A Stable Isotopic Examination of Particulate Organic Matter During

*Karenia brevis*

Blooms on the Central West Florida Shelf: Hints at

Nitrogen Sources in Oligotrophic Waters

by

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A thesis submitted in partial fulfillment of the requirements for the degree of
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Date of Approval:  
May 10, 2004

Keywords: stable isotope, nitrogen, carbon, phytoplankton

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I would like to acknowledge my committee members, Dr. Gabriel Vargo, Dr. Cynthia Heil and Dr. David Hollander for their continual support throughout this project. I would like to extend special thanks to Danylle Spence, Susan Murasko and Merrie Beth Neely for help with sampling, data processing and moral support. In addition, thanks to Dr. Deborah Bronk, Dr. Judith O’Neill, Dr. Marjorie Mullholland and Marta Sanderson for help with sampling. Last but not least; thanks to the crews of the R/V Suncoaster, R/V Bellows, R/V Pelican and R/V Walton Smith.
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A Stable Isotopic Examination of Particulate Organic Matter During Karenia brevis Blooms on the West Florida Shelf: Hints at Nitrogen Sources in Oligotrophic Waters

Julie Ann Havens

ABSTRACT

Blooms of the red tide dinoflagellate Karenia brevis occur annually on the west Florida shelf. In the late summer/early fall months, background concentrations increase from 10^3 cells L^{-1} to excesses of 10^6 cells L^{-1}. Blooms are most common between Tampa Bay and Charlotte Harbor, and may be maintained for months. The region’s hydrography may play a role in the initiation, maintenance and termination of blooms.

The west Florida shelf is depauperate in inorganic nutrients. Inorganic nitrogen and phosphorus rarely exceed the limits of detection, whereas dissolved organic nitrogen is often present at concentrations of 15 to 20 µM. Because K. brevis exhibits the ability to utilize both organic nitrogen and phosphorus, the organic pool may serve as an important nutrient source. The source of nutrients for K. brevis blooms is the focus of much scientific research.

Nitrogen is considered to be the limiting nutrient in marine waters and may have several sources. Potential sources of inorganic and organic nitrogen are estuarine outflow, atmospheric deposition, upwelling, dissolved organic nitrogen released from N_2 fixing cyanobacteria, diatom blooms, decaying seagrasses, fish or other organic matter.

The natural abundance stable isotopic signatures of particulate bloom material (δ^{15}N and δ^{13}C) associated with K. brevis blooms during 1998 to 2001 was analyzed and
compared with known isotopic values of potential nutrient sources. Data was analyzed from blooms occurring from 1998 to 2001. Extensive analysis of the 2001 bloom showed that the $\delta^{15}$N of bloom material ranged from $2^{\text{o}}/_{00}$ to $5^{\text{o}}/_{00}$. $\delta^{13}$C of bloom material ranged from $-22^{\text{o}}/_{00}$ and $-17^{\text{o}}/_{00}$. Non-bloom material was considerably more variable in both $\delta^{15}$N and $\delta^{13}$C. $\delta^{13}$C values were higher near shore than offshore during the 2001 bloom, suggesting lower dissolved inorganic carbon levels due to high temperature and/or high biomass.

$\delta^{15}$N of bloom material fell within the range of the $\delta^{15}$N values of potential nitrogen sources. It appears that *K. brevis* utilizes the available nitrogen sources opportunistically, and that isotopically more depleted sources are more important. More enriched sources such as upwelled nitrate or sewage nitrogen can be excluded as significant sources based on the isotopic data.
Chapter One

Introduction

Blooms of the toxic dinoflagellate *Karenia brevis* are a common seasonal phenomenon off of Florida’s west coast. In the past century, these blooms have received much attention from the scientific community, in an effort to understand both the ecology and physiology of the organism responsible, and the characteristics of the West Florida Shelf (WFS) that make it such a suitable environment for toxic algal blooms.

Bloom events, commonly known as “red tides,” have been observed in this region since the 16th century, when people noticed the associated discolored water and fish mortalities. It was not until 1947 that the causative organism was discovered, and named *Gymnodinium brevis* (Davis 1948). Since then, owing to new structural and physiological information (Steidinger et al. 1998), the organism has undergone several taxonomic changes. Today, it is known as *Karenia brevis* (Daugbjerg et al. 2000).

A resident population of *K. brevis* exists in the Gulf of Mexico (Geesey and Tester 1993), and it is transported throughout its range by the Gulf Loop Current, the Florida Current and the Gulf Stream. It has been recorded throughout the U.S. South Atlantic Bight (Tester et al. 1993), but rarely occurs in shelf waters north of Cape Hatteras, North Carolina. While *K. brevis* blooms have been reported by all states surrounding the Gulf of Mexico, they are most common off the west coast of central Florida (Tester and Steidinger, 1997). The impacts of these blooms can be extensive. For
example, in the 1970’s, 2 bloom events lasting from 3 to 5 months cost local communities somewhere between $15 and $20 million (Habas and Gilbert 1974, 1975).

It is reasonable to assume that there is something unique about this region of the west Florida shelf that allows _K. brevis_ to outcompete other phytoplankton and persistently achieve bloom concentrations. The hydrography of the region may play a role in the initiation, maintenance and termination of these blooms (Vargo et al. 2001).

Florida’s western continental shelf is shallow and broad, and is characterized by oligotrophic waters and representative hydrographic features. Surface heating and subsequent water column stratification in the summer months gives way to thorough vertical mixing in the fall when thermal and salinity fronts pass through the region (Yang et al. 1999). Upwelling and downwelling events that occur near the coast as a result of the region’s wind patterns may influence the onshore/offshore movement of blooms (Weisberg et al. 2000). Rainfall is highest in the late summer months, and may stimulate increased nutrient discharge into the estuaries (Heil et. al 1999), but inorganic nitrogen and phosphorous levels are often at the limits of detection in coastal waters.

Background concentrations of _K. brevis_ of < 1,000 cells L⁻¹ are present in the eastern Gulf year round (Geesey and Tester, 1993). Almost annually, in the late summer and early fall, _K. brevis_ cell concentrations increase and a “bloom” ensues. It takes about 2 to 8 weeks for bloom conditions to reach fish killing intensity (1 – 2.5 x 10⁵ cells L⁻¹), (Tester and Steidinger, 1997). When concentrations reach 5 x 10³ cells L⁻¹, shellfish bed closures may become necessary. At levels of 10⁵ cells L⁻¹, fish and manatee mortalities may occur, and at 10⁶ cells L⁻¹, water discoloration becomes apparent to the human eye, and may cause respiratory irritation (Tester et. al, in press).
In the past 50 years, considerable progress has been made in understanding what conditions allow these blooms to initiate and be maintained, often for months, at concentrations that cause considerable economic and human health impacts. One hypothesis is that blooms are initiated between 18 and 74 km offshore, and may be transported to near-shore waters given appropriate current and wind conditions (Steidinger, 1975). Additionally, intrusions from the Loop Current and associated thermal and salinity fronts may help to push blooms inshore and concentrate them (Haddad and Carder, 1979; Steidinger and Haddad, 1981). Once blooms are transported to nearshore waters, coastal nutrient inputs may serve to maintain them, but are not likely to play a large role in bloom initiation. Furthermore, although Tampa Bay estuaries are typically enriched in dissolved inorganic phosphorus (DIP), dissolved inorganic nitrogen (DIN) is often present at the limit of detection suggesting that estuarine N sources are insufficient to support bloom biomass (Vargo et. al, in press). Past records of nutrient data indicate that there is rarely sufficient inorganic nitrogen in the Southwest Florida coastal waters to support observed \textit{K. brevis} bloom biomass (Finucane and Dragovich, 1959; Dragovich et al., 1961; Dragovich et al., 1963).

The main sources of DIN to this region are river outflow and atmospheric deposition during the rainy season and upwelling from deeper waters off the shelf break (Heil et. al, 1999). Despite the fact that WFS waters are often depleted in both DIN and DIP, large \textit{K. brevis} blooms with concentrations exceeding $10^6$ cells L$^{-1}$ have been maintained for months. N:P ratios are near Redfield when bloom concentrations are $\leq 10^5$ cells L$^{-1}$, suggesting that cells have access to sufficient N and P sources to grow at their maximum rate (Heil et. al, 2001). When cell concentrations exceed $10^5$ cells L$^{-1}$, N:P
ratios are higher suggesting P-limitation (Vargo et. al, 2002). Other, as yet unidentified nutrient sources must exist to support these blooms.

One possible source is dissolved organic nitrogen (DON). While DIN is often at or below the limits of detection in oligotrophic waters, DON is found at much higher concentrations. In the open ocean, DON ranges from 3 to 7 µM (Capone 2000), and values are even higher in coastal waters (Sharp 1983). On the WFS, DON has been found to range from 5 to 10 µM when DIN is at nearly undetectable levels (Heil et al., 2001).

The DON pool consists of a wide variety of compounds, varying greatly in size, complexity and lability (Zehr and Ward 2002). The more refractory forms make up the dominant portion of the ambient pool, but the labile forms are far more important as potential nitrogen sources. The compounds that have been identified include urea, dissolved combined amino acids (DCAAs), dissolved free amino acids (DFAAs), humic and fulvic substances and nucleic acids (Bronk 2002). The remainder of the pool is a heterogeneous mixture of unidentified compounds.

