MEMORANDUM

DATE: August 11, 2006

TO: Sanibel City Council

FROM: Judie Zimomra, City Manager

SUBJECT: Supplemental Packet Information – August 15, 2006

Please find the following supplemental material attached for the August 15, 2006 City Council meeting:

- Agenda Item - to be added
  - Industry Appreciation Week Proclamation

- Agenda Item 7(c)
  - Letter of objection from resident to sewer rate increase dated August 7, 2006

- Agenda Item 10(a)4
  - Staff Report with attached back-up material

- Agenda Item 10(d)
  - Map of Inventory and Analysis of Public Accesses to Dinkins and Clam Bayous

- Agenda Item 15(a)1
  - Composite Report from Business Roundtable Discussion Groups and next steps

Please feel free to contact me with any questions regarding the above items.

JAZ/jkg

C: Ken Cuyler, City Attorney
Pamela Smith, City Clerk

Agenda Item - to be added

ATTACHED IS THE INDUSTRY APPRECIATION PROCLAMATION TO BE ADDED TO AGENDA

MEMORANDUM

TO: CITY COUNCIL MEMBERS

FROM: JUDIE ZIMOMRA, CITY MANAGER

DATE: AUGUST 11, 2006

SUBJECT: INDUSTRY APPRECIATION WEEK

We were just informed by the Horizon Council that Industry Appreciation Week is September 18 through September 22, 2006. The Industry Appreciation Luncheon will be held on September 22, 2006, Harborside, 11:30 a.m.. Eight seats are available at the City table. In Pamela Smith's absence, please inform Carol Reed if you will attend the luncheon.

The enclosed Industry Appreciation Week Proclamation is added to the August 15, 2006 agenda due to the City Council meeting schedule prior to Industry Appreciation Week.

Industry in Lee County is vital in the communities health; and

WHEREAS:	*Lee County's existing industries are the key to a prosperous future; and*
WHEREAS:	*The expansion of those industries accounts for the majority of new jobs created; and*
WHERAS:	*Lee County's industries help sustain our quality of life; and*
WHERAS:	*Public knowledge of the contributions made by industry is essential to maintenance of good community industry relationships.*

NOW, THEREFORE, I, Carla Brooks Johnston, Mayor of the City of Sanibel, Lee County, Florida on behalf of the members of Sanibel City Council and the citizens of Sanibel do hereby declare September 18 through 22, 2006 as INDUSTRY APPRECIATION WEEK and urge all residents to salute our industries and their employees for their contribution to our community.

IN WITNESS WHEREOF, I have hereunto set my hand and caused the seal of the City of Sanibel to be affixed hereto.

7. Utilities Division

c. RESOLUTION 06-117 ADOPTING AND ESTABLISHING A REVISED SCHEDULE OF RATES, FEES AND CHARGES FOR THE SANIBEL SEWER SYSTEM; PROVIDING FOR AN INCREASE IN RESIDENTIAL AND COMMERCIAL CUSTOMER RATES; AND PROVIDING EFFECTIVE DATES

THE ATTACHED IS A LETTER OF OBJECTION TO THE ABOVE RESOLUTION FOR SEWER RATE INCREASES.

Aug 7 2006

To: City of Sanibel

Re: Rate Increase Hearing
Sewer Charge

1- If you increase the sewer charge, which I am very opposed to, the entire rate structure should be rethought. Could not the rates be tied to square footage of the house or the number of bathrooms or both ???

2- I live in an older 1 bedroom cottage. I have one bathroom (1950 vintage), no dishwasher, no trash disposal, no outdoor spigot. That I pay the same as the McMansions and the huge estates is really outrageous. The logic and fairness of that type of charge is baseless and faulty.

3- Do rethink everything.

Thank You.

Sincerely,
Candace Hines

10. OLD BUSINESS

a. Water Quality Issues

4. Staff Report regarding the red tide correlation regarding nutrients

ATTACHED IS THE STAFF REPORT AND BACK-UP MATERIALS

Red Tide (*Karenia brevis*) Literature Review

City of Sanibel
Department of Natural Resources

Summary

This literature review is the result of a request from the Sanibel City Council to examine the scientific literature regarding the relationship between nutrients and Florida red tide (*Karenia brevis*). Although this literature review was extensive, it is not all-inclusive of all of the information related to *K. brevis*.

There are numerous theories regarding the origin of red tide blooms and what sustains them, but the direct link between nutrients and bloom events are still poorly understood. A majority of the work in the past pointed to an offshore bloom initiation which moved inshore with currents and wind. These studies argued that land-based nutrients were not the driving force behind Florida red tides. However, recent work from Lapointe and Brand indicate that land-based runoff and elevated nutrient loads from river inputs may result in bloom initiation inshore. In addition, recent work by Heil *et a*l suggests that there may be an indirect link between nutrient runoff via *Trichodesmium*, a cyanobacteria that is limited by iron, which has the ability to fix nitrogen making it available to fuel red tide blooms.

Below is a list of articles that were reviewed by the Department of Natural Resources. We have selected some key papers regarding the relationship between red tide and nutrients and have pulled some key points from each of them to highlight the current theories.

Lenes, J.M. *et al.* 2001.
Iron fertilization and the *Trichodesmium* response on the West Florida shelf

- Iron plays a critical role in N-fixation by the cyanobacteria, *Trichodesmium*, and iron deposition, in the form of Saharan dust, may play a major role in blooms of the organism.
- Blooms of *Trichodesmium* have been observed within 75 km of the west coast of Florida for more than 50 years.
- Suggests that the organic nitrogen that supported the October 1999 Florida red tide was the result of increased N-fixation by the cyanobacterium, *Trichodesmium spp*.

Anderson, D.M. *et al.* 2002.
Harmful Algal Blooms and Eutrophication: Nutrient Sources, Composition, and Consequences

- The sources of nutrients potentially stimulating algal blooms are numerous.
- The overall effect of eutrophication on harmful algal species is species specific.
- Karenia brevis specifically: It has been suggested that production of reduced nitrogen by *Trichodesmium* fuels red tide blooms of the coast of Florida
- Eutrophication is one of several mechanisms by which harmful algae appear to be increasing in extent and duration in many locations. Although important, it is not the only explanation for blooms or toxic outbreaks.

Gilbert *et al.* 2006
Escalating worldwide use of urea – a global change contributing to coastal eutrophication

- Worldwide use of urea as a nitrogen fertilizer and feed additive has increased more than 100-fold in the past 4 decades
- There is evidence that urea differentially stimulates the growth of some phytoplankton species and may promote a shift in community composition to those species that are more noxious to the ecosystem and to human health.
- Elevated urea concentrations were measured at the mouth of the Caloosahatchee River and surrounding areas following Hurricane Charley.
- *K. brevis* has been shown to increase its production of brevetoxin up to 6x when exposed to elevated urea levels (although urea levels used in this experiment far beyond natural conditions)

Murdock, J.F. 1954
A preliminary survey of the effects of releasing water from Lake Okeechobee through the St. Lucie and Caloosahatchee estuaries

- Suggests that water releases from the Caloosahatchee may be a contributing cause to red tide outbreaks; however, the flows from the Caloosahatchee are minimal as compared to contributions of the Peace River and other drainage systems
- Ultimately concludes that the damage caused by releases through the Caloosahatchee is small and any changes that do occur are not believed to be serious.

Lapointe, B.E., Bedford, B., Brand,L., and Yentsch, C.S. 2006
Harmful algal blooms in coastal waters of Lee County, FL: Bloom dynamics and identification of land-based nutrient sources. Phase II Final Report

- There is general agreement among scientists that increasing runoff pollution from land-based sources is a major cause of the global increase in HABs (Gilbert et al. 2005).
- An analysis of existing data of cell counts for Red tide (*Karenia brevis*) from the 1950's and 1990's showed that these blooms have intensified an average of 15-fold since the 1950's and they occur primarily in nearshore (not offshore) waters, and that the duration of the blooms has increased (Brand and Compton, in press).
- The total dissolved nitrogen to total dissolved phosphorus ratio "…varied between 8.5 and 83.5 with the lowest value associated with a red tide bloom in 30 ‰ salinity water off Sanibel Island supports the idea that nearshore red tides on Florida's southwest coast are associated with high phosphorus coastal waters associated with freshwater runoff of the Peace and Caloosahatchee rivers."
- "The dense red tide sampled on September 8th off southern Sanibel Island had an acerage ^{15}N value of =7.83$\pm$ 1.14 ‰, which is also within the range of sewage nitrogen."
- The high ^{15}N values in *K. brevis* "…provide strong evidence that these blooms were supported by land-based nitrogen discharges, particularly the massive releases from Lake Okeechobee and the Caloosahatchee River that occurred in 2004/2005 following hurricanes Charley, Frances, and Jeanne."
- "These ^{15}N data do not support the hypothesis that red tide off Sanibel Island was supported by Nitrogen fixation from the cyanobacterium *Trichodesmium* as suggested by Lenes et al. (2001), which would have produced much lower ^{15}N values of ~0 ‰ to +1 ‰"

Lapointe, B.E. and Bedford, B.J. 2006.
Drift rhodophyte blooms emerge in Lee County, FL: Evidence of escalating eutrophication. Harmful Algae, in press.

- "Land-based nutrient discharges to bays and coastal waters along southwest Florida have long been linked to the development of macroalgae and phytoplankton blooms."
- "In coastal waters of southwest Florida, Ketchum and Keen (1947) correlated red tide blooms off Sarasota, FL, with unusually high P concentrations in the water column and suggested "the excessive nutrient content may be the result of terrigenous contamination of fertilization of the waters.""

- "Slobodkin (1953) reported that the red tide outbreaks off southwest Florida may be initiated by the development of a stratified water mass characterized by reduced salinity and elevated nutrients resulting from discharges of the combined Charlotte Harbor-Caloosahatchee River drainage basins."

Tester, P.A., and K.A. Steidinger. 1997.
***Gymnodinium breve* red tide blooms: Initiation, transport and consequences of surface circulation. Limnology and Oceanography 42(5):1039–1051.**

- Tester and Steidinger propose that red tide blooms initiate "offshore and in association with shoreward movements of the Loop Current or spinoff eddies."
- Phycotoxicans in tropical Atlantic waters were recognized and reported as far back as 1530-1550 in ships logs. According to Feinstein et al. 1955, accounts of *G. breve* (*K. brevis*) blooms were linked with noxious "gases" and massive fish kills along the west coast of Florida as far back as 1844.
- "Throughout the Gulf of Mexico and the U.S. South Atlantic Bight, *G. breve* is found in background concentrations (1-1,000 cells/l) except in areas off the Texas coast and the west Florida coast where circulation may play a role."
- "Bloom concentrations first appear offshore
- "Fronts represent a dynamic area of nutrient regimes and light conditions which can favor accumulation and growth of dinoflagellates." Bloom species such as *G. breve* are well adapted to such environments and can grow throughout the euphotic zone.
- "In addition to their ability to exploit light regimes, both species have advantages in nutrient dynamics." "Both assimilate Nitogen at low light and are able to utilize organic as well as inorganic nutrients."
- The bloom model using 80-100 yr observations starts with an offshore bloom initiation in late summer or fall in conjunction with a Gulf Loop intrusion on the outer continental shelf. The *G. breve* (*K.brevis*) cells concentrate on the midshelf and wind induced up-welling or down-welling assist the bloom. The bloom is then carried inshore by currents and wind.

Kirkpatrick et al. 2004.
Literature review of Florida red tide: implications for human health effects. Harmful Algae 3 (2004) 99-115.

- "Recent prolonged red tides in the Gulf of Mexico have been associated with environmental, human health, and economic impacts."
- This paper is a literature review and outlines the health effects to humans associated with red tides. It also discusses the symptoms and treatment of neurotoxic shellfish poisoning (NPS)
- The authors state that the most effective way to prevent adverse health effects is to prevent exposure to the toxins and organisms associated with red tide blooms.

Hu, C. F.E. Muller-Karger, and P.W. Swarzenski. 2006.

Hurricanes, submarine groundwater discharge, and Florida's red tides. Geophysical Research. 11:L11601.

- The authors of this paper hypothesize that the unusual number of hurricanes in 2004 resulted in high runoff and higher than normal submarine groundwater discharge off the west Florida coast throughout 2005, which initiated and fueled the persistent HAB of *K. brevis.*
- They argue that the Saharan dust hypothesis does not explain the timing extent and longevity of the 2005 red tide. The relationship between Saharan dust deposition and red tide seems unlikely because the dust storms would have an effect on a larger geographic area and not just affect a small area between Sarasota and Sanibel where the blooms occurred.
- The authors feel that rivers are clearly an important nutrient source to coastal blooms, but the amount of dissolved inorganic nitrogen and dissolved inorganic phosphorous was not sufficient to maintain the 2004-2005 bloom and that other nutrient inputs from submarine groundwater discharge are a large nutrient source that fuels Florida red tides.

*Several articles have been ordered, but have not yet been received from the FWRI website. Copies of the pertinent articles will be provided to Council upon receipt and review by the Department of Natural Resources.

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Iron fertilization and the *Trichodesmium* response on the West Florida shelf

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Abstract

Prior laboratory studies of *Trichodesmium* have shown a high iron requirement that is consistent with the biochemical demand for iron in the enzyme nitrogenase. Summer delivery of iron, in the form of Saharan dust, may provide an explanation for *Trichodesmium* blooms observed in offshore waters of the West Florida shelf over the last 50 yr. During ecology and oceanography of harmful algal blooms (ECOHAB) field studies, background iron levels (0.1–0.5 nmol kg^{-1}) were found at the surface during periods of minimal dust delivery (May 2000 and October 1999). In contrast, total dissolved iron concentrations on the order of ~16 nmol kg^{-1} were measured at the West Florida shelf-break after a July 1999 Saharan dust event that was identified by advanced very high resolution radiometer (AVHRR) imagery, ground-based radiometers, air mass analysis, and aerosol samples (dust and non–sea-salt nitrate) collected throughout South Florida. The *Trichodesmium* response following this July dust event was a 100-fold increase over background biomass, reaching a surface stock of ~20 colonies L^{-1}. Surface dissolved concentrations of both inorganic and organic phosphorus decreased below detectable limits during this bloom. Dissolved organic nitrogen concentrations associated with the bloom (15–20 μM) were 3–4-fold greater than background and much larger than ambient NO_3^- concentrations (<0.5 μmol kg^{-1}). If all dissolved organic nitrogen (DON) is converted to urea and ammonium, this organic nitrogen could have supported the red tide of >20 μg chl L^{-1} of the toxic dinoflagellate, *Gymnodinium breve*, found along the West Florida coast during October 1999.

Iron availability has been characterized as an important controlling factor in the primary production and nutrient cycles of oceanic ecosystems (Martin and Fitzwater 1988; Barber and Chavez 1991). Laboratory studies indicate that iron plays a critical role in nitrogen fixation by the cyanobacterium *Trichodesmium spp.* (Rueter 1988; Rueter et al. 1990; Paerl et al. 1994). In this context, blooms of *Trichodesmium erythraeum* have been observed within 75 km of the west coast of Florida for more than 50 yr (King 1950), where ambient nitrate concentrations within 5 km of the coast are less than 0.50 μmol kg^{-1} (Steidinger et al. 1998). Accurate depictions of fluctuations in surface iron concentrations in response to Saharan dust deposition and cyanobacterial uptake has not been explored within this 100–150-km wide, oligotrophic shelf ecosystem (Fig. 1).

Duce (1986) and Martin and Gordon (1988) indicated that a majority of phytoplankton Fe-requirements might be supplied by atmospheric deposition. Direct uptake of particulate iron is of negligible significance in most phytoplankton (Rich and Morel 1990), whereupon iron bioavailability to

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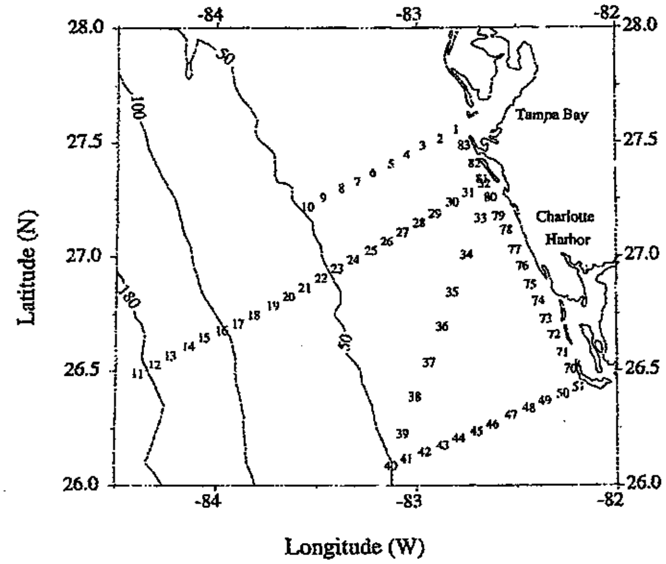

Fig. 1. ECOHAB cruise track of monthly surveys on the central West Florida shelf, between Tampa Bay and Charlotte Harbor.

algal assemblages is controlled by dissolved iron species. In contrast to this generalization for phytoplankton, Rueter et al. (1990, 1992) suggested that *Trichodesmium* may take up both dissolved and particulate iron associated with dust.

Saharan dust in vast quantities is swept into air streams over West Africa during the dry summer months and is transported thousands of kilometers across the Atlantic Ocean to the Caribbean and eastern United States (Schütz et al. 1981). Desert dust often contains iron oxides. Recent investigations (Carder et al. 1991; Young et al. 1991) suggest that aerosols may be an important source of iron to phytoplankton in several oligotrophic oceanic regions. Indeed, aeolian input is believed to be responsible for 30–96% of the dissolved iron in the photic zone of the Sargasso Sea and 16–76% in the central North Pacific gyre (Duce 1986).

Concentrations of Fe(II) are generally much lower in seawater than in freshwater (Miller et al. 1995) due to rapid Fe(II) oxidation rates (Millero and Sotolongo 1989) and Fe(III)-oxide solubility limitations (Byrne and Kester 1976). At ambient seawater pH, maximum Fe(II) concentrations range from 4 to 8% of total iron concentrations (Miller et al. 1995). The low solubility and high reactivity of ferric iron, plus the obligate role of iron in metabolic processes, limits dissolved iron concentrations to nanomolar levels (Waterbury et al. 1997). On the West Florida shelf, summer iron stocks should be controlled by two dominant factors: (1) Local riverine inputs (Kim and Martin 1974; U.S.G.S. 1976–1981) and (2) far-field aerosol dust (Carder et al. 1991; Prospero 1999). This input iron will be depleted by biological uptake, particulate scavenging, sediment deposition, and physical export.

Previous assessments of iron inputs to the West Florida shelf have not included direct measurements of iron concentrations. Instead, estimates of iron inputs have been based on time series dust records at Fort Myers and Miami, dust composition, and relative wet (75%) and dry (25%) mineral deposition rates (Walsh and Steidinger in press). With a combined wet and dry deposition rate of $\sim$1.25 g m^{-2} yr^{-1} (Prospero et al. 1987; Landing et al. 1995) and a $\sim$3.5% mass fraction of iron in mineral aerosols (Duce et al. 1991; Zhu et al. 1997), about 80% of the estimated annual loading (0.6 mM Fe m^{-2}) may be deposited in 1 month on the West Florida shelf.

The large (2.2 $\times$ 10^{-3}) Fe/N ratio for the diazotroph *T. erythraeum* (Rueter et al. 1992) compared, for example, to less than 2 $\times$ 10^{-4} for diatoms and flagellates (Sunda and Huntsman 1995) is a reflection of the high iron levels required for optimal nitrogenase enzyme activity. Diazotrophs are a source of ammonium during population growth (Prufert-Bebout et al. 1993) and, as well, after bloom collapse (Devassy et al. 1978). Since 50–100% of the dissolved organic nitrogen (DON) excreted by *Trichodesmium* is amino acids (Capone et al. 1994; Glibert and Bronk 1994), diazotrophs are capable of eliminating or mitigating nitrogen limitation for other components of the phytoplankton community and the microbial loop. Thus we postulated that large pools of released DON might accumulate in the water column during periods of Fe availability on the outer shelf.

Nitrogen half-saturation constants, k_N, for the toxic dinoflagellate *Gymnodinium breve* range from $\sim$130 μmol kg^{-1} for amino acids (Baden and Mende 1979) to $\sim$1.1 μmol kg^{-1} for urea and $\sim$0.5 μmol kg^{-1} for ammonium, nitrite, and nitrate (Steidinger et al. 1998). The high k_N values for amino acids indicate (Fukami et al. 1991; Gentien 1998) that when amino acids are available, *G. breve* depends upon bacterial transformation of amino acids into urea and ammonium for fueling subsequent red tides. Alternatively, during periods of iron-limited growth and reduced nitrogen fixation, the ammonium released by some *Trichodesmium* populations might be directly used by *G. breve* (Prufert-Bebout et al. 1993). As an example, elevated inorganic nutrients (NH_4, PO_4) and organic nutrients (DON) associated with short-term (i.e., 7–10 d) *Trichodesmium* blooms in the Great Barrier Reef lagoon have been shown to significantly influence phytoplankton and zooplankton community dynamics (O'Neil et al. pers. comm.).

