey took place on September 19-22, 1999. No major effects from this storm were seen on land in the area adjacent to this study area. Hurricane Gordon occurred September 14-18, 2000. Its intensity was strongest on September 17, approximately 165 nautical miles southwest of Tampa. On land, the damage was felt by many, as more than 20,000 homes were without power for more than six hours. In addition, numerous homes along the immediate Florida west coast from the Tampa Bay area northward to Cedar Key experienced some minor roof damage (NOAA/National Weather Service- National Hurricane Center data). Hurricane Gabrielle occurred September 11-19, 2001. Many rivers experienced major flooding, including the lower St. Johns River, Manatee River, Little Manatee River, Myakka River, Peace River, and Horse Creek (NOAA/National Weather Service- National Hurricane Center data). All September sampling cruises were run prior to each of these storms. All October sampling cruises were run approximately 2 weeks after the end of each storm. These storms, and the associated increased precipitation, probably account for the sharp drop in temperature (Virmani and Weisberg 2003), salinity, and therefore density in September and October in each year (Fig. 3 A, B).

4.2 Particulate Matter and Associated Ratios

HYPOTHESIS: Particulate matter (C, N, and P) and their ratios change seasonally, spatially, and annually.

Phytoplankton are largely responsible for the primary production in the ocean and therefore are an important source of particulate matter (Qian et al. 2003). The amount of particulate matter and the associated ratios measured in this study area varied annually (Figs. 14 and 20). Seasonal variations in particulate matter are also evident (Fig. 16). Two estuaries bound this study area: Tampa Bay in the north and Charlotte Harbor in the south. The heavy rainfall in June-October of each year, as well as the hurricanes in October 2000 and 2001, created increased river flow within these watersheds. This led to increased nutrient loads in the water, and resulted in more nutrients available to the phytoplankton (Hecky and Kilham 1988; Sigua et al. 2000; Vargo et al. 2001; Ringuet et al. 2003). Table 6 shows the increase in average particulate C:P and N:P ratios in the rainy season. The large increase ($>0.35 \text{ mg L}^{-1}$) in particulate nitrogen during the summer and early fall of 1999 (Fig. 16B), as well as the high particulate carbon values in October 2000 and 2001 (Fig. 16A), could also be due to the increased nutrient availability from these atmospheric events.

Spatial variations in the amount of particulate matter can also be seen. The input of estuarine water seemed to have an effect on the amounts of particulate C and P, as concentrations increased at the end stations (Fig. 15A, C) (Vargo et al. 2001). Greater urbanization, especially in the Tampa-St. Petersburg area, may account for these differences (Vargo et al. in review). Interestingly, the estuaries did not appear to be a source of particulate N (Vargo et al. 2001). Some spatial variations in particulate ratios can also be seen (Fig. 22).

The Redfield ratio is typically around 106:16:1 (C:N:P) (Redfield 1958; Redfield et al. 1963). According to Goldman (1980), the chemical composition of phytoplankton typically exhibits ratios close to or at Redfield at very high growth rates. However, others have found phytoplankton to be more flexible in their stoichiometry (Rhee 1978; Sterner and Elser 2002; Klausmeier et al. in press), primarily due to the presence of stored nutrients (Klausmeier et al. 2004). Klausmeier et al. (2004) assert the Redfield N:P ratio of 16:1 is not “universally optimal,” and competitive equilibrium selects high N:P values. In fact, some studies have found that the N:P stoichiometry differs significantly from Redfield more often than not, and should not be unexpected (Duarte 1992; Hecky et al. 1993; Elser and Hassett 1994; Karl et al. 2001). While

particulate C:N ratios from this study fell within or close to the range of reported values (Heil 1986, Shanley and Vargo 1993), the other nutrient ratios did not (Fig. 23, Table 4). The mean particulate N:P and C:P molar values found in this study were more than double typical ratios found by Heil (1986), and were well above Redfield ratios.

The ratios determined by Heil (1986) and Shanley and Vargo (1993) were for pure cultures, while the water samples used in this study contained an assemblage of other microorganisms. Therefore the variations in C:P and N:P ratios in this study could be due to the presence of other organisms or detritus in the water. Harris (1986) found the proportions to exceed Redfield ratios at low growth rates, which could be another explanation for these discrepancies. High N:P ratios could be a result of growth limitation by trace elements (Valiela 1995). As cells accumulate N and P, their growth could be slowed by the lack of something else, such as a trace element, resulting in high N:P ratios. This type of limitation may be particularly important in oligotrophic waters. Finally, variations in the Redfield ratio could also be attributed to changes in algal nutrient status (Guildford and Hecky 2000) or from surface adsorption of P (Sanudo-Wilhelmy et al. 2004).

According to Hecky and Kilham (1988), “Deviance from the optimum nutrient ratio can lead to limitation by one or the other nutrient.” While Ryther and Dunstan (1971) found nitrogen to be “the critical limiting factor to algal growth”, Karl et al. (2001) found increasing N:P ratios indicative of P-limitation in surface ocean waters. Myers and Iverson (1981) found P to be the nutrient most limiting to phytoplankton growth in estuarine areas in the northeastern GOM. In this study, the elevated N:P and C:P molar values suggest that *K. brevis* growth was P-limited, which is puzzling given the fact that the presence of inland phosphate deposits results in P-enriched watersheds (Vargo et al. in press). Therefore, one would expect high P flux into the coastal zone. However, Vargo and Shanley (1985) described P-limited blooms within Charlotte Harbor. While Heil et al. (2001) and Vargo et al. (2001) described both estuaries as being N-limited, C:N ratios that fell close to Redfield imply populations with adequate nitrogen supplies (Vargo et al. in press). Therefore, if nitrogen is not limiting, as the C:N ratios suggest, then the elevated N:P ratios are suggestive of P-limitation (Vargo et al. in press). It is possible that the type of limiting nutrient may actually vary with the time of year, location, age, and/or biomass of each bloom (D’Elia et al. 1986; Fisher et al. 1992; Pennock and Sharp 1994; Vargo et al. in press). The identification of the limiting factor is of

the utmost importance in understanding the ecology of the local water system and to water management practices (Beardall et al. 2001).

4.3 Particulate Ratios in Bloom and Non-bloom Periods

HYPOTHESIS: There are differences in particulate matter ratios between bloom and non-bloom periods.

There were clearly differences in particulate matter ratios between bloom and non-bloom periods (Fig. 23, Table 5). Many stations without *K. brevis* blooms had average particulate C:N ratios that were below the Redfield ratio, while most stations with *K. brevis* blooms were above the Redfield ratio (Fig. 23A). Every station without *K. brevis* blooms had average particulate C:P ratios that were above the Redfield ratio, as did every station with *K. brevis* blooms except for one (Fig. 23B).

The majority of the stations with *K. brevis* blooms had average particulate N:P ratios that were greater than the Redfield ratio but less than 60 (Fig. 23C). The highest value was 69.37. However, the values in 1999 were below the Redfield ratio. There were more variations in the non-bloom stations, where most values were also less than 60, but the highest value was 177.46.

However, when values from all stations with *K. brevis* blooms were averaged, and values from all stations without blooms were averaged, the particulate C:N, C:P, and N:P ratios from this study area were all above the Redfield ratios (Table 5). There was no systematic relationship between any ratio and bloom or non-bloom condition.

There were also differences between the blooms. The particulate N:P ratios for the bloom stations in 1999 were generally lower than the other two years, while the ratios in 2001 were generally the highest (Fig. 24). It is interesting to note that the densest *K. brevis* blooms were found in 1999 (Appendix C).

4.4 Dissolved Nutrients

HYPOTHESIS: Dissolved nutrient concentrations vary seasonally, spatially, and interannually.

Dissolved nutrients play an important role in regulating the amount and type of phytoplankton present (Turpin and Harrison 1979). For example, Hodgkiss and Ho (1997) demonstrated that the increasing dissolved phosphate and nitrate levels resulted in large increases in standing crop of phytoplankton and an increase in red tide blooms. The DOC pool, one of the largest organic carbon pools

on earth, can also have a strong impact on phytoplankton (Farrington 1992).

Estuaries are susceptible to cultural eutrophication (Hecky and Kilham 1988), and this study area is no exception. The amount of P-loading from point sources is 85% in Charlotte Harbor and 90% in Tampa Bay (Turner and Rabalais 1999). This study area is clearly impacted by these estuarine inputs of P (Fig. 18C). The flux increases during the rainy season due to intensified river flow, and results in increased nutrient loads in the water (Hecky and Kilham 1988; Vargo et al. 2001). As expected, the data show that the dissolved inorganic nutrients appeared to increase slightly in the rainy season (Fig. 19), however, there are several months where these data are missing. Vargo et al. (in press) found a similar pattern for DOP.

While the amount of dissolved nutrients seemed to fluctuate annually (Fig. 17), spatial patterns in dissolved nutrients could be seen in this study area. The outwelling of PO_4 typically accompanied fluxes of estuarine water onto the shelf, particularly from Charlotte Harbor (Fig. 18C). There was no significant estuarine outwelling of NO_{3+2} due to the elevated levels of PO_4 in both Tampa Bay and Charlotte Harbor (Heil et al. 2001; Vargo et al. 2001). Therefore both estuaries are typically N-limited (Pennock et al. 1999; Vargo et al. 2001), display very low dissolved inorganic nitrogen: dissolved inorganic phosphorus (DIN:DIP) (Vargo et al. 2001), and cannot be considered a major source of DIN for coastal waters (Vargo et al. in review). While estuarine input clearly influenced the concentration of P at the 10 m isobath, not all of the nutrients are transported quite so far. Vargo et al. (in review) found TN, DON, and DIN concentrations at the 10 m isobath were as much as 70% lower than those found at the mouth of Tampa Bay and Charlotte Harbor.

In addition to estuarine input, sources of dissolved nutrients in marine waters can include sedimentation, cultural eutrophication, and other biogeochemical processes (Hecky and Kilham 1988). Eppley et al. (1973) and Dugdale (1976) also found the regeneration of nutrients in the euphotic zone to be an important source of nutrients for phytoplankton growth. Finally, the cyanophyte *Trichodesmium* have been associated with *K. brevis* blooms in Florida (Walsh and Steidinger 2001), and they release nearly 4-fold larger amounts of DON than background after episodic Saharan dust events on the WFS (Lenes et al. 2001). All of these sources can potentially result in large-scale temporal and spatial nutrient patchiness (Turpin and Harrison 1979), which could also affect the location and amount of phytoplankton present. In

fact, Pennock et al. (1999) found that Tampa Bay changed from a seagrass- to a plankton-dominated habitat as a result of eutrophication (Pennock et al. 1999).

4.5 Dissolved Nutrients in Bloom and Non-bloom Periods

HYPOTHESIS: The dissolved nutrient concentrations differ between bloom and non-bloom periods.

A primary regulator of phytoplankton processes is nutrient availability (Boynton et al. 1982). In this study, there were no major differences in the dissolved inorganic nutrient concentrations between bloom and non-bloom periods (Fig. 25, Table 5). The average nitrite and nitrate values were only slightly greater at the non-bloom stations than at the stations with blooms (Table 5). One reason for this could be that DIN in Tampa Bay is very scarce, often occurring at or below the limits of detection (Heil et al. 2001). There was virtually no difference in the PO₄ and total dissolved phosphate values between stations with and without blooms. This correlates with results found by Heil et al. (2001), and is indicative of the oligotrophic nature of the WFS. Vargo et al. (in press) found water column DIN:DIP molar ratios in this study area to be generally less than 1.0, most likely as a result of the limited DIN supply. These values also suggest P-enrichment from estuarine inputs rich in phosphate deposits (Vargo et al. in press).

The relationship between DON and *K. brevis* is not quite as clear. While Vargo et al. (in review) did find DON concentrations to be elevated during the summer and fall periods of 1998 and 1999, this did not correspond with the presence of *K. brevis* blooms. Lester et al. (2001) also did not find any patterns in DON relative to *K. brevis* biomass. However, blooms of the N₂ fixing cyanobacteria *Trichodesmium* sp., and the associated accumulation of DON have been found in the GOM (Lenes et al. 2001). Large *K. brevis* blooms can occur at the same time as, or just after the *Trichodesmium* blooms (Walsh and Steidinger 2001). This evidence points to a possible correlation between *K. brevis* blooms and increased levels of DON. Finally, Boynton et al. (1982) found strong relationships between annual N loading and peak values of phytoplankton production.

Other studies have conclusively demonstrated associations between dissolved nutrients and *K. brevis* biomass. Vargo et al. (in review) found peaks in DOP in November 1999 and 2001, as well as in October 2000 that all coincided with *K. brevis* blooms. Lester et al. (2001) found DOP concentrations to be

elevated during a bloom in November 1998-February 1999, but only during the highest concentrations of *K. brevis*.

4.6 Chlorophyll *a* and Physical and Chemical Parameters

HYPOTHESIS: Relationships exist between biological indicators of blooms (i.e., chlorophyll *a*) and physical and chemical parameters of the WFS.

One useful method of investigating of nutrient limitation in phytoplankton is by measuring chlorophyll *a* fluorescence (Beardall et al. 2001). The association of C and chlorophyll are important because they are often used as an estimate of biomass, which can then be used to estimate relative growth rates (Harris 1986; Cullen et al. 1992). However, the amount of cellular chlorophyll, as well as particulate N and P, is highly dependent on species and growth conditions (Goldman 1980).

There are clear relationships between chlorophyll *a* and the associated chemical parameters. For example, chlorophyll concentrations in Tampa Bay increased one to two orders of magnitude during the 1970s and 1980s as a result of PO₄ loading from phosphate mining operations (Boler 1995). Positive relationships between chlorophyll *a* and nutrients have also been found in Florida Bay, another marine dominated estuary (Pennock et al. 1999), as well as in Apalachicola Bay, FL (Pennock et al. 1999), Jinhae Bay in Korea (Yang 1989), and other areas (Boynton et al. 1982). In this study, C:Chl, N:Chl, and P:Chl weight ratios all fell within or close to the range of reported values (Shanley 1985; Heil 1986) (Table 7). However, all ratios were more than 40% higher during non-bloom months (Table 5). The P:Chl ratios during blooms were indicative of P limitation (Vargo et al. in press), while the C:Chl ratios from the blooms indicate that *K. brevis* could have utilized organic sources of C (Heil et al. 2001).

Interestingly, the highest C:Chl did not occur in conjunction with highest counts of *K. brevis* (Fig. 26) (Heil et al. 2001). A linear trend can be seen between particulate carbon and chlorophyll concentrations during months without *K. brevis* blooms (Fig. 26B). However, the R² value of 0.26 indicates that this is not a very good linear fit. No strong relationship was observed between particulate carbon and chlorophyll during months with *K. brevis* blooms (Fig. 26A). Nutrient concentrations in most estuaries in the Gulf of Mexico are generally lower than those in these other systems at higher latitudes in

North America. As a result, chlorophyll *a* concentrations are lower during bloom events and there is less accumulation of unassimilated phytoplankton material in stratified bottom waters (Cowan et al. 1996).