Much of the recent DON research has focused on the potential of this pool as a nutrient source for HABs. While diatom abundance tends to correlate with high nitrate concentrations, addition of DON tends to correlate with microflagellate abundance (Bronk 2002). Like other dinoflagellates, *K. brevis* can take up a variety of organic compounds (e.g. vitamins, amino acids) as nitrogen sources (Steidinger et al., 1998). In culture, *K. brevis* cell yields increased dramatically upon additions of glycine, leucine and aspartic acid (Shimizu et al., 1995).
Several potential sources of DON are available to *K. brevis* blooms. Among these are atmospheric inputs (Paerl et al., 2002; Seitzinger and Sanders, 1999; Mopper and Zika, 1987), terrigenous and estuarine inputs (Seitzinger and Sanders, 1997), DON from nutrient rich waters upwelled at the shelf break, atmospheric nitrogen fixed by cyanobacteria and subsequently released as DON (Glibert and Bronk, 1994), and that released from diatom blooms, floating seagrasses, dead fish or other decaying organic materials (Vargo et al. 2001).

All of these sources may contribute to the regenerated nitrogen pool in WFS waters. The ammonium released in the zooplankton grazing and microbially mediated regeneration processes are readily available for phytoplankton utilization, especially after bloom initiation (Bronk et al., 2003). It has recently been proposed that the fish kills associated with *K. brevis* blooms may also supply regenerated N in sufficient amounts to sustain blooms during their maintenance phase (Walsh, submitted) and laboratory experiments have demonstrated the ability of *K. brevis* to use fish extracts as a nutrient source (Wilson and Collier, 1955).

Atmospheric deposition processes are highly variable in terms of the magnitude of DIN and DON delivered. In general, continentally derived storm events deliver higher DIN loads than oceanic fronts (Fogel and Paerl, 1993). While no comprehensive studies to date have been done to describe and quantify the process in the WFS region, studies of other coastal areas may be comparable (Paerl et al., 2002). Citing the first recorded *K. brevis* bloom off the coast of North Carolina in 1988, (Paerl et al. 1994) suggest that the recent geographic expansion of these blooms may indicate increasing N loading along the eastern seaboard, much of which comes from atmospheric sources. Estimates suggest
that from 20% to 50% of annual “new” nitrogen may come from atmospheric deposition in geographically diverse regions (Fisher et al., 1988).

The WFS receives the majority of its annual rainfall from July to October. While no studies have been conducted to quantify the amount of DON deposition in this region, estimates of DIN deposition range from 0 to 18 kg/ha, with elevated values occurring during the rainy season.
Nitrogen Utilization by Phytoplankton

Phytoplankton nitrogen metabolism is complex, largely because of the number of different forms of nitrogen available for phytoplankton uptake and assimilation. Phytoplankton are able to assimilate dissolved DIN in the form of nitrate, nitrite and ammonium. It is generally agreed that they prefer NH$_4^+$ to NO$_3^-$ because of the need to reduce NO$_3^-$ before assimilation, but this is not a universal preference (Zehr and Ward, 2002). In oligotrophic regions, low concentrations of DIN often limit primary productivity in the surface layer (Zehr and Ward, 2002). The major source of NO$_3^-$ in such areas is upwelling of NO$_3^-$ rich deep waters, while the major source of NH$_4^+$ is via regeneration, resulting from the degradation of organic matter by bacterial processes or animal excretion (McCarthy, 1980), although atmospheric deposition of DIN may be important sporadically (Fogel and Paerl, 1993).

It has been shown that a large fraction of the DIN assimilated by phytoplankton can be released as DON (Bronk and Ward 1999; Ward and Bronk 2001), and it is known that phytoplankton and cyanobacteria can assimilate components of this pool, such as some amino acids and urea (Antia et al., 1991). Recent work shows that many phytoplankton have cell-surface enzymes that allow them to take up DON in larger amounts than previously thought (Palenik and Morel, 1990). This suggests that phytoplankton may be a sink for, as well as a source of DON (Palenik and Morel 1990).
Seitzinger and Sanders (1997) reported that diatoms and dinoflagellates accounted for > 90% of the phytoplankton biomass in treatments receiving DON from rainwater. *Karenia brevis* is much like other dinoflagellates in that it exhibits the ability to utilize both inorganic and organic forms of nitrogen. It has been shown to have a relatively high affinity for NO$_3^-$, NH$_4^+$, urea and glutamate in kinetic experiments (Bronk et al., 2003). Growth of *K. brevis* in a seawater medium containing no detectable NO$_3$ or NO$_2$ has been reported (Wilson, 1967). It has been shown to assimilate organic forms of both N (Baden and Mende, 1979; Shimizu and Wrensford, 1993; Shimizu et al. 1995; Steidinger et. al 1998) and P (Vargo and Shanley, 1985) in culture studies.
Stable Isotopes: Inferring Nutrient Sources

Natural abundance stable isotopic ratios are often used in ecological studies as a means of understanding trophic structure. Such studies utilize stable isotope ratios of elements common in organic material; most commonly nitrogen ($^{15}\text{N}/^{14}\text{N}$), carbon ($^{13}\text{C}/^{12}\text{C}$), hydrogen (D/H) and sulfur ($^{34}\text{S}/^{32}\text{S}$). An advantage of the natural abundance stable isotopic approach is that it is a relatively quick analysis, and does not involve time intensive uptake/kinetics, or the use of radioactivity. Differences in isotopic ratios of various materials are expressed relative to a universal standard material, in terms of “delta” notation as follows:

$$\delta = [(R_{\text{sample}}/R_{\text{standard}}) – 1] \times 1000$$

where $R_{\text{sample}}$ and $R_{\text{standard}}$ are the isotopic ratios of the sample and standard materials. The notation is $\delta/_{\text{oo}}$, or “per mil.”

The underlying premise of such stable isotopic analyses is that the isotopic compositions of organisms should reflect those of their diets to some difference in $\delta/_{\text{oo}}$, with the consumer being enriched in the heavier isotope relative to it’s current food source (Peterson and Fry 1987). Such studies are aided by some knowledge of the isotopic signatures of the primary producers in the environment, which may vary spatially and temporally with the nutrient pool sources and concentrations (O’Reilly and Hecky, 2002).
Another approach is analysis of the isotopic signatures of the primary producers themselves to gain information about the nutrient sources supporting them. This may be useful for placing constraints about the potential nitrogen sources sustaining *K. brevis* blooms on the WFS. This technique is based on the isotopic fractionation that occurs during enzyme mediated biological reactions. The lighter isotope of a given element will enter into such a reaction at a higher rate than the heavier one, so that the product of the reaction is depleted in the heavier isotope relative to the reactant. If something is known about the amount of fractionation that occurs in a given reaction type, such as that which occurs during the uptake and assimilation of a nutrient by phytoplankton, then a nutrient source can be inferred. The difference in the isotopic signatures of the dissolved species and the particulate matter it becomes assimilated into is the “fractionation factor”. The $\delta^{15}N$ signature of the particulate organic matter associated with a monospecific *K. brevis* bloom should reflect the $\delta^{15}N$ signature of the nitrogen source supporting the bloom, which should differ substantially between potential sources.
Stable nitrogen isotopes at natural abundance

There are a few complications involved with using isotopic ratios of POM as a tool for tracking potential nitrogen sources. First, $\delta^{15}$N values of nitrogen sources vary among nitrogen species, (NO$_3$ vs. NH$_4$ vs. dissolved organic nitrogen) and among sources of these species. Both N species and source are often variable temporally and spatially. In addition, *in situ* nitrogen transformation processes such as atmospheric nitrogen (N$_2$) fixation (Hoering and Ford 1960, Macko et al. 1982), bacterial nitrification and denitrification (Miyake and Wada 1971, Checkley and Miller 1989) can modify the $\delta^{15}$N of the nitrogen source pools. Furthermore, the isotopic composition of a primary producer at one time may reflect a combination of sources utilized over it’s lifetime, creating an issue of “time averaging” (O’Reilly and Hecky 2002). In coastal or offshore systems where mixing of nitrogen from two or more isotopically distinct sources is important, the $\delta^{15}$N signature will reflect a combination of these (Fry, 1988).

A second complication is the variability associated with the amount of fractionation involved in nutrient uptake and assimilation. The isotopic fractionation associated with nitrogen utilization by phytoplankton is a very significant fractionation process in the biogeochemical cycle of N in the ocean, but the amount of fractionation is not always known, and the mechanisms controlling it are not well understood (Handley and Raven 1992; Goeriche et al. 1994). In general, phytoplankton discriminate between $^{14}$N and $^{15}$N during uptake and assimilation, leaving biomass more depleted than the
source. Variability in fractionation occurs in terms of nitrogen availability (and thus physiological state), N sources, and phytoplankton species composition (Waser et al. 1998). In laboratory cultures, reported fractionation during the growth of marine microorganisms on both NO$_3$ and NH$_4$ varies greatly (Wada and Hattori 1976; Wada 1980; Montoya and McCarthy 1995; Pennock et al. 1996). It has also been shown to vary with light intensity, N substrate and growth rate (Wada and Hattori, 1978; Wada, 1980).