In this work, we examine changes of *Trichodesmium* abundances, dissolved iron stocks, PO_4 and DON/DOP concentrations across the West Florida shelf in relation to observations of air mass optical properties at St. Petersburg and Dry Tortugas, and atmospheric dust and non–sea-salt nitrate at Miami. The transport of Saharan dust to southern Florida was monitored through the use of AVHRR imagery. The arrival of dust at the West Florida shelf is described in terms of increases in the concentration of dissolved iron, diazotrophs, and labile organic nitrogen, with associated depletion of PO_4 and DOP. The proposed causal relationship of Walsh and Steidinger (in press), that *Trichodesmium* provides a nitrogen source for *G. breve,* investigated in this work will allow future research into the impact of cyanobacterial nitrogen fixation on food chain nutrient supply and thus prediction of red tides along the West Florida coast.

Methods

Iron sampling and analysis—Sampling for total dissolved iron (Fe_T) in the surface ocean was conducted aboard the R/

V *Suncoaster'* and R/V *Bellows* in August of 1998, during monthly cruises from June to October 1999, and in May 2000. As part of the ECOHAB Florida project, 44 stations were sampled as far offshore as the 180-m isobath (Fig. 1).

The sampling device consisted of a 150-ml Teflon bottle fitted with a specialized cap that allowed water to enter from the side of the cap while air exits through the top.

The Teflon bottle was placed snugly inside a Delrin bottle, with a special cap that allowed for water and air flow in the same manner as the Teflon cap. The bottle was cast ahead of the ship with a fishing rod as the ship headed into the wind at 1 knot. The bottles typically filled with seawater in 30–45 s from the top 2 m of the water column. All samples were analyzed within 10 min after collection.

Seawater samples were analyzed for total dissolved iron, without filtration, using spectrophotometric procedures similar to those of Waterbury et al. (1997). Four hundred microliters of 0.01 M hydroxylamine hydrochloride were added to 100 ml of the seawater sample to reduce Fe(III) to Fe(II). Next, 200 μl of 0.01 M ferrozine (Sigma) reagent was added to 50 ml of this solution and the solution was introduced to the 10-m waveguide using a peristaltic pump. The concentration of iron in the solution was determined from the absorbance of the Fe(II)-ferrozine complex at 562 nm. The absorbance baseline for these measurements was obtained using the seawater sample combined with hydroxylamine hydrochloride without added ferrozine. The 10-m pathlength liquid core waveguide (LCW) used in this work produced a detection limit for total iron on the order of 0.1 nmol kg^{-1}.

The spectrophotometric system was calibrated using an iron stock solution prepared from ferrous ammonium sulfate in 0.01 M HCl. Calibration curves showing absorbance plotted against iron concentration ($[Fe_T]$) consistently conformed to Beer's law ($A = \epsilon \times [Fe_T] \times l$), where ϵ is the molar absorptivity of the iron ferrozine complex and l is pathlength. The molar absorptivity (ϵ) obtained in these calibrations was essentially identical to that obtained using a 1-cm pathlength and a conventional spectrophotometer.

Atmospheric optical properties—Aerosol optical depth (τ_a) is a measure of atmospheric turbidity. Clean maritime atmospheres possess optical depths from a reference wavelength at 500 nm [$\tau_a(500)$] of approximately 0.15, whereas this value for Saharan dust over the tropical North Atlantic is often between 0.3 and 0.5 (Reddy et al. 1990; Korotaev et al. 1993). Aerosol optical depth is commonly related to wavelength by $\tau(\lambda) \propto \lambda^{-\eta}$, where η is the Angstrom exponent (Angstrom 1964). Air mass origin may be characterized by this exponent. Small aerosols (e.g., maritime or tropospheric) display a strong spectral nature with Angstrom exponents between 1 and 2 (Hoppel et al. 1990; Reddy et al. 1990). Larger dust aerosols (e.g., Saharan) evince a more nonspectral behavior, with Angstrom values less than 0.8 and often less than 0.5 (Tanré et al. 1988; Reddy et al. 1990).

Measurement of aerosol optical depth was taken by two different instruments. The CIMEL (CIMEL Électronique) sun and sky radiometer retrieves aerosol optical depth in eight spectral bands. This instrument comprises a federation of ground-based remote sensing stations (AERONET) dedicated to assessing global aerosol optical properties (Holben et al. 1998). We obtained the daily optical depths from a CIMEL operating in the Dry Tortugas (http://www.aeronet.gsfc.nasa.gov:8080/). From these data we calculated the daily Angstrom exponent using a least-squares fit of optical depth versus wavelength between 400 and 870 nm. The Dry Tortugas (24.63°N, 82.89°W) are free of anthropogenic influence yet often experience the same air masses as Miami and St. Petersburg. The Microtops, a five-channel hand-held sunphotometer, measured aerosol optical depth in St. Petersburg to establish the presence of Saharan dust over the offshore oceanic sampling sites. These local measurements, combined with air mass back trajectory calculations from hybrid single particle Lagrangian integrated trajectory (HYSPLIT) and CIMEL optical depths in the Dry Tortugas, afford a complete air mass classification (Smirnov et al. 1995) capable of distinguishing Saharan dust from aerosols of continental origin. The HYSPLIT model is supplied by the Air Resources Laboratory of the National Oceanic and Atmospheric Administration (NOAA) (http://www.arl.noaa.gov/ready). Trajectories of 90-h duration were calculated at 1800 UTC (universal time coordinates) for heights of 500, 1,000, and 3,000 m above sea level.

Aerosol sampling of atmospheric dust and nitrate—Daily aerosol samples were obtained by drawing ~1,500 m^3 of air through Whatman filters located ~30 m above ground on an island approximately 4 km east of mainland Miami (Prospero 1999). The filters were extracted with deionized water and the extracts were then analyzed for major soluble inorganic ions. Non–sea-salt (NSS) nitrate was determined by suppressed ion chromatography (Savoie et al. 1989). The filter residue, obtained by ashing filters over 14 h at 500°C in a muffle furnace (less the ashed blank), was considered mineral dust. To compensate for the loss of soluble and volatile soil minerals, an adjustment factor of 1.3 (Prospero 1999) was applied to these dust data.

Trichodesmium counts—During monthly ECOHAB surveys, the concentration of *Trichodesmium* in surface water at selected stations was determined (within 3 h of collection) over a 72-h period by direct microscopic count. Surface water containing *Trichodesmium* was collected with 8-liter Nisken bottles, drained into a 10-liter Nalgene carboy, and pumped through a 49-mm Whatman GF/F filter at ~70 ml min^{-1}. Filters were placed cell side up in a petri dish and both single trichomes and colonies ("puffs" and "tufts") of *Trichodesmium* were counted with a Meiji Model EMZ-TR dissecting microscope. Colony size and single trichomes were noted.

Dissolved organic matter—Nitrogen and phosphorus samples were collected from Nisken bottles and filtered through precombusted (2 h at 450°C) Whatman GF/F filters. Total dissolved nitrogen (TDN) concentrations were determined using the persulfate oxidation method of Solórzano and Sharp (1980*a*). Inorganic nitrogen values were determined using methods recommended by Gordon et al. (1993). DON was then determined as the difference between the inorganic nitrogen and TDN estimates.

Total dissolved phosphorus (TDP) measurements were

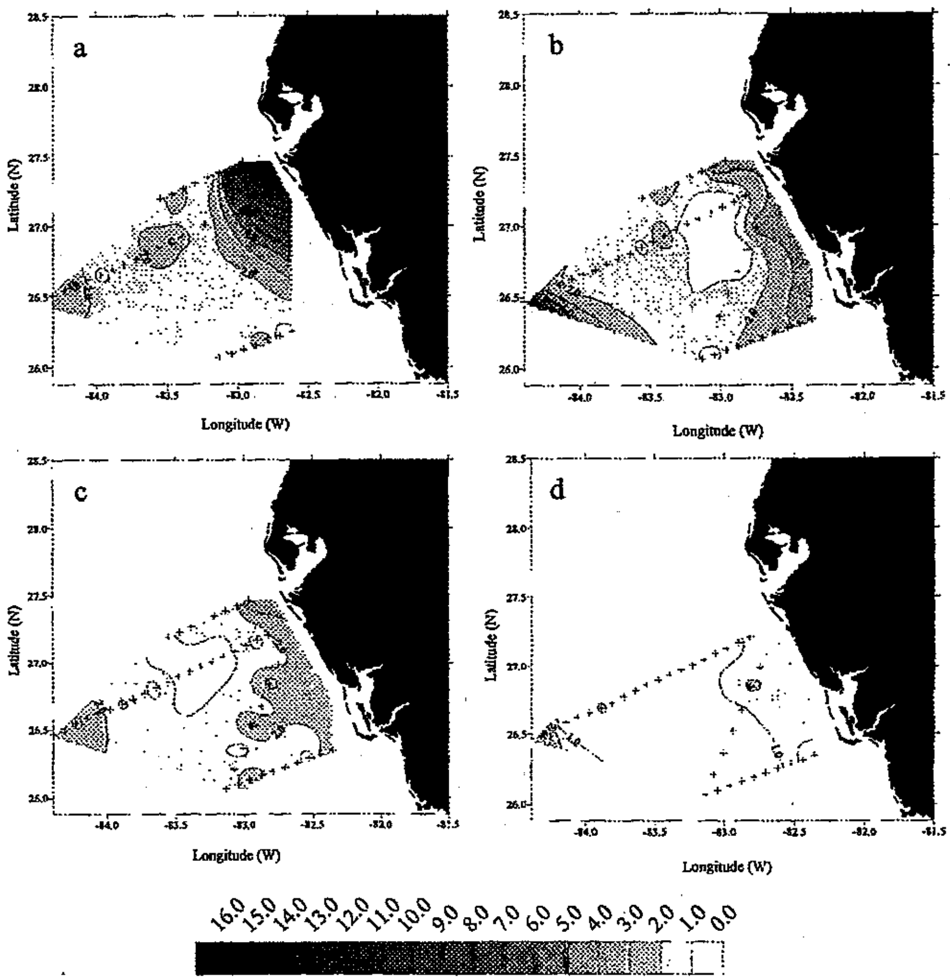

Fig. 2. The 1999 surface distributions of dissolved iron (nmol Fe kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

made by using the high temperature–hydrolysis technique of Solórzano and Sharp (1980*b*). Inorganic phosphorus values were again determined using methods recommended by Gordon et al. (1993). Dissolved organic phosphorus (DOP) was then determined as the difference between the inorganic phosphate and TDP estimates.

Sampling of surface salinity—Surface salinities along the 1999 ECOHAB cruise tracks (Fig. 1) were measured with a Falmouth Scientific microCTD-model MBP sensor. Measurements were averaged over 30 s intervals over the 3-d cruise track. During August 1998 only CTD data were available, whereupon discrete surface observations from individual stations were obtained.

Results

Dissolved iron levels—Total dissolved iron concentrations measured on the 5–7 July 1999 cruise (Fig. 2b), following the Saharan event of Fig. 3, reached ~16.0 nmol kg^{-1} at Sta. 11. In contrast, the iron found off the West Florida shelf during the October 1999 cruise, in the absence of Saharan dust input, represents mean background levels <0.1 nmol kg^{-1} at Stations 11–22 (Table 1) between the 50- and 200-m isobaths (Fig. 1). The same background concentrations of Fe were found in May 2000. Similar results were also obtained from the August 1998 cruise, with a mean of 0.2 nmol kg^{-1} at these offshore stations. High iron content of the West Florida river systems (~3,000 nmol kg^{-1} within the Peace River at Arcadia, Florida) led to elevated iron concentrations (1–2 nmol kg^{-1}) at the 10-m isobath in October 1999, May 2000, and August 1998.

Four Saharan dust events were observed in Miami during June–July 1999 (16–17 June, 26 June–4 July, 8–13 July, 19–21 July) with a mean interval of 6.3 d (Fig. 4a). The observed surface iron stocks at stations remote from riverine supplies (Stations 11–22) were averaged to yield a July mean of 3.0 nmol kg^{-1} (Table 1). Dissolved iron concentrations exhibited a cross-shelf minimum (Fig. 2b) of <0.1 nmol kg^{-1} at salinities greater than 36.0 (above the 20–50-m isobaths). This iron minimum at a salinity >36 lies between the offshore salinity minimum (~34.5) and low local river-

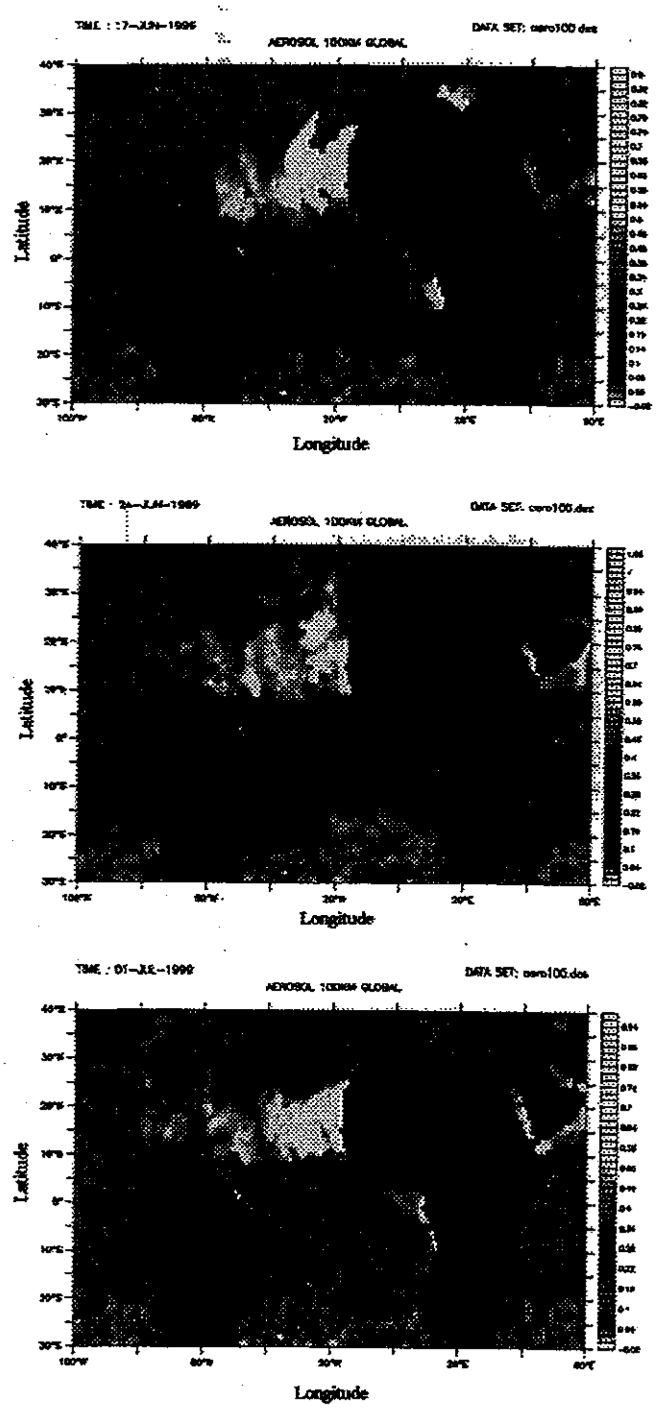

Fig. 3. AVHRR imagery of the 1999 aerosol optical thickness of the atmosphere, adjacent the Sahara Desert and above the Gulf of Mexico, during (a) 17 June, (b) 24 June, and (c) 1 July—from the Satellite Active Archive at PMEL (Pacific Marine Environmental Laboratory).

influenced salinities (~32.0) where iron concentrations were >3.0 nmol kg^{-1}. The mean 3.0 nmol kg^{-1} per event iron influx, as measured in July 1999, would lead to a cumulative 1-month input of ~12.0 nmol kg^{-1} within the 5-m surface mixed layer (Walsh and Steidinger in press).

The 6–8 August 1999 cruise occurred during a large Saharan dust event observed at both Miami (Fig. 4a) and Dry Tortugas (Table 1). Owing to an anticyclonic trajectory in the Gulf of Mexico similar to that shown in Fig. 5, this dust took a few days longer to arrive at St. Petersburg (Fig. 4b). Thus, offshore iron concentrations at the time of shipboard sampling (mean $[Fe_T]$ ~ 1.5 nmol kg^{-1} at Stations 11–22) were lower than iron concentrations in July ($[Fe_T]$ ~ 3.1 nmol kg^{-1}). By September 1999, Saharan dust supply gives way to continental sources, further reducing dissolved iron concentrations (Fig. 2d) from earlier months. A mean of 1.1 nmol kg^{-1} was found during 7–9 September following a continental dust event (Fig. 5).

In contrast, at the beginning of the dust season (5–8 June 1999), the dissolved iron at these stations was 2.0 nmol kg^{-1} (Fig. 2a). Nearshore concentrations exhibited a 14 nmol Fe kg^{-1} maximum, presumably representing a mixing event during the rough seas encountered. The lower salinity plume (~35.5) originating at the mouth of Tampa Bay extended farther offshore in June (Fig. 6a) than July (Fig. 6b). The linear regression between offshore dissolved iron concentration (June–October 1999) and the mean dust collected at Miami each month during all events (>10 $\mu g\ m^{-3}$) had a coefficient of determination (r^2) of 0.92.

Diazotroph populations—Background populations of *Trichodesmium* on the outer shelf during October 1999 were 0.1–0.2 colonies L^{-1}. During the ECOHAB survey of 5–8 June 1999 (Fig. 7a) populations were tenfold greater than these background levels. *Trichodesmium* abundance on the West Florida shelf during July 1999 exhibited a second tenfold increment after a Saharan dust event, reaching ~20.0 colonies L^{-1} at Sta. 16 above the 100-m isobath (Fig. 7b).

The local maximum of *Trichodesmium* stocks on the outer shelf in June corresponded to the iron minimum (Fig. 2a). Similarly, the July iron minimum of 1.3 nmol kg^{-1} between Stations 15 and 22 (Fig. 2b) also corresponded to the location of maximal *Trichodesmium* abundance. This implies removal of dissolved iron from the surface waters as the summer *Trichodesmium* populations grow on the West Florida shelf. A similar relation between dissolved iron and *Trichodesmium* was also observed across the Great Barrier Reef (Jones et al. 1986).

Likewise, a high *Trichodesmium* affinity for inorganic phosphorus (Karl et al. 1992) led to a July depletion of phosphorus stocks from the midshelf areas. Whereas June concentrations were ~0.50 μmol DOP kg^{-1} and ~0.30 μmol PO_4 kg^{-1} (Figs. 8a and 9a), after the July *Trichodesmium* population increase, P stocks within the bloom decreased to nearly undetectable levels for both organic and inorganic phosphorus (Figs. 8b and 9b). A high alkaline phosphatase activity (Yentsch et al. 1972) would provide rapid use of organic phosphorus within the population during periods of growth.

At Sta. 16 the surface stock decrease of *Trichodesmium*

Table 1. The dates of ECOHAB cruise in relation to (1) duration of the Saharan and Continental aerosol events (dates) and (2) backward trajectories of air masses from St. Petersburg, (3) mean weight ratios of atmospheric nitrate/dust concentrations ($\mu g\ m^{-3}$) sampled at Miami, (4) mean Angstrom exponents from the Dry Tortugas CIMEL, (5) total Tampa rainfall (cm), (6) mean aerosol optical thickness, $\tau_{aer}(500)$, above St. Petersburg, and (7) mean dissolved iron (nmol kg^{-1}) within surface waters of the West Florida shelf at Stations 11–22, between the 50 m and 200 m isobaths.

ECOHAB cruise	Dust event	Air mass trajectory	Miami NO_3/dust	Dry Tortugas exponent	Tampa rainfall	St. Petersburg $\tau_{aer}(500)$	W. Florida iron
1–3 May 2000	none	—	—	—	0.0	—	0.2
5–8 Jun 1999	—	—	0.49	—	0.3	0.19	2.0
	16–17 Jun	SE	0.08	0.60	3.8	—	—
	26 Jun–4 Jul	SE	0.07	0.27	5.9	—	—
5–7 Jul 1999	—	—	0.18	0.57	0.8	0.19	3.1
	8–13 Jul	SE	0.05	0.27	1.3	0.24	—
	19–21 Jul	SE	0.05	0.29	0.0	0.15	—
	28–31 Jul	NW	0.30	—	0.0	0.48	—
6–8 Aug 1999	7–11 Aug	SE	0.09	0.44	2.7	0.18	1.5
	27–30 Aug	NW	0.19	1.64	0.0	0.28	—
	3–6 Sep	NW	0.50	1.80	1.3	0.33	—
7–9 Sep 1999	—	—	0.24	1.10	0.8	—	1.1
5–7 Oct 1999	none	—	—	0.16	—	—	<0.1
6–10 Aug 1998	none	—	0.36	—	7.3	—	0.2

between July and August (Fig. 7c) mirrored the decrease in mean iron concentrations (Table 1). Although the local diazotroph maximum was still associated with iron minima (Fig. 2c), other limiting factors may also have been operative. By September 1999, despite levels of dissolved iron (Fig. 7d) at the half-saturation value of ~1.1 nmol kg^{-1} (Table 1), the offshore *Trichodesmium* abundance is minimal, with only ~0.5 colonies L^{-1} found at Sta. 16 (Fig. 8d). In contrast, a maximum concentration of 8.5 colonies L^{-1} was then located just off the mouth of Charlotte Harbor, where surface inorganic phosphorus was ~0.20 μmol PO_4 kg^{-1} and DOP was nearly undetectable (Fig. 9d and 8d).