Boler (1995) found chlorophyll *a* concentrations were highest during the summer and early fall months in Tampa Bay. Boynton et al. (1982) found similar results in a study of 63 different estuarine systems. They also found chlorophyll *a* to be well above the mean at times of peak productivity. This concurs with the chlorophyll peaks found in this study in October 1999 and 2001 (Figs. 12 and 13), which correspond with the presence of very dense blooms of *K. brevis* (Fig. 2).

Chlorophyll *a* concentration seemed to be associated with hydrographic parameters, as shown in Figure 27. During bloom months, chlorophyll *a* primarily occurred in a temperature range of 20-28°C, while the range was larger during non-bloom months. Chlorophyll *a* was predominant at salinities ranging from 34-37 ppt, but was primarily at salinities of 34-36 ppt during bloom months. During bloom months, chlorophyll *a* was present at a density range of 22-26 kg m⁻³, while the density ranged from 21-27 kg m⁻³ during non-bloom months. The highest concentrations of chlorophyll *a* associated with *K. brevis* bloom events were typically found over a very narrow range of temperature and salinity, and therefore density.

5. CONCLUSIONS

The physical and chemical features of both the WFS and *K. brevis* blooms are multifaceted and sometimes unpredictable. However, this study has found the following trends and relationships:

1. The surface distribution of *K. brevis* populations changed seasonally and spatially in relation to estuarine derived density fields.
2. Particulate matter (C, N, and P) and their ratios varied spatially and interannually. Monthly variations were observed, but did not follow any specific seasonal pattern.
3. Particulate ratios indicated P-limited *K. brevis* blooms in this study area.
4. Particulate matter ratios differed between bloom and non-bloom periods.
5. Dissolved nutrient concentrations varied spatially and interannually. Values varied monthly, but there were no seasonal patterns observed.
6. The dissolved inorganic nutrient concentrations did not differ between bloom and non-bloom periods.
7. Relationships existed between biological indicators of blooms (i.e., chlorophyll *a*) and physical and chemical parameters.

K. brevis blooms are a regular occurrence on the WFS, and they can often have devastating effects on the local fauna. Many researchers have tried to find a way to permanently mitigate these blooms, but have yet to succeed. This study shows that *K. brevis* populations are strongly affected by factors such as hydrography, particulate matter, and dissolved nutrients. Therefore future studies should include a solid understanding of the physical and chemical parameters of the area in order to fully understand the density and distribution of *K. brevis*.

Table 1. ECOHAB stations, alongshore transect.

Station	Latitude	Longitude
70	26.4848	82.2249
72	26.6350	82.2683
74	26.7861	82.3347
76	26.9292	82.3849
78	27.0901	82.5464
80	27.2408	82.6270
82	27.3936	82.7132

Table 2. Average water temperature, salinity, and density (± 1 standard deviation), and ranges throughout the study period. *K. brevis* blooms occurred in months shown in bold type.

Month	Avg. Temp. (°C)	\pm S.D.	Range	Avg. Sal. (ppt)	\pm S.D.	Range	Avg. Dens. (kg m ⁻³)	\pm S.D.	Range
Jan 99	17.11	0.49	16.11-17.53	34.15	0.29	33.63-34.45	24.83	0.13	24.64-25.02
Feb	21.88	0.47	21.8-22.44	34.60	0.35	34.35-34.78	23.92	0.38	23.02-24.54
Mar	19.17	0.38	18.62-19.63	34.51	0.31	34.08-34.86	24.60	0.15	24.38-24.75
Apr	23.54	0.48	22.42-24.62	35.08	0.12	34.85-35.25	23.82	0.22	23.37-24.23
May	24.40	0.49	23.36-25.38	35.56	0.17	35.16-35.91	23.93	0.20	23.57-24.52
Jun	ND			ND			ND		
Jul	ND			ND			ND		
Aug	30.73	0.26	30.30-31.53	35.56	0.19	34.82-35.79	21.89	0.18	21.20-22.13
Sep	29.95	0.17	29.57-30.40	34.97	0.62	31.61-35.43	21.69	0.48	19.15-22.06
Oct	27.91	0.22	27.72-28.25	33.81	0.76	32.96-34.94	21.54	0.62	20.55-22.44
Nov	ND			ND			ND		
Dec	ND			ND			ND		
Jan 00	20.27	0.50	19.55-20.95	35.54	0.34	35.13-35.91	25.10	0.31	24.21-25.58
Feb	ND			ND			ND		
Mar	20.70	0.66	19.64-22.20	36.01	0.40	34.71-36.89	25.34	0.44	24.02-26.30
Apr	ND			ND			ND		
May	ND			ND			ND		
Jun	28.60	0.42	28.13-29.52	36.80	0.12	36.20-36.92	23.55	0.20	22.81-23.74
Jul	29.25	0.33	28.64-29.88	36.76	0.25	36.35-37.17	23.31	0.26	22.82-23.64
Aug	30.32	0.25	29.95-30.86	36.60	0.43	34.53-37.22	22.82	0.35	21.12-23.24
Sep	ND			ND			ND		
Oct	28.33	0.27	27.96-28.73	35.79	0.38	35.33-36.03	22.88	0.27	21.40-23.06
Nov	24.06	0.15	23.88-24.23	36.47	0.13	36.19-36.60	24.74	0.13	24.47-24.90
Dec	18.32	0.51	17.22-18.78	36.30	0.30	35.56-36.52	26.19	0.11	25.88-26.29
Jan 01	12.95	0.68	11.66-13.81	35.95	0.25	35.46-36.33	27.14	0.10	26.95-27.52
Feb	15.73	0.61	14.53-16.50	36.07	0.33	35.36-36.45	26.63	0.15	26.13-26.80
Mar	19.34	0.47	18.72-20.20	36.36	0.24	35.93-36.85	25.97	0.13	25.59-26.30
Apr	20.56	0.57	19.76-21.83	35.51	0.53	32.73-36.71	25.33	0.40	22.62-25.87

ND=No Data

Table 2 (Continued)

May	22.22	0.28	21.91- 22.48	36.44	0.13	36.13- 36.92	25.25	0.14	24.95- 25.70
Jun	28.36	0.57	27.49- 29.59	36.58	0.35	35.50- 37.34	23.46	0.22	22.38- 23.79
Jul	29.66	0.33	28.40- 30.22	36.61	0.30	35.57- 37.45	23.26	0.18	22.27- 23.57
Aug	29.18	0.06	29.03- 29.25	35.89	0.20	35.31- 36.10	22.68	0.15	22.26- 22.83
Sep	30.38	0.32	30.13- 30.74	36.14	0.26	35.89- 36.03	22.49	0.24	21.51- 22.77
Oct	26.90	0.38	26.24- 27.39	34.21	0.55	33.55- 34.81	22.15	0.33	21.37- 22.55
Nov	21.60	0.10	21.54- 21.69	35.46	0.19	35.19- 35.58	24.68	0.13	24.46- 24.84
Dec	23.69	0.20	23.48- 23.90	35.47	0.58	35.03- 35.73	24.14	0.21	23.68- 24.39

ND=No Data

Table 3. *K. brevis* cell counts (cells L⁻¹). Water samples were obtained from 0 meters using a CTD sampler.

1999	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Station												
70	200000	0	0	0	0	0	0	0	0	7500	ND	0
72	0	1000	0	0	0	0	0	0	0	32500	ND	2000
74	0	0	0	0	0	0	0	0	0	640000	ND	3000
76	4000	5000	0	0	0	0		0	0	3557500*	ND	0^
78	0	8000	0	0	0	0			0	2975000*	ND	0
80	0	244000	1000	0	0	0			0	5270000*	ND	0
82	0	422000	0	0		0			0	662000*	ND	0
2000	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Station												
70	4000	ND	1000	No	0	ND	0	0	0	0	0	ND
72	18000	ND	1000	Cruise	0	ND	0	0	0	1000	2000	ND
74	4000	ND	0		0	ND	0	0	0	61000	1000	ND
76	19000	ND	2000		0	ND	0	0	0	2000	0	ND
78	6000	ND	2000		0	ND	0	0	0	4000	5000	ND
80	5000	ND	1000		0	ND	0	0	0	1000	4000	ND
82	0	ND	0		0	ND	0	0	0	3000		ND
2001	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Station												
70	0	ND	0	0	ND	ND	0	0	3000	0		176000
72	0	ND	0	0	ND	ND	0	0	8000	8000	66000	16000
74	0	ND	0	0	ND	ND	0	0	211000	70000		44000
76	0	ND	0	1000	ND	ND	0	0	0	128000	254000	68000
78	0	ND	0	0	ND	ND	0	0	1000	107000	342000	58000
80	0	ND	0	0	ND	ND	0	0	0	17000		22000
82	0	ND	0	0	ND	ND	0	0	1000	28000		

ND=No data

^ *Rhizosolenia* bloom

*Dead fish present on surface

Table 4. Annual data summary of particulate molar nutrient ratios.

Year	Molar C:N Mean(Range)	Molar C:P Mean(Range)	Molar N:P Mean(Range)
1999	7.46 (0.09-33.45)	238.39 (15.22-672.22)	68.92 (10.90-712.10)
2000	9.66 (2.01-35.27)	280.43 (114.51-699.59)	38.71 (6.91-177.59)
2001	8.97 (3.11-13.21)	234.10 (104.74-488.93)	31.89 (12.87-140.54)

Table 5. Data summary of water column, cellular, and particulate ratios for bloom and non-bloom months during this study period (± 1 standard deviation).

	Bloom Months¹	Non-Bloom Months	
	Mean (\pm S.D.)	Mean (\pm S.D.)	Range
Avg NO ₂ ($\mu\text{mol L}^{-1}$)	0.03 (0.04)	0.07 (0.11)	0.00-1.05
Avg NO ₃ ($\mu\text{mol L}^{-1}$)	0.03 (0.07)	0.16 (0.41)	0.00-2.59
Avg PO ₄ ($\mu\text{mol L}^{-1}$)	0.16 (0.11)	0.17 (0.18)	0.00-1.45
Avg TDP ($\mu\text{g-at L}^{-1}$)	0.58 (0.46)	0.58 (0.68)	0.005-4.41
Particulate C:N	9.73 (5.64)	8.63 (3.78)	0.31-35.27
Particulate C:P	234.89 (80.46)	258.13 (72.38)	15.22-699.59
Particulate N:P	43.60 (50.21)	40.53 (28.13)	6.91-712.10
C:Chl (wt:wt)	356.52(205.08)	525.29 (260.22)	6.85-1705.70
N:Chl (wt:wt)	52.19 (39.33)	94.77 (56.04)	5.67-1014.39
P:Chl (wt:wt)	3.05 (1.36)	5.89 (2.71)	0.45-17.97
Avg Temp ($^{\circ}\text{C}$)	24.21 (4.14)	24.05 (5.64)	11.72-31.30

Bloom months=Jan 99, Feb 99, Oct 99, Jan 00, Oct 00, Nov 00, Sep 01, Oct 01, Nov 01, Dec 01

Table 6. Data summary of particulate ratios and particulate C, N, and P to chlorophyll ratios for wet season and dry season.

	Wet* Season		Dry Season		
	(Mean)	St Dev	(Mean)	St Dev	Range
Molar C:N	7.53	3.83	9.91	4.46	0.31-35.27
Molar C:P	279.71	153.67	242.52	86.02	15.22-699.59
Molar N:P	52.16	39.14	34.03	30.48	6.91-712.10
P:Chl (wt:wt)	4.93	3.14	5.25	2.45	0.45-17.97
N:Chl (wt:wt)	86.27	61.67	80.42	51.26	5.67-1014.39
C:Chl (wt:wt)	404.50	241.68	537.52	256.53	6.85-1705.70

*Wet season is June through October

Table 7. Annual average (wt:wt) ratios of particulate C,N, and P to chlorophyll.

	P:Chl (wt:wt) Mean(Range)	N:Chl (wt:wt) Mean(Range)	C:Chl (wt:wt) Mean(Range)
1999	4.57 (0.45-13.86)	109.40 (11.28-1014.39)	422.14 (6.85-1400.65)
2000	5.47 (1.47-13.86)	84.77 (17.07-259.65)	577.33 (70.00-1705.70)
2001	5.13 (0.60-17.97)	71.00 (5.67-338.21)	445.87 (53.58-1218.25)

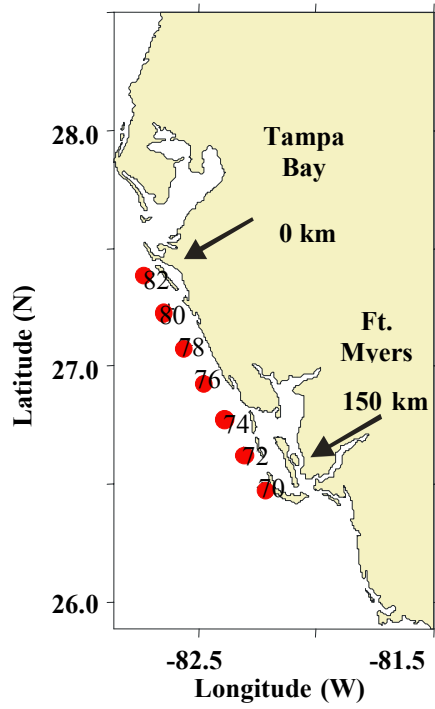


Figure 1. ECOHAB Bellows transect with locations of stations 70-82.