Much information on isotopic fractionation by phytoplankton has been gained with the use of laboratory cultures, which may not always be a good proxy for field conditions. Most past culture studies have employed substrates at concentrations that are usually much higher than those found in oceanic environments and may overestimate fractionation occurring in the natural environment. Montoya and McCarthy (1995) found evidence of variation among species, with lower fractionation factors for a flagellate compared with a diatom. An investigation of the nitrogen isotope fractionation during uptake of 4 different nitrogen sources by a marine diatom showed fractionation values ranging from 0.8 to 20 $^{\circ}/_{00}$ (Waser et al. 1998), and demonstrated the importance of urea and NO$_2$ as nitrogen sources in addition to NO$_3$ and NH$_4$.

The variability in $^{\delta^{15}}$N signatures of marine phytoplankton and associated particulate organic matter (POM) has often been explained by the geographical variation in nitrogen dynamics in oceanic surface waters (Nakatsuka, 1992). The low $^{\delta^{15}}$N of plankton in low latitudinal areas has been associated with N$_2$ fixation (Wada and Hattori, 1987; Minagawa and Wada, 1986), while in high latitudes, it has been associated with large isotopic fractionation during the uptake of NO$_3$ (Wada and Hattori, 1978). Alternatively, Checkley and Miller (1989) suggested that large isotopic fractionation
during ammonium excretion by zooplankton could explain the low $\delta^{15}N$ of plankton in low latitudes. Literature values for phytoplankton and POM $\delta^{15}N$ range from around -1 to 12 $^{0}/_{00}$.

If some information were available about the $\delta^{15}N$ values of the potential forms and sources of DIN and DON on the WFS, and this information could be related to the isotopic signature of *K.brevis* during a bloom, then it may be possible to infer which ones are most useful in sustaining such large blooms. Fig. 1 shows $\delta^{15}N$ values for potential sources and sinks of nitrogen in a coastal shelf environment.
Potential sources of nitrate on the WFS include: fertilizer and/or sewage NO$_3^-$ introduced via terrigenous runoff, upwelled NO$_3^-$ from beyond the shelf break, and NO$_3^-$ delivered via atmospheric deposition. Each of these source pools should have a distinct characteristic isotopic signature. For terrigenous inputs, fertilizer DIN is typically isotopically depleted ($\delta^{15}$N: -2 to 2 $^{0/00}$), while sewage NO$_3^-$ is enriched, ranging from 5 to 11 $^{0/00}$ (Paerl et al. 1993). Atmospherically deposited nitrate varies considerably, depending on the source of the combined nitrogen to the atmosphere. Where the source is high temperature combustion from pollution, $\delta^{15}$N should be close to 0 $^{0/00}$; whereas if the source is soil nitrification, it may be more depleted (Fogel and Paerl, 1993). Values range from $\delta^{15}$N ~ -5.5 to 1 $^{0/00}$ (Paerl et al. 1994, Fogel and Paerl, 1993). Upwelled NO$_3^-$ varies geographically, but tends to be relatively enriched. In deep, low oxygen regions where microbially mediated denitrification is occurring, $\delta^{15}$N ~ 15 $^{0/00}$ (Michener and Schell, 1994), and where this process is not as prominent, it is ~ 5 $^{0/00}$ (Mahaffey et al., 2003).

Wide variability in fractionation factors for NO$_3^-$ have been reported, ranging from 0.7 to 23 $^{0/00}$ (Wada and Hattori, 1978). As studies have begun to employ micromolar substrate concentrations, fractionation values of NO$_3^-$ uptake have been reported that are much less than previously determined. Most recent values range from about 2-5 $^{0/00}$ (Waser et al., 1999).
Ammonium ($NH_4^+$)

Potential $NH_4^+$ sources on the WFS include: terrigenous runoff of sewage and/or fertilizer, atmospheric sources, or that remineralized within the water column and sediments. These source pools also differ isotopically. Terrigenous inputs of $NH_4^+$ from sewage are $\delta^{15}N \sim 8^{0/00}$ (Paerl et al. 1993), while atmospherically deposited $NH_4^+$ is relatively depleted, at $\delta^{15}N \sim -3.1^{0/00}$ (Paerl and Fogel, 1994). Isotopic values of remineralized $NH_4^+$ vary. In estuarine environments, they tend to be more enriched, at $\delta^{15}N \sim 13^{0/00}$ (Paerl et al. 1993), while in oligotrophic environments it is more depleted, at $\delta^{15}N \sim -3.5^{0/00}$ (Miyake and Wada, 1971). For $NH_4^+$ many uncertainties remain, but fractionation may range from 6.5 - 9 $^{0/00}$ in eutrophic systems (Cifuentes et al., 1989; Montoya et al., 1991) to as low as 0 $^{0/00}$ in N-depleted environments (Waser et al. 1999).
Dissolved Organic Nitrogen (DON)

DON may be atmospherically deposited or produced by regeneration processes within the water column. It may be released from the primary producers (*K. brevis* and other phytoplankton, *Trichodesmium* spp., decaying seagrass on the WFS), or from consumers (fish, benthic consumers). These different sources will likely vary isotopically, although there is very little information in the literature concerning δ^{15}N of DON due to methodological problems associated with its measurement. Values obtained from samples taken at various locations and depths spanning the Atlantic and Pacific Oceans and the Gulf of Mexico range from 6.6 to 10.2 ‰, the most depleted value coming from a surface sample from the Sargasso Sea, suggesting a contribution from N_{2} fixation (Benner et al. 1997).

As is the case for δ^{15}N values for DON, there is very little information regarding isotopic fractionation factors for DON. As isolation and characterization of this pool becomes more routine, this may prove to be valuable information, as DON has been shown to be an important N source to estuarine ecosystems (Sietzinger and Sanders 1997, 1999). It has also been shown that the release of DON by *Trichodesmium* spp. is, on average, 50% of the N_{2} fixation rate (Glibert and Bronk, 1994), and that *K. brevis* has the ability to exploit this pool (Bronk et al., 2003).
Fig. 1: δ$^{15}$N in a coastal shelf environment.
Stable carbon isotopes at natural abundance

To overcome some of the issues involved in isotopic analysis of ecosystem processes, natural abundance studies often examine ratios of 2 or more compounds simultaneously. Ecological studies using $\delta^{15}N$ are often done in conjunction with $\delta^{13}C$, because the different fractionation factors and processes associated with these 2 elements often compliment one another in interpretation of the data.

Isotopic enrichment of both carbon and nitrogen has been shown to occur as one moves up the trophic ladder, but $\delta^{13}C$ is more variable at the base of the food chain, and tends to better conserve it’s primary source signature with increasing trophic level (Zanden and Rasmussen, 1999). $^{13}C$ enrichment has been estimated at about $1^{\circ}/_{00}$ per trophic level, and $^{15}N$ enrichment at 3-4 $^{\circ}/_{00}$ (Fry and Sherr, 1984). Continuous flow isotope ratio mass spectrometry (IRMS) provides a rapid way to analyze both at the same time.

Differences in $\delta^{13}C$ values of organic matter reflect different photosynthetic pathways; (C3 vs. C4) (Boutton, 1991). In the marine environment, photosynthesis occurs mainly via the C3 pathway, which fractionates to a greater extent relative to the C4 pathway utilized by some terrestrial plants. However, $\delta^{13}C$ values of marine primary producers often differ from those of C3 photosynthesizing terrestrial ones due to a combination of factors associated with isotopic fractionation during photosynthesis. Fractionation has been shown to vary with aqueous CO$_2$ concentration and algal growth rate (Fry and Wainright, 1991). As a result, it can be a function of temperature and
salinity (Boutton, 1991). It may also be dependent on the growth-rate limiting resource (Burkhardt et al., 1999b).

Raven et al. (1993) suggested that variations in carbon isotopic fractionation may be linked to bicarbonate (HCO$_3^-$) utilization, or a non-passive inorganic carbon uptake mechanism during periods of CO$_2$ limitation. Differences in cell size (Fry and Wainright, 1991) and cell membrane permeability (Francois et al., 1993) can also modify fractionation.

Depending on temperature and pH, the concentration of HCO$_3^-$ in seawater is much greater than that of free CO$_2$, (about 2.5 mM and 10-12 µM, respectively), (Falkowski, 1991). It is generally agreed that phytoplankton primarily utilize CO$_2$ for photosynthesis (Raven et al. 1993). Utilization of HCO$_3^-$ would require the C4 photosynthesis pathway. The presence of this pathway in marine phytoplankton is still under debate. Results by Falkowski (1991) show a wide range (24.2 $^{0}/_{00}$) in δ$^{13}$C values for 13 species of phytoplankton grown in culture. This range along with the lack of a clear dichotomy in these values suggests variability in the capacity to assimilate HCO$_3^-$, with diatoms having a greater ability than dinoflagellates or cyanobacteria. However, it has been suggested that C3 vs C4 photosynthesis pathways cannot be determined on the basis of δ$^{13}$C values (Wong, 1976).