Despite abundant iron (>2 nmol kg^{-1}) and phosphorus stocks within these nearshore waters, by 5–7 October 1999 the diazotroph population had been reduced to 0.5 colonies L^{-1} off Charlotte Harbor when a red tide of $>2 \times 10^6$ cells L^{-1} (i.e., >20 μg chl L^{-1}) was found. With an estimated saturation light intensity of ~300 $\mu E\ m^{-2}\ s^{-1}$ for *Trichodesmium* (Carpenter and Roenneberg 1995), compared to a noon PAR of ~1,500 $\mu E\ m^{-2}\ s^{-1}$ at the surface of the West Florida shelf (Penta pers. comm.), these diazotrophs must balance their iron nutrition needs (atmospherically derived) against the costs of near surface photoinhibition. In the absence of sufficient colored dissolved organic matter (CDOM) sunscreen (Keiber et al. 1990), termination of surface diazotroph blooms in both offshore and nearshore waters of the West Florida shelf may result from cumulative photolytic losses, since grazing losses seem to be minimal (O'Neil et al. 1996).

Dissolved organic nitrogen—Dissolved organic nitrogen released within surface waters by *Trichodesmium* populations provides a source of new nitrogen. The mean DON concentration across the West Florida shelf was ~4 μmol kg^{-1} in September 1998, following the occurrence of minimal iron concentrations during August (Fig. 10b). These 1998 DON concentrations are similar to midshelf values of ~5 μmol kg^{-1} in September 1999 (Fig. 11d). In contrast, larger DON values (~20 μmol kg^{-1}) were found in June 1999, just beyond the 100-m isobath, whereas nearshore values remained ~5 μmol kg^{-1} (Fig. 11a). These observations are consistent with a threefold increment of DON (5 μmol kg^{-1} to 14 μmol kg^{-1}) observed off Hawaii after a *Trichodesmium* bloom (Karl et al. 1992).

Although the *Trichodesmium* abundance increased by an order of magnitude from June to July (Fig. 7b), DON stocks declined from 20 to 14 μmol kg^{-1} (Fig. 11b). This may reflect uptake of labile amino acids (C/N ~ 4.3) released by the diazotrophs (Capone et al. 1994). In contrast, nearshore concentrations of DON composed, presumably, of more refractory (C/N > 20) riverine carbohydrates (Gardner et al. 1996) increased to ~22 μmol kg^{-1} during July. This coastal influx of DON was associated with low salinities off Charlotte Harbor (Fig. 6b) after a July rain event preceding the cruise by a few days (Fig. 12).

The concentrations of nearshore DON in August (Fig. 11c) and September (Fig. 11d) continued to be associated with low salinity plumes from Tampa Bay and Charlotte Harbor (Fig. 6c,d). The regression between dissolved organic nitrogen and salinity along the 10-m isobath during the June–October 1999 ECOHAB cruises (Fig. 1) produced an r^2 of 0.95, indicating that DON was a conservative property. In contrast, the DON versus salinity relationship at stations between the 50- and 100-m isobaths, with an r^2 of only 0.29, is consistent with less refractory offshore pools of DON. Although the Mississippi River influence on salinity (Del Castillo et al. pers. comm.) increased on the outer shelf (Fig. 6c,d), the concentration of apparently labile DON offshore (Figs. 11c,d) was significantly reduced (~8 μmol kg^{-1} in August and ~5 μmol kg^{-1} in September). Within offshore waters, DON uptake presumably continued for at least a month while, as indicated by the absence of surface populations of *Trichodesmium* (Fig. 7d), nitrogen fixation had ceased.

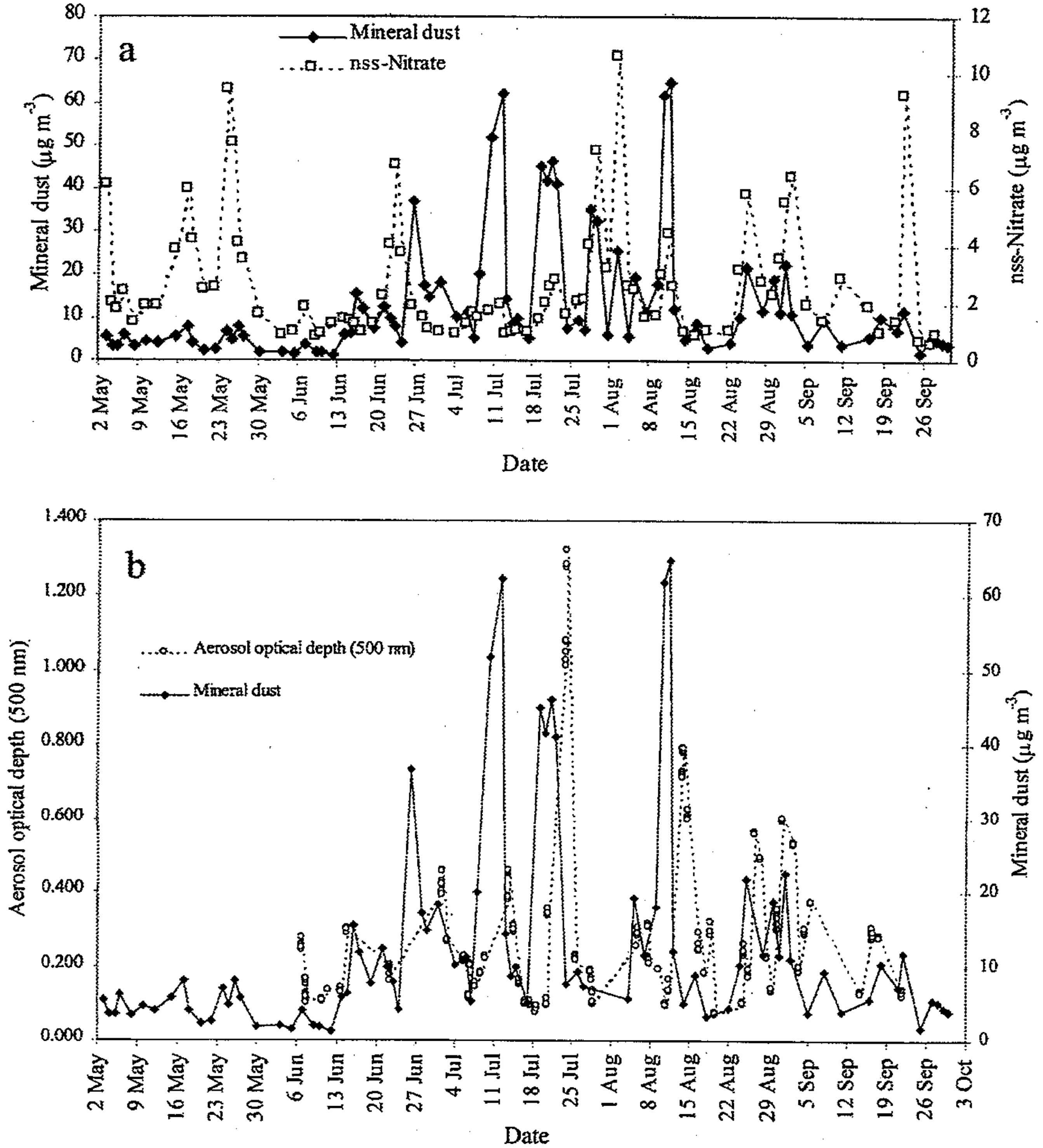

Fig. 4. Daily observations of mineral dust ($\mu g\ m^{-3}$) of the atmosphere above Miami during May–September 1999 in relation to (a) non-sea-salt nitrate ($\mu g\ m^{-3}$) of air 30 m above ground at Miami, and (b) aerosol optical thickness at 500 nm, $\tau_{aer}(500)$, above St. Petersburg.

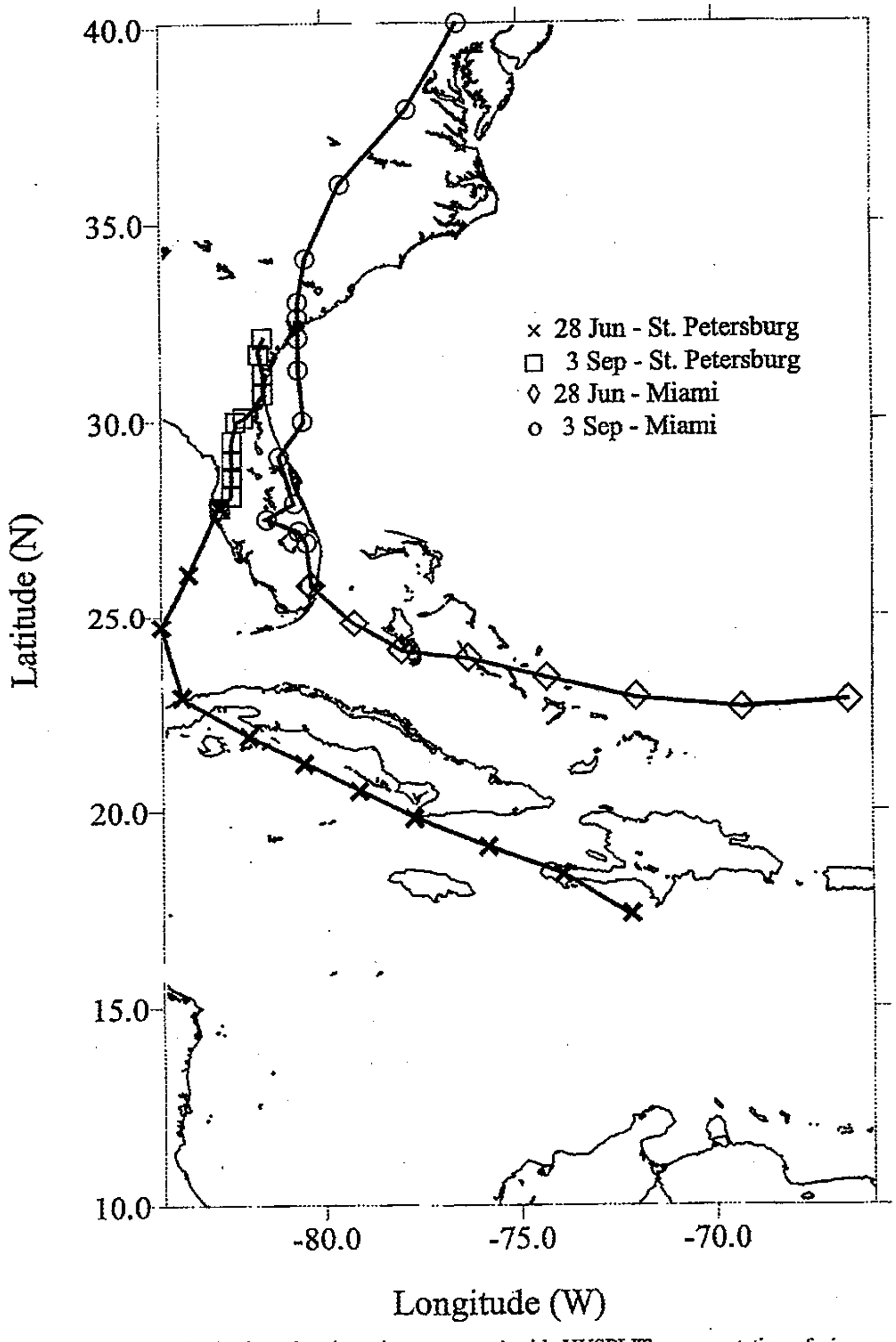

Fig. 5. The daily backward trajectories, computed with HYSPLIT, representative of air mass flow at 500, 1,000, and 3,000 m above ground/sea level over a 90-h period ending at 1800 h on 28 June 1999 and on 3 September 1999 from St. Petersburg and Miami.

Saharan dust episodes—The history of the first major Saharan dust event of 1999 was traced with AVHRR imagery. Figure 3a indicates the beginning of a Saharan dust pulse on 17 June 1999, with the highest optical thickness, i.e., highest concentration of dust, found directly off the African coast. As the winds transported the dust across the Atlantic, a large fraction settled, thereby reducing the amount that eventually reached the West Florida shelf. In Fig. 3b, troughs of higher

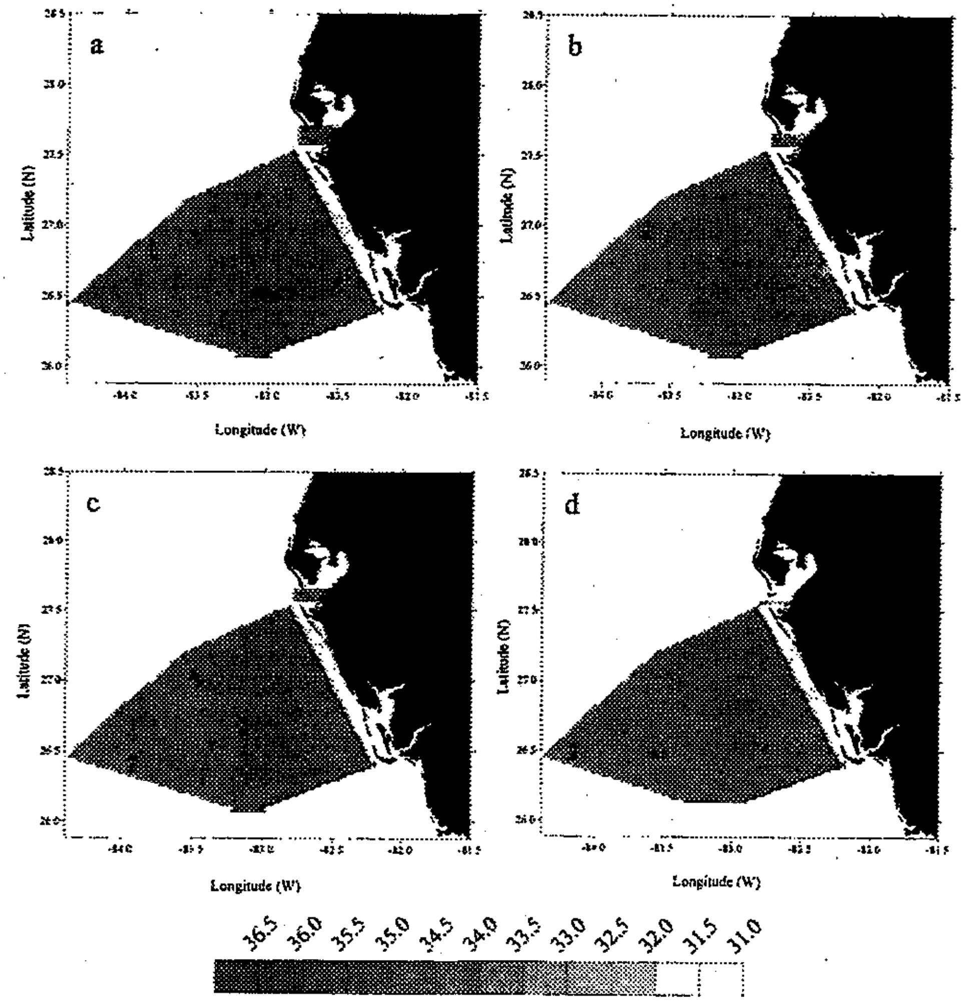

Fig. 6. The 1999 surface distributions of salinity across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

optical thickness are observed on 24 June above the equatorial Atlantic Ocean, reflecting waves of dust supplied to Barbados. A week later (Fig. 3c) the dust front was west of Miami in the Gulf of Mexico.

The winds at Miami are southerly or southeasterly (Fig. 5) during episodes of high optical thickness. This is also seen in back trajectories from St. Petersburg on 28 June for air masses at a height of 1,000 m (Fig. 5). Mean summer wind speeds are 3–5 m s^{-1}, and the path for a southeast wind from Miami to St. Petersburg is such that direct air mass transit (~400 km) between the two locations should take between 20 and 32 h. However, the prevailing wind patterns at St. Petersburg are variable (Henry et al. 1994). Saharan dust can then arrive via westerly or northwesterly winds after turning sharply from its original course over south Florida (Fig. 5). Such a track will increase the distance that must be covered by an air mass, leading to a more usual transit time of ~60 h.

The aerosol sampling system at ~30 m above the ground in Miami caught 37 and 18 $\mu g\ m^{-3}$ of mineral dust (Fig. 4) during successive 27 June and 1 July 1999 rainfall events. The atmospheric nitrate concentrations were minimal. A mean 0.07 nitrate/dust weight ratio (Table 1) reflects little contribution from continental aerosols. The CIMEL spectral radiometer at Dry Tortugas in the southern West Florida shelf confirmed that the mean Angstrom exponents of aerosols during this southeast wind event were typical ($\eta = 0.27$) of pure Saharan dust (Tanré et al. 1988; Dubovik et al. 2000). The mean $\tau_a(500)$ value, seen by CIMEL over 26 June–1 July, was 0.26.

Microtops II estimates of $\tau_a(500)$ above St. Petersburg were not available in late June, but an optical depth of 0.42 at 500 nm was found on 1 July (Fig. 4b). During seven other dust events, a daily $\tau_a(500) > 0.30$ was also found, when dust concentrations were >10 $\mu g\ m^{-3}$ at Miami. Of these eight large June–September dust events, the three during 28–31 July, 27–30 August, and 3–6 September were of continental rather than Saharan origin (Table 1). For example, the NSS-nitrate/dust ratio was ≤0.50, air mass trajectories were from the north (Fig. 5), and the mean Angstrom exponent

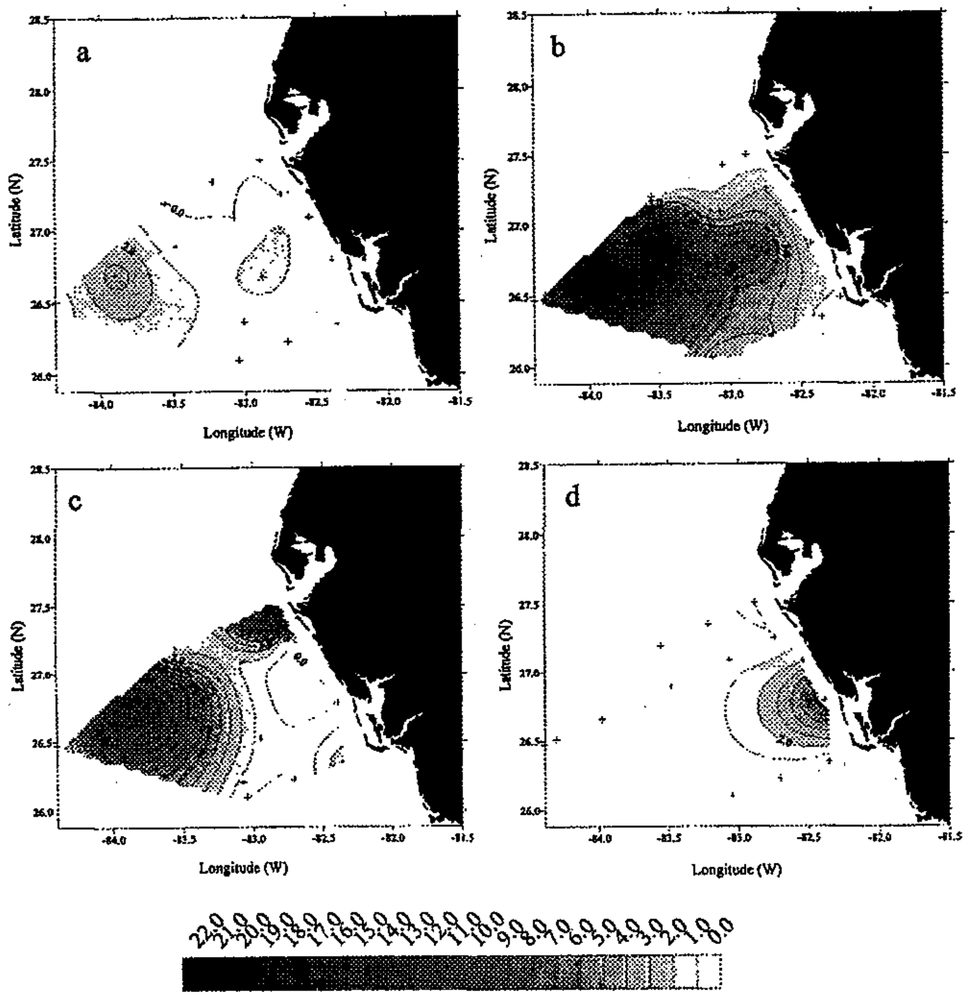

Fig. 7. The 1999 surface distributions of *Trichodesmium* populations (colonies L^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

was 1.80 during 3–6 September. By matching the peaks in the mineral dust concentration at Miami and the aerosol optical depth at St. Petersburg during the Saharan events, a 60 h transit time with an r^2 of 0.98 over seven data bins was calculated.