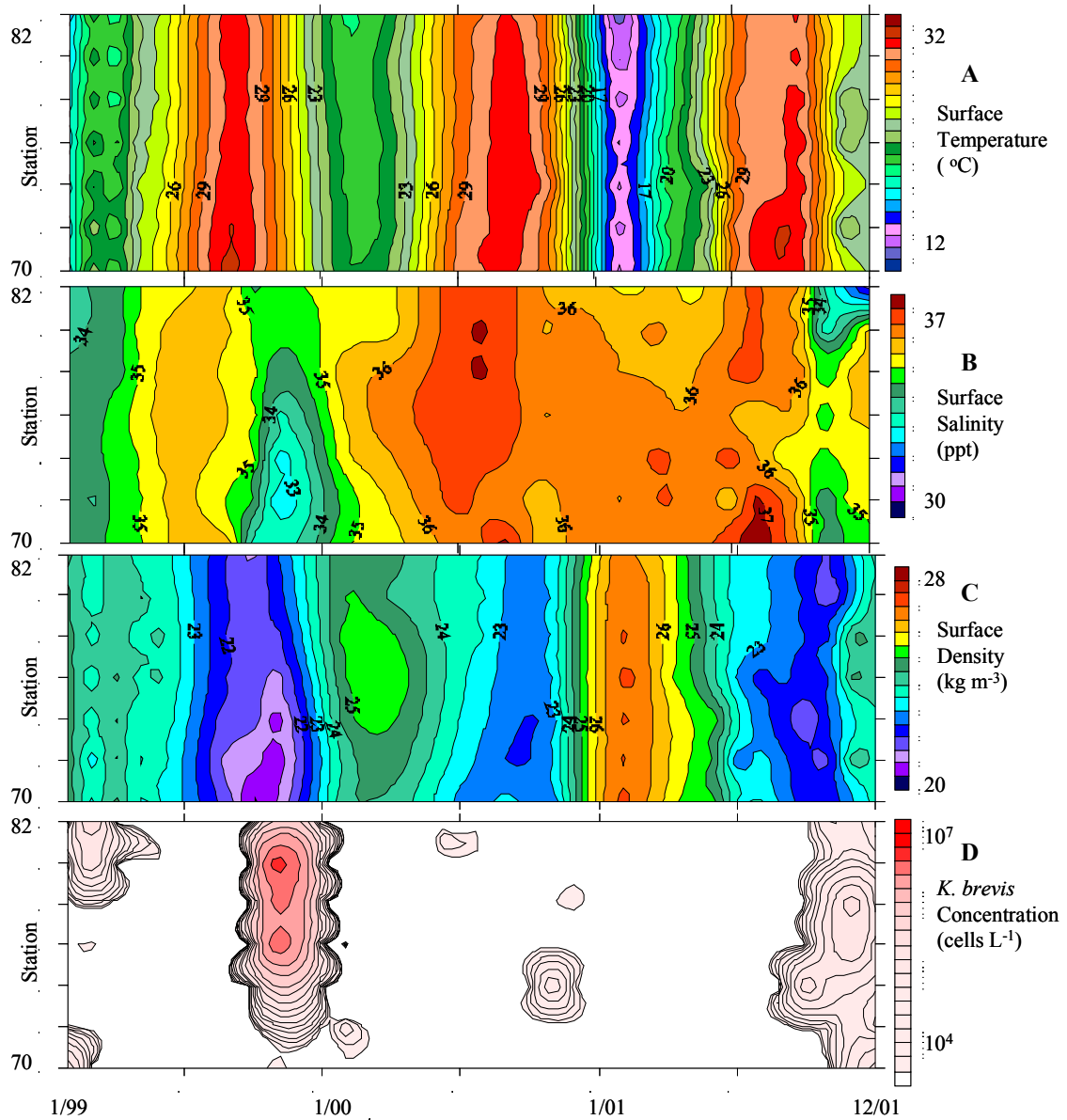


Figure 2. Surface (A) water temperature, (B) salinity, (C) density, and (D) *K. brevis* concentration at all stations

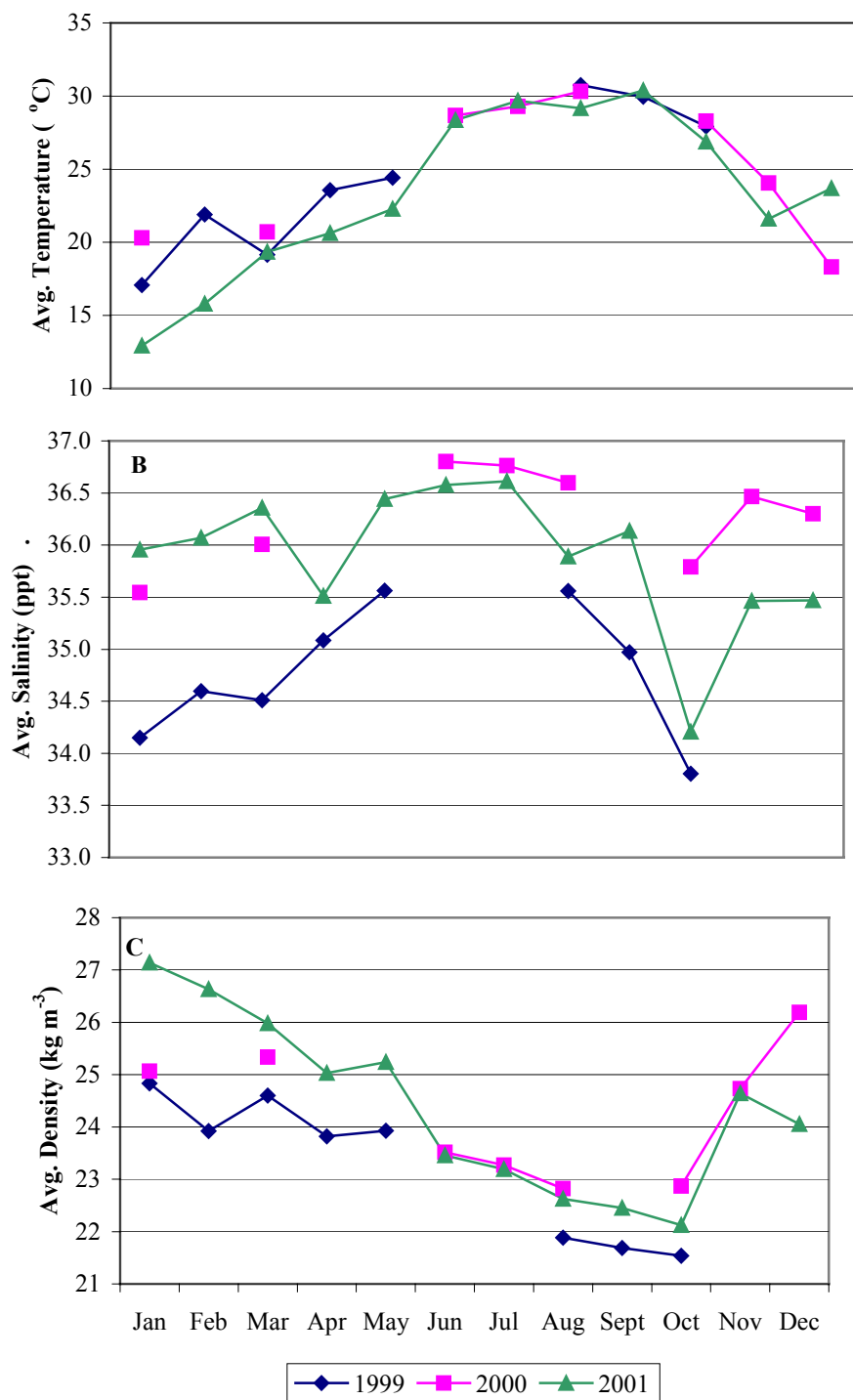


Figure 3. Average (A) water temperature, (B) salinity, and (C) density at all stations over time.

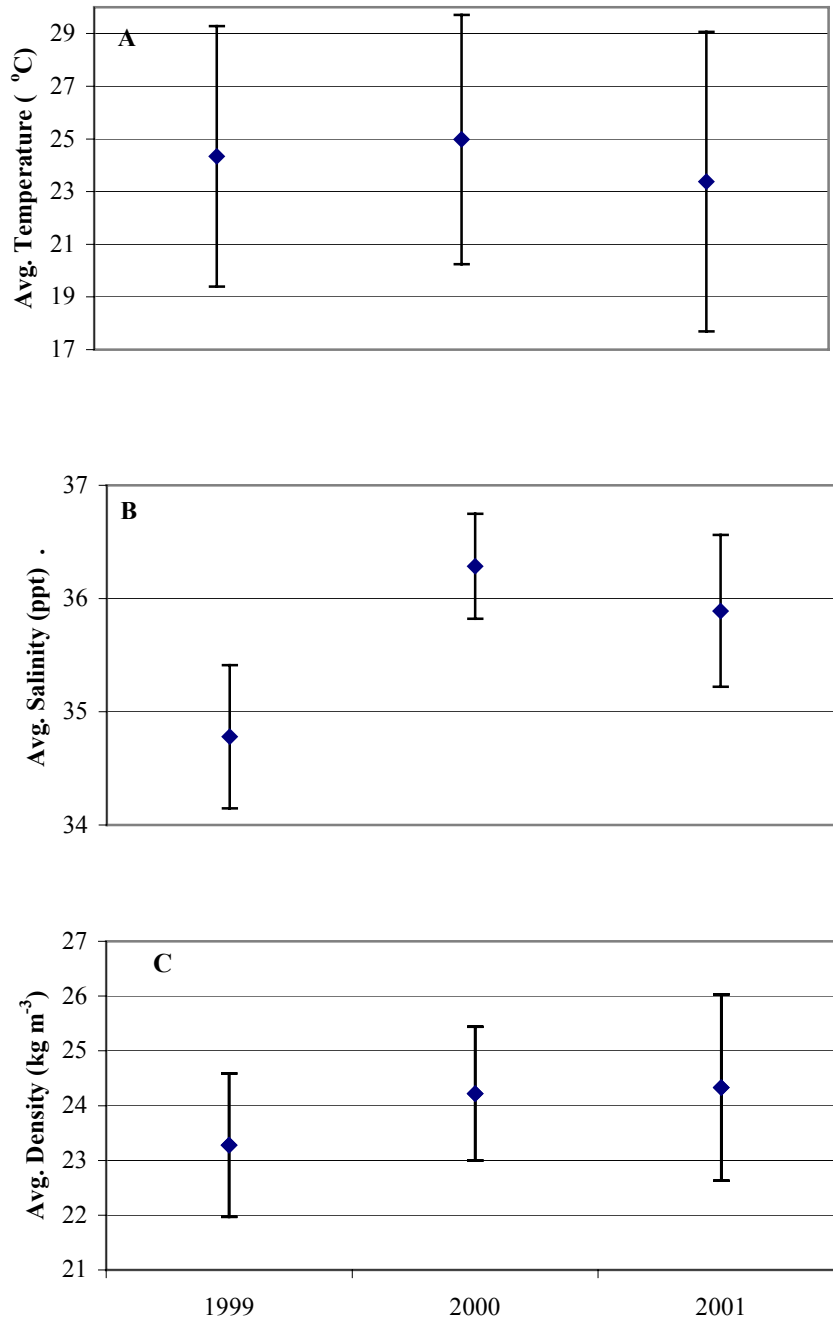


Figure 4. Annual average (A) water temperature, (B) salinity, and (C) density at all stations. Error bars represent one standard deviation.

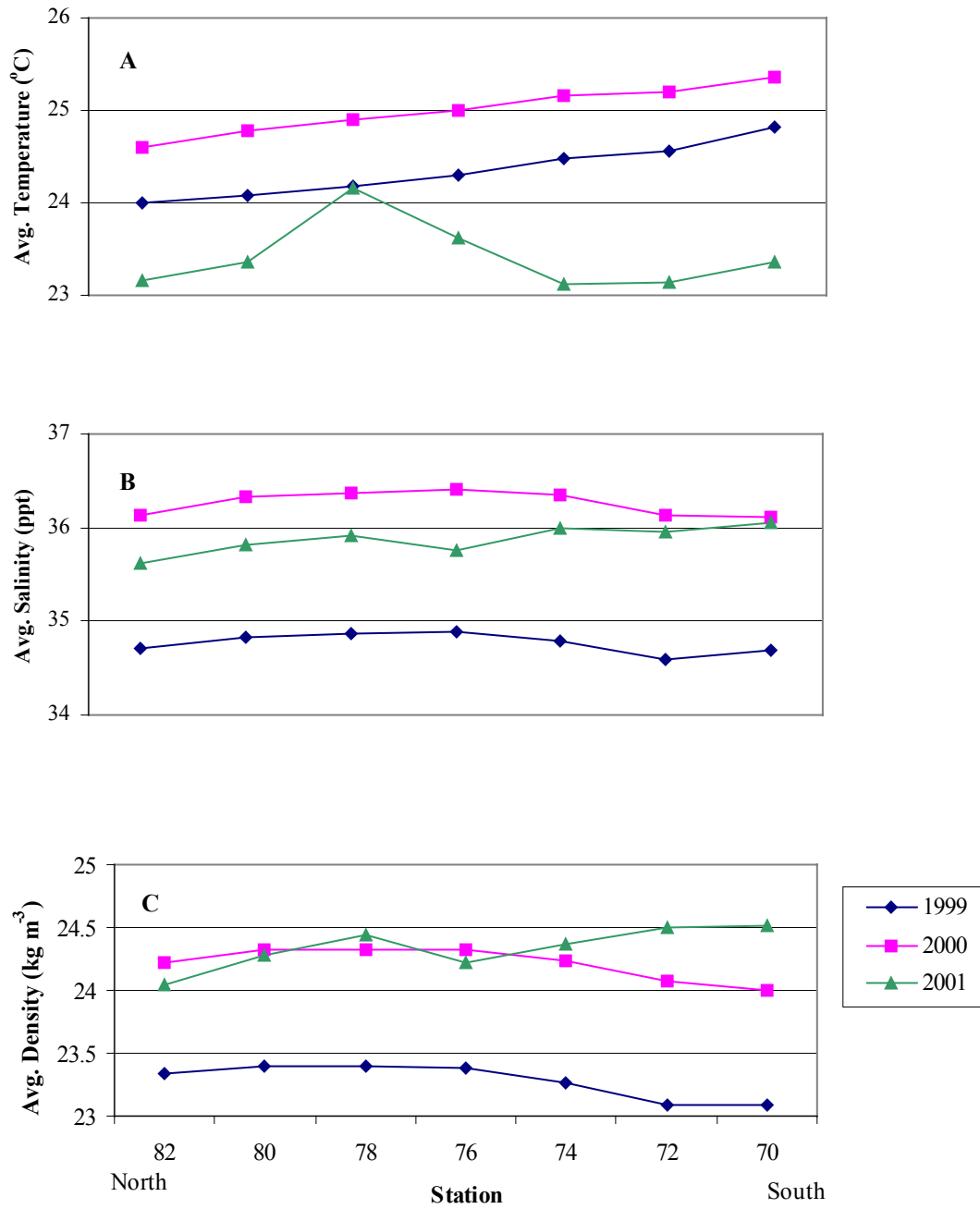


Figure 5. Annual average (A) water temperature, (B) salinity, and (C) density along the cruise track.