Despite the uncertainty associated with carbon isotopic fractionation and DIC utilization in marine phytoplankton, δ$^{13}$C values are typically more enriched than those of terrestrial C3 plants. Sackett et al. (1986) showed that the sedimentary organic carbon in Tampa Bay and adjacent riverine systems becomes more depleted in $^{13}$C with increasing distance upriver; ranging from -20 $^{0}/_{00}$ in the middle of Tampa Bay to -28 $^{0}/_{00}$ up the
rivers. This same study found relatively enriched $\delta^{13}C$ values, (~10 $^{\circ}/_{oo}$), in several small bays along the Gulf of Mexico coastline. These enriched values are thought to reflect a contribution of organic material from seagrasses ($\delta^{13}C$ -5 to -10 $^{\circ}/_{oo}$), and/or decreased isotopic fractionation in warm waters, as seen in an earlier study (Sackett et al. 1965). $\delta^{13}C$ values of marine phytoplankton range from –30 to –18 $^{\circ}/_{oo}$, but are typically around –22 $^{\circ}/_{oo}$, while terrestrial plant material and soil organic matter averages around 27 $^{\circ}/_{oo}$ (Boutton, 1991). Fig. 2 shows $\delta^{13}C$ values of potential sources and sinks of carbon in a coastal shelf environment.
Dissolved Inorganic Carbon (DIC)

Dissolved carbon dioxide (CO₂) and bicarbonate (HCO₃⁻) are the most abundant forms of DIC in the oceans, with HCO₃⁻ comprising > 99% of ΣDIC (Smit, 2001). Variation in the chemical equilibrium of DIC can alter the δ¹³C of this pool. In the ocean, both ΣDIC and CaCO₃ have mean δ¹³C values ~ 0 ‰, reflecting the small amount of fractionation between the carbonate ion (CO₃²⁻) and CaCO₃ (Boutton, 1991). In estuarine waters, the δ¹³C of DIC may be modified depending on the source of CO₂. The classical weathering reaction (CaCO₃ + CO₂ + H₂O = 2HCO₃⁻ + Ca²⁺) can be used to explain variations in δ¹³C. If CaCO₃ has a δ¹³C~0 ‰ and organically derived CO₂ has a δ¹³C~ -26 ‰, then weathering should produce HCO₃⁻ with a δ¹³C~ -13 ‰ (Sackett et al., 1997). The HCO₃⁻ can undergo further exchange with atmospheric CO₂ or additional organically derived CO₂ to shift its isotopic composition further in either direction. As photosynthesis discriminates against ^¹³C, residual DIC in surface waters tends to be slightly enriched, ranging from about 1 to 3 ‰ (Smit, 2001).
Dissolved organic carbon is the largest pool of organic carbon in marine waters, and globally has a reservoir size similar to atmospheric CO₂ (Fry et al., 1998). In contrast to DIC, DOC is relatively depleted due to the enzymatic fractionation of the DIC pool associated with photosynthesis. DOC in marine waters consists largely of soluble products of plankton decomposition, and has an average isotopic signature of δ¹³C ~ -23 ‰, similar to that for phytoplankton (Boutton, 1991).

Riverine DOC is more depleted, reflecting the contribution to this pool of more depleted freshwater riverine plankton (δ¹³C ~ -30 to -25 ‰) and surrounding terrestrial vegetation (δ¹³C ~ -27 ‰), (Boutton, 1991). This variation in δ¹³C values between marine and freshwater DOC is often used to trace the source of dissolved organic carbon (Simenstad and Wissmar, 1985) to coastal marine ecosystems, which can be important in understanding the contribution of terrestrial nutrient sources.
Fig. 2: $\delta^{13}C$ in a coastal shelf environment.
Objectives and Methodology

Research Objectives

The overall objective of this research is to measure the stable isotopic signatures of POM associated with *K. brevis* blooms and to use these signatures to constrain the potential sources of nitrogen that support them. Specific objectives were to:

1. Examine spatial and temporal stable isotopic behavior of particulate organic matter (POM) associated with the 2001 *K. brevis* bloom

2. Utilize this analysis in conjunction with previous bloom isotopic behavior and measured chemical and biological parameters to infer possible nutrient sources sustaining blooms

3. Assess the feasibility of using dual stable isotopic analysis of POM as a means of constraining nutrient sources supporting harmful algal blooms
Sampling

Sampling for this research occurred on the monthly ECOHAB cruises from 1998 to 2001. ECOHAB cruises consisted of 4 day quasi-synoptic sampling of approximately 75 stations located along 3 transects extending from Tampa Bay and Ft. Myers out to the 50 meter isobath and from Sarasota out to the 200 meter isobath. The area within these transects comprised the ECOHAB control volume (Fig. 3a). Additionally, more extensive sampling was done monthly from September through December 2001. During this time, a large bloom of *K. brevis* was present throughout the ECOHAB control volume.

Continuous underway measurements of surface temperature, salinity and fluorescence were taken on all cruises with a Falmouth Scientific underway CTD system. The CTD was placed in a large, darkened cooler and seawater was continuously pumped through it. Vertical water column measurements of these parameters were also taken on station with a Seabird CTD coupled with a rosette sampler consisting of 12 8L Niskin bottles. During the October (DotGOM; Fig. 3b)) 2001 cruise, additional samples were taken of the surface layer (0 to 10 cm) by filling a plastic bucket over the side of the ship.

Particulate samples for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis were obtained via rosette sampling during CTD casts. For September and October 2001, ~1.25 L of water was immediately taken from the Niskin bottle and filtered through precombusted (2 hr, 450°C) 25 mm Whatman GF/F filters under mild (10 – 15 psi) vacuum pressure. For
November and December sampling, 4L of water was transferred directly from the Niskin bottles into 20L metal canisters and filtered through precombusted 47 mm Whatman GF/F filters using pressurized (10 to 15 psi) N₂ gas. All samples were taken in duplicate, folded, placed in precombusted (2 hr, 450°C) foil packets and immediately frozen for later analysis.

Total dissolved phosphorus (TDP), total dissolved nitrogen (TDN), chlorophyll \( a \) \( (\text{chl}) \), particulate carbon, nitrogen and phosphorus and \( K. \ brevis \) cell concentration were also sampled. Duplicate samples for chl concentration were obtained by filtering 285 ml of water drawn directly from Niskin bottles through 25 mm Whatman GF/F filters. Samples were either immediately placed in 10 ml of methanol and extracted for ~ 48 to 76 hr., or were folded and placed in foil packets and immediately frozen in darkness. Samples stored in foil were placed in 10 ml. of methanol within 24 hrs. of the end of each cruise. All samples were analyzed fluorometrically for chl \( a \) according to Holm-Hansen et al. (1978). Duplicate samples for particulate C and N analysis were obtained by filtering 50 to 200 ml water through 13 mm precombusted (2 hr, 450°C) Whatman GF/F filters and were rinsed with 1 ml of 10% HCL to remove inorganic carbonate, followed by a filtered sea water rinse to remove the acid, folded and placed in fired foil packets and immediately frozen for later analysis. Total dissolved and particulate phosphorus samples were analyzed according Solorzano and Sharp (1980a, b). For particulate phosphorus, 585 ml of water was taken directly from the Niskin bottle and filtered through 25 mm precombusted (2 hr, 450°C) Whatman GF/F filters, briefly washed with 4 ml of 0.17M \( \text{Na}_2\text{SO}_4 \), placed into precombusted (2 hr, 450°C) 20 ml scintillation vials containing 2 ml of 0.017M \( \text{MgSO}_4 \) and frozen until analyzed. For total dissolved
phosphorus, 10 ml of water was taken directly from the Niskin bottle and filtered through precombusted (2 hr, 450°C) 25 mm Whatman GF/F filters and the filtrate placed into precombusted (2 hr, 450°C) scintillation vials. 0.2 ml of 0.17M MgSO₄ was added to each vial and all vials were immediately frozen for later analysis. Duplicate samples for total dissolved nitrogen were obtained by filtering 50 ml samples through precombusted (2 hr, 450°C) 25mm Whatman GF/F filters into 60 ml polypropylene bottles for analysis. Samples for inorganic nutrient (NO₃, NO₂, NH₄, PO₄ and SiO₄) analysis were collected directly from the Niskin bottle into 20 ml polypropylene bottles and immediately frozen for later analysis. Inorganic nutrient samples taken on the September, November and December ECOHAB cruises were not filtered prior to freezing while inorganic nutrient samples taken on the 2001 October cruise were filtered through precombusted (2 hr, 450°C) 25 mm Whatman GF/F filters. Chl a samples and all particulate and nutrient samples were stored at between –20°C and 4°C on board for later analysis. In most cases, *K. brevis* was counted live shortly after sample collection (according to Heil et al. 1999), but some samples were preserved in Lugol’s Iodine and transported back to the lab. *Karenia brevis* concentrations were determined by five replicate counts of 0.2 ml water at 100X using a dissection microscope.

Locations for sampling were selected to represent a wide range of *K. brevis* cell concentrations within the bloom. In addition to surface water samples taken within the bloom, samples were occasionally taken at 5m intervals throughout the water column (when the depth was <50m) or at 10m intervals (when the depth was >200m). Depths were chosen to sample the deep chlorophyll maximum (DCM) for comparison of 2 distinct phytoplankton populations. Samples of *Trichodesmium* spp. were also obtained
when blooms of this cyanobacterium were encountered during a *K. brevis* bloom. Individual *Trichodesmium* spp. colonies were picked from samples with inoculating loops and placed onto precombusted (2 hr, 450°C) 25mm Whatman GF/F filters, placed in precombusted (2 hr, 450°C) foil packets and immediately frozen. Zooplankton samples were obtained from zooplankton net tows and frozen in the same manner. In addition, samples of floating seagrass and *Sargassum* spp. were obtained when encountered by placing them into plastic bags and freezing immediately.