Continental dust episodes—NSS-nitrate/dust ratios can help discriminate source regions. Low ratios indicate mineral dust of Saharan origin, whereas high ratios are often associated with polluted air masses (Prospero 1999). The dust collected at Miami decreases and non–sea-salt nitrate increases during the latter half of August and early September (Fig. 4a). By 27–30 August, winds at Dry Tortugas were from the northwest with a mean Angstrom exponent equal to 1.64 (Table 1). Concurrently, the mineral dust at Miami was only 12 $\mu g\ m^{-3}$, with a NSS-nitrate/dust ratio of 0.19. Increased NSS-SO_4 concentrations, closely related to NSS-NO_3 concentrations, have been associated with trajectories traced back to the Gulf of Mexico and then north into the central United States (Prospero et al. 2001). It will be shown that less dissolved iron was found on the West Florida shelf after these periods of continental dust supply.

Salinity fields—Although the outflow of the Apalachicola River is larger than the sum of all other Florida rivers between Capes San Blas and Romano (Nordlie 1990) (peak discharge of ~1,300 $m^3\ s^{-1}$ in February–April; Gilbes et al. 1996), this freshwater signal does not influence the summer salinity regime of the ECOHAB study site (Fig. 1). Furthermore, the smaller Peace River influx to Charlotte Harbor (~65 $m^3\ s^{-1}$; McPherson et al. 1990) during the local mid-June to September summer rains (Fig. 12), was observed only as surface nearshore, low salinity plumes. Salinities of 32–34 at the 10-m isobath were observed during July–September 1999 (Fig. 6b,c,d), compared to 35.5 in June 1999 (Fig. 6a). The freshwater efflux from Tampa Bay was smaller, with local minima of 34.5–35.0 at the 10-m isobath during July–September.

Along the break and outer shelf of the central West Florida shelf, low salinity surface lenses between 34 and 35 were

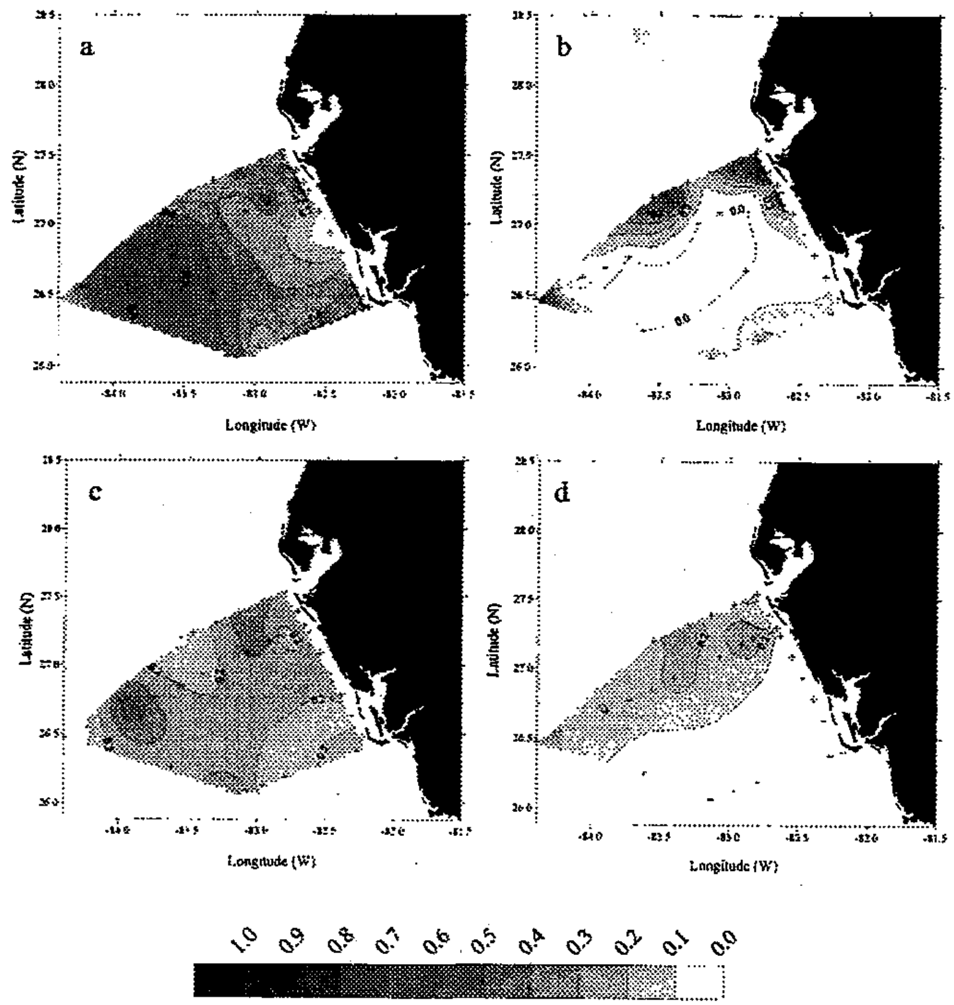

Fig. 8. The 1999 surface distributions of dissolved organic phosphorus (μmol DOP kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

found above the 50–100-m isobaths during August 1999 (Fig. 6c), with an attributed Mississippi River origin (e.g., Gilbes et al. 1996). Furthermore, during August 1998, the low salinity water on the outer shelf was associated with high amounts of colored dissolved organic matter of Mississippi origin (Del Castillo et al. pers. comm.). Since terrestrial runoff is a source of iron, with ~3,000 nmol kg^{-1} found in the Peace River (U.S.G.S. 1976–1981), these local and far-field freshwater influxes are potentially dominant sources of dissolved iron on portions of the West Florida shelf.

Interannual variation—Two types of iron input conditions are encountered on the West Florida shelf in relation to local rainfall and Saharan dust caught at Miami. Variations in [Fe_T] between a low dust/low rain summer (1998) and high dust/high rain summer (1999) demonstrate the impact of Saharan dust input. During August 1998, for example, the total monthly rainfall at Tampa Airport was 16.6 cm and the cumulative dust caught at Miami was 90.3 μg m^{-3}, compared to 21.2 cm and 144.5 μg m^{-3} in August 1999. The mean dissolved iron stocks on the outer West Florida shelf were 0.2 nmol kg^{-1} (Table 1) during August 1998 (Fig. 10b) and 1.5 nmol kg^{-1} in August 1999 (Fig. 2c), which reflects smaller dust loading (Fig. 10c) and less wet deposition (Fig. 12) in 1998.

Since the August 1999 salinities within this region were no lower than 34.5 (Fig. 6c), compared to 31.0 during August 1998 (Fig. 10a), the Mississippi River can be eliminated as a major iron source to the West Florida shelf. Furthermore, when dust loading and wet deposition were low, as during August 1998, observed iron stocks were also low, and only a small *Gymnodinium breve* concentration (~5 × 10^4 cells L^{-1}) was found during November 1998 within 10 km of the coast. Subsequent to a tenfold iron stock increase due to greater aeolian supplies (August 1999), a large red tide of >5 × 10^6 cells L^{-1} occurred (October 1999). Correlation of dust arrival, total iron concentrations, diazotroph abundance, DON accumulation, and PO_4/DOP use provide clues into the interdynamics of this complex shelf ecosystem. In the absence of intrusions of particle-rich water of

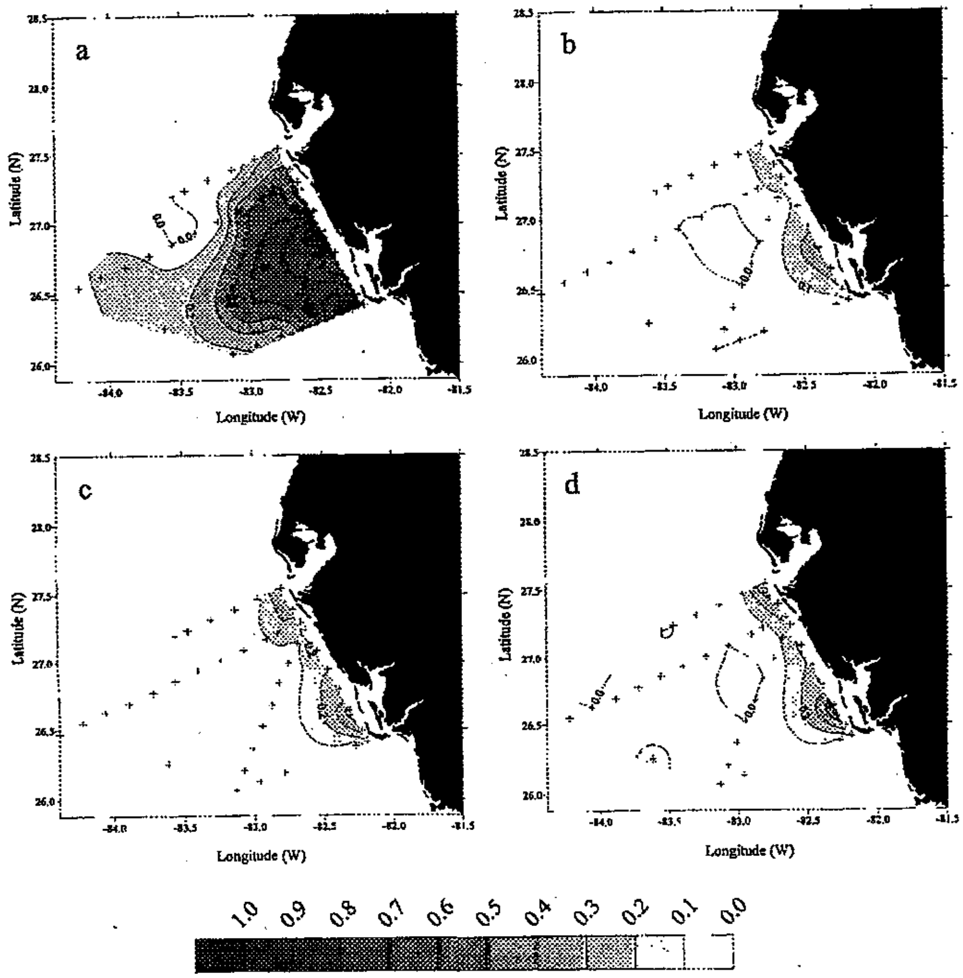

Fig. 9. The 1999 surface distributions of inorganic phosphorus (μmol PO_4 kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

the Loop Current (Haddad and Carder 1979), the shelf system depends upon aeolian sources of iron-mediated nitrogen supply.

Discussion

Daily aerosol sampling carried out previously in Fort Myers on the southwest coast of Florida and in Miami on the East coast (Prospero et al. 2001) showed maximal dust input over the summer months (June–August). If one has $\tau_a(500)$ as an independent assessment the aerosol type, the Miami dust data can be used as a proxy for dust loading to the West Florida shelf. One approach for verification of Saharan events is the use of atmospheric non–sea-salt nitrate as an index of local pollutants at Miami, with a nitrate/dust weight ratio criterion of $\leq$0.1 for dust events. Both air mass trajectories and the Angstrom exponent of mineral dust can provide additional source corroboration.

The optical depths measured by the CIMEL sunphotometer in the Dry Tortugas mirrored those of the Microtops with little time lag in July and the first half of August, but these time series became asynchronous afterward. Late summer in the Gulf of Mexico usually marks changing meteorological conditions—sluggish winds, a northward shift in the prevailing wind patterns, and a sharply increased frequency of tropical disturbances. All of these features decrease the consistency of the prevailing wind patterns (Henry et al. 1994). At Dry Tortugas, fluctuating Angstrom exponents then suggest an infrequent presence of dust and inconsistent delivery of iron to the ocean.

At only monthly sampling intervals, the persistence of aeolian derived iron in surface waters of the West Florida shelf cannot be directly observed. Sampling frequency at any particular station was limited due to the large size of the ECOHAB area. However, during iron fertilization experiments in the equatorial Pacific, Martin et al. (1994) measured a similar (6.2 nmol kg^{-1}) dissolved iron concentration within the core of their patch 4 h after surface fertilization. Owing to convective mixing of the water column, concentrations dropped rapidly to 3.6 nmol kg^{-1} after the first day, at which point concentrations decreased ~15% per day over 6–7 d.

Rainfall during 1–4 July 1999 (4.1 cm at the Tampa Air-

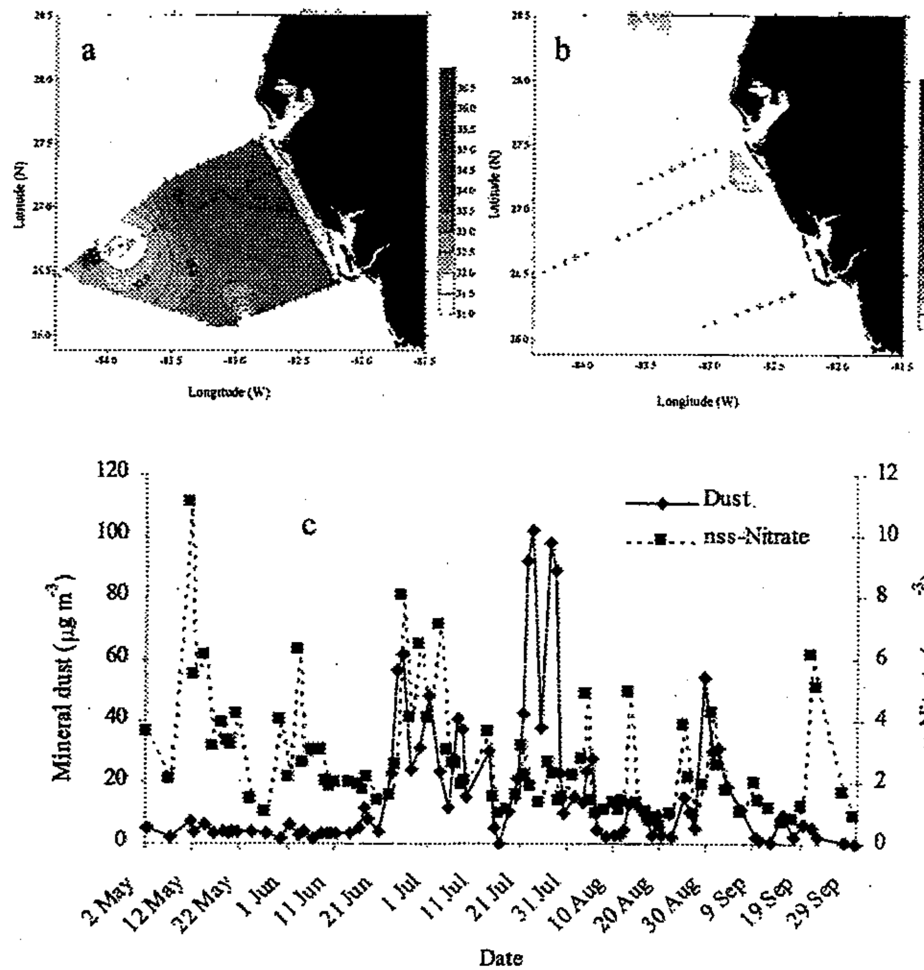

Fig. 10. The surface distributions of (a) salinity and (b) dissolved iron (nmol Fe kg^{-1}) across the West Florida shelf during 6–10 August 1998 in relation to (c) mineral dust ($\mu g\ m^{-3}$) and non-sea-salt nitrate ($\mu g\ m^{-3}$) of air sampled daily 30 m above ground at Miami during May–September 1998.

port) provided local washout of Saharan dust. During a similar precipitation event on 6 August 1999 (Fig. 12), an iron concentration of 52.4 nmol kg^{-1} was observed in rainwater at Sta. 3. Mixed throughout the 5-m surface mixed layer in July 1999, such an influx would produce a concentration near 10.5 nmol kg^{-1}, as was observed in offshore waters. A cumulative iron fertilization of ~12 nmol kg^{-1} within the surface mixed layers of the outer West Florida shelf can be estimated from the four Saharan dust events during 16 June–21 July 1999. If we assume a further loading of ~3 nmol kg^{-1} from the last (28–31 July 1999) Saharan event, and ~1 nmol kg^{-1} from each of the three continental events (Table 1), the estimated 1999 summer aeolian influx to the surface mixed layer of the West Florida shelf is 18 nmol kg^{-1}.

Most *Trichodesmium* colonies on the West Florida shelf had a small number of trichomes (filaments), also found when populations were sampled discretely with bottles off Barbados (Borstad 1978). Assuming a colony size of 3×10^3 cells (Borstad 1978), instead of 3×10^4 cells for large colonies collected with nets (Carpenter 1983), and a cellular chlorophyll content of 1.2×10^{-6} μg $cell^{-1}$ (Borstad 1982), a range of 3–20 colonies L^{-1} in July (Fig. 7b) yields a pigment biomass of 0.01–0.07 μg chl L^{-1}. With an observed mean total chlorophyll stock of 0.14 μg chl L^{-1}, the diazotrophs would constitute 7–50% of the phytoplankton community biomass. Letelier and Karl (1996) found that *Trichodesmium* populations off Hawaii constituted a similar range (10–40%) of their total observed biomass of 0.12 μg chl L^{-1}.

Our measured concentrations of *Trichodesmium* may underestimate the actual stocks, since our surface sampling did not account for vertical migration or for the presence of subsurface peak abundances. Indeed, off Barbados during the Saharan dust season of July–October 1974, 20 of 23 stations exhibited subsurface diazotroph maxima (Borstad 1978). *Trichodesmium* concentrations at 16.3 m were 3.2 times larger than the surface populations, with significant abundance to a depth of 50 m. The ability to migrate (Villareal and Carpenter 1990) at a mean velocity of 2 m h^{-1} (Kromkamp and Walsby 1992) allows *Trichodesmium* to move over a 50-m water column within 1 d.

For a population with a C/chl weight ratio of 220 (Car-

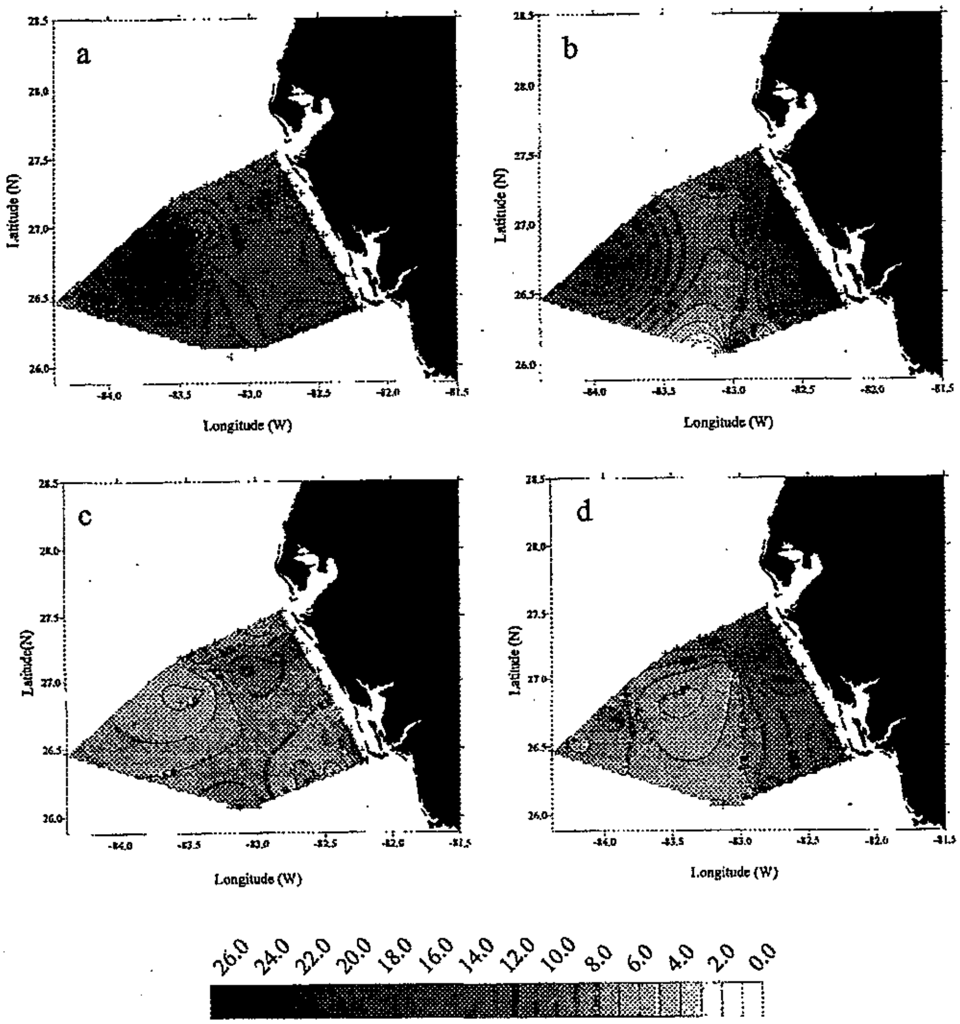

Fig. 11. The 1999 surface distributions of dissolved organic nitrogen (μmol DON kg^{-1}) across the West Florida shelf during (a) 5–8 June, (b) 5–7 July, (c) 6–8 August, and (d) 7–9 September.

penter 1983), a molar C/N ratio of 6.1 (McCarthy and Carpenter 1979), and a molar N/Fe ratio of 465 (Rueter et al. 1992), a surface stock of 0.07 μg chl L^{-1} of *Trichodesmium* represents a minimal iron demand of ~0.45 nmol Fe kg^{-1}. Since these diazotrophs can excrete up to ~50% of their fixed nitrogen in the form of DON (Glibert and Bronk 1994), a total iron demand of ~0.9 nmol Fe kg^{-1} might be required for a 0.42 μmol kg^{-1} increment of both forms of organic nitrogen (DON + PON). The measured July depletion of iron at Stations 15–22 was indeed 1.7 nmol Fe kg^{-1}, compared to the mean (3.1 nmol kg^{-1}) found at all of Stations 11–22 across the outer shelf (Table 1), fueling both surface and possibly larger subsurface populations.