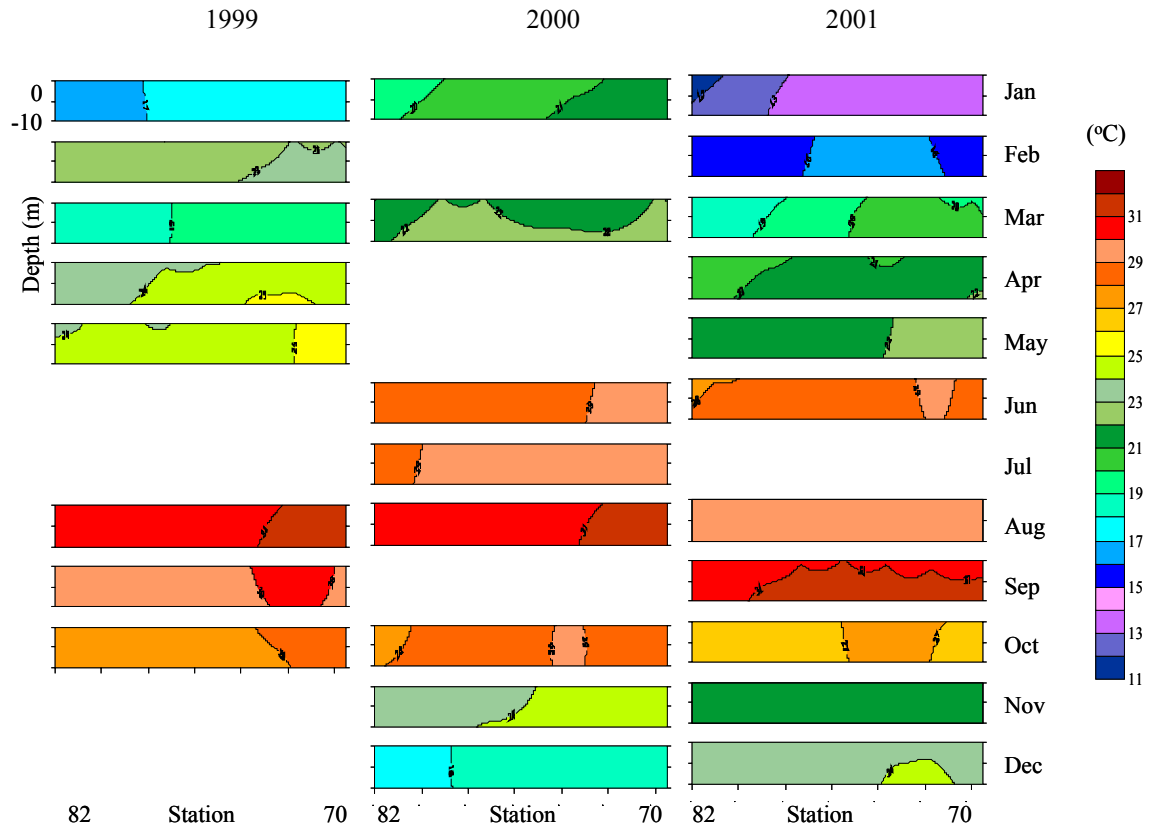


Figure 6. Average water temperature with depth.

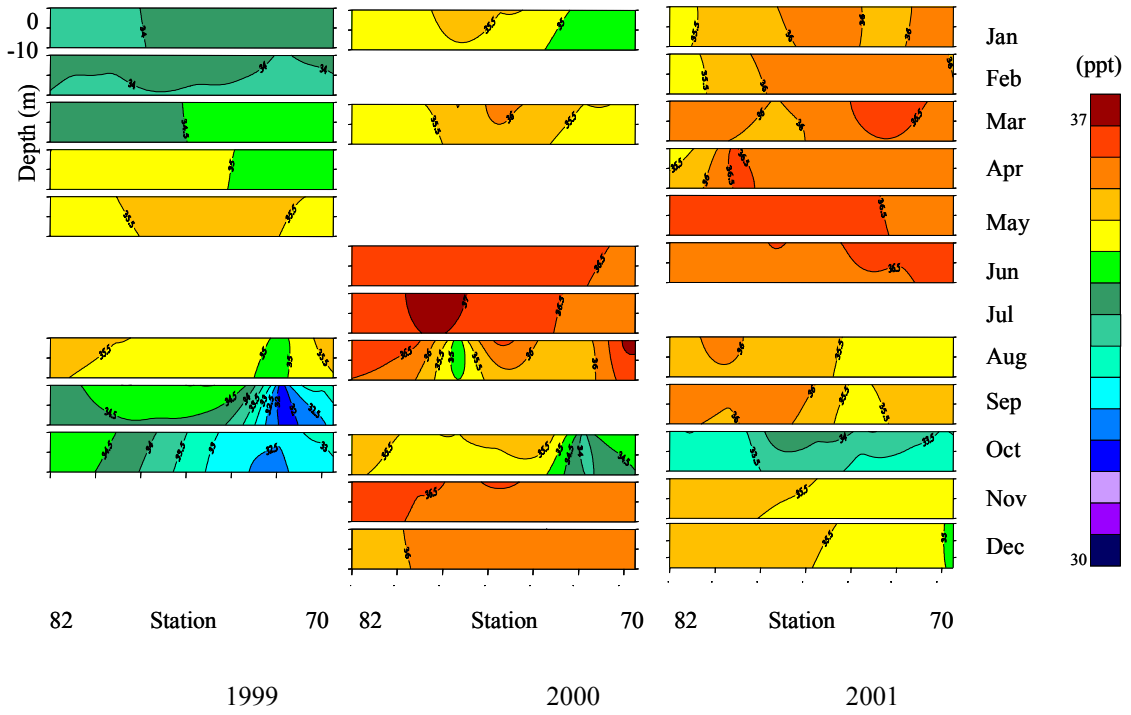


Figure 7. Average salinity with depth.

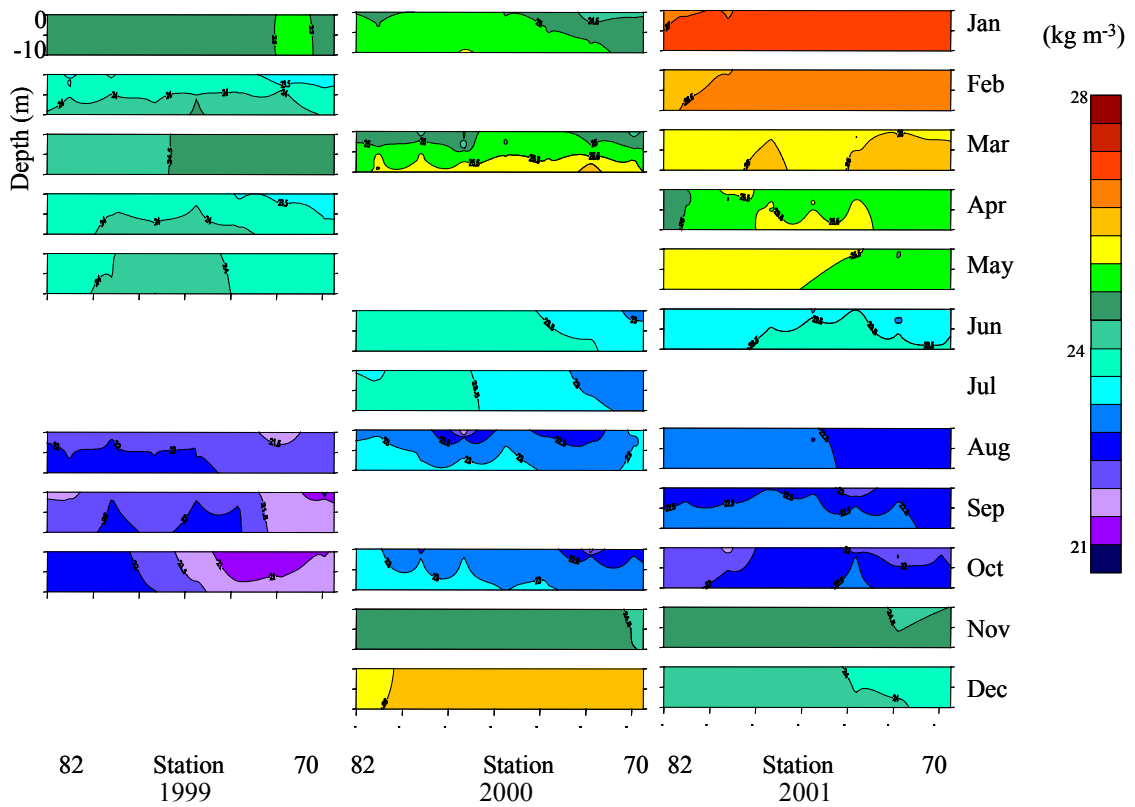


Figure 8. Average density with depth.

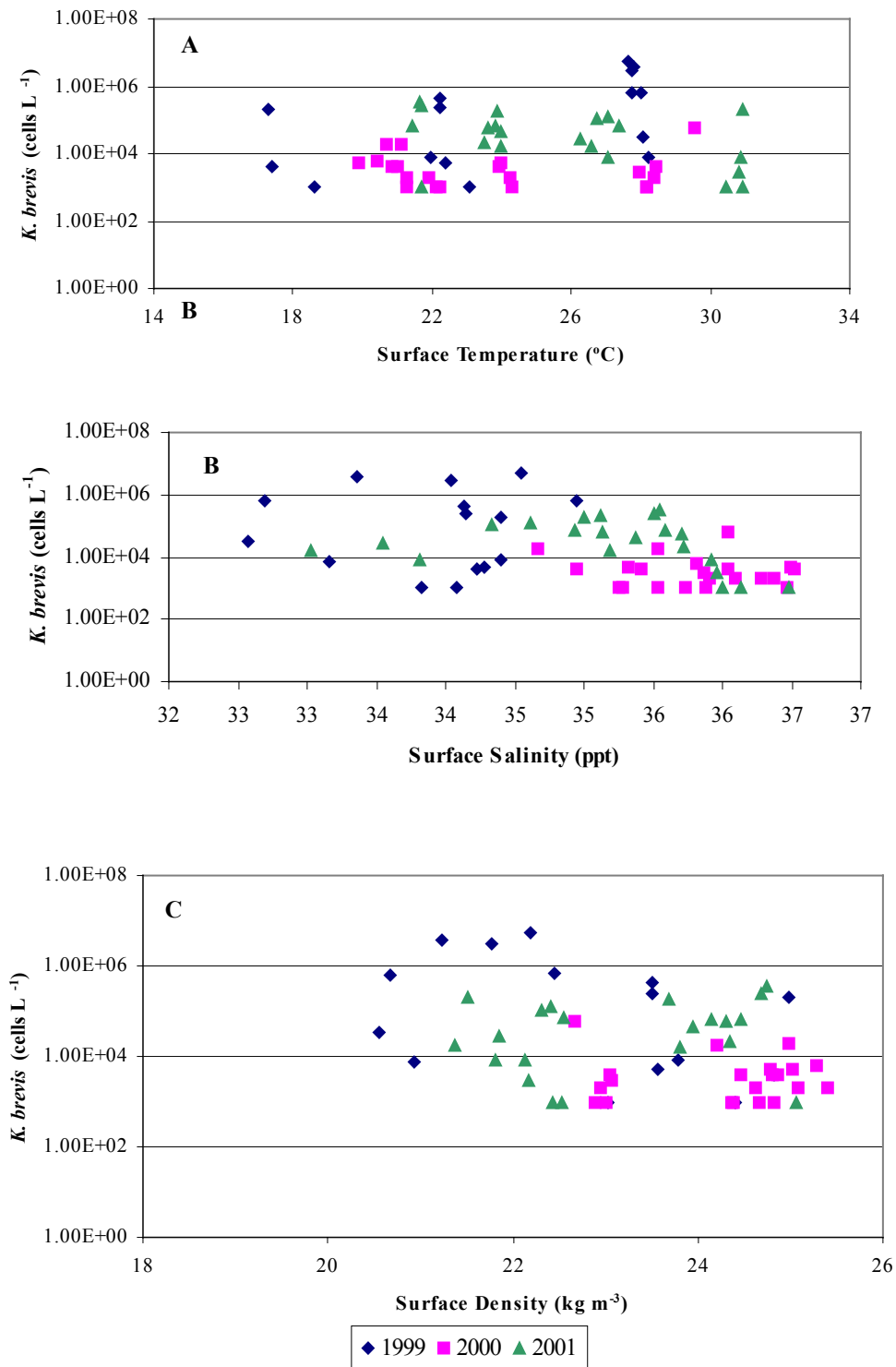


Figure 9. Surface (A) temperature, (B) salinity, and (C) density vs. surface *K. brevis* concentration, at stations where *K. brevis* was present.

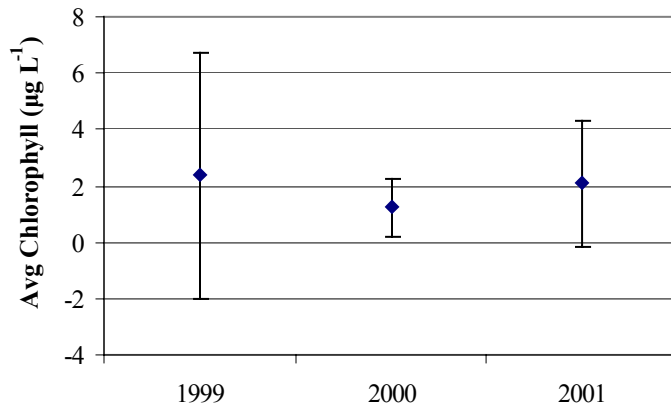


Figure 10. Annual average chlorophyll values ($\mu\text{g L}^{-1}$) at all stations. Error bars represent one standard deviation.

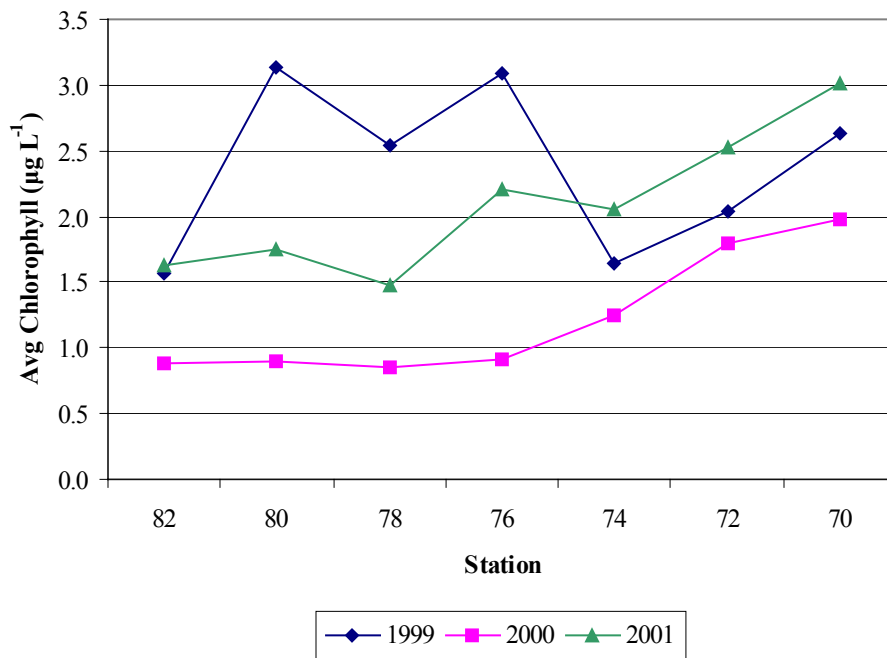


Figure 11. Annual average chlorophyll values ($\mu\text{g L}^{-1}$) along the cruise track.

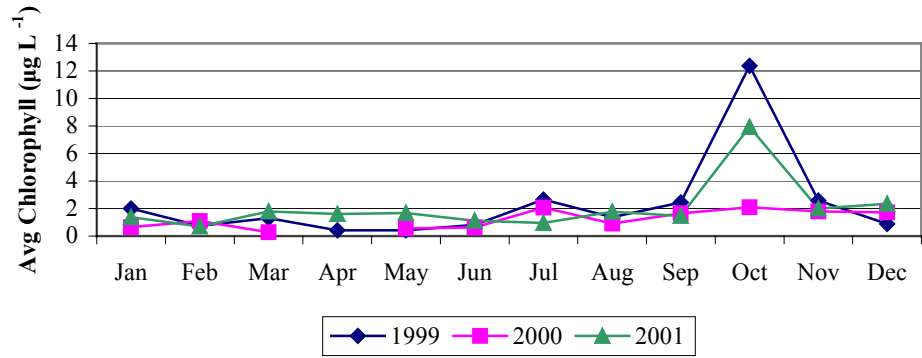


Figure 12. Annual average chlorophyll values ($\mu\text{g L}^{-1}$) at all stations over time.