![Station map from ECOHAB: Florida cruises.](image)

Fig. 3a: Station map from ECOHAB: Florida cruises.
Fig. 3b: Station map from DotGOM2 (Oct. 2001) cruise.
Laboratory Processing

Isotopic analysis of particulate bloom samples was conducted on a continuous flow dual analysis Isotope Ratio Mass Spectrometer. The frozen particulate filters were rinsed with 1 ml of 10% HCL to remove any carbonate material, lyophilized, and the filters cut into pieces from which subsamples were taken to establish material homogeneity on the filter. Filters were introduced into the mass spectrometer via combustion with a Carlo-Erba Elemental Analyzer.

Particulate carbon and nitrogen concentrations were determined using a Carlo-Erba Model 1106 Elemental Analyzer. TDN (total dissolved nitrogen) concentrations were determined using the persulfate oxidation method of Solorzano and Sharp (1980). Inorganic nutrients (NO₂, NO₃, PO₄) were determined on a Alpkem RFA II segmented-flow nutrient analyzer according to Gordon et al. (1993). NO₃, NO₂ or PO₄ were subtracted from total N or P, respectively, to give concentrations of dissolved organic nitrogen and phosphorus.
Statistical Methodology

Statistical analysis was performed with STATISTICA software. Stable isotopic data (both $\delta^{15}$N and $\delta^{13}$C) was subdivided into temporal and spatial categories. The Shapiro-Wilks W test for normality was performed on each data set to determine distribution. All data sets were determined to have a non-normal distribution.

Nonparametric methods were used to test for statistically significant spatial and temporal differences. The Mann-Whitney U test was employed to test for differences in stable isotopic signature between surface bucket samples and 0 meter Niskin samples, between 0 meter and depth samples, and between samples taken within and outside of the 2001 K. brevis bloom. The Kruskal-Wallis ANOVA test was employed to test for temporal differences between the 4 months of the 2001 K. brevis bloom.
Results

The 2001 *K. brevis* Bloom

*Cell Abundance and Biomass*

The 2001 *K. brevis* bloom was first encountered in September outside the mouth of Charlotte Harbor. Maximum cell concentrations at this time were $3.76 \times 10^5$ cells L$^{-1}$ (fig. 4a). The bloom intensified and moved north to the mouth of Tampa Bay in October when cell concentrations in the 0 meter Niskin bottle sample reached $10^6$ cells L$^{-1}$ (fig. 4b), and $9.00 \times 10^6$ cells L$^{-1}$ in the surface layer (1 to 10 cm). The bloom remained in this area in November at the same intensity (fig. 4c). In December, cell concentrations decreased to a maximum of $2.24 \times 10^5$ cells L$^{-1}$, and the bloom became “patchier,” spreading along the coast between Tampa Bay and Charlotte Harbor (fig. 4d).

Surface (0 meter) chlorophyll concentrations follow the same pattern, except in November where there was an additional phytoplankton population located south of the *K. brevis* bloom (Fig. 5a-c). Due to sampling/processing error, no data was obtained for the month of December. Chlorophyll *a* concentrations increased steadily with increasing bloom biomass in September 2001, and continued to increase as 0 meter *K. brevis* populations reach maximum at around $10^6$ cells L$^{-1}$ in October and November. Chlorophyll *a* was higher in the surface (0 to 10 cm) layer; reaching 24 $\mu$M at one station. Concentrations decreased as *K. brevis* populations decreased in December (Fig. 6).
Surface contours of C:N showed a larger variation in regions outside of the bloom when compared to bloom regions (Fig. 7a-d). During September and October, C:N of bloom POM were near Redfield (6), but increased during November and December to > 9 as cell populations and chlorophyll concentrations stabilized and then decreased (Fig. 7a-d).
Nutrient Distributions

Surface maps of monthly nutrient concentrations show small patches of DIN (0.25 µM) off the mouths of both Tampa Bay and Charlotte Harbor in September (fig. 8a). As the bloom moved north to Tampa Bay in October, DIN decreased to the limit of detection (0.03 µM) in the 0 meter samples (fig. 8b), and remained depleted in November and December (fig. 8c & 8d). Yearly average values of atmospheric DIN deposition show an annual maximum of ~ 10 kg/ha/yr (fig. 12) being delivered to the WFS.

Surface concentrations of DON varied spatially during all months of the 2001 bloom, ranging from ~5 to ~20 µM over the sampling volume (Fig. 9a-d). DON concentration is much higher than DIN over the entire sampling volume; ranging from ~5 to ~25 µM (Fig. 9a-d).

Dissolved silica concentrations in the surface layer exhibited clear on/offshore gradients during all 4 months, with maximum concentrations of ~26 µM in December (Fig. 10a-d). Highest concentrations are found near the mouth of Charlotte Harbor in September (Fig. 10a), November (Fig. 10c) and December (Fig. 10d).

Surface layer concentrations of DIP were highest (1.25 µM) in September (Fig. 11a) in a patch off the coast of Charlotte Harbor. This level decreased within bloom areas over the next 3 months (Fig. 11b-d).
Stable Isotopes

Surface maps (using 0 meter Niskin samples) of $\delta^{15}$N of POM showed a wide range of values over the sampling area, including samples taken from within and outside of the bloom (Fig. 13a-d). During September, $\delta^{15}$N ranged from $-2.10$ $^{0}/_{00}$ to $9.18$ $^{0}/_{00}$, showing no discernible pattern of distribution (Fig. 13a). In October, values ranged from $-0.58$ $^{0}/_{00}$ to $4.52$ $^{0}/_{00}$, exhibiting a gradient with $\delta^{15}$N decreasing with distance from shore (Fig. 13b). In November, this gradient disappears, (Fig. 13c) exhibiting a patchier distribution, with one patch along the 50m isobath having an elevated $\delta^{15}$N signature. In December, the range narrows to between $2.24$ $^{0}/_{00}$ and $5.43$ $^{0}/_{00}$ (Fig. 13d). $\delta^{15}$N values of samples taken within the bloom are between ~2 and 5 $^{0}/_{00}$ during all 4 months (Table 1).

Surface maps (0 meter Niskin samples) of $\delta^{13}$C of POM show a gradient with $\delta^{13}$C decreasing with distance offshore in all 4 months (Fig. 14a-d). $\delta^{13}$C values are within a range between $-17$ and $-22$ $^{0}/_{00}$ within the bloom and are more variable outside the bloom during all 4 months (Table 2).

Isotopic signatures of both nitrogen and carbon are comparable to those of phytoplankton and associated POM in various U.S. coastal regions, while $\delta^{15}$N of POM associated with this $K. brevis$ bloom on the West Florida shelf is slightly more depleted (Table 3). Stable isotopic signatures of floating seagrass, *Sargassum* spp., *Trichodesmium* spp. and zooplankton on the WFS increase in the increment between primary producers and consumers (Table 4). The $\delta^{15}$N of these samples is comparable to that of bloom associated POM on the WFS, while the $\delta^{13}$C is more isotopically enriched.
Monthly averages of POM $\delta^{15}\text{N}$ from August 1998 to October 2000 show more variation between months than spatially within the same month (Fig. 15). Values from months when a bloom occurred are less variable and fall within a range of 2 to $\sim6.5\,^0/_{00}$. Isotopic variability does not appear to be related to distance from shore during these months, although monthly averages are comprised of samples taken over the entire ECOHAB:Florida control volume. $\delta^{15}\text{N}$ of POM is depleted during April 1999 and May 2000, when *Trichodesmium* spp. were abundant (Fig. 15).
Statistical Analysis

A significant difference was found between $\delta^{13}$C (POM) of surface bucket samples and 0 meter Niskin samples ( >99% confidence, $p = .00$). Significant differences were also observed between surface samples taken inside and outside of the bloom in both $\delta^{15}$N (91% confidence, $p = .09$) and $\delta^{13}$C (100% confidence, $p = .0$). Variance in either $\delta^{15}$N or $\delta^{13}$C with time over the 4 month period was not statistically significant.
Discussion

Several sources of nitrogen and carbon are available for utilization by *Karenia brevis* on the WFS. Fig. 1 & 2 show these potential sources and their corresponding $\delta^{15}$N and $\delta^{13}$C values ($^0/_00$). Because the intense *K. brevis* bloom of 2001 was first encountered in September (Fig. 4a) off the mouth of Charlotte Harbor, it seems obvious to consider estuarine sources of nitrogen first. Indeed, sampling revealed small patches of DIN (0.1 $\mu$M) and DIP (0.5 $\mu$M) in this region at this time (Fig. 8a & Fig. 11a). The relationship between *K. brevis* and DIN concentration during the 4 months of the 2001 bloom shows a wide range of cell concentrations in the presence of low DIN (fig. 17a). When chlorophyll concentrations are maximum, DIN concentration is at and below the limits of detection; $\sim$ 0.03 $\mu$M (Fig. 17b).

$\delta^{15}$N values of POM collected from areas with detectable DIN ($\sim$ 2 $\mu$M) ranged from 3 to 5 $^0/_00$ (Fig. 13a); a range of values that overlaps those of both atmospheric and estuarine (fertilizer) DIN (fig. 1). This suggests that either of these are possible nitrogen sources to support growth in this bloom.