With a molar N/P ratio of 16 for *Trichodesmium* (Walsh 1996), the combined 0.42 μmol kg^{-1} production of PON + DON (calculated from Sta. 16 on July 1999) would require a phosphorus supply of ~0.03 μmol P kg^{-1}. Indeed, a mean surface concentration of 0.02 μmol PO_4 kg^{-1} was still present at Stations 11–22 in July 1999 (Fig. 9b), i.e., after phosphate depletion. In June 1999, the phosphate stock was instead a mean of 0.08 μmol PO_4 kg^{-1} (Fig. 9a).

Since diazotrophs exhibit both alkaline phosphatase activity (Yentsch et al. 1972) and a high affinity for phosphomonoesters (McCarthy and Carpenter 1979), continued phosphorus demands during subsequent dust events could be met, as well, by the observed surface organic stocks of ~0.22 μmol DOP kg^{-1} (Fig. 8) on the outer shelf. Therefore the absence of DOP could indicate a growing population.

Using an N/P ratio of 16 for *Trichodesmium* colonies and a 50% excretion/fixation ratio for nitrogen, a mean diazotroph biomass of 1.4 μg chl L^{-1} and 4.2 μmol DON kg^{-1} would be produced over ~90 d of cumulative iron supply within the surface waters. Following bacterial degradation of the released DON and photolysis of the intact *Trichodesmium* colonies, a new total nitrogen supply of 8.4 μmol kg^{-1} might thus be derived from nitrogen fixation and might have been available to *G. breve* during summer of 1999. A PON/chl ratio of 0.4 for these shade-adapted dinoflagellates

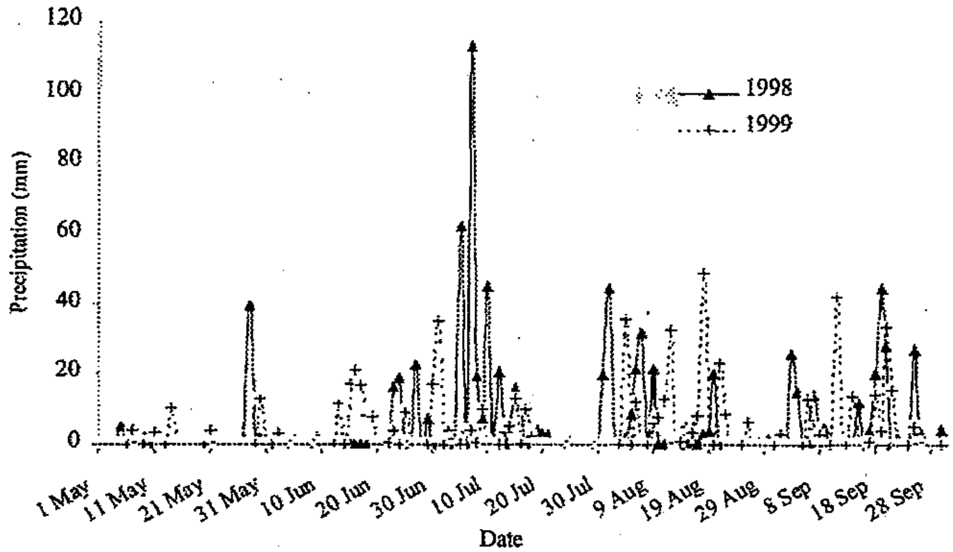

Fig. 12. The daily rainfall (mm day^{-1}) at Tampa International Airport during June–August 1998 and 1999.

(Walsh and Steidinger in press) then suggests a cumulative red tide of 21 μg chl L^{-1}, as was actually observed in coastal waters off West Florida during October 1999.

An associated phosphorus demand of 0.52 μmol kg^{-1} over the 90 d could be partially met by residual phosphorus stocks of ~0.20 μmol PO_4 kg^{-1} and ~0.13 μmol DOP kg^{-1} that are always present within 2–4 km of the Florida coast once the *T. erythraeum* and *G. breve* blooms (Steidinger et al. 1998) are near shore. Indeed, during October 1986, 0.3 μmol PO_4 kg^{-1} were left behind by ~10 μg chl L^{-1} of *T. erythraeum* and ~20 μg chl L^{-1} of *G. breve* above the 20-m isobath (Walsh and Steidinger in press). Furthermore, the ~0.42 μmol PO_4 kg^{-1} phosphate at a depth of 75 m during July 1999 at Sta. 16 could provide a significant phosphorus source for migrating *Trichodesmium* (Karl et al. 1992) in offshore waters.

Conclusion

During summer months, Saharan dust is carried across the Atlantic by prevailing winds, which fertilize the ocean with iron. In oligotrophic basin and shelf ecosystems of the Gulf of Mexico, this iron frequently removes a nutrient limitation for many species of phytoplankton, including the diazotroph *T. erythraeum* and, subsequently, the nitrogen-starved toxic dinoflagellate *G. breve* within phosphorus-replete coastal waters (Walsh and Steidinger in press). The 1999 time series of optical thickness data at St. Petersburg and Dry Tortugas are consistent with observations of aerosol dust at Miami and AVHRR imagery and demonstrate the efficacy of satellite-borne estimates of dust/iron inputs. Future ecological models of multiple plankton groups initialized with satellite observations will allow a more quantitative examination of the causal relationships posed by these ECOHAB cruise results.

Implication of *Trichodesmium* in the nutrient dynamics of *G. breve* red tides is not a new idea: "The physiology, metabolism, and tactic responses of *G. breve* . . . must be understood and the source . . . of nutrients determined before it is possible to suggest a solution or remedy. . . . red tide organisms might be able to utilize atmospheric nitrogen as some of the blue-green algae are capable of doing" (Lasker and Smith 1954). We do present, however, new observations on the mechanisms by which these processes may occur, thus providing constraints on future numerical models of red tide forecasts. The role of *Trichodesmium* on the West Florida shelf is not only to influence the competitive success of red tide organisms, but to also have a major impact on the nitrogen and phosphorus cycles during summer months.

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Harmful Algal Blooms and Eutrophication: Nutrient Sources, Composition, and Consequences

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ABSTRACT: Although algal blooms, including those considered toxic or harmful, can be natural phenomena, the nature of the global problem of harmful algal blooms (HABs) has expanded both in extent and its public perception over the last several decades. Of concern, especially for resource managers, is the potential relationship between HABs and the accelerated eutrophication of coastal waters from human activities. We address current insights into the relationships between HABs and eutrophication, focusing on sources of nutrients, known effects of nutrient loading and reduction, new understanding of pathways of nutrient acquisition among HAB species, and relationships between nutrients and toxic algae. Through specific, regional, and global examples of these various relationships, we offer both an assessment of the state of understanding, and the uncertainties that require future research efforts. The sources of nutrients potentially stimulating algal blooms include sewage, atmospheric deposition, groundwater flow, as well as agricultural and aquaculture runoff and discharge. On a global basis, strong correlations have been demonstrated between total phosphorus inputs and phytoplankton production in freshwaters, and between total nitrogen input and phytoplankton production in estuarine and marine waters. There are also numerous examples in geographic regions ranging from the largest and second largest U.S. mainland estuaries (Chesapeake Bay and the Albemarle-Pamlico Estuarine System), to the Inland Sea of Japan, the Black Sea, and Chinese coastal waters, where increases in nutrient loading have been linked with the development of large biomass blooms, leading to anoxia and even toxic or harmful impacts on fisheries resources, ecosystems, and human health or recreation. Many of these regions have witnessed reductions in phytoplankton biomass (as chlorophyll *a*) or HAB incidence when nutrient controls were put in place. Shifts in species composition have often been attributed to changes in nutrient supply ratios, primarily N:P or N:Si. Recently this concept has been extended to include organic forms of nutrients, and an elevation in the ratio of dissolved organic carbon to dissolved organic nitrogen (DOC:DON) has been observed during several recent blooms. The physiological strategies by which different groups of species acquire their nutrients have become better understood, and alternate modes of nutrition such as heterotrophy and mixotrophy are now recognized as common among HAB species. Despite our increased understanding of the pathways by which nutrients are delivered to ecosystems and the pathways by which they are assimilated differentially by different groups of species, the relationships between nutrient delivery and the development of blooms and their potential toxicity or harmfulness remain poorly understood. Many factors such as algal species presence/abundance, degree of flushing or water exchange, weather conditions, and presence and abundance of grazers contribute to the success of a given species at a given point in time. Similar nutrient loads do not have the same impact in different environments or in the same environment at different points in time. Eutrophication is one of several mechanisms by which harmful algae appear to be increasing in extent and duration in many locations. Although important, it is not the only explanation for blooms or toxic outbreaks. Nutrient enrichment has been strongly linked to stimulation of some harmful species, but for others it has not been an apparent contributing factor. The overall effect of nutrient overenrichment on harmful algal species is clearly species specific.

Introduction

Algal blooms, including toxic events, can be natural phenomena. Historically, indigenous tribes avoided shellfish at certain places or times of year (e.g., Lescarbot 1609 cited in Prakash et al. 1971), and the logs of early mariners such as Captains James Cook and George Vancouver (Vancouver and Robinson 1798 cited in Prakash et al. 1971) describe discolored water and poisonous shellfish. Over the last several decades coastal regions throughout the world have experienced what appears to be an escalation in the incidence of blooms that are toxic or otherwise harmful. Commonly called red tides, these events are now grouped under the descriptor harmful algal blooms or HABs. Although most of the species involved are plant-like, photosynthetic algae, a few are actually animal-like protozoans without the

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ability to photosynthesize on their own. HABs have one unique feature in common—they cause harm, either due to their production of toxins or to the manner in which the cells' physical structure or accumulated biomass affect co-occurring organisms and alter food web dynamics. Impacts of these phenomena include mass mortalities of wild and farmed fish and shellfish; human illness and death from toxic seafood or from toxin exposure through inhalation or water contact; illness and death of marine mammals, seabirds, and other animals; and alteration of marine habitats and trophic structure.

A distinction must be made between two different types of HABs—those that involve toxins or harmful metabolites, such as toxins linked to wildlife death or human seafood poisonings, and those which are nontoxic but cause harm in other ways. Some algal toxins are extremely potent, and low-density blooms can be dangerous, sometimes causing poisonings at concentrations as low as a few hundred cells l^{-1}. Many HAB species that do not produce toxins are able to cause harm through the development of high biomass, leading to foams or scums, the depletion of oxygen as blooms decay, or the destruction of habitat for fish or shellfish by shading of submerged vegetation.

Eutrophication is the natural aging process of aquatic ecosystems. The term was formerly used mostly in reference to the natural aging of lakes wherein a large, deep, nutrient-poor lake eventually becomes more nutrient-rich, more productive with plant and animal life, and slowly fills in to become a pond, then a marsh (Wetzel 1983). More recently, the term has been used to refer to cultural or accelerated eutrophication of lakes, rivers, estuaries, and marine waters, wherein the natural eutrophication process is advanced by hundreds or thousands of years by human activities that add nutrients (Burkholder 2000). Nixon (1995, p. 95) defined eutrophication as "the process of increased organic enrichment of an ecosystem, generally through increased nutrient inputs."

Two nutrients in human-derived sources, phosphorus (P) and nitrogen (N), are of most concern in eutrophication. In freshwaters, P is the least abundant among the nutrients needed in large quantity (macronutrients) by photosynthetic organisms, so it is the primary nutrient that limits their growth (Schindler 1977). P can also limit or co-limit algal growth in estuarine and marine environments that are sustaining high N inputs (Rudek et al. 1991; Fisher et al. 1992). In many temperate and polar coastal marine waters, N is the most important nutrient that limits primary production of photosynthetic organisms (Dugdale and Goering 1967; Glibert 1988). N is often the nutrient that first limits primary production at the estuarine interface between marine and freshwater habitats. In lower estuaries both N and P can co-limit phytoplankton production (Rudek et al. 1991; Fisher et al. 1992). If improved sewage treatment reduces P loading within freshwater segments of a given river system, corresponding reductions in freshwater phytoplankton blooms will allow more inorganic N to be transported down to estuarine segments where it can support larger blooms (Fisher et al. 1992; Mallin et al. 1993). Both N and P are considered here, and these nutrients should be co-managed in the development of strategies to minimize HABs. Other nutrients such as silicon (Si) and iron (Fe) also can significantly influence the outcome of species dominance and the structure and abundance of phytoplankton communities under cultural eutrophication (Heckey and Kilham 1988; Wilhelm 1995).

For more than 50 years scientists have recognized that noxious blooms of toxic or otherwise harmful cyanobacteria (blue-green algae), the most common harmful algae in freshwater lakes, reservoirs, and slow flowing rivers, are stimulated by P enrichment (reviewed in Schindler 1977; Smith 1983). These organisms can form rotting hyperscum mats up to ca. 1 m thick, with billions of cells ml^{-1} and chlorophyll *a* (chl *a*; index of algal biomass) as high as 3,000 $\mu g\ l^{-1}$ (Zohary and Roberts 1989). Many species produce bioactive compounds, including potent hepatotoxins and neurotoxins that have caused livestock and wildlife death in most countries throughout the world (Skulberg et al. 1993; Codd et al. 1997) and, more rarely, death of humans as well (Chorus and Bartram 1999). The relationship between cyanobacteria and P is sufficiently strong that in many lakes of moderate depth ($\geq$ 10 m) with low abiotic turbidity, the spring-season concentration of total P in lakes (specifically, during lake overturn or total water column mixing) has been used with reasonable success to predict the late summer maximum in cyanobacterial biomass (as water-column chl *a*; Wetzel 1983). This relationship has also held in estuarine and brackish coastal waters of Scandinavia and Australia, where blooms of the toxic cyanobacterium, *Nodularia spumigena,* have been related to excessive P enrichment (Chorus and Bartram 1999).

In freshwater reservoirs and rivers, mixing and flushing dynamics are more complex, and abiotic turbidity from episodic sediment loading is appreciable. Light can be the primary resource limiting algal growth, rather than nutrients. The increased flow and mixing maintains relatively high nutrient supplies, and P has not been used successfully to predict the occurrence and extent of late summer cyanobacterial blooms (Canfield and Bachmann 1981; Thornton et al. 1990). Modest success in understanding nutrient stimulation of harmful algae, and in being able to reliably predict HABs from nutrient inputs, has been achieved to date only for cyanobacteria in clear-water lakes of moderate depth and dependable mixing regimes. Reliable prediction of the growth of HAB species in rivers (including run-of-river impoundments), estuaries, and coastal waters, characterized by highly complex and stochastic mixing and flushing patterns, has remained a challenge (Thornton et al. 1990; Burkholder 2000).

The nature of the global HAB problem in estuarine and coastal waters has changed considerably over the last several decades, both in extent and its public perception (Anderson 1989; Smayda 1990; Hallegraeff 1993). Virtually every coastal country is now threatened by multiple harmful or toxic algal species, often in many locations and over broad areas. This trend has been referred to as the apparent global expansion of HABs because for many locations, poor historic data are available. It is not clear as to how much of the increase reflects heightened scientific awareness and scrutiny of coastal waters and seafood quality versus an actual increase in the number, severity, or frequency of outbreaks (Anderson 1989). Many new bloom species are believed to reflect the discovery of hidden flora populations (Smayda 1989) which had existed in those waters for many years, but which had not been detected or recognized as harmful until the advent of more sensitive toxin detection methods or an increase in the number and training of observers (e.g., Anderson et al. 1994). The number of known toxic dinoflagellates has increased from roughly 20 only a decade ago to at least 55 today (Burkholder 1998), yet none of these more recently known species appear to be mutants or species that have suddenly become toxic. Geological records or past monitoring data, where available, indicate that in many locations these species were present in the plankton all along, but were not discovered until recently. As underscored by Hallegraeff and Bolch (1992), the accidental introduction of HAB species into an area via ballast water discharge can also be a contributing factor to the global expansion.

Of considerable concern, particularly for coastal resource managers, is the potential relationship between the apparent increase in HABs and the accelerated eutrophication of coastal waters due to human activities. Linkages between HABs and eutrophication have been noted within the past two decades (e.g., Officer and Ryther 1980; Lam and Ho 1989; Smayda 1989, 1990; Riegman 1995; Richardson and Jorgensen 1996; Richardson 1997). Coastal waters are receiving massive and increasing quantities of industrial, agricultural, and sewage effluents through a variety of pathways (Vitousek et al. 1997). In many urbanized coastal regions, these anthropogenic inputs have altered the size and composition of the nutrient pool which may, in turn, create a more favorable nutrient environment for certain HAB species.

From innovative syntheses of available databases worldwide, Smayda (1989, 1990) made a compelling case for the increase in blooms of some HAB species being a result of coastal eutrophication. He presented a unifying framework that stressed analogies in phytoplankton community response across geographic regions and encouraged scientists and resource managers to consider the previously neglected role of accelerated eutrophication in HABs. Now, more than a decade later, the heavy public and scientific attention given to HABs and apparent increasing trends, new outbreaks, or, in a few cases, outbreaks that have diminished in size or frequency, suggest that it is time to assess scientific progress in some of the issues that relate to possible human-induced changes in HAB distribution and dynamics. In particular, emphasis is needed on the physiological, ecological, and environmental mechanisms involved. There is no question that nutrients are required by HABs, as they are by all algal species. Here we address current insights into the relationships between HABs and eutrophication, focusing on sources of nutrients, the known effects of nutrient loading and reduction, new understanding of pathways of nutrient acquisition among HAB species, and the specific relationships between nutrients and toxic algae. Through local, regional, and global examples of these various relationships, we offer both an assessment of the state of understanding, and the uncertainties that require future research efforts.

Sources of Nutrients and their Relationship with HABs

Many sources of nutrients can stimulate harmful algal blooms, including sewage and animal wastes, atmospheric deposition, and groundwater inflow, as well as agricultural and other fertilizer runoff. Yet another source is the growing aquaculture industry in many coastal areas.

Human activities have had a tremendous impact on the global cycling of nutrients in coastal systems. The export of P to the oceans has increased 3-fold compared to pre-industrial, pre-agricultural levels, and N has increased even more dramatically, especially over the last 4 decades (Caraco 1995; Smil 2001). During that time, the flux of N increased 4-fold into the Mississippi River and more than 10-fold into the rivers entering the North Sea

(National Research Council 2000; Smil 2001). Human activity is estimated to have increased N inputs to the coastal waters of the northeastern United States generally and to Chesapeake Bay specifically by 6–8-fold (Boynton et al. 1995; Howarth 1998).

Point sources generally are less important nutrient contributors than nonpoint sources, when considered on an annual basis (National Research Council 2000). Point sources can be a major source of nutrients for small watersheds within, or adjacent to, major population centers. Wastewater contributes an estimated 67% of the N inputs to Long Island Sound annually, largely due to sewage from New York City. Sewage treatment plants deliver from 40–80% of the N to Kaneohe Bay, Hawaii, and to Narragansett Bay, Rhode Island (Nixon and Pilson 1983; National Research Council 1993). More rarely, point sources can be major components of nutrient loads to moderately sized watersheds. One point source, the world's largest phosphate mine, added 50% of the total P loading to the mostly agricultural Tar-Pamlico watershed of the Albemarle-Pamlico estuarine system in North Carolina for nearly 30 years (ca. 2,800 metric tons of free phosphate dust added per day to the Pamlico Estuary; reduced by > 90% in the early 1990s; North Carolina Department of Environment, Health and Natural Resources [NC DEHNR] 1994).

Nonpoint sources of nutrients (from agricultural activities, fossil-fuel combustion, and animal feeding operations) are often of greater concern than point sources because they are larger and more difficult to control. Howarth et al. (1996) estimated that sewage contributes only 12% of the flux of N from the North American continent to the North Atlantic Ocean. Only ca. 25% of the N and P inputs to Chesapeake Bay come from wastewater treatment plants and other point sources (Boynton et al. 1995). Even in relatively large watersheds the importance of point source contributions increases during summer low-flow conditions, when treated and untreated wastewater can represent 50% or more of the river flow (e.g., the Neuse estuary of the Albemarle-Pamlico estuarine system; NC DEHNR 1994). This point becomes especially important, given the fact that many harmful algal species are most active in summer low-flow periods.