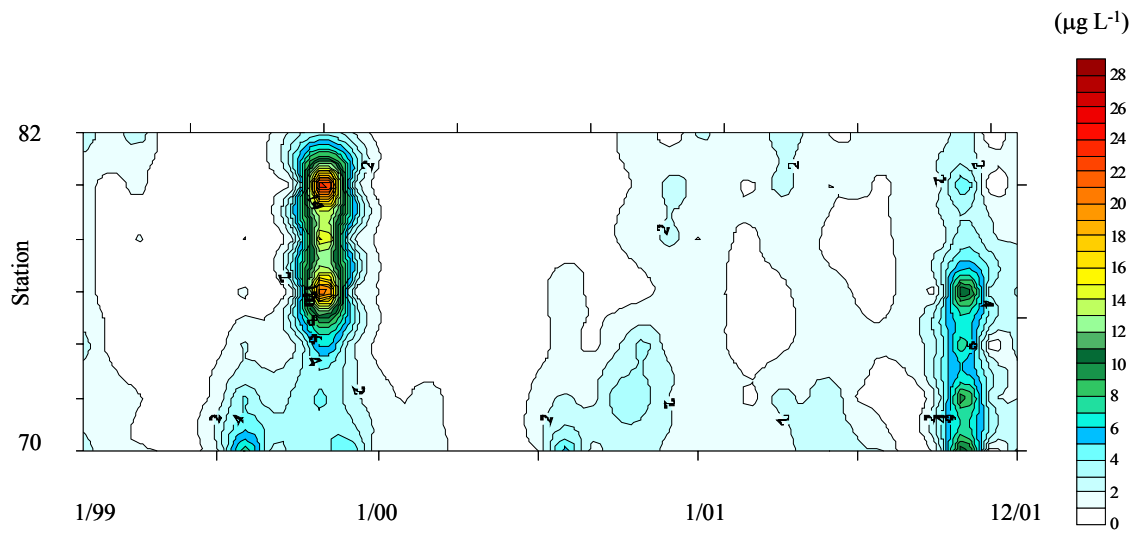


Figure 13. Average surface chlorophyll values ($\mu\text{g L}^{-1}$).

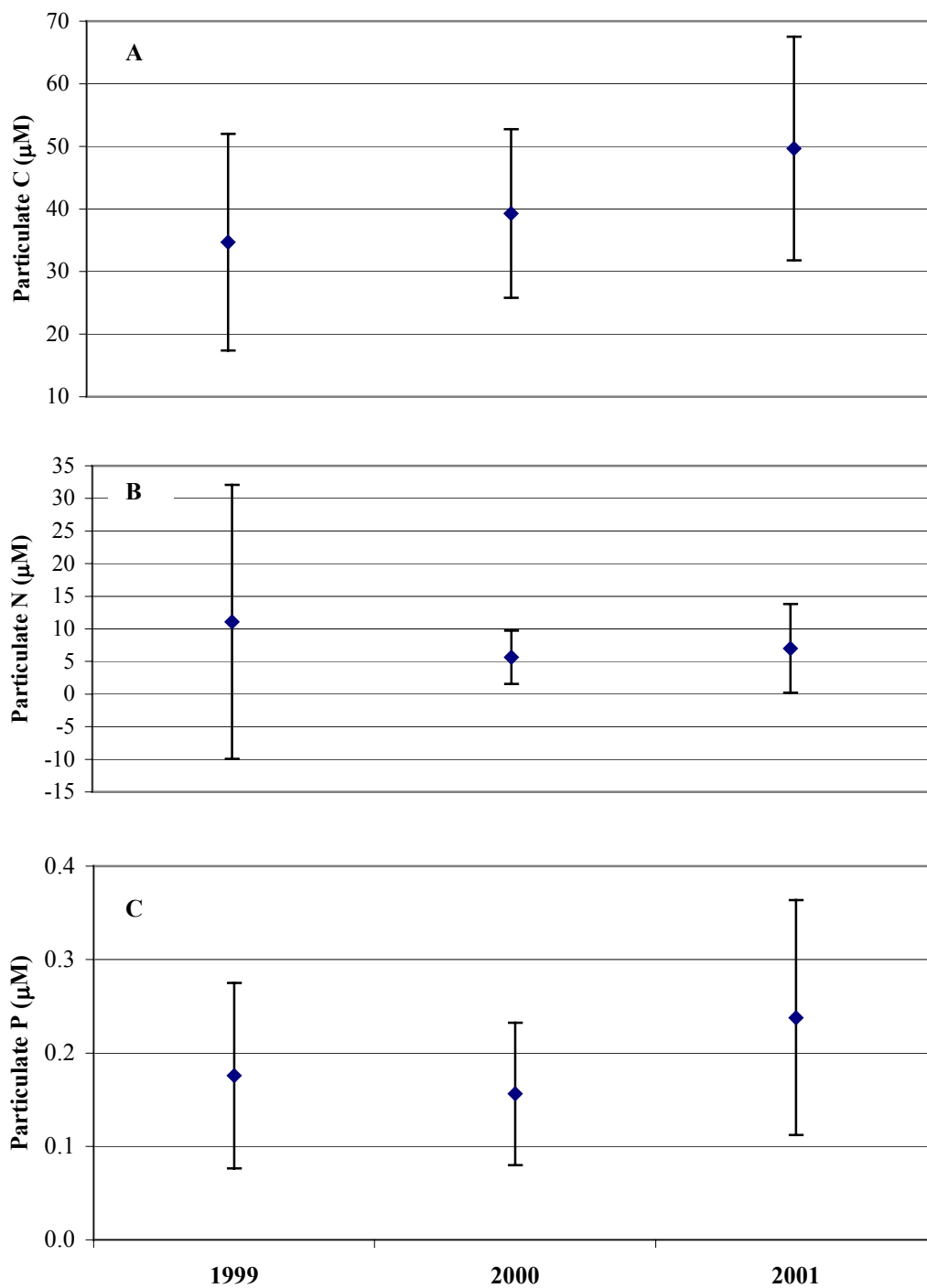


Figure 14. Annual average molar values of particulate (A) carbon, (B) nitrogen, and (C) phosphorus at all stations. Error bars represent one standard deviation.

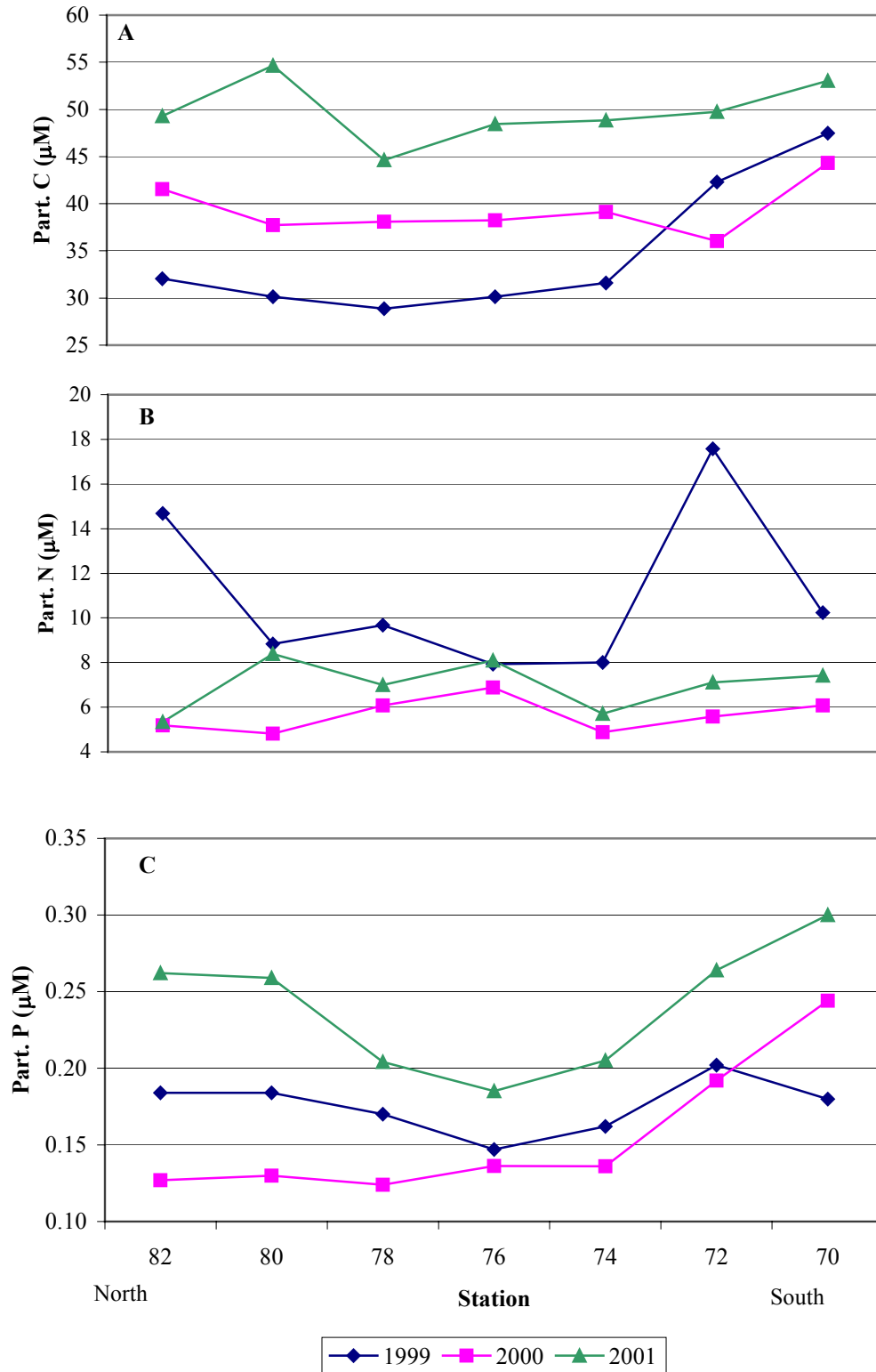


Figure 15. Annual average molar values of particulate (A) carbon, (B) nitrogen, and (C) phosphorus along the cruise track.

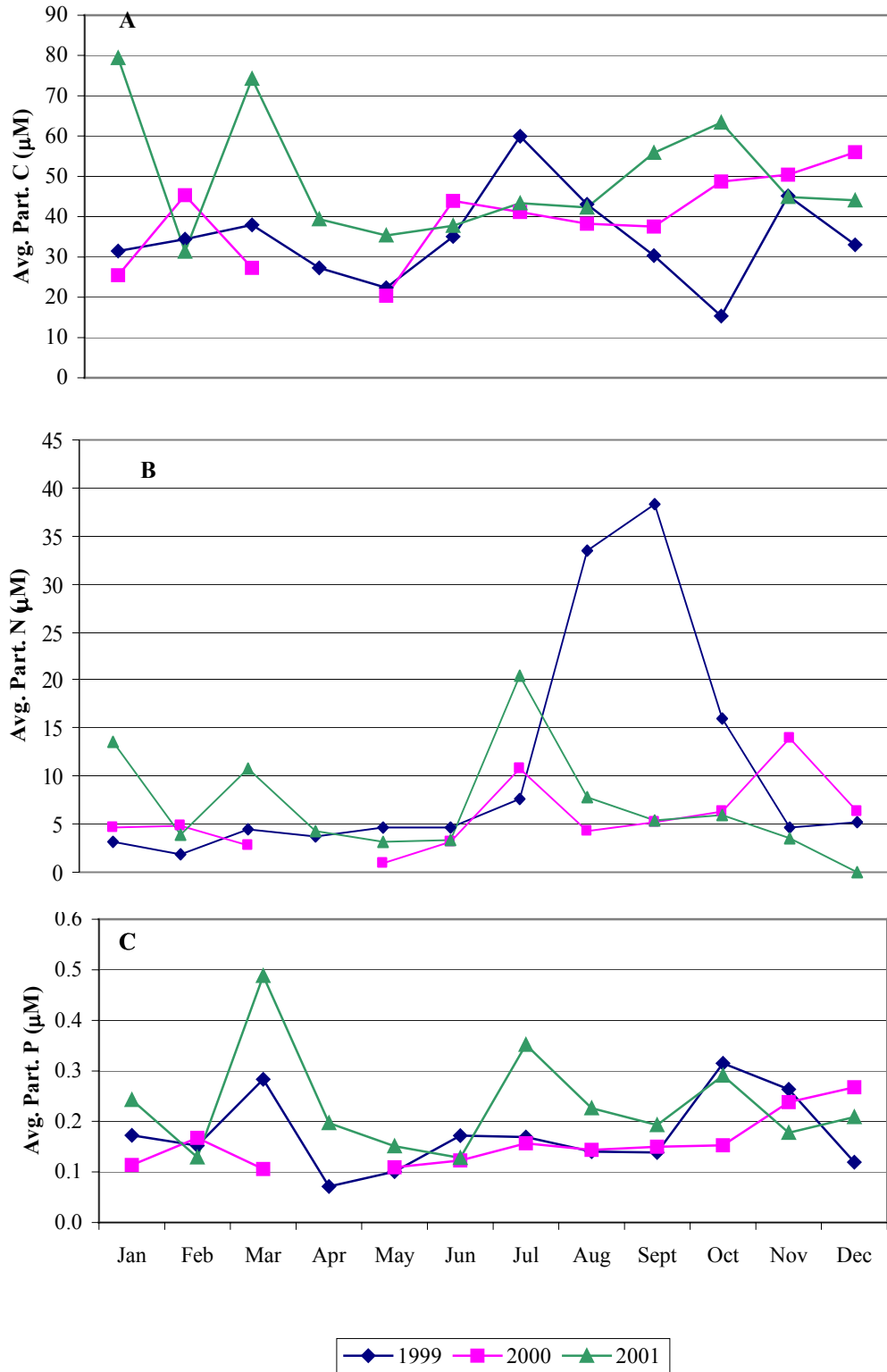


Figure 16. Average molar values of particulate (A) carbon, (B) nitrogen, and (C) phosphorus at all stations over time.