However, reviews of historical cruise track data suggested that *K. brevis* blooms originate on the mid WFS, between 18 and 74 km offshore. This was verified by subsequent offshore cruise track data showing increased cell concentrations appearing offshore and then onshore several weeks later (Tester and Steidinger 1997). Estuarine outflow on the WFS does not reach this far; moreover, estuarine outwelling has been
found to provide phosphorus enriched waters with NO₃: PO₄ of <2 (Vargo et al., 2003). Even in the summer and fall when increased rainfall may contribute to higher nutrient outflow, this same process can serve to create salinity fronts that concentrate the nutrients inshore (Vargo et al. 2001).

In addition to an estuarine source, upwelling is a potential source of inorganic nitrogen. Haddad and Carder (1979) note that wind speeds are rarely sufficient to drive upwelling at the edge of the WFS except in winter. One exception occurred in the spring of 1998, when strong west winds caused an upwelling event causing the near bottom isopleth of 1 µmol NO₃ kg⁻¹ to penetrate to the 20m isobath in the Panhandle, Big Bend and Southeast regions of the WFS by May (Walsh, in review). In addition, intrusions of the Gulf Loop Current have been documented prior to K. brevis blooms (Haddad and Carder 1979), and may be a source of deeper waters containing elevated DIN concentrations.

Theoretically, these events could supply DIN, as K. brevis has been found down to depths of 50 meters (Steidinger 1998). However, natural populations tend to concentrate at the surface (Steidinger 1998). At one station in this study, cell concentrations were 8 times as high in the thin 0 to 10 cm surface layer as in the 0 to 1 m layer. Another problem is that NO₃ supplies from either upwelling or the Loop Current yield both pelagic and benthic diatoms (Khromov, 1969; Saunders and Glenn, 1969) instead of dinoflagellates. Heil et al. (1999) found that upwelled NO₃⁻ on the WFS fueled near bottom diatom blooms. This is hardly surprising considering that diatoms grow ~ 10 times faster than K. brevis, and that dinoflagellates have a half-saturation constant for
NO3 that is ~ 7 times that for diatoms (Smayda, 1997). This leads to the question of the importance of any source of NO3 to blooms of K. brevis.

Atmospheric deposition (AD) is another potential source of DIN. It is estimated that the nitrogen deposition to the global ocean from the atmosphere is equal to that from riverine sources (Fogel and Paerl, 1993). Complex chemical reactions result in a wide range of δ15N values of nitrogen-bearing gases in the atmosphere (Kendall, 1998). Seasonal and meteorological variations, types of anthropogenic inputs, proximity to pollution sources and distance from the ocean are all factors contributing to this range. In general, NO3 in rain has a more enriched δ15N value than the co-existing NH4 (Fig. 1).

There are no studies to date examining the δ15N signature of the atmospheric nitrogen source pools on the WFS. In the Atlantic coastal waters of North Carolina, however, AD is a major source (35 to 80%) of new nitrogen (Fogel and Paerl, 1993). In this region, combined DIN (NO3 + NH4) has a range of δ15N values from -13 to 2 ‰ (Fig. 1) (Fogel and Paerl 1994).

A medium sized K. brevis bloom amounting to 50 – 100 mg chl m⁻² and having a PON:chl (µmol/µg) of 0.4 and a C:chl of 30 requires that at least 20 – 40 mmol N m⁻² of new nitrogen be delivered to the WFS (Walsh & Steidinger 2001). NO3 stocks on the WFS above the 40 m isobath are generally < 0.25 µmol NO3 kg⁻¹, or < 10 mmol NO3 m⁻² (Walsh and Steidinger, 2001). High-sensitivity fluorometric methods have provided an even lower estimate for background NO3 stocks of < 0.01 µmol NO3 kg⁻¹ (Masserini and Fanning, 2000). It seems that there must be an additional source of nitrogen.

Because K. brevis is known to have the ability to use organic nitrogen, it seems that this is a potential source pool. During all four months or the 2001 bloom, DON was
present at high concentrations in all regions of the sampling area reaching 20 µM in some places (Fig. 9a-d). The relationship between K. brevis concentration and DON concentration shows elevated cell concentrations where DON ranges from between 10 to 20 µM (Fig. 18a). A similar pattern is seen with chlorophyll concentration (fig. 18b).

There are several source pools of DON on the WFS. Nearshore sources include estuarine, atmospheric, resuspension from near-bottom diatom populations (Lester et al. 2001) and release from decaying floating seagrasses. It is thought that riverine inputs (Seitzinger & Sanders, 1997) and atmospheric inputs (Seitzinger and Sanders 1999) of DON may contribute much more to estuarine and shelf eutrophication than was previously expected. Offshore sources include releases from N₂ fixing Trichodesmium spp. (Walsh and Steidinger, 2001).

Regenerated DON in the global ocean at various depths displays a range from 6.6 to 10.2 0/00 (Benner et al. 1997). In the Gulf of Mexico, this range narrows to 9.5 - 10.2 0/00 (fig. 1) (Benner et al. 1997). Because of methodological difficulties associated with the isolation of DON, the literature is lacking in δ¹⁵N values for this pool.

The lack of sufficient nitrate to sustain red tides on the WFS led to an early hypothesis that K. brevis could fix atmospheric nitrogen (Lasker and Smith, 1954). It now appears that the N₂ fixing diazotroph Trichodesmium spp. may play an important role in the nitrogen economy of large K. brevis blooms in coastal waters of the southeastern U.S. This is the dominant species of colonial N₂ fixer on the west coast of Florida (Walsh and Steidinger, 2001).

Blooms of Trichodesmium on the WFS have been related to annual summertime wind-induced deliveries of iron from the Sahara Desert (Lenes et al. 2001; Walsh and
Steidinger, 2001). Iron is necessary for the enzymatic reaction controlling nitrogen fixation. When iron limitation is alleviated and phosphorus needs are met by the surface P stocks reaching 0.4 µmol P kg\(^{-1}\) at times (Lenes et al., 2001), conditions are prime for *Trichodesmium* blooms.

It has been demonstrated that Trichodesmium releases DON at 50\% the rate of nitrogen fixation (Glibert and Bronk, 1994). During a 1999 ECOHAB cruise, increments of DON elevation were observed following population increases of *Trichodesmium* (Lenes et al, 2001). Further investigation has shown the capability of *K. brevis* to utilize \(^{15}\text{N}\) labeled DON released from Trichodesmium as a result of N\(_2\) fixation (Bronk et al., 2003).
Stable Isotopes and Other Parameters

The isotopic signatures of POM both within and outside of the *K. brevis* bloom were plotted against other parameters to examine the relationships between them. The relationship between the isotopic values of POM and surface DIN concentration shows a wide range of isotopic values for both carbon and nitrogen with the low DIN concentrations seen over the 4 month period (Fig. 20 a & b). A sample taken within the bloom in September where DIN was ~ 2.5 µM had a δ¹⁵N value of 5.1 ‰ and a δ¹³C value of −20.5 ‰ (Fig. 20b). δ¹⁵N and δ¹³C of surface POM exhibit wide variability over the large range of DON concentration (Fig. 21a & b).

There is no clear relationship between the elemental C:N and the isotopic signatures of POM. While C:N increases with bloom progression, both δ¹⁵N and δ¹³C vary in a different manner. δ¹⁵N becomes more constrained in December, and δ¹³C becomes more depleted (Fig. 22 a & b).

Ranges of δ¹⁵N and δ¹³C POM values become restricted with increasing dissolved silica concentration during all 4 months (Fig. 23a & b). Ranges narrow to between 3 and 5 ‰ for δ¹⁵N and −20 to −16 ‰ for δ¹³C.

δ¹⁵N values of the POM within the *K. brevis* bloom in September of 2001 ranged from 4.93 to 5.10 ‰ (Table 1). This isotopic value in combination with the nearshore proximity of the bloom during this time suggests a combination of estuarine sources (fertilizer and sewage DIN) and atmospheric DIN were potentially supporting the bloom.
(Fig. 1). However, the uncertainties associated with the isotopic fractionation of phytoplankton during nitrogen assimilation (Handley and Raven 1992; Goeriche et al. 1994) complicate this interpretation. Nonetheless, this value is at the top of the range of $\delta^{15}N$ values observed during this bloom, and is low when compared to $\delta^{15}N$ values of POM from other coastal regions (Table 3) suggesting that some of the nitrogen utilized by this bloom came from a $^{15}N$ depleted source pool.

$\delta^{13}C$ values of POM within the bloom in this region ranged from -24.1 to -18.7 $\%$ (Table 2). This wide range in carbon isotopic signatures reflects both typical values seen for POM in coastal regions (Table 3), and the more enriched values found in nearshore waters in this study (Fig. 14 a-d). *K. brevis* cell concentrations within the bloom during September averaged ~ 75 x 10$^3$ cells L$^{-1}$. Elemental C:N from samples within the bloom were close to Redfield, suggesting that the nitrogen required for maximum cell growth was present (Fig. 7a).

The bloom was found north of the mouth of Tampa Bay the following month with cell concentrations reaching 9 x 10$^6$ cells L$^{-1}$ in the surface (0 to 10 cm) layer. Both DIN and DIP were at detectable, but very low levels in this region (Fig. 8b & 11b). During this month, both $\delta^{15}N$ and $\delta^{13}C$ values of POM (Table 1 & 2) from within the bloom fall within ranges of 2 to 6 $\%$ and -22 to -17 $\%$, respectively (Fig. 19a & b). The range of $\delta^{15}N$ is similar to that seen in September, and suggests that *K. brevis* is relying on similar source pools or source pool combinations throughout the course of the bloom.