Fertilizer application on land remains a major contributor to nonpoint nutrient pollution, and this source is still increasing at an alarming rate in many geographic regions (Vitousek et al. 1997). Both industrial and developing nations are using significantly higher loadings of fertilizer in agriculture, with global N and P fertilizer usage increasing 8-fold and 3-fold, respectively, since the early 1960s (Constant and Sheldrick 1992; Caraco 1995; Matson et al. 1997; Smil 2001). There is a direct relationship between population development, fertilizer applications, and riverine N and P fluxes (Fig. 1a,b; Caraco 1995; Smil 2001). When these nutrient supplies reach lower rivers, estuaries, and coastal waters, they are available for phytoplankton uptake and growth. The nitrate component of fertilizers can travel long distances. For example, Mallin et al. (1993) demonstrated a significant relationship between nitrate, carried ca. 400 km downstream to the lower Neuse estuary (over a 2-wk period), and increased phytoplankton productivity.

Nutrient inputs from runoff vary not only in quantity (influenced by rainfall and other environmental factors), but also in composition (based on the form of fertilizer in use), and this has important implications for HAB development. A dramatic trend in world fertilizer production is the increased proportion of urea in world N production, especially in third-world countries (Fig. 1c; Constant and Sheldrick 1992). Urea now comprises roughly 40% of all N fertilizers produced (Constant and Sheldrick 1992). This is significant because data indicate that in some areas, this shift in fertilizer composition has resulted in a shift in the nutrient composition of runoff, potentially favoring some HAB species.

Ground water has also been identified as an important source of nutrients to receiving surface waters. Human population growth and agricultural practices have increased nutrient loadings to ground water, and this has the potential to affect algal growth in adjacent rivers, lakes, estuaries, and coastal zones. In lakes the linkages between groundwater nutrient inputs and HABs (mostly as cyanobacteria) has been clearly demonstrated; Jones and Bachmann (1975) and Dillon and Rigler (1975) were able to reliably predict late summer phytoplankton biomass in natural lakes by taking into account the P supplied from septic effluent leachate. In coastal areas such linkages can be more complex and more difficult to prove conclusively.

Some success has been achieved relating groundwater flow to the growth of the harmful brown tide species *Aureococcus anophagefferens* in Long Island, New York. This species has been associated with loss of eelgrass meadows and reduction in reproduction and growth of shellfish (Tracey 1988; Dennison et al. 1989; Gallagher et al. 1989). LaRoche et al. (1997) hypothesize that in specific coastal bays, years with high inputs of ground water lead to high dissolved inorganic nitrogen (DIN) concentrations. *A. anophagefferens* is not a strong competitor when DIN is high, as

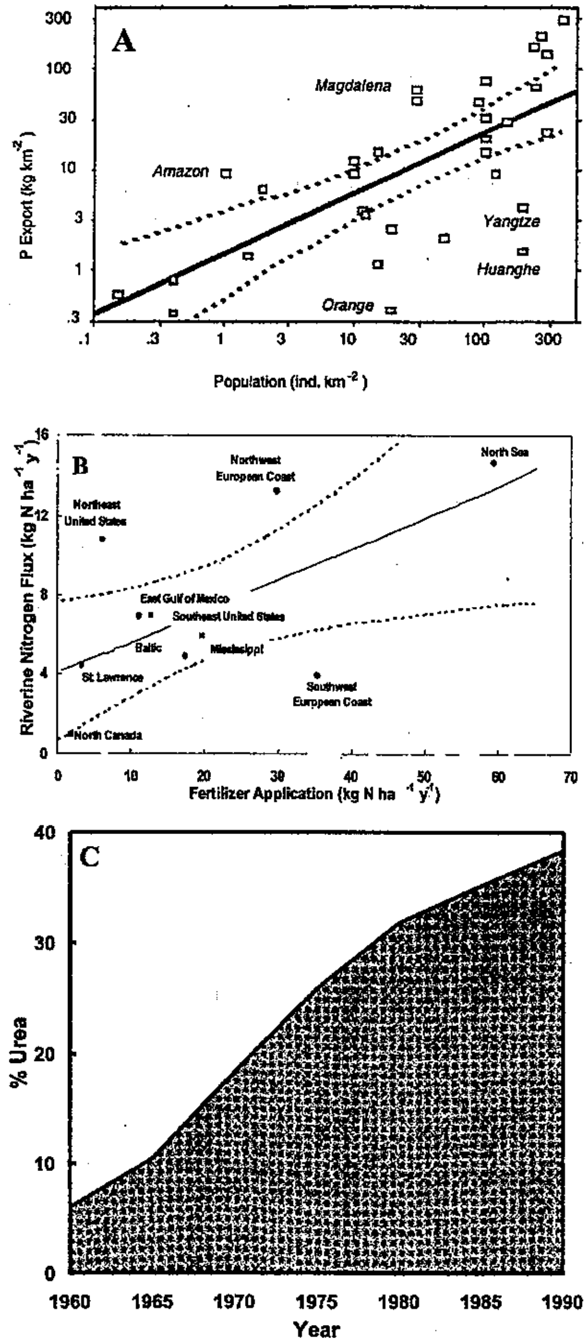

Fig. 1. Nutrient inputs to the world's oceans. A) The relationship between population density in watersheds and export of soluble reactive phosphorus (SRP) in river water, considering 32 major rivers (from Caraco 1995). B) The relationship between the rate of fertilizer applications and the flux of riverine nitrogen in many of the world's coastal ecosystems (from Smil 2001). C) Trends in the proportion of the contribution of urea to world N fertilizer production from 1960 to 1990 (from Constant and Sheldrick 1992).

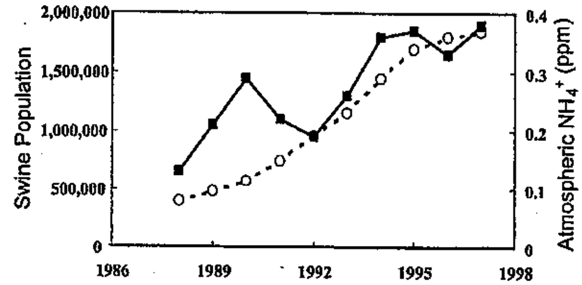

Fig. 2. Example of localized, significant increase in atmospheric ammonium (squares) from concentrated animal operations (circles; Sampson County, North Carolina, where there are 48 swine per person [ca. 2 million swine in total]). Approximately 72% of the variability in airborne ammonia during the past decade can be explained by the expansion of the county's swine population, alone. Much of the nitrogen volatilized as ammonia during spray-application of swine effluent onto fields is deposited into receiving rivers and streams within a distance of ca. 100 km radius (modified from Mallin 2000).

shown in nutrient enrichment studies in mesocosms, where the cell density of *A. anophagefferens* was inversely correlated with DIN concentrations (Keller and Rice 1989). When groundwater input is low, decay of the algal biomass created in previous years from high DIN leads to elevated levels of dissolved organic nitrogen (DON) which *A. anophagefferens* can use efficiently (Berg et al. 1997). A groundwater index relationship has been formulated that correctly hindcasts brown tide blooms in 9 of 11 years on Long Island, but the relationship has not held for all embayments in which this species blooms (Gobler 1999; Lomas et al. 2001; Borkman and Smayda unpublished data). If the groundwater hypothesis is valid, the LaRoche et al. (1997) study also suggests that there can be a significant time lag between human activities that enrich the ground water (such as heavy fertilizer usage) and the eventual HAB impact. In Long Island Sound, it is possible that the massive brown tides which began suddenly in 1985 may reflect heavy fertilizer usage on land 10 or 20 years earlier.

On local to global scales, one of the most rapidly increasing sources of nutrients to both freshwaters and the coastal zone is the atmosphere (Figs. 2 and 3). Phosphate adsorbed onto fine particulates, and nitrate derived from particulate or oxidized nitric/nitrous oxides in wet and dry deposition, have long been recognized as important sources of nutrients to streams and lakes, and can be major sources especially for softwater, nutrient-poor freshwater systems (Likens et al. 1979; Kilham 1982; Swedish Ministry of Agriculture 1982). In estuarine and coastal waters, it has been estimated that 20–40% of N inputs can be of atmospheric origin, from industrial, agricultural, and urban sources (Duce 1986; Fisher and Oppenheimer 1991; Paerl 1995,

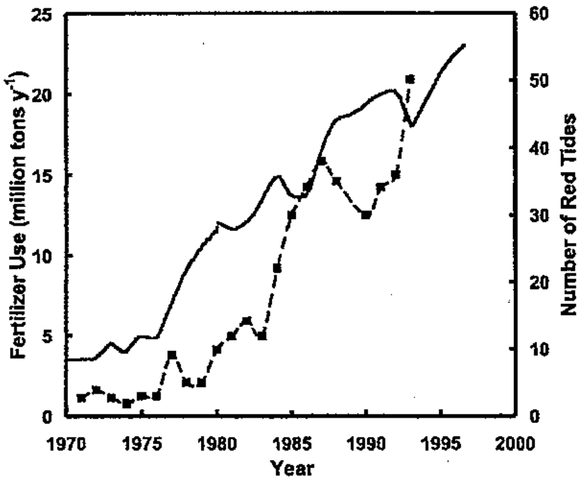

Fig. 3. Trends in fertilizer use and the number of red tides reported for Chinese coastal waters (data redrawn from Smil 2001 and Zhang 1994). While the general pattern is increasing for both parameters, it is thought that atmospheric deposition may also play an important role in the development of these blooms.

1997; Driscoll et al. 2001). In other areas more removed from such sources, this proportion can be lower, such as in the Gulf of Mexico where atmospheric inputs (1–2% of the total) are overwhelmed by contributions from the Mississippi and Atchafalaya Rivers (Paerl et al. 2000).

Atmospheric inputs are important not only because of their magnitude, but because the mix of atmospheric nutrients, like other nutrient sources, can stimulate some phytoplankton species disproportionately over others. Experimental manipulations have shown that rainwater can enhance productivity more than the addition of a single N source (Paerl 1997). The high proportion of DON in rainwater, representing up to 40% of its total N, is thought to be significant in this enhancement (Timperley et al. 1985; Paerl 1997). Blooms in the Yellow Sea of China, which have escalated in frequency over the past several decades (Fig. 3), have been related to atmospheric deposition in addition to direct nutrient runoff (Zhang 1994). It is estimated that a typical rain event over the Yellow Sea may supply sufficient N, P, and Si to account for 50–100% of the primary production of a HAB event (Zhang 1994).

The atmosphere, through both wet and dry deposition, may also be a source of key trace metals such as Fe (Church et al. 1991; Duce and Tindale 1991). Phytoplankton in many estuaries and coastal waters (where most HAB species occur) can be Fe-limited (e.g., Wells 1999), and additions of atmospheric Fe could therefore contribute to some bloom events (Martin and Fitzwater 1988; Cullen 1991; Coale et al. 1996). Interactions between Fe and N can influence plankton community structure (e.g., DiTullio et al. 1993), and may be a factor in the regulation of growth and encystment of dinoflagellates (Doucette and Harrison 1991) and possibly in the toxicity of diatoms such as *Pseudo-nitzschia* spp. (Rue and Wells unpublished data).

Aquaculture ponds and cage culture systems represent another source of nutrients, provided as feed or fertilizer and by the biological transformations occurring in these high biomass systems. It has been suggested that these enriched systems may promote the growth of harmful species not previously detected in the source water (Anderson 1989; Hallegraeff 1993). The cultured animals retain only a fraction of their food, the rest decomposes in the water column or settles to the bottom and decomposes, and either way, the nutrients released from this decomposition can stimulate phytoplankton growth (Cho et al. 1996; Burford 1997; Burford and Glibert 1999). The effect can be worsened if the aquaculture site is constructed in wetlands (e.g., salt marshes or mangrove swamps) that otherwise would serve as a sink rather than a source of nutrients to the system.

Sakamoto (1986) calculated that nutrients released from fish culture sites affect an area 3–9 times the size of the aquaculture zone. In a quiescent system, this sustained input could affect productivity in the area, but the extent of the nutrient impact may diminish with higher rates of flushing by tides and currents. Recognizing the need for dilution, fish farming operations in the northwestern U.S. have shifted from easily accessible but poorly flushed bays and coves to areas with much stronger currents resulting in a significant reduction in particulate and dissolved nutrient buildup and reduced planktonic and benthic impacts (Rensel personal communication). Many fish farms in developing countries are located in shallow, easily accessible bays where nutrients can accumulate and stimulate algal blooms (e.g., Wu et al. 1994). Benthic nutrient regeneration of the accumulated feces and decomposing feed may be a significant and sustained source of nutrients in such systems. The situation in these environments was described in harsh terms by Romdhane et al. (1998, p. 82), in referring to fish farms in Tunisian lagoons, "... eutrophication following increased human activity in and around these lagoons influences the magnitude and frequency of toxic blooms. Lagoons may function as traps for toxins or other exudates from algae. We therefore stress that aquaculture inside lagoons is a hazardous business."

There is no simple generalization about the impacts of aquaculture operations on plankton communities, or specifically, on HABs, although it is clear that in waters with a high density of aquaculture operations and poor flushing, the cumulative input of nutrients has impacts on plankton productivity. As is the case with the other sources of nutrients to coastal waters, the increased nutrient loading will lead to increased phytoplankton production, but whether this leads to toxic impacts depends on whether toxic species are present and on the relative abundance of the nutrient elements, the mixing and hydrographic characteristics of the area, and other factors such as grazing intensity or light availability.

Nutrient Loadings, Nutrient Reductions, and High-Biomass HABs

On local, watershed, and global scales, strong correlations have been shown between total P input into freshwaters, and between total N input into estuaries and coastal waters and total phytoplankton production (Schindler 1977; Wetzel 1983; Nixon 1992; Mallin et al. 1993). HAB species, like all plant-like organisms require certain major and minor nutrients for their nutrition, and these can be supplied either naturally from freshwater and marine biogeochemical processes or through human activities such as pollution. These nutrient sources include dissolved inorganic and organic compounds of various types, as well as particulate nutrients in the form of other organisms or detritus.

In attempting to understand the impacts of nutrient availability and nutrient loading on an aquatic ecosystem, it is important to make the distinction between effects on physiological processes or productivity versus biomass accumulation. As initially developed conceptually by Caperon et al. (1971) and applied more recently to the Chesapeake Bay (Malone et al. 1996), nutrient loading responses can be viewed in a manner analogous to a saturating response curve (Fig. 4). The effects of nutrients may fall in the minimal response region, which is dominated by rapid physiological adjustment and low biomass accumulation, or alternatively, in the maximum response region, in which physiological processes have become saturated, but biomass accumulations continue. The minimum response region of the curve also represents the period of bloom initiation, whereas the maximum response region represents bloom maintenance. As the period of bloom initiation is characterized by minimal increases in biomass, the role of nutrients in bloom initiation is far less understood than for the period during which a bloom may have been maintained. Ultimately, the entire response may be saturated at exceptionally high loading rates due to limitation by some other factor. Within this framework, it is important to recognize that in

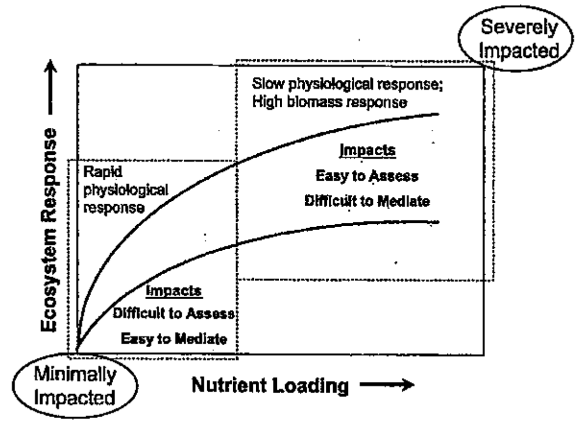

Fig. 4. Generalized ecosystem response to nutrient loading. At low levels of nutrient loading, the organismal response may be rapid, but biomass changes would be few. At high rates of nutrient loading, the physiological responses of the organism would be expected to be at or near saturating rates, and would show little increase, yet on a longer time scale, biomass would increase.

the minimum response region, impacts are few, difficult to detect, and easy to reverse, while in the maximum response region, impacts are large and often easy to detect, but substantially more difficult to reduce and control.

Nutrients can stimulate or enhance the impact of toxic or harmful species in several ways. At the simplest level, harmful phytoplankton may increase in abundance due to nutrient enrichment, but remain in the same relative fraction of the total phytoplankton biomass. Even though non-HAB species are stimulated proportionately, a modest increase in the abundance of a HAB species can cause it to become noticeable because of its toxic or harmful effects.

A more frequent response to nutrient enrichment occurs when a species or group of species begins to dominate under the altered nutrient regime. In deeper freshwater, estuarine, and coastal marine systems, phytoplankton dominate the algal flora. Macroalgae and benthic microalgae often dominate many lakes and shallow, poorly flushed estuaries, lagoons, and upper embayments, as well as coral reefs and rocky intertidal/subtidal habitats (Harlin 1993). In surface waters across the entire salinity gradient, there are many examples of overgrowth and high biomass blooms by phytoplankton, benthic microalgae (especially epiphytes), and macroalgae. In many cases, the responding dominant species are not toxic and, in fact, are beneficial to coastal productivity until they exceed the assimilative capacity of the system, after which anoxia and other adverse effects occur. When that threshold is reached, seemingly harmless species can have negative impacts.

In this context, much has been written about the links between freshwater flow, nutrient loading (as total P and phosphate), and increased nontoxic (as well as toxic) cyanobacterial blooms in lakes, and the associated bottom-water anoxia, benthic animal mortalities, and fish kills that can follow these outbreaks (Vallentyne 1974). Freshwater flow and nutrient loading (mostly as nitrate) have been linked to increased numbers of estuarine algal blooms (as diatoms and other typically benign microalgae or as macroalgae), followed by oxygen deficits and finfish and/or shellfish kills (Harlin 1993; Mallin et al. 1993).

Increases in high biomass phytoplankton blooms have been reported from the south China Sea (Qi et al. 1993), the Black Sea (Bodeanu and Ruta 1998), Hong Kong (Lam and Ho 1989), and many other locations, typically in parallel with the nutrient enrichment of coastal waters. In Chesapeake Bay, high phytoplankton biomass is typically observed in the spring, associated with high riverine nutrient inputs (Glibert et al. 1995; Malone et al. 1996). These large spring blooms eventually settle to the bottom, where heterotrophic bacteria process a major fraction of the organic material. This can result in depletion of oxygen as temperatures warm (Malone et al. 1986; Shiah and Ducklow 1994), leading to anoxia and benthic mortalities (e.g., Boynton et al. 1982; Malone et al. 1983; Fisher et al. 1988, 1992; Glibert et al. 1995). As another example, spring eutrophication from the N loading of the Mississippi and Atchafalya Rivers to the Gulf of Mexico has resulted in enhanced phytoplankton production and the development of anoxia in the Gulf of Mexico, a so-called dead zone that has altered benthic food web dynamics substantially (Turner and Rabalais 1994; Rabalais et al. 1996).

One of the clearest examples of the direct development of a toxic species in response to increased nutrient loading is the development of *Pseudo-nitzschia* spp. on the Louisiana shelf in the extended plume of the Mississippi River. Blooms of *Pseudo-nitzschia* spp. develop in high abundances during the spring when nutrient loading is highest (Dortch et al. 1997; Parsons et al. 1998, 1999; Pan 2001). Both historical data and frustules preserved in cores (Dortch et al. 1997, 2000; Parsons et al. 2002) indicate a large increase in *Pseudo-nitzschia* spp. abundance since the 1950s, concomitant with increases in nutrient loading. Studies in mesocosms have also demonstrated a disproportional increase in *Pseudo-nitzschia* spp. following nutrient pulsing (Dortch et al. 2000).

Flushing rate or turnover time (the rate at which all of the nutrient-laden water is exchanged or moved out of the lake, river, or estuary) and water depth play a major role in the duration of the period in which nutrients are available to algal assemblages. Lakes and reservoirs with high flushing rates and high P loading have significantly less algal production than similar systems with poor flushing (e.g., Dillon 1975; Canfield and Bachmann 1981). The same is true of flushing in estuaries and coastal waters, where shallow systems typically support more algal growth than deeper systems (Wetzel 1983; Day et al. 1989). Chesapeake Bay has an estimated mean turnover time of ca. 35 d and a mean depth of ca. 9 m (Magnien et al. 1992). N and P loads are estimated at ca. 80×10^6 kg N yr^{-1} and 4×10^6 kg P yr^{-1}, of which 55–70% is delivered during the winter-spring freshet (Magnien et al. 1992; Boynton et al. 1995). Phytoplankton biomass during early spring blooms that are supported by these nutrient supplies can exceed 50 μg chl *a* l^{-1} (Glibert et al. 1995; Malone et al. 1996). The Neuse estuary has a mean water turnover time of ca. 80 d and a mean depth of ca. 3.5–4 m (Glasgow and Burkholder 2000; Glasgow et al. 2001a). In this smaller, poorly flushed, shallow system, loadings of ca. 5×10^6 kg N yr^{-1} and $6–8 \times 10^5$ kg P yr^{-1} have supported late winter-spring blooms of benign (nontoxic) dinoflagellates with biomass as high as 300 μg chl *a* l^{-1} (Glasgow and Burkholder 2000; Glasgow et al. 2001a).