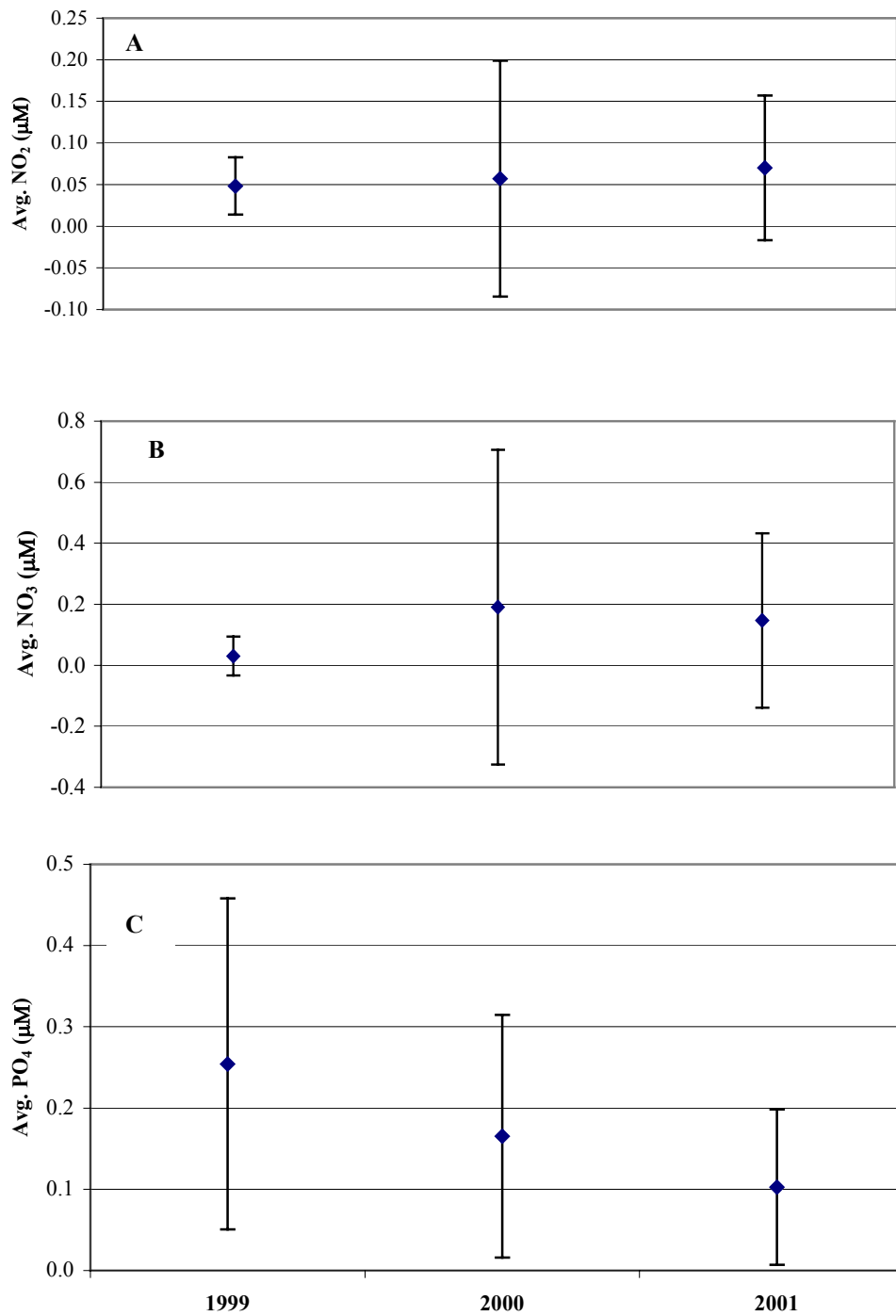


Figure 17. Annual average values of inorganic (A) nitrite, (B) nitrate, and (C) phosphate at all stations. Error bars represent one standard deviation.

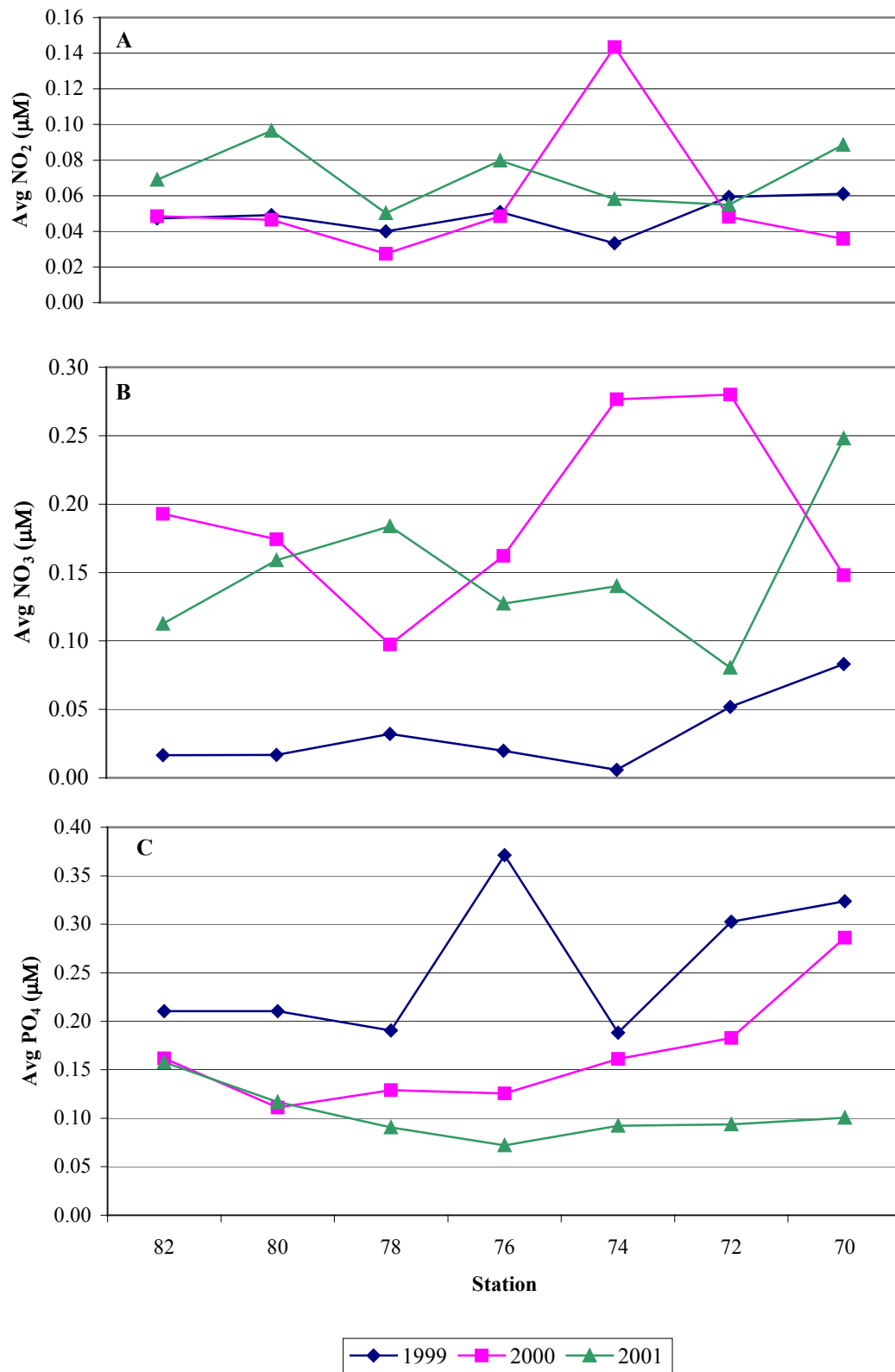


Figure 18. Annual average values of inorganic (A) nitrite, (B) nitrate, and (C) phosphate along the cruise track.

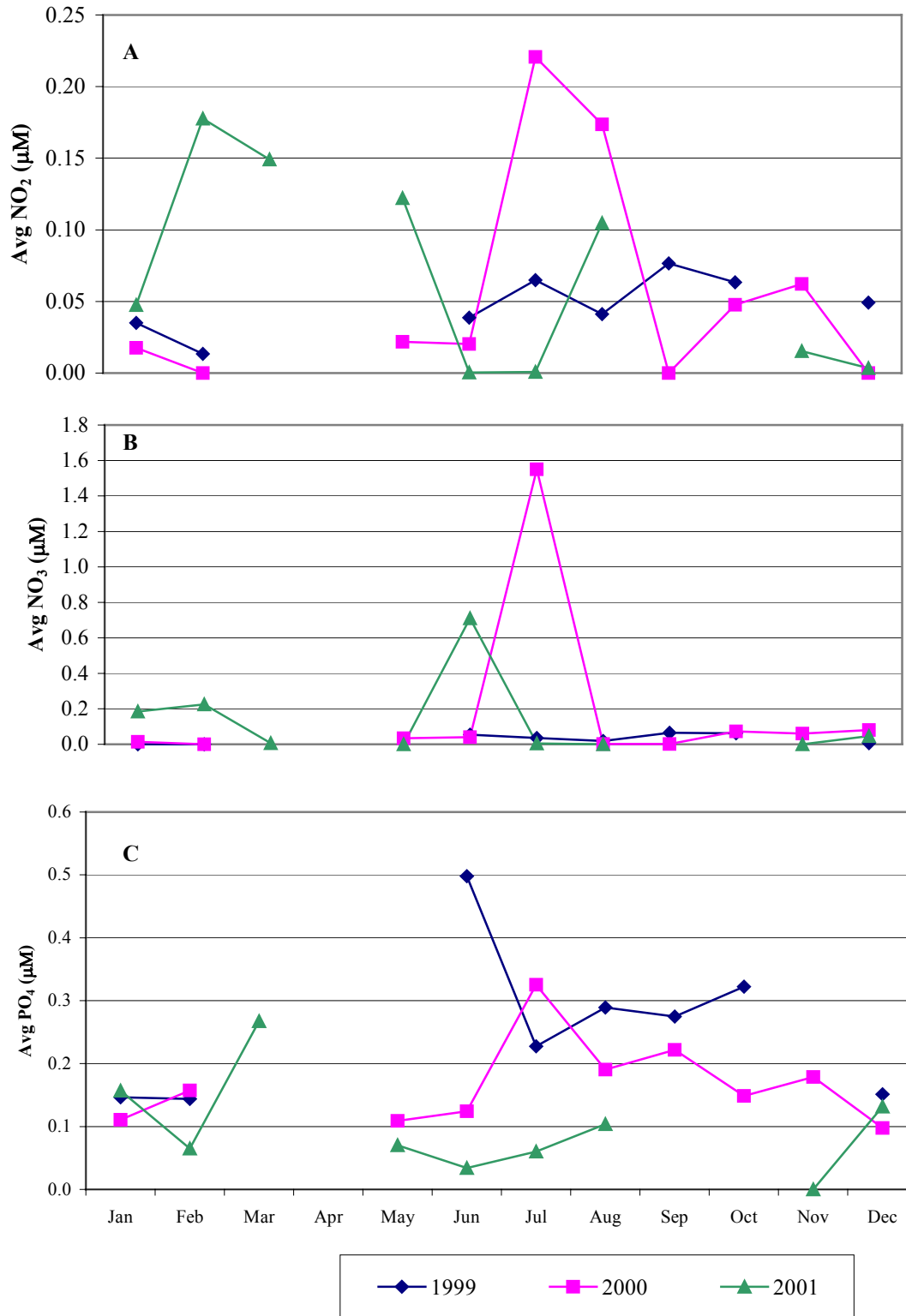


Figure 19. Average monthly values of inorganic (A) nitrite, (B) nitrate, and (C) phosphate at all stations over time.

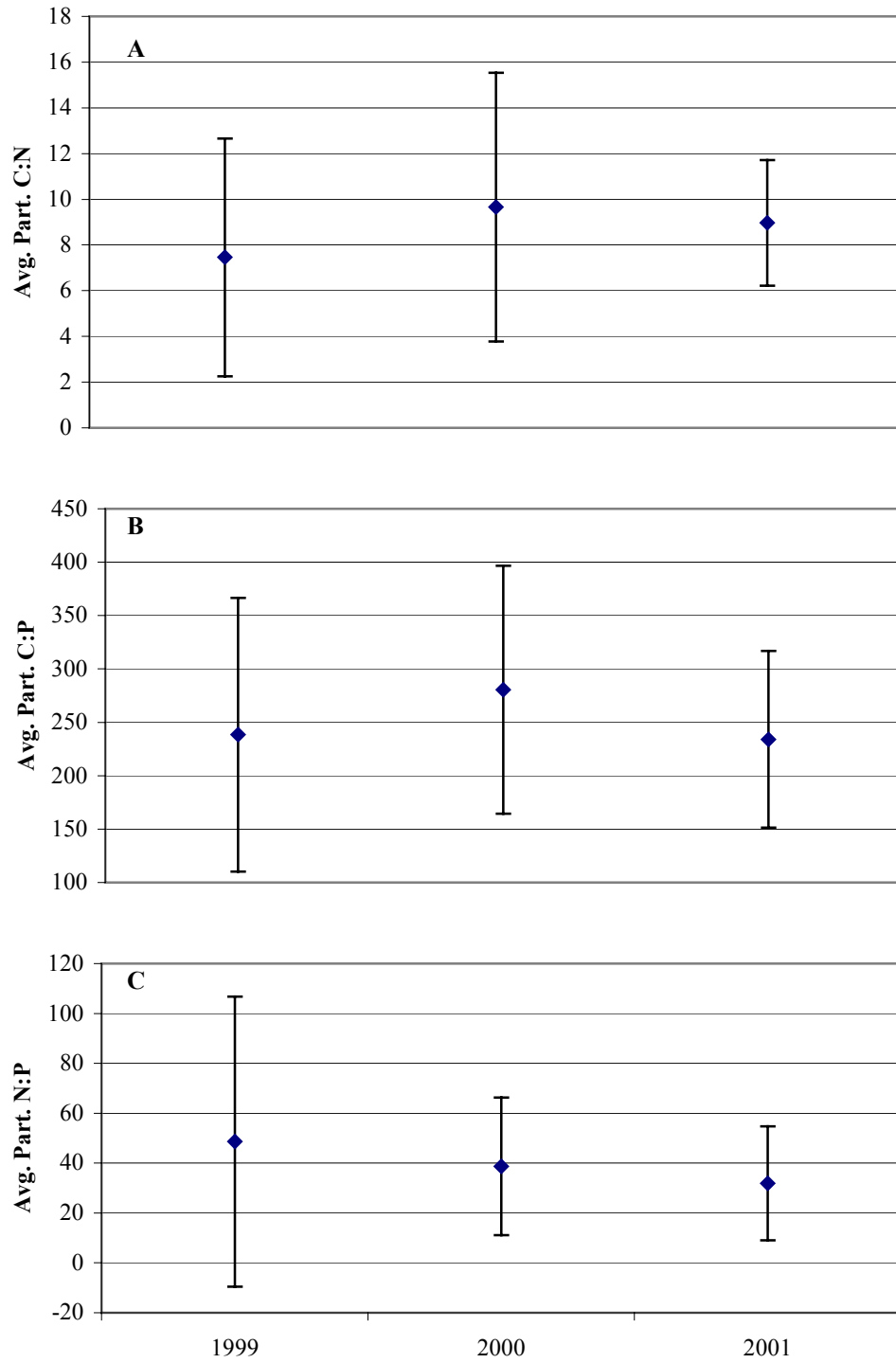


Figure 20. Annual average molar particulate ratios at all stations: (A) C:N, (B) C:P, (C) N:P. Error bars represent one standard deviation.