Fig. 1 shows a depleted isotopic signature for regenerated NH$_4$ in oligotrophic environments, and an enriched signature for DON. It is important to note that these values were not obtained form WFS samples, and are dependent upon the sources of
nitrogen supplied for the regeneration process. For NH₄, this depleted signature is not unrealistic in an environment where a significant source of DON is from *Trichodesmium* spp., as this isotopically depleted pool is likely to become even more depleted with regeneration (Walsh and Steidinger 2001).

The enrichment in $^{13}$C seen at maximum bloom concentrations could suggest a depletion of DIC as a result of high cell density and/or elevated temperature. Elemental C:N within the bloom during October were close to Redfield, suggesting that cells were growing at maximum growth rates in a nitrogen replete environment (Fig. 7a).

In November of 2001, cell concentrations began to decrease, but still remained in the $10^6$ cells L$^{-1}$ range (Fig. 4c). Inorganic nutrient concentrations were at the limit of detection, but DON concentrations were still elevated in some regions (Fig. 9c), suggesting that this source pool may be regenerated within the bloom. Isotopic signatures of both carbon and nitrogen (Table 1 & 2) remained within the ranges characteristic of those seen in high ($\geq 5 \times 10^3$ cells L$^{-1}$) cell populations, further suggesting the occurrence of nitrogen regeneration processes within the bloom (Fig. 19a & b). C:N ratios during this month began to increase above Redfield. This is the first suggestion that cells were depleting their nutrient sources. Alternatively, it may suggest elevating amounts of detritus associated with the bloom.

During December, maximum cell concentrations decreased to around $3 \times 10^5$ cells L$^{-1}$ (Fig. 4d). Inorganic nutrient concentrations remained at the limits of detection (Fig. 8d & 11d), but there remained a surplus of DON (Fig. 9d). $\delta^{15}$N and $\delta^{13}$C of POM
within the bloom remained constrained (Fig. 19a & b). C:N remained above Redfield, suggesting further nutrient depletion or detrital contribution (Fig. 7d).

\[ \delta^{13}C \] of POM becomes more enriched as silica concentration increases in all 4 months (Fig. 23b), suggesting an inflow of freshwater into the bloom region. Some diatoms were found to occur in bloom regions, but at much lower concentrations than \textit{K. brevis}, so it is likely that the elevated silica is coming from a riverine source. At high silica concentrations, \[ \delta^{15}N \] ranges from ~2 to 5 \(^{0/00}\), suggesting that if nitrogen is being provided by freshwater inflow, it is not coming from sewage, as this would be more isotopically enriched (Fig. 1). Estuarine outflow of inorganic fertilizer is one source possibility, with isotopic values ranging from 0 to 3 \(^{0/00}\) (Fig. 1).

The relationship between \textit{K. brevis} concentration and chlorophyll concentration (Fig. 6) indicates that \textit{K. brevis} is responsible for most of the surface biomass in the sampling area. This means that samples that were taken within the bloom reflect bloom characteristics, and not those of other phytoplankton. Indeed, C:N, (Fig. 16a & b), \[ \delta^{15}N \] (Fig. 19a) and \[ \delta^{13}C \] (Fig. 19b) are much more variable in areas of low \textit{K. brevis} concentration.

Samples from past ECOHAB cruises have provided \[ \delta^{15}N \] data similar to that seen in 2001. The monthly averages shown in Fig. 15 show that during bloom months, \[ \delta^{15}N \] falls between a range of ~ 2 – 5 \(^{0/00}\). During months when there was no bloom the isotopic signatures are much more variable. This suggests that \textit{K. brevis} opportunistically
uses whatever nitrogen source it can “find”, and regenerates this nitrogen within the bloom as it progresses, to give such a constrained isotopic signature range.

Table 4 presents some $\delta^{15}N$ and $\delta^{13}C$ values for samples of biological material found in close proximity to the bloom in 2001. One nitrogen source possibility is decaying seagrass that is often floating in bloom regions. The $\delta^{15}N$ of this seagrass averages 2.30 $^0/_{00}$, similar to that found in seagrasses sampled in the Florida Keys (Anderson 2003). The previously cited study demonstrates that isotopic signatures of seagrasses can be used to monitor nitrogen source pools in a region. The relatively depleted signatures seen in Florida waters likely reflect the isotopically depleted source pools. The relatively enriched $\delta^{13}C$ of seagrasses could be one source of detritus present within the bloom which could contribute to an enrichment of bloom POM $\delta^{13}C$, if the observed enrichment is to be explained by detritus and not depleted DIC concentration.

*Trichodesmium* spp. sampled from around the *K. brevis* bloom gave a characteristic $\delta^{15}N$ value of -0.6 $^0/_{00}$. DON released from this diazotroph would be isotopically depleted as well. Recent studies (Bronk et al. submitted) have shown that *K. brevis* has the ability to utilize $^{15}$N-labelled DON which was released by *Trichodesmium* after fixing $^{15}$N-labelled N$_2$. Since this organism is common in the oligotrophic WFS waters and is found to co-occur in and around *K. brevis* blooms, it seems that this may be one source of nitrogen contributing to the lower end of the $\delta^{15}N$ range seen in bloom POM.
Figures 1 and 2 give a schematic representation of the isotopic values of possible nitrogen source pools and various types of biomass found in coastal areas. All of the sources represented are potentially available to supply nitrogen for use by *K. brevis*, although based on data from past studies and the isotopic values of bloom POM from this study, some seem more likely than others. Given the relatively narrow and isotopically depleted range of $\delta^{15}$N found within blooms on the WFS, it seems that terrigenous input of sewage material can be excluded as a significant source. In addition, upwelled nitrate is probably not significant, given the isotopic discrepancy and the rarity of this process on the WFS. It is likely that a combination of the other source pools are responsible, and are probably exploited by *K. brevis* opportunistically.

If *K. brevis* blooms are initiated in offshore waters, then offshore sources of nitrogen must support the initiation process. Walsh and Steidinger (2001) concluded that the likelihood of a large *K. brevis* bloom at the shoreline increases with the co-occurrence of seasonal Saharan dust events (and dissolution of iron delivered); sufficient rainfall; seed stocks of both *Trichodesmium* spp. and *K. brevis*; release of DON to all dinoflagellate competitors; selective grazing stress on diatoms and other dinoflagellates; and onshore flow to facilitate congregation inshore. They note that smaller red tide events are more enigmatic, given that there are multiple sources of nitrogen inshore that may serve to initiate and maintain smaller *K. brevis* stocks. Indeed, POM associated with a small event ($10^5$ cells L$^{-1}$) in December 1998 had an isotopic signature of 4.8‰. This value is intermediate between values for *Trichodesmium* spp., (0.3‰, Walsh and Steidinger 2001; -0.62‰, this study), and 7.3‰ for diatoms above the 30-40 m isobath.
(Walsh and Steidinger 2001). This value falls in the middle of the range seen in the present study, and may reflect a $^{15}$N enriched DON substrate modified by bacterial processing. Alternatively, it may reflect the isotopic composition of DON from another source, such as estuarine (Seitzinger and Sanders 1997) or atmospheric (Seitzinger and Sanders 1999).

The similarities in the isotopic data from this and past studies indicates that there is a source or combination of sources of nitrogen being utilized that is unchanging over time. The greater incidence of blooms in the late summer early fall adds a seasonal component that, in combination with offshore bloom initiation, seems to suggest a relationship with release of DON by *Trichodesmium* spp. The more depleted isotopic signatures for bloom associated POM corroborate this, and together the data suggest that release of DON by cyanophytes may serve to initiate large blooms.

Once blooms are transported to nearshore waters, other nitrogen sources may serve to maintain them, and bacterial processing may serve to regenerate the nitrogen pool, thereby modifying it’s isotopic signature. It appears that over the course of a typical *K. brevis* bloom, various sources are utilized opportunistically. The isotopic data in this study suggest that sources exhibiting relatively depleted isotopic signatures ($< 5$ \(^{0/00}\)) are more important than those that are more isotopically enriched.