Repeated incidence of increased, high-biomass blooms provide evidence of a broadly based, stimulatory effect on phytoplankton from anthropogenic nutrients. The evidence for this relationship is further strengthened by repeated observations that HABs tend to decrease when nutrient loading is reduced. Among the most cited early reports of partial reversal of cultural eutrophication in freshwater involved removing sewage discharges from Lake Washington within metropolitan Seattle, Washington (Edmondson 1970). This lake had sustained noxious cyanobacteria blooms prior to the 1920s because of raw sewage inputs. Zero discharge of sewage to Lake Washington was imposed in 1968, and the cyanobacterial blooms declined. In a much larger system, Great Lake Erie, the green macroalga *Cladophora* had choked much of the west basin with massive growth until improved wastewater treatment and detergent phosphate bans in the early 1980s led to significant reduction in the nuisance blooms (Ashworth 1986).

Reduced nutrient loading similarly has promoted declines in estuarine and marine coastal HABs. Sewage discharges to the Mumford Cove, a shallow estuary in Connecticut were rerouted to another waterway in the late 1980s, and within two years massive nuisance blooms of the macroalga, *Ulva*

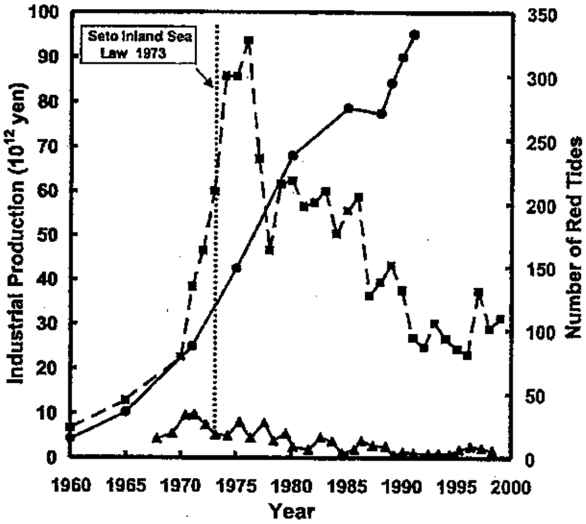

Fig. 5. Trends in industrial production (circles) and the number of visible red tides (squares) in the Seto Inland Sea of Japan. The vertical line represents the passage of the Seto Inland Sea Law in 1973, after which nutrient loadings were reduced to one-third of 1974 levels. The triangles denote the number of red tides with fisheries impacts (redrawn from Okaichi 1997 with additional data from Fukuyo).

lactuca, were eliminated (Harlin 1993). In the Seto Inland Sea in Japan between 1965 and 1976, the number of red tide outbreaks (high biomass blooms) increased 7-fold (Okaichi 1997), in parallel with the increase in industrial production and chemical oxygen demand (COD) from domestic and industrial wastes (Fig. 5). In 1973, Japanese authorities instituted the Seto Inland Sea Law to reduce COD loadings to half of the 1974 levels over a 3-yr period. The number of red tides began to decrease in 1977, eventually falling to less than 30% of the peak frequency, which had been in excess of 300 blooms yr^{-1} (Fig. 5). This lower level of bloom incidence has been maintained to the present. These data demonstrate a general increase in phytoplankton abundance due to overenrichment, and a proportional decrease in blooms when that loading was reduced. It is interesting that toxic blooms (in this instance, those that cause fish mortalities or other fisheries damage) also decreased after the loadings were reduced (Fig. 5).

Another important observation from the Seto Inland Sea is that as the waters became less eutrophic and large biomass blooms decreased, there was a shift in species composition, leading to a greater prevalence of some that are responsible for shellfish poisonings in humans, such as *Alexandrium tamarense* and *A. catenella.* Paralytic shellfish poisoning (PSP) caused by these species was not reported in the Inland Sea several decades ago, but is common now (Fukuyo personal communication). This emphasizes a common dilemma faced by coastal managers, namely that effluent controls may reduce the number of phytoplankton blooms, but those actions may not result in fewer HAB impacts. This can happen because some species (and their high biomass blooms) may decrease in frequency or disappear as the waters become cleaner, but there are other harmful or toxic species that can fill that niche and have negative impacts. This reflects the great variation among HAB species in the levels of nutrients that are optimal for growth. In some cases, oligotrophic HAB species that are not good competitors when nutrient loads are high can thrive as loadings from land diminish. PSP-producing *Alexandrium* spp. have long occurred in Alaska, northeastern Canada, and northern Japan; all areas with relatively unpolluted and historically pristine waters (e.g., Horner et al. 1997). On Long Island, shellfishermen who have been devastated by recurrent *A. anophagefferens* brown tides since 1985 point out that immediately prior to the outbreaks, the affected waters are cleaner with more transparency compared to the past when brown tides did not occur (McElroy 1996). Reductions in nutrients generally will reduce blooms, but may not necessarily reduce all the potentially harmful impacts of HABS or all of the HAB species.

Another example of the effect of nutrient reduction comes from the freshwater-to-brackish Potomac River, a tributary of the Chesapeake Bay, where phosphate removal from sewage began in the late 1970s. This region had previously experienced repeated blooms of *Microcystis* spp. with chlorophyll concentrations in surface waters exceeding 70 $\mu g\ l^{-1}$, but after the nutrient reductions, there were sustained decreases both in total chlorophyll and in the frequency and intensity of the *Microcystis* blooms (Jaworski 1990). Chlorophyll levels were generally $< 20\ \mu g\ l^{-1}$.

A final example is from the northwestern Black Sea, which experienced heavy pollution loading in the 1970s and 1980s due to industrialization, fertilizer use, and urbanization in eight countries within that watershed, followed by reductions in these loads in the 1990s. Significant increases in inorganic and organic nutrients were noted over that initial 20-yr interval: nitrate was 2.5–8 times higher, and phosphate was up to 20-fold higher (Bodeanu 1993). A consequence of this enrichment was an increase in the frequency and magnitude of algal blooms, as well as changes in the species composition. In the 1960s, high biomass blooms were rare, but during the two decades of intense eutrophication pressure, blooms became recurrent, with cell densities greatly exceeding past abundance levels (Bodeanu 1993). During the 1980s, when nutrient loadings peaked, 49 major blooms were reported, of which 15 had > 10 million cells l^{-1} (Bodeanu and Ruta 1998). Anoxia, fish mortalities, and other impacts were frequent. A characteristic of this interval was the decreased abundance of diatoms and larger algae, and their replacement by flagellates and nanoplankton. In a striking reversal, algal blooms began to decrease in 1991, both in number and size, and this trend has continued to the present. Diatoms became more dominant, and nanoplankton and flagellates decreased. From 1991–1996, there were only three blooms with cell concentrations in excess of 10 million cells l^{-1}. This reduction in blooms coincided with significantly decreased fertilizer usage as a result of the loss of economic subsidies that accompanied the breakup of the former Soviet Union (Bodeanu and Ruta 1998). It will be interesting to see if the positive trend in bloom incidence of recent years is reversed when economic development, and thus fertilizer usage, increase in the coming years.

There are a number of examples where increases and decreases in nutrient loadings due to human activities have resulted in parallel increases or decreases in bloom incidence. Many of these examples are of high biomass blooms, that cause harm through excessive population development and its decay. Other factors need to be considered in understanding phytoplankton compositional changes that lead to development of HAB outbreaks, but not necessarily to high biomass production.

Nutrient Composition and HAB Development

Many factors affect phytoplankton species composition and bloom development, and among these is the composition of the nutrient pool—the forms of the nutrients supplied, as well as the relative abundance of the major nutrient elements. Some generalities are beginning to emerge with respect to the preference of many bloom-forming species for specific forms of nutrients, as well as the tendency for some blooms to occur when the ratios of nutrient availability or supply are altered. The latter concept is based largely on the nutrient ratio hypothesis (Tilman 1977; Smayda 1990, 1997) which argues that environmental selection of phytoplankton species is associated with the relative availability of specific nutrients in coastal waters, and that human activities have altered these nutrient supply ratios in ways that change the natural phytoplankton community composition and possibly favor harmful or potentially toxic forms.

Perhaps the clearest demonstration of the effect of altered nutrient supply ratios involves the stimulation of non-diatom species following changes in the availability of N or P relative to silicate. Diatoms, the vast majority of which are harmless, require silica in their cell walls, whereas most other phytoplankton do not. Since silica is not abundant in sewage effluent but N and P are, the N:Si or P:Si ratios in some lakes, rivers, estuaries, and coastal waters have increased over the last several decades (Shelske et al. 1986; Smayda 1989, 1990; Rabalais et al. 1996). In theory, diatom growth will cease when silica supplies are depleted, but other phytoplankton classes can continue to proliferate using the excess N and P.

Research is ongoing in various geographic regions to further examine this concept, which is supported by several data sets. From a long-term database in Great Lake Michigan, Schelske et al. (1986) found evidence of silica depletion that was correlated with increased anthropogenic P loading through the early 1970s. By the 1980s, cyanobacteria and colonial green algae had increased to co-dominance with diatoms, but at that point P inputs began to decline. The phytoplankton community then shifted from ca. 50% cyanobacteria and colonial greens to replacement by flagellates in summer with diatoms dominant in the spring. Similarly, in marine waters of Tolo Harbor in Hong Kong, there was an 8-fold increase in the number of red tides (mainly dinoflagellates) per year between 1976 and 1989, in parallel with a 6-fold increase in human population density and a 2.5-fold increase in nutrient loading in that watershed that altered the nutrient ratios (Lam and Ho 1989). In the mid to late 1980s, as pollution loadings decreased due to the diversion of sewage effluent to Victoria Harbor, there was a resurgence of diatoms and a decrease in dinoflagellates and red tides (Yung et al. 1997).

These blooms in Tolo Harbor show a distinct relationship with nutrient ratios, but not just N:Si or P:Si. Hodgkiss and Ho (1997) demonstrated that the numbers of dinoflagellate red tides increased as the annually averaged N:P ratio fell from 20:1 to 11:1 between 1982 and 1989 (Fig. 6). In more detailed analysis of the patterns during a single year, Hodgkiss (2001) showed that whenever the N:P ratio fell below ~10:1 in Tolo Harbor, dinoflagellate cell numbers increased. These two inverse correlations are consistent with experimental data, whereby the three major dinoflagellate species in Tolo Harbor in the 1980s (*Prorocentrum micans, P. sigmoides,* and *P. triestinum*) were shown to have optimal N:P ratios for growth of 5–10, 4–15, and 8–15:1, respectively, all significantly below Redfield proportions. As the N:P ratio in Tolo Harbor decreased between 1982 and 1989, these species increased in abundance.

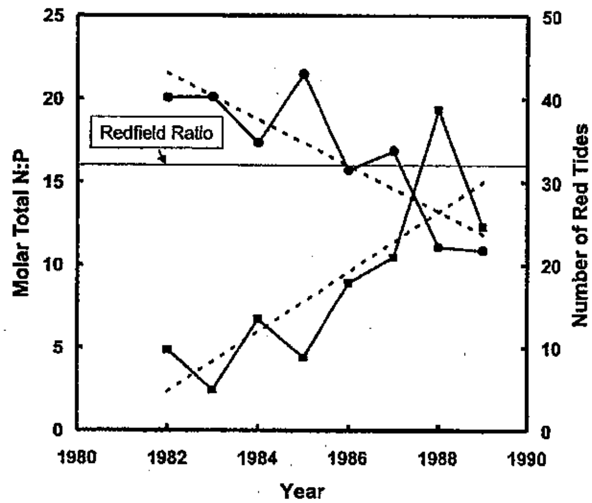

Fig. 6. Trends in the N:P molar ratio (circles) and the number of reported red tides (squares) in Tolo Harbor, Hong Kong from 1980 to 1990 (redrawn from Hodgkiss and Ho 1997).

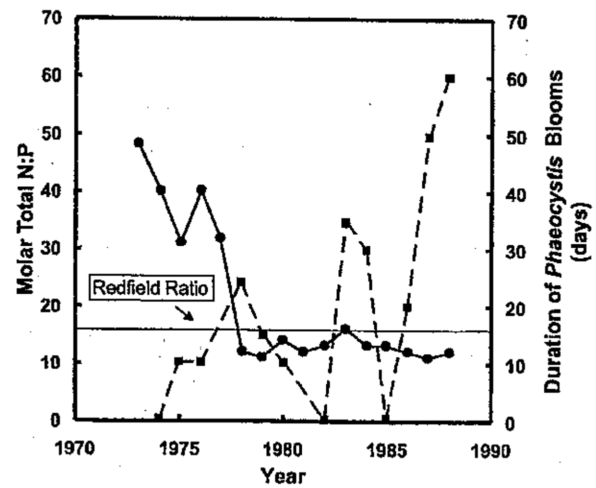

Fig. 7. Change in N:P molar ratio (circles) in Dutch coastal waters coincident with increase in *Phaeocystis* blooms (squares; redrawn from Riegman 1995).

In Tunisian lagoons where *Gymnodinium aureolumi* (formerly *Gyrodinium aureolum*) was found to be the cause of repeated fish kills in aquaculture systems, blooms occurred when the N:P ratio (which was normally very high) began to decline in the autumn (Romdhane et al. 1998). There is evidence to suggest that the ichthyotoxic dinoflagellate *Pfiesteria piscicida* may do disproportionately well when the ratio of N:P decreases following an increase in the availability of phosphate (Burkholder and Glasgow 1997; Burkholder et al. 2001b; Glasgow et al. 2001b).

Another prominent example of the importance of nutrient supply ratios in determining phytoplankton species composition is seen with the foam-producing prymnesiophyte *Phaeocystis poucheti*. A 23-year time series off the German coast documents the general enrichment of these coastal waters with N and phosphate and a 4-fold increase in the N:Si and P:Si ratios (Radach et al. 1990). This was accompanied by a decrease in the diatom community and an increase in the occurrence of *Phaeocystis* blooms. Mass occurrences of this species began in 1977 in the North Sea (Cadée and Hegeman 1986) and increased in cell abundance and bloom duration through 1985. The general N and P enrichment of that coastal area resulted in winter concentrations an order of magnitude higher than those in adjacent Atlantic waters (Lancelot 1995). The abundance of these nutrients is less of an issue than their relative proportions. These blooms were first related to the increase in N:Si ratios, particularly following the spring diatom blooms which depleted the silica but not the nitrate (Cadée and Hegeman 1986; Smayda 1990). Riegman (1995) further showed that in mixed phytoplankton assemblages in the laboratory, *P. poucheti* became dominant only when N:P ratios were 7.5 or lower, and at N:P ratios of 1.5, there was almost complete *P. poucheti* dominance. These relationships are consistent with the trends for summer blooms of *P. poucheti* in Dutch coastal waters, which accompanied a shift from P-limitation to N-limitation in the area; lower N:P ratios coincided with higher, and more variable, *P. poucheti* abundance (Fig. 7).

Nutrient ratios may also be affected by other types of human development in addition to direct nutrient pollution. The building of dams has numerous associated environmental problems, including the potential for altered water quality. Dam construction, coincident with increased P loading, has led to diatom blooms, and thus to the sequestration of silica (Turner and Rabalais 1991). In the development of the massive Three Gorges Dam in the upstream region of the Changjiang (Yangtze River), the potential for eutrophication and other massive environmental and cultural damage has been greatly debated (Zhang et al. 1999). In this system, it is thought that by the year 2010, silica will be significantly reduced due to diatom uptake and sediment trapping by the dam, and this combined with the trend of increasing N loading will lead to very high N:Si and N:P ratios downstream. As the Changjiang watershed supplies nearly 10% of the total world population's water resources and 40% of the Chinese national food production, the societal benefits from the dam are significant, as is the potential for negative impacts on the health of coastal ecosystems (Zhang et al. 1999).

The nutrient ratio concept has recently been expanded to include the relative abundance of different chemical forms of nutrients, such as organic versus inorganic N and carbon (C) compounds. Recent studies in enriched coastal areas have shown that while productivity may increase quantitatively with overall N availability, the DON component may contribute disproportionately to the changes in phytoplankton succession, apparently favoring the development of some HABs (Paerl 1988; Berg et al. 1997; LaRoche et al. 1997; Lomas et al. 2001). The DON pool is composed of a wide range of compounds from small amino acids and urea to complex molecules such as proteins and humic acids. Some are available for assimilation by the phytoplankton, whereas many other compounds are highly refractory and not readily used. One component of the DON pool, urea, has been shown to be highly correlated with the outbreak of harmful dinoflagellates in estuarine fish ponds (Glibert and Terlizzi 1999), where elevated levels of urea were associated with significant dinoflagellate outbreaks 73% of the time, but urea concentrations of < 1.5 μM were not associated with any dinoflagellate blooms. In several Chesapeake Bay tributaries, high urea concentrations have also been found to precede large blooms of the dinoflagellate *Prorocentrum minimum* (Glibert et al. 2001). The trend toward increasing applications of urea fertilizer (Constant and Sheldrick 1992) may increase the likelihood of blooms of organisms that grow well on this nutrient.

Several HABs have been shown to be related to an elevation in the ratio of dissolved organic carbon (DOC):DON. Three separate blooms in Chesapeake Bay occurring over a 3-yr period, including *P. piscicida*, *P. minimum*, and *A. anophagefferens*, were all correlated with elevated DOC:DON ratios relative to the long-term mean (Glibert et al. 2001; Fig. 8). The elevation in this ratio for these particular blooms was a reflection of both elevated levels of DOC as well as a depletion of DON. Lomas et al. (2001) have shown this relationship to be robust for numerous brown tide blooms in Long Island, New York (Fig. 8). During a bloom of *Gymnodinium* spp. in Kuwait Bay, the ratios of DOC:DON for stations collected within the bloom were approximately twice those determined for non-bloom stations with a mixed phytoplankton assemblage (Heil et al. 2001; Fig. 8). This relationship is deserving of additional study in other bloom conditions. Of particular interest in this context is the potential change in DOC:DON preceding blooms.

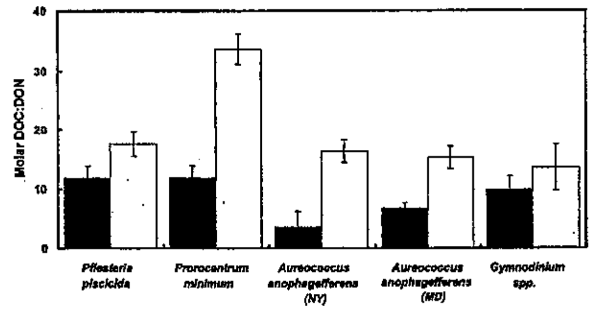

Fig. 8. Relationship between DOC:DON for numerous bloom periods and locations. In each case, the dark bars represent either long-term average non-bloom periods for the same sites or comparable sites outside of the bloom region. The gray bars represent the periods during the peak of bloom occurrence. The non-bloom data from the *P. piscicida* and *P. minimum* blooms represent long-term monitoring results for tributaries of Chesapeake Bay. The *P. piscicida* bloom occurred in these same tributaries in Maryland in 1997, and the *P. minimum* bloom occurred in the same region in 1998. The *A. anophagefferens* blooms were sampled either in New York or Maryland coastal bays in 1999. The *Gymnodinium* spp. bloom was sampled during a red tide event in Kuwait Bay, 1999 (data were derived and redrawn from Glibert et al. 2001; Lomas et al. 2001; and Glibert unpublished data).

Pathways of Nutrient Acquisition

An understanding of physiological responses is further complicated by the fact that the rate of nutrient supply will not necessarily correlate with the rate of nutrient assimilation by the algae, as the latter is controlled by nutritional preferences, uptake capabilities, and physiological or nutritional status. The response by either the total phytoplankton community or individual species within the community also depends on many factors, including interactions with grazers and physical forcings such as turbulence. Grazers may inhibit the development of phytoplankton biomass through their feeding, while at the same time, enhance the regeneration of nutrients through their release and excretion. This in turn will alter the balance of reduced versus oxidized forms of N (Glibert 1998).

The assimilation of nutrients by phytoplankton depends on environmental factors such as light, temperature, and water column stability with different environmental effects having differential impacts on different nutrient substrates. The uptake of ammonium and urea are usually thought to be less light dependent than the uptake of nitrate (MacIsaac and Dugdale 1972; Fisher et al. 1982), and the temperature dependence of ammonium uptake may also differ from that of nitrate (Lomas and Glibert 1999a). Water column stability is another critical factor influencing species composition. Blooms of *Karenia* cf. *mikimotoi* have been associated with warm, stable conditions, and can persist for extended periods with low light and low nutrients (Dahl and Tangen 1993). In Norwegian waters, these blooms initiate at the pycnocline in the summer or early autumn in offshore waters, then collect at hydrographic fronts in nearshore waters (Dahl and Tangen 1993). In Tunisian lagoons, where blooms of *G. aureolum* have caused repeated fish kills, a correlation has been found between the development of blooms and decreasing day length, consistent with the frequency of these blooms being greater in late summer or autumn (Romdhane et al. 1998). Any potential effects of nutrient stimulation on HAB biomass or productivity must be considered within the physical and environmental tolerances of the particular species of concern.