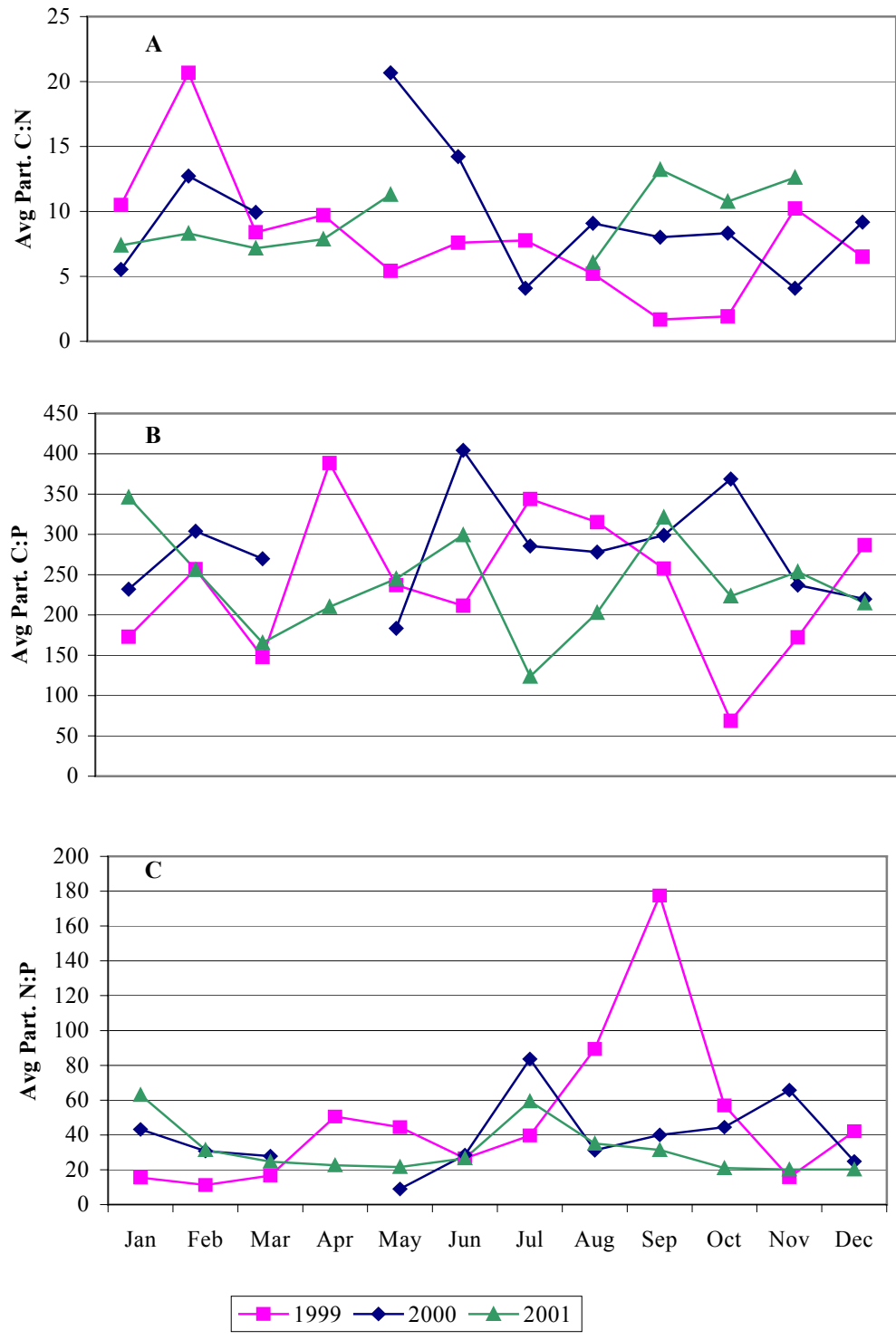


Figure 21. Average particulate molar ratios at all stations over time. (A) C:N, (B) C:P, (C) N:P.

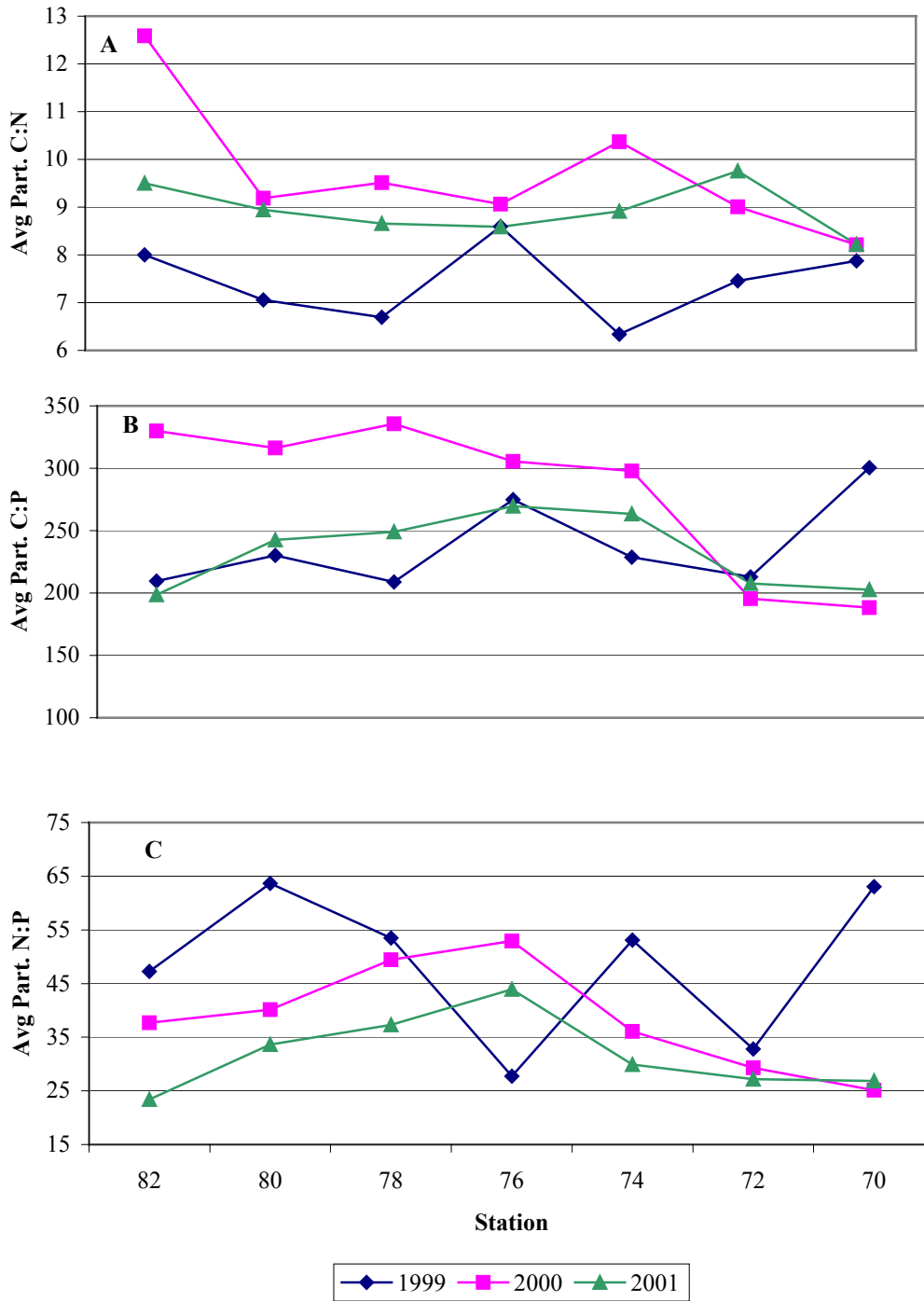


Figure 22. Annual average particulate molar ratios along the cruise track. (A) C:N, (B) C:P, (C) N:P.

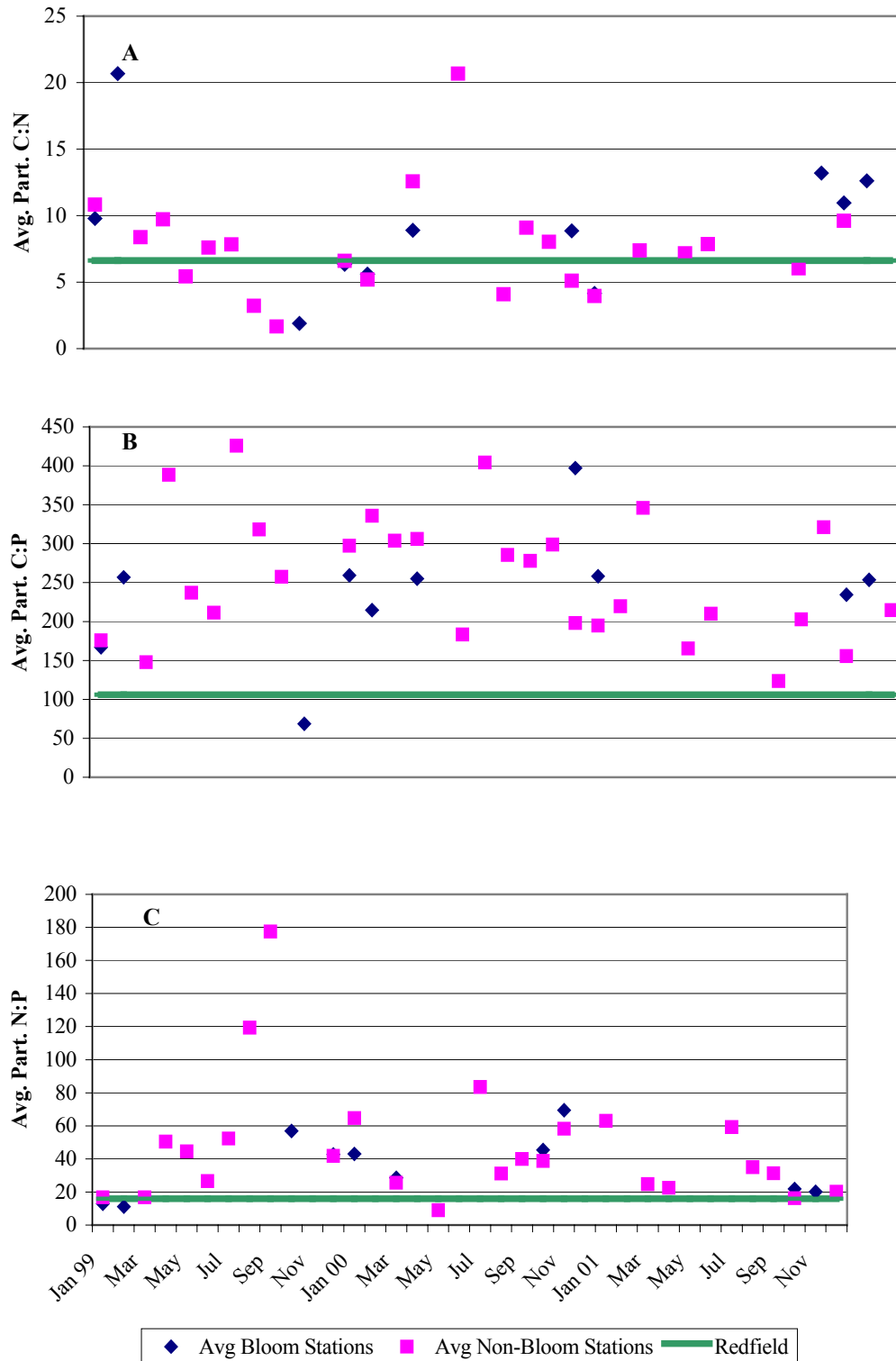


Figure 23. Average particulate molar ratios for stations with and without *K. brevis* blooms. (A) C:N, (B) C:P, (C) N:P.

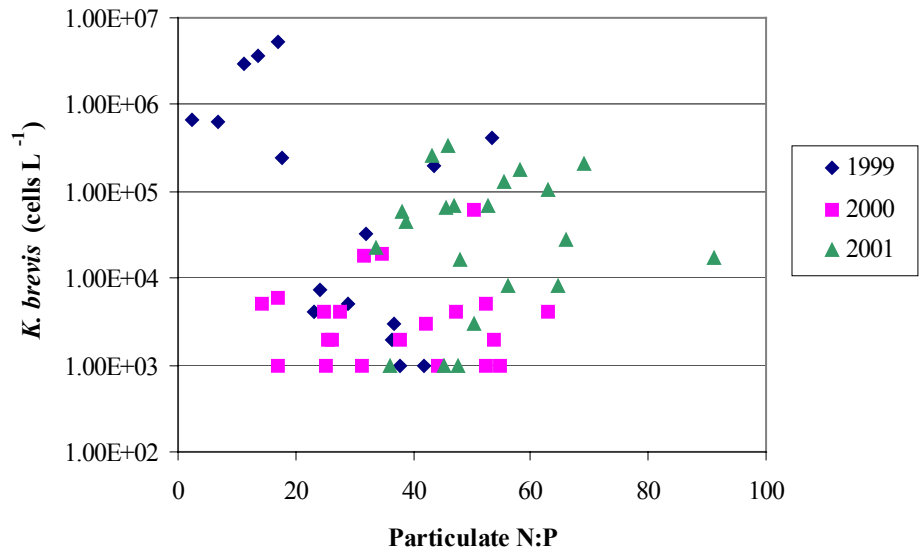


Figure 24. Surface particulate molar N:P values at all stations where *K. brevis* was present.