Given the affinity *K. brevis* has for organic nitrogen and the large supply of it on the WFS (in contrast to the lack of inorganic nitrogen), it is likely that the DON pool is the most important substrate serving to initiate and maintain blooms. This pool contains a diverse array of compounds coming from several different potential sources. Future
research should focus on the relative contribution of each potential source to the WFS, and on the isotopic compositions of each source. Answers to these questions will help us to find out why Florida’s oligotrophic gulf coastal waters are such a prime habitat for this red tide dinoflagellate.
Fig 4: Surface contour of *Karenia brevis* concentrations (x 10^3 cells L^-1) in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), Nov. (c), and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 5: Surface contour of chlorophyll \( a \) concentrations (\( \mu \text{g L}^{-1} \)) in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), and Nov. (c) of 2001. Stations sampled are indicated by the black dots. *No data for Dec.
Fig. 6: Relationship between surface *Karenia brevis* concentration (cells L$^{-1}$) and surface chlorophyll $a$ concentration (µg L$^{-1}$) during the 2001 bloom. October samples are comprised of both 0 meter Niskin bottle samples and surface bucket samples while other months are 0 meter Niskin bottle samples only.
Fig. 7: Surface contour of carbon: nitrogen elemental ratios (µM) of particulate organic matter in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), Nov. (c) and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 8: Surface contour of dissolved inorganic nitrogen concentrations (µM) in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), Nov. (c) and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 9: Surface contour of dissolved organic nitrogen concentrations (µM) in the 0 meter Niskin bottle for Sept. (a), Oct. (b), Nov. (c) and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 10: Surface contour of dissolved silica concentrations (µM) in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), Nov. (c) and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 11: Surface contour of dissolved inorganic phosphorus concentrations (μM) in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), Nov. (c) and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 12: Atmospheric deposition of inorganic nitrogen on the west Florida shelf: 1996 – 2003.
Fig. 13: Surface contour of $\delta^{15}$N values (‰) of particulate organic material in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), Nov. (c) and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 14: Surface contour of δ^{13}C values (‰) of particulate organic material in the 0 meter Niskin bottle sample for Sept. (a), Oct. (b), Nov. (c) and Dec. (d) of 2001. Stations sampled are indicated by the black dots.
Fig. 15: Monthly averaged $\delta^{15}$N ($^\circ/1000$) of particulate organic material from ECOHAB: Florida cruises: 1998-2000. Averages are from Aug. 1998 to Nov. 2000 along the 10, 30 and 50 meter isobaths and offshore at ~200 meters. The arrow indicates the month where high *Trichodesmium* spp. concentrations were observed.
Fig. 16: Relationship between the carbon: nitrogen elemental ratios (µM) of particulate organic material with *Karenia brevis* concentration (cells L⁻¹) (a) and chlorophyll *a* concentration (µg L⁻¹) (b) over the course of the 2001 bloom. Samples were taken from the 0 meter Niskin bottle.
Fig. 17: Relationship between the dissolved inorganic nitrogen concentration (µM) with *Karenia brevis* concentration (cells L⁻¹) (a) and chlorophyll *a* concentration (µg L⁻¹) (b) over the course of the 2001 bloom. October samples are comprised of 0 meter Niskin bottle samples and surface bucket samples while other months are 0 meter Niskin samples only.
Fig. 18: Relationship between the dissolved organic nitrogen concentration (µM) with *Karenia brevis* concentration (cells L$^{-1}$) (a) and chlorophyll *a* concentration (µg L$^{-1}$) (b) over the course of the 2001 bloom. Samples are from the 0 meter Niskin bottle.
Fig. 19: Relationship between *Karenia brevis* concentration (cells L$^{-1}$) and the $\delta^{15}$N ($^{\circ}$/oo) (a) and $\delta^{13}$C ($^{\circ}$/oo) (b) of particulate organic material over the course of the 2001 bloom. Data is from all stations and all depths sampled.
Fig. 20: Relationship between dissolved inorganic nitrogen concentration (μM) and the δ¹⁵N (‰) (a) and δ¹³C (‰) (b) of particulate organic material over the course of the 2001 bloom. October data is comprised of 0 meter Niskin bottle samples as well as surface bucket samples while other months are 0 meter Niskin samples only.
Fig. 21: Relationship between dissolved organic nitrogen concentration (µM) and the δ¹⁵N (%oo) (a) and δ¹³C (%oo) (b) of particulate organic material over the course of the 2001 bloom. October data are comprised of 0 meter Niskin bottle samples as well as surface bucket samples while other months are 0 meter Niskin samples only.
Fig. 22: Relationship between the elemental carbon:nitrogen ratio (µM) of particulate organic material with the δ¹⁵N (‰) (a) and δ¹³C (‰) (b) over the course of the 2001 bloom. Data are from all stations and depths sampled.
Fig. 23: Relationship between dissolved silica (µM) and the δ¹⁵N (‰) (a) and δ¹³C (‰) (b) of particulate material over the course of the 2001 bloom. Data is from all stations and depths sampled.
Table 1: Spatial $\delta^{15}$N during the 2001 *K. brevis* bloom. Values are the means with ranges given in parenthesis where N>1. “Bloom” signifies the presence of *K. brevis* in the sample at concentrations $>$ 5000 cells L$^{-1}$.

<table>
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<td></td>
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<td>3.77</td>
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<td>4.51</td>
<td>5.43</td>
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<td>*</td>
<td>*</td>
<td>4.26</td>
<td>(4.06 to 4.60)</td>
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<td>*</td>
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<td>*</td>
<td>10.43</td>
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Table 2: Spatial $\delta^{13}C$ during the 2001 *K. brevis* bloom. Values are the means with ranges given in parenthesis where N>1. “Bloom” signifies the presence of *K. brevis* in the sample at concentrations > 5000 cells L$^{-1}$.

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<td>Tampa Bay (inside)</td>
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<td>Longshore</td>
<td>-20.6 N=1</td>
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<td>Tampa Bay (mouth)</td>
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<tr>
<td>Charlotte Harbor (mouth)</td>
<td>-21.7 N=3</td>
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<td>Longshore</td>
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<td>Offshore Non-bloom</td>
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<tr>
<td>Outside Tampa Bay</td>
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</tr>
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<td></td>
<td></td>
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<td>Outside Charlotte Harbor</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
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<tr>
<td>50m isobath</td>
<td>-23.8 N=1</td>
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<tr>
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<tr>
<td>200m isobath</td>
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Table 3: $\delta^{15}$N and $\delta^{13}$C of phytoplankton and associated particulate organic material from various U. S. coastal regions.

<table>
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<tr>
<th>Region</th>
<th>Material</th>
<th>$\delta^{15}$N</th>
<th>$\delta^{13}$C</th>
<th>Source</th>
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<tr>
<td>George’s Bank</td>
<td>POM</td>
<td>5.1 +/- 1.8</td>
<td>-21.3 +/- 1.6</td>
<td>Fry, 1988</td>
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<td>Wood’s Hole Harbor</td>
<td>POM (mostly Diatoms)</td>
<td>7.5 to 12</td>
<td>-19 to -25</td>
<td>Wainright and Fry, 1994</td>
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<td>Mississippi salt marsh</td>
<td>Edaphic Algae</td>
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<td>-20</td>
<td>Sullivan, 1990</td>
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<td>Salt marsh estuary, Sapelo Island, Georgia</td>
<td>POM</td>
<td>8.6 +/- 1</td>
<td>-23 +/- 1.1</td>
<td>Peterson, 1987</td>
</tr>
<tr>
<td>San Fransisco Bay</td>
<td>phytoplankton</td>
<td>5 to 11</td>
<td>-27 to -17</td>
<td>Cloern et al. 2002</td>
</tr>
<tr>
<td>N.W. Gulf of Mexico</td>
<td>POM</td>
<td>7.5 +/- 0.8</td>
<td>-21 +/- 1.4</td>
<td>Macko et al. 1984</td>
</tr>
<tr>
<td>South Florida</td>
<td>POM (Tricho. present)</td>
<td>-0.9 +/- 1.4</td>
<td>-19.4 +/- 1.2</td>
<td>Macko et al. 1984</td>
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<tr>
<td>Delaware Estuary</td>
<td>POM</td>
<td>8 to 11</td>
<td>no data</td>
<td>Fogel and Paerl, 1993</td>
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<tr>
<td>North Carolina Estuary</td>
<td>POM</td>
<td>3 to 6</td>
<td>no data</td>
<td>Fogel and Paerl, 1993</td>
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<tr>
<td>West Florida shelf</td>
<td>POM (2001 K. brevis bloom material)</td>
<td>2 to 5</td>
<td>-22 to -17</td>
<td>*this study</td>
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<td>*typical estuarine phytoplankton</td>
<td>phytoplankton</td>
<td>6 to 20</td>
<td>no data</td>
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Table 4: $\delta^{15}$N and $\delta^{13}$C of miscellaneous primary producers on the west Florida shelf. Samples include floating seagrass and *Sargassum* spp., zooplankton samples from tows and hand-picked *Trichodesmium* spp. collected during the 2001 *K. brevis* bloom. Values are means with ranges given where N>1.

<table>
<thead>
<tr>
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<th>Average $\delta^{15}$N ($^{\circ}/oo$)</th>
<th>Average $\delta^{13}$C ($^{\circ}/oo$)</th>
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<tr>
<td>Floating Seagrass</td>
<td>2.307 N=7</td>
<td>-11.843 N=7</td>
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<td>(-.204 to 3.616)</td>
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<td>Floating <em>Sargassum</em> spp.</td>
<td>3.201 N=1</td>
<td>-18.698 N=1</td>
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<td>Zooplankton</td>
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<tr>
<td>10 µm tow</td>
<td>5.673 N=4</td>
<td>-20.287 N=5</td>
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<tr>
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<td>(5.387 to 6.441)</td>
<td>(-23.664 to -14.976)</td>
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<td>64 µm tow</td>
<td>5.948 N=3</td>
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<tr>
<td></td>
<td>(4.826 to 6.757)</td>
<td>(-15.826 to -13.927)</td>
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<tr>
<td>153 µm tow</td>
<td>6.126 N=9</td>
<td>-17.323 N=9</td>
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<td>(4.952 to 7.974)</td>
<td>(-18.992 to -13.681)</td>
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<tr>
<td><em>Trichodesmium</em> spp.</td>
<td>-.619 N=1</td>
<td>-13.146 N=1</td>
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References


Appendices
Appendix A: *K. brevis* counts from 2001

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<thead>
<tr>
<th>Date</th>
<th>Station</th>
<th>lat. (°N)</th>
<th>long. (°W)</th>
<th>Depth</th>
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