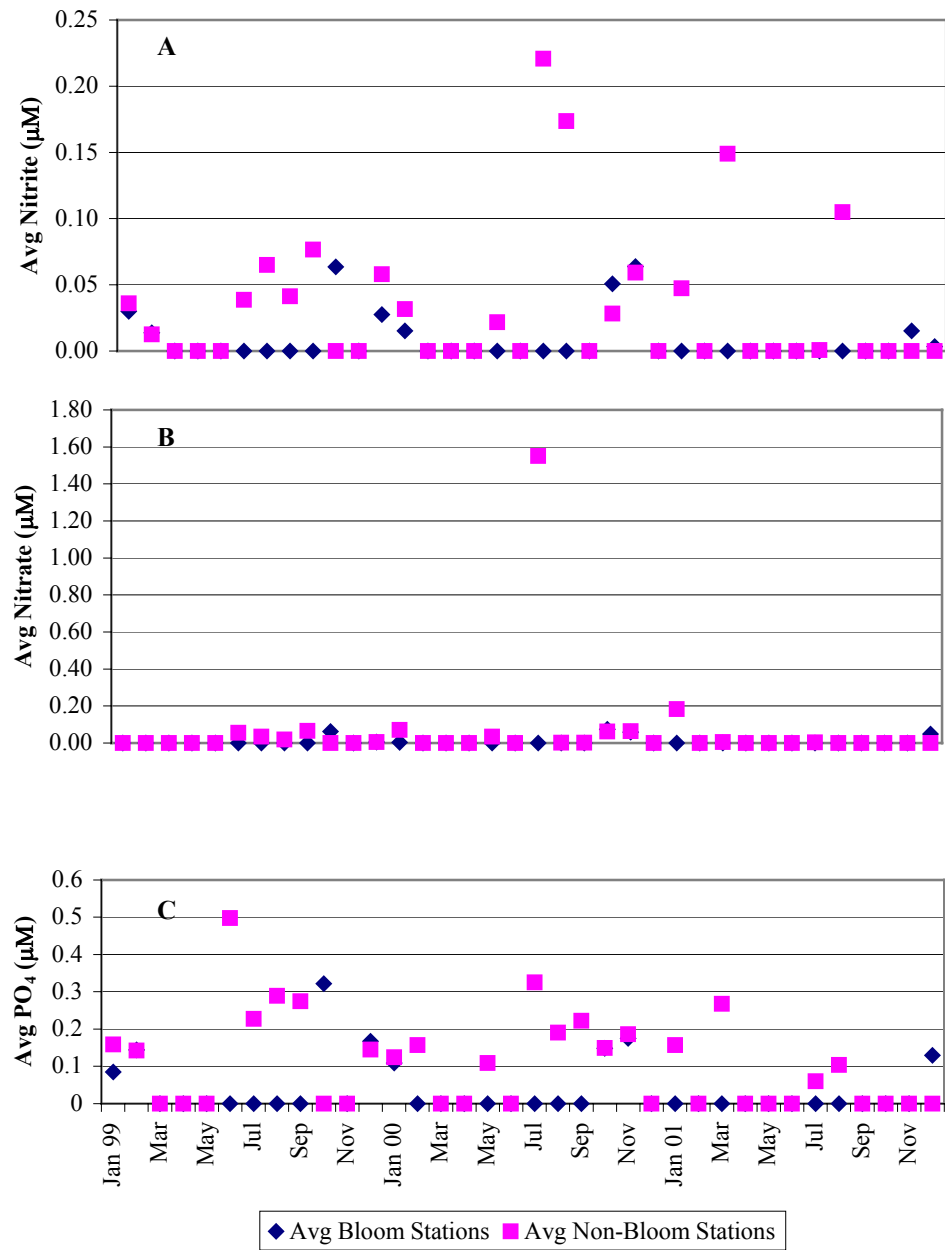


Figure 25. Average dissolved nutrient concentrations for stations with and without *K. brevis* blooms. (A) Nitrite, (B) nitrate, and (C) phosphate..

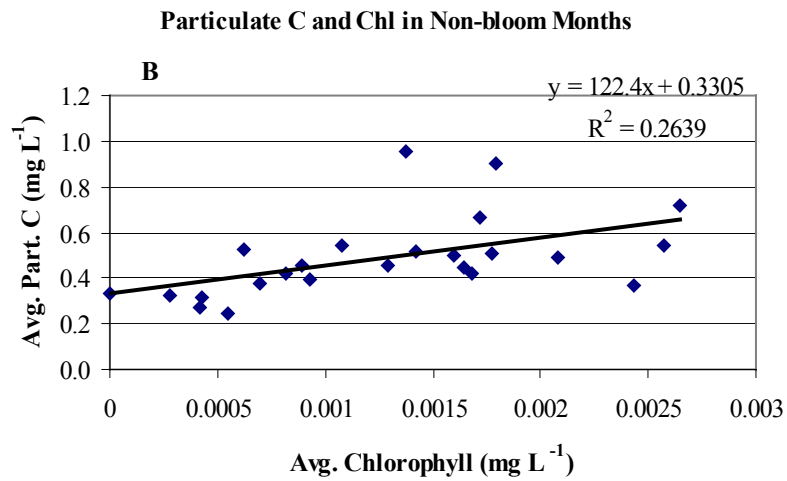
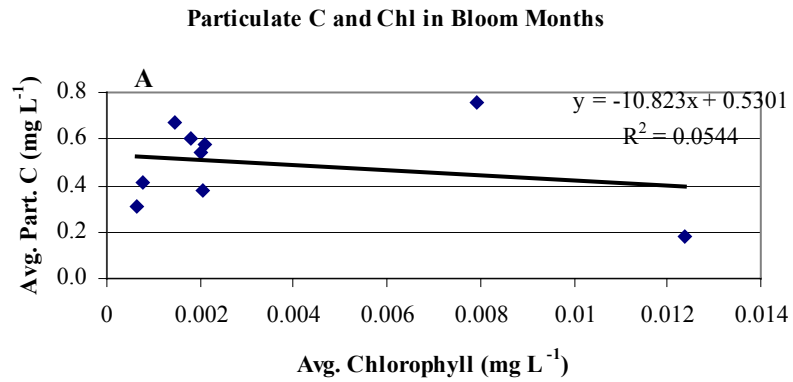


Figure 26. Average particulate carbon and chlorophyll values for (A) bloom months and (B) non-bloom months.

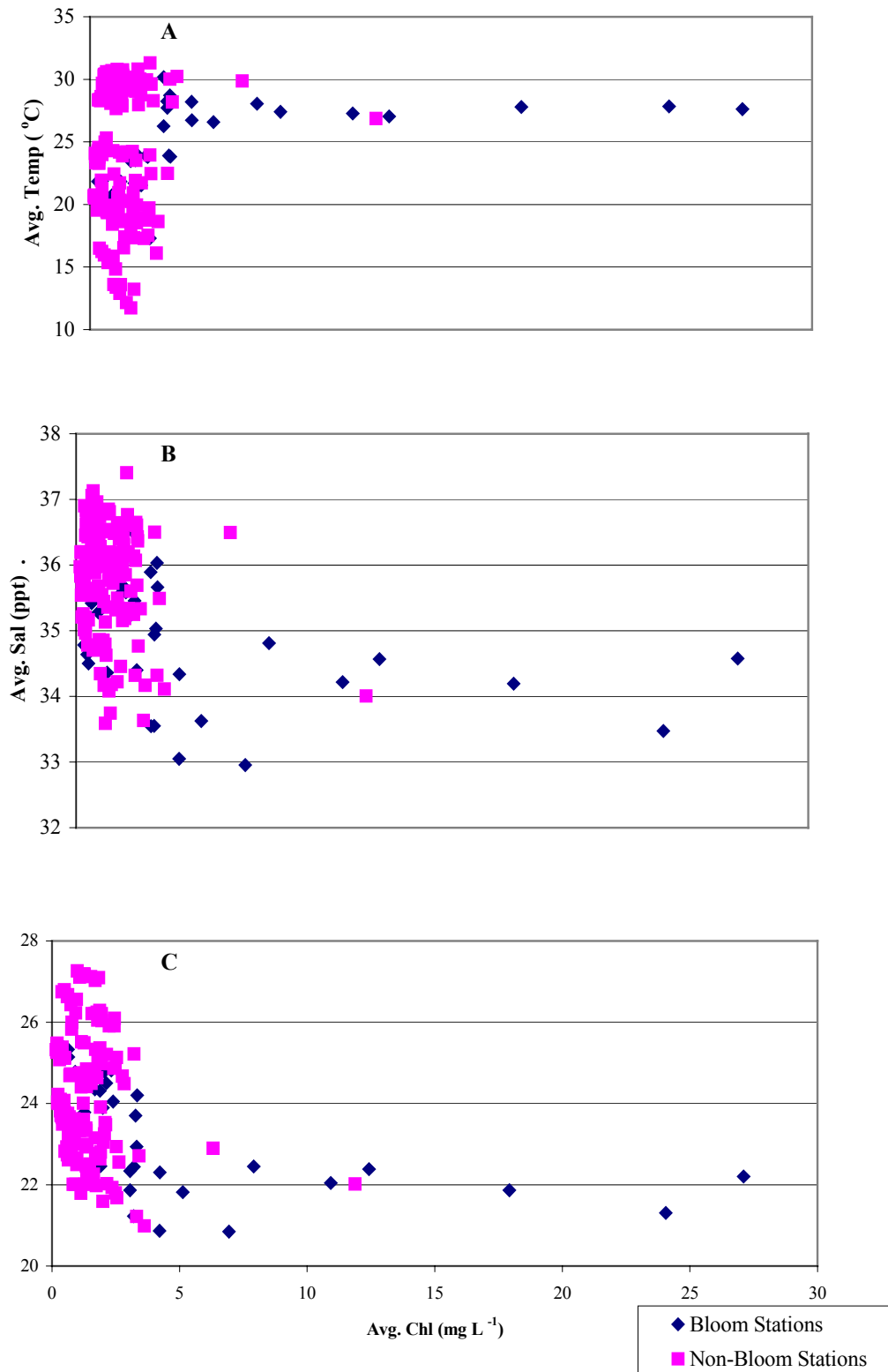


Figure 27. Average (A) temperature, (B) salinity, and (C) density values versus average chlorophyll values at stations with and without blooms.

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6. APPENDICES

Appendix A: Rainfall Data.

Table 8. Rainfall data in inches. Values are shown as rainfall amount for that month/average monthly amount 1915-2001.

		Manatee Co.	Sarasota Co.	Charlotte Co.
1999	Jan	3.87/1.77	4.35/2.32	2.77/2.13
	Feb	0.24/2.82	0.11/2.64	0.05/2.32
	Mar	0.66/3.15	1.62/3.04	1.18/2.74
	Apr	0.86/2.40	0.56/2.40	0.48/2.22
	May	3.82/3.19	2.06/3.10	3.45/3.54
	Jun	9.43/7.47	9.18/7.49	11.45/8.47
	Jul	5.63/8.71	7.58/8.25	8.11/8.02
	Aug	10.12/8.77	14.79/8.50	9.71/7.97
	Sep	5.37/7.66	7.36/7.97	7.43/8.03
	Oct	3.56/3.18	5.04/3.38	3.57/3.54
	Nov	0.97/1.90	0.72/1.88	1.18/1.68
	Dec	1.95/2.01	2.41/1.97	1.44/1.73
2000	Jan	1.13/1.77	2.41/2.32	3.50/2.13
	Feb	0.58/2.82	0.47/2.64	0.16/2.32
	Mar	1.14/3.15	1.72/3.04	1.78/2.74
	Apr	1.74/2.40	2.03/2.40	1.21/2.22
	May	0.31/3.19	1.06/3.10	1.20/3.54
	Jun	7.42/7.47	8.30/7.49	7.73/8.47
	Jul	11.51/8.71	9.44/8.25	9.59/8.02
	Aug	6.46/8.77	7.45/8.50	7.72/7.97
	Sep	9.40/7.66	9.87/7.97	8.01/8.03
	Oct	0.43/3.18	0.80/3.38	0.59/3.54
	Nov	1.99/1.90	1.42/1.88	0.89/1.68
	Dec	0.84/2.01	1.34/1.97	0.53/1.73
2001	Jan	0.30/1.77	0.20/2.32	0.13/2.13
	Feb	0.01/2.82	0.13/2.64	0.00/2.32
	Mar	7.98/3.15	7.27/3.04	6.33/2.74
	Apr	0.18/2.40	0.41/2.40	0.53/2.22
	May	1.41/3.19	1.18/3.10	1.05/3.54
	Jun	10.04/7.47	9.87/7.49	7.67/8.47
	Jul	12.40/8.71	10.62/8.25	16.51/8.02
	Aug	4.95/8.77	4.69/8.50	6.37/7.97
	Sep	14.49/7.66	14.95/7.97	11.06/8.03
	Oct	1.73/3.18	1.39/3.38	2.87/3.54
	Nov	0.05/1.90	0.14/1.88	0.28/1.68
	Dec	0.76/2.01	0.59/1.97	1.01/1.73

Source: Southwest Florida Water Management District Data.

Appendix B: Monthly Average Rainfall.

The higher than average rainfall in March 2001 could be attributed to a higher than normal number of extratropical fronts, storms, and weather events, including waterspouts, thunderstorms, and hail (National Oceanic and Atmospheric Administration/National Climatic Data Center data <http://www4.ncdc.noaa.gov/cgi-win/wwcgi.dll?wwevent~storms>). The higher than average rainfall in July 2001 could be part of the natural rainy season at this time of year in Florida. The higher than average rainfall in September 2001 was probably a direct result of Hurricane Gabrielle.

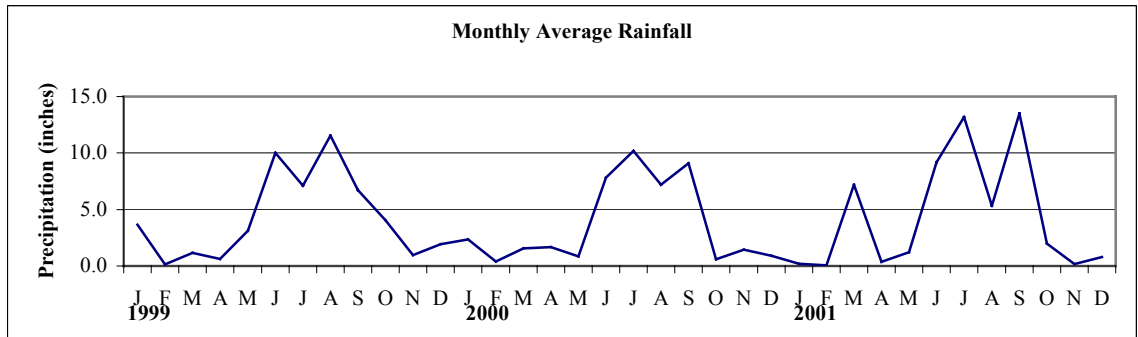


Figure 28. Monthly average rainfall amount (for Manatee, Sarasota, and Charlotte counties combined). Source: Southwest Florida Water Management District Data.

Appendix C: ECOHAB: Florida Cruise Log.

Table 9. Cruise log for this study period.

		R/V Suncoaster	R/V Bellows	
Month	Year	Day of Month	Day of Month	Comments
January	1999	11, 12, 13		Ran cruise track backward due to bad weather
February	1999	8, 9, 10		
March	1999	1, 2, 3		
April	1999	5, 6, 7		
May	1999	2, 3, 4, 5		
June	1999	5, 6, 7, 8		
July	1999		5, 6, 7, 8	R/V Suncoaster not available Started on 6th & returned to port due to weather, restarted on 7th
August	1999	6, 7, 8, 9		
September	1999	7, 8, 9		
October	1999	5, 6, 7		
November	1999	6, 7, 8		
December	1999		4	Start of R/V Bellows Cruises
January	2000		4	
February	2000		11	All personnel at HAB2000 Meeting
March	2000		3	
April	2000		No Cruise	
May	2000		3	
June	2000		13	
July	2000		1	
August	2000		3	
September	2000		12	
October	2000		3	
November	2000	7, 8, 9, 10		Used CTD from Bellows
December	2000		5, 6	New UW system on-line
January	2001		5, 6	
February	2001		6, 7	
March	2001		6, 7	Very rough weather, anchored overnight off Egmont Key
April	2001		2, 3	
May	2001		1, 2	
June	2001		2, 3	
July	2001	June 30-July 3		Ran Bellows line on Suncoaster
August	2001		1, 2	Bad storm, had to cut off cruise Suncoaster did Sta 70-75; Bellows did 70a-80a, 81-83 (added new stations in red tide)
September	2001	Aug 28, 29, 30, 31	Aug 28, 29	
October	2001		1, 2	

Appendix C: (Continued)

November 2001	17, 18, 19, 20	Ran Bellows line on Suncoaster
December 2001	11, 12, 13, 14	Ran Bellows line on Suncoaster