In recent years, the physiological strategies by which different groups of species acquire their nutrients have become better understood. Rapidly growing marine diatoms have been highly correlated with large and/or frequent additions of nitrate, in part because they have physiological adaptations which allow them to exploit nitrate-rich conditions (Takahashi et al. 1982; Goldman 1993; Lomas and Glibert 1999a,b, 2000). Microflagellates, including dinoflagellates, are most frequently associated with low nitrate concentrations, higher ammonium, urea, or DON supply, and consistent physiological preference for reduced N forms (e.g., Berg et al. 1997; Carlsson et al. 1998; Lomas and Glibert 1999b). Most estuarine and coastal marine HAB species are microflagellates. Harmful estuarine dinoflagellates tend to occur in waters that have seasonally high phosphate and nitrate, as well as high DOC and other organic nutrient forms (Burkholder and Glasgow 1997; Burkholder et al. 1997, 2001a,b; Magnien et al. 2000; Glasgow et al. 2001a; Glibert et al. 2001). Indeed, the brown tide species that blooms in Texas, *Aureoumbra lagunensis* is incapable of nitrate uptake, and thus must use reduced N forms (DeYoe and Suttle 1994).

An important physiological adaptation of many flagellate species, including some HAB species, is the ability to acquire both N and C via particle ingestion or by the uptake of dissolved organic compounds (reviewed in Granéli and Carlsson 1998). Such mixotrophic or heterotrophic tendencies have been linked with the ability of these cells to thrive in environments where inorganic nutrients or light may otherwise be insufficient to meet their nutritional or C demands. Toxic *Chrysochromulina polylepis* cultures have been shown to consume more algal food when limited by P compared to nutrient-replete and N-limited conditions (LeGrand et al. 1996). Mixotrophy is now considered essential for the survival and growth of many *Dinophysis* species, including those responsible for diarrhetic shellfish poisoning (DSP). This is supported by uptake of ^{14}C in the dark, either from direct ingestion of labelled algal prey or dissolved organic substances released by those algae (Granéli et al. 1997). Using different methods, Jacobson and Anderson (1996) found food vacuoles containing prey fragments (probably ciliates) in *Dinophysis norvegica* and *D. acuminata*, confirming these species' ability to ingest particulate food. Other common HAB species have also been shown to be mixotrophic, including *Heterosigma carterae* (= *H. akashiwo*), *A. tamarense* (Nygaard and Tobiesen 1993), and *Gyrodinium galatheanum* (= *Karlodinium micrum*; Li et al. 2000, 2001). Given the importance of mixotrophy in many species, as well as the development of new methods to measure ingestion and C uptake (Schnepf and Elbrächter 1992; Stoecker 1999; Stickney et al. 2000), the number of HAB species known to be mixotrophic will likely increase as more are examined for this characteristic (Burkholder and Glasgow 1995, 1997; Burkholder et al. 2001b).

A unique example of mixotrophic nutrition is the toxic *Pfiesteria* complex (two species—*P. piscicida* and *Pfiesteria shumwayae*; Burkholder et al. 2001a,b). These dinoflagellates are heterotrophs, yet they can be stimulated directly and indirectly by inorganic as well as organic nutrient enrichment (Burkholder and Glasgow 1997, 2001; Burkholder et al. 1998a, 2001a,b; Glasgow et al. 2001b; Parrow et al. 2001). Like other heterotrophic dinoflagellates (Schnepf and Elbrächter 1992), they can take up inorganic and organic nutrients directly (e.g., dissolved amino acids: Burkholder and Glasgow 1997; Glasgow et al. 1998; nitrate, ammonium, and urea: Lewitus et al. 1999a). *Pfiesteria* spp. are not capable of photosynthesis on their own, but zoospores can retain chloroplasts from algal prey (Burkholder and Glasgow 1997; Lewitus et al. 1999a,b; Glasgow et al. 2001c). This phenomenon, kleptochloroplastidy, is increasingly recognized in dinoflagellates and some protozoan ciliates (Stoecker 1998; Skovgaard 1998).

Kleptochloroplastidy allows *Pfiesteria* spp. to function as mixotrophs for hours to days (Lewitus et al. 1999a). In this mode, cells can take up N directly (Lewitus et al. 1999a). *Pfiesteria* spp. have also been shown to be stimulated indirectly by nutrient enrichment, mediated through the abundance of algal prey that they consume when fish are not present (Burkholder and Glasgow 1995, 1997; Glasgow et al. 1998; Parrow et al. 2001). The ability to consume an array of prey ranging from bacteria to mammalian tissues, as well as dissolved substrates, allows *Pfiesteria* spp. to thrive where food is abundant (Burkholder and Glasgow 1995, 2001; Burkholder et al. 2001b). Toxic *Pfiesteria* outbreaks have occurred in shallow, poorly flushed estuaries that have been highly impacted by nutrient overenrichment, including the Neuse, Pamlico, and New River estuaries of North Carolina and the tributaries of Maryland's eastern shore (Burkholder et al. 1995, 1997; Lewitus et al. 1995; Burkholder and Glasgow 1997; Glasgow et al. 2001a). In both laboratory and field studies, *Pfiesteria* zoospore production has been shown to be stimulated by human and animal wastes (Burkholder and Glasgow 1997, 2001; Burkholder et al. 1997). Nutrients provide a food-rich habitat for *Pfiesteria* spp., but other environmental conditions are required for toxic *Pfiesteria* activity, especially poor flushing, fish in abundance, and brackish salinities (Burkholder and Glasgow 1997; Glasgow et al. 2001a). The ability of these heterotrophic dinoflagellates to function photosynthetically, and to switch between modes of nutrition and among an array of prey types as conditions change, represents a significant survival mechanism.

Many phytoplankton have the ability to acquire some of their nutrients via extracellular oxidation or hydrolysis. Extracellular amino acid oxidation has been shown to occur in a wide range of flagellates and in a range of ecosystems, although this process appears to be expressed to a greater degree when ambient inorganic nutrient levels are at or near depletion (Palenik and Morel 1990a,b; Pantoja and Lee 1994; Mulholland et al. 1998). Proteins and peptides may also be hydrolyzed at the cell surface, producing smaller compounds that can be taken up by the cells (Hollibaugh and Azam 1983; Keil and Kirchman 1992; Pantoja et al. 1997; Pantoja and Lee 1999). While much is still to be learned about the role of this process in the development of HABs, there is some evidence that certain HAB species possess this ability (Mulholland et al. 2000).

The uptake of organic compounds may contribute to the C requirements of HAB cells, in addition to their N or P requirements. The suggestion that C acquisition may stimulate algal growth rates through organic uptake is by no means new (Schell 1974; Wheeler et al. 1974; Lewitus and Kana 1994). Specific examples of the linkage between DOC uptake and HAB development, however, are only now beginning to emerge. In 1998, a new species of dinoflagellate, *Kryptoperidinium carolinium* (sp. ined.; formal description ongoing by Lewitus unpublished data), was observed in the waters of coastal South Carolina. Following intensive monitoring of all forms of inorganic and organic nutrients, it was concluded that bloom initiation followed the pulsed delivery of organic nutrients (Lewitus et al. 2001). Bloom development was coincident with a greater than 3-fold decrease in both DOC and DON. These findings underscore the need to incorporate organic nutrients and heterotrophic potential in both monitoring and models of HAB population dynamics.

Indirect Nutrient Linkages with HABs

All too frequently, public perception of whether nutrient over-enrichment has reached undesirable levels has been based on acute, obvious or easily measured symptoms, such as high biomass algal blooms, massive fish kills, and oxygen deficits. Because of this focus, a broad array of indirect, chronic, often-subtle but serious impacts of nutrient pollution on aquatic ecosystems remain underemphasized and, in some cases, poorly understood. The available data indicate that these chronic, indirect impacts can be important in controlling the growth of HAB species over the long term in lakes, rivers, estuaries, and marine coastal waters.

As eutrophication progresses, for example, shifts in phytoplankton communities toward declines in certain diatom species in favor of less desirable nanoplankton and flagellates can lead to subtle but important changes at higher trophic levels. Some freshwater diatom species that grow best in low nutrient regimes produce lipids that are essential for zooplankton sexual reproduction. Under nutrient over-enrichment, these species are replaced by species that produce low or negligible quantities of these lipids (Kilham et al. 1997). In estuarine waters, spawning of green sea urchins and blue mussels appears to be triggered by a heat-stable metabolite that is released in high abundance by certain species of phytoplankton that decline with cultural eutrophication (Starr et al. 1990). Replacement species that thrive under nutrient enrichment produce low or negligible quantities of the substance. At the same time, excessive nutrient loading has led to the decline and, eventually, the disappearance of rooted vegetation that is critically important to the survival of animals such as certain zooplankton, finfish, and/or shellfish which graze on algae. Overfishing has led to significant declines in some shellfish species, such as oyster populations in Chesapeake Bay (Newell 1988; Rothschild et al. 1994). Such factors would interact in depressing grazing activity which, in turn, would indirectly encourage growth of phytoplankton, including HAB species, under nutrient enrichment (Burkholder 2000).

Nutrient loading seldom occurs alone. Atmospheric deposition contains nutrients as well as acid-imparting contaminants and toxic substances such as pesticides; cropland runoff carries not only nutrients, but pesticides and suspended sediments (Miller 2000). Nutrients in poorly treated human sewage and animal wastes are added to surface waters along with heavy metals and other toxic substances, suspended solids, estrogens and estrogen-mimic substances, and a wide array of microbial pathogens (Burkholder et al. 1997; Mallin 2000;

Miller 2000). Excessive nutrients act in concert with these other, co-associated pollutants to cause physiological stress and disease in sensitive grazing fauna which, again, could indirectly help to promote the growth of harmful algae through lowered grazing pressure and facilitated access to weakened fish by some harmful algae that consume them as prey.

Other factors such as suspended sediments or grazing pressure may reduce or negate a potentially stimulatory nutrient effect. In turbid lakes and reservoirs with high episodic sediment loading, and systems with relatively rapid flushing rates, high P loading may not stimulate phytoplankton blooms because of light limitation and short water turnover times (Dillon 1975; Cuker et al. 1990; Burkholder et al. 1998b). Cyanobacteria can bloom under low light availability by taking advantage of periods between episodic sediment loading events when the water clears, or by using mechanisms for buoyancy regulation to position themselves near the water surface (Burkholder et al. 1998b; Dortch unpublished data). In lakes with low to moderate nutrient loading, grazing pressure from large-bodied zooplankton can significantly reduce the populations of most phytoplankton species, balancing the nutrient stimulation effect (Harper 1992).

Similar observations have been reported in estuaries and coastal waters. The Pearl River estuary supplies a huge pollution load to the waters of the south China Sea, including the western waters of Hong Kong, yet the number of red tides and general chlorophyll levels are low compared to the conditions in Victoria Harbor and areas to the east. Tang et al. (2001) hypothesized that this inverse relationship between nutrient loading and algal biomass is due to the high sediment loads that accompany the Pearl River discharge. Light limitation would prevent the full utilization of the nutrients supplied to the phytoplankton.

In San Francisco Bay, increased nutrient loads have resulted in increased secondary production in the benthos, which in turn modulates the algal biomass (Cloern 1982). In an analogous manner, primary production in the Bay of Brest, France, is nutrient limited, even with large nutrient loadings from its tributaries. Nutrient inputs have increased 3-fold since 1975, yet chlorophyll levels have not changed significantly (Le Pape et al. 1996; Le Pape and Ménesguen 1997). Primary productivity has increased slightly, but grazing pressure has as well, particularly in the benthos. In this case, the main control of eutrophication pressures appears to relate to a strong tidal influence and hydrodynamic exchange. The resulting stirring hinders the formation of a persistent surface mixed layer where phytoplankton have access to nutrient inputs and to light. Horizontal tidal currents cause significant water exchange with the Iroise Sea, and reduce the accumulation of nutrients and plankton in the Bay. As has been observed in certain other systems, nutrient loading has been beneficial in that it supports increased productivity. Such beneficial effects should continue as long as those loadings fall within the assimilative capacity of the system.

In some cases, indirect relationships between nutrient loading or availability and the development of a HAB species may be difficult to establish, due to the complexities of the nutrient cycling pathways involved. These may be on short temporal and spatial scales, or on longer-term scales. One example of such pathways potentially leading to HAB development involves the release of DON following N fixation. Blooms of the N-fixing cyanobacterium *Trichodesmium* have been found to release a significant fraction of their newly fixed N in the form of ammonium and DON (Capone et al. 1994; Glibert and Bronk 1994). In dense blooms of this organism, the concentration of reduced N forms can be enriched several-fold over control sites (Karl et al. 1992; Glibert and O'Neil 1999; O'Neil et al. submitted). It has been suggested that this production of reduced N fuels red tide blooms of *Karenia brevis* (= *Gymnodinium breve*) off the coast of Florida (Walsh and Steidinger 2001; Lenes et al. 2001). Likewise, DON release by *Trichodesmium* has been shown to be correlated with an increase in the development of dinoflagellates such as *Dinophysis* off the coast of Australia (O'Neil et al. submitted).

Another example of indirect stimulation of HAB species by nutrients is the ichthyotoxic dinoflagellate, *P. piscicida*. In toxic strains of this organism, temporarily nontoxic zoospores are the precursors of actively toxic zoospores. These nontoxic zoospores have been found to increase in response to elevations in chlorophyll (Burkholder and Glasgow 1997; Glasgow et al. 2001a), and their growth rates have been shown to vary widely depending on the form of algal prey (Burkholder and Glasgow 1995; Glasgow et al. 1998; Burkholder et al. 2001a; Parrow et al. 2001). Nutrients may select for certain phytoplankton species which may promote *Pfiesteria* growth in temporarily nontoxic mode.

Links between Nutrients and Toxicity

The discussion thus far has centered on nutrient pools as they affect the growth and accumulation of HAB cells. There is evidence that nutrients can play a major role in the regulation of toxicity in some HAB species, and this can have significant implications to toxin monitoring programs and public health decisions. In some cases, toxicity can increase or decrease dramatically depending on the limiting nutrient. Saxitoxin production by *A. tamarense* can be 5–10-fold higher in P-limited versus N-limited cells (Boyer et al. 1987; Anderson et al. 1990). Likewise, domoic acid production by *Pseudo-nitzschia multiseries* is inversely correlated with the ambient Si concentration in batch culture (Pan et al. 1996a). In that study, cells began accumulating this toxin only when the division rate declined as a result of partial or total depletion of silica. When cultures were N-limited, no toxin was produced. Toxin production was greatly enhanced under P-deficient conditions in continuous cultures (Pan et al. 1996b). Recent results also suggest that Fe limitation can enhance toxicity in *Pseudo-nitzschia* spp. (Rue and Wells unpublished data).

For other HAB species a similar picture emerges: toxin production varies significantly with different degrees and types of nutrient limitation. The dinoflagellate *D. acuminata* produced elevated levels of the DSP toxin, okadaic acid, under both N and P limitation, but the enhancement was 6-fold larger with N-limitation (Johansson et al. 1996). In an analogous although opposite manner, *Chrysochromulina polylepis* was 6-fold more toxic under P enrichment than N-limited conditions (Johansson and Granéli 1999a). Another prymnesiophyte, *Prymnesium parvum*, increased toxicity under N-limited or P-limited conditions (Johansson and Granéli 1999b).

The chemical form of the nutrient supplied to the HAB species can also affect toxicity, although this is an area that has received relatively little study. *K. brevis* has been shown to increase its production of brevetoxin up to 6-fold when exposed to elevated urea levels of 0.5 to 1.0 mM in batch culture compared to controls without urea enrichment (Shimizu et al. 1993). The urea levels used in that experiment far exceed those found under natural conditions, but the implication is that certain compounds are more readily assimilated and incorporated into algal toxins than others. With the addition of urea or glycine, the cells switched from autotrophic to heterotrophic nutrition, using the C skeleton only after the N was used. In this study, toxicity was not influenced by the addition of leucine or aspartic acid (Shimizu et al. 1993).

The ecological implications of nutrient effects on toxicity are significant. What is not yet clear is how often the conditions that induce these changes actually occur in natural waters, and how human activities, and specifically eutrophication, affect overall toxin potential. One can envision several scenarios for eutrophic waters, depending on the extent of nutrient enrichment, the resulting nutrient availability ratios, and the HAB species and toxin involved. Due to the nutrient enrichment, HAB cells might be more abundant, but because of the altered nutrient ratios, their cellular toxicity could be higher or lower than with non-eutrophic conditions. Depending on the species, the net effect could thus be an increase, decrease, or no change in overall toxicity from a public health, fisheries, or ecosystem impact perspective. This is an area of obvious importance, but further research is needed before useful insights about nutrient form and HABs can be provided to coastal resource managers.

HABs with Little Apparent Link to Nutrient Enrichment

A common assumption by the public and the press is that new or unusual HAB events are somehow linked to pollution, and that all nutrient increases will result in algal blooms. The situation is far from that simple, but in many cases a link between blooms and eutrophication can be identified. It should be emphasized though that there are HABs that do not appear to have this linkage. These are blooms for which there may be no nutrient relationship, or one that has not yet been identified. There may be other factors that exert more control in regulating plankton community dynamics. This is true for some new outbreaks and for expansions of recognized or recurrent blooms. PSP toxicity from toxic *Alexandrium* species is a present-day problem in the relatively pristine waters of the Gulf of Maine, as well as along most of the U.S. west coast including Alaska. The blooms that occur undoubtedly use some nutrients that derive from human activities, given their proximity to the coast, but other factors seem to better explain the recent spreading of these organisms. The PSP problem has expanded into southern New England and into Puget Sound on the U.S. west coast over the last several decades, but these increases are thought to reflect the transport of cyst-forming *Alexandrium* species into those regions by natural storms and currents and with the deposition of cysts that have allowed the species to colonize the areas (e.g., Rensel 1993; Anderson et al. 1994). For *Alexandrium* spp. in the Gulf of Maine, increased nutrient loading and composition appear to be secondary factors influencing growth.

Conclusions and Cautions

Eutrophication is a global problem, and coastal areas throughout the world have been affected. There is little question that nutrient loading fuels high biomass algal blooms, and increases in chlorophyll have been shown to parallel increases in nutrient concentrations. There is clear evidence for direct stimulation of some HABs by nutrient over-enrichment. The linkages between other HABs and eutrophication, however, are more complex and include indirect as well as direct pathways; and linkages between some oligotrophic HAB species and eutrophication are not known. There have been many significant advances in our understanding of the physiological requirements for, and the mechanisms of nutrient acquisition by, HAB species. We have gained much knowledge of how certain nutrients, and their proportions, can regulate some species or groups of species.

It is important to recognize that the impacts of nutrient loading depend on many factors, from the species composition and nutritional state of the organisms at the time of the loading, to the physical features of the environment at that point in time, as well as the existence of grazers. Similar nutrient loads will not necessarily have the same effect on a different environment, or on the same environment at a different point in time. It is important to avoid ascribing the apparent global increase in HABs solely to pollution or eutrophication, although the public and the press often assume this linkage. There are many causes for the expansion and eutrophication is but one of these mechanisms.

Although there have been many successes in relating nutrient quantity and composition to outbreaks of HABs, in general the relationships between nutrient delivery and the development of blooms of many HAB species, and between nutrient enrichment and the potential toxicity of blooms or outbreaks of those species, remain poorly understood. Local, regional, and worldwide coordinated efforts, particularly those targeting comparative ecosystems that include both highly eutrophic waters and those that have experienced altered nutrient inputs will be required to better understand the underlying direct and indirect mechanisms that interact to control the complexities of these relationships.

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Escalating worldwide use of urea – a global change contributing to coastal eutrophication

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Abstract. While the global increase in the use of nitrogen-based fertilizers has been well recognized, another change in fertilizer usage has simultaneously occurred: a shift toward urea-based products. Worldwide use of urea has increased more than 100-fold in the past 4 decades and now constitutes >50% of global nitrogenous fertilizer usage. Global urea usage extends beyond agricultural applications; urea is also used extensively in animal feeds and in manufacturing processes. This change has occurred to satisfy the world's need for food and more efficient agriculture. Long thought to be retained in soils, new data are suggestive of significant overland transport of urea to sensitive coastal waters. Urea concentrations in coastal and estuarine waters can be substantially elevated and can represent a large fraction of the total dissolved organic nitrogen pool. Urea is used as a nitrogen substrate by many coastal phytoplankton and is increasingly found to be important in the nitrogenous nutrition of some harmful algal bloom (HAB) species. The global increase from 1970 to 2000 in documented incidences of paralytic shellfish poisoning, caused by several HAB species, is similar to the global increase in urea use over the same 3 decades. The trend toward global urea use is expected to continue, with the potential for increasing pollution of sensitive coastal waters around the world.

Introduction

Global increases in total nitrogen fertilizer use in recent decades are well documented (Galloway et al. 1995, 2003; Howarth et al. 2000; Smil 2001; Galloway and Cowling 2002), and there is ample evidence of the detrimental effects of these increases on aquatic and forested ecosystems (Howarth et al. 2002; Nosengo 2003). However, little consideration has been given to the recent and dramatic changes in composition of fertilizer nitrogen that are occurring throughout most of the world. In particular, worldwide use of urea as a nitrogen fertilizer and feed additive has increased more than 100-fold in the past 4 decades, with a doubling in just the past decade alone (Figure 1a). Indeed, the 1990s were hailed as an 'especially joyous time' for urea sales

(International Raw Materials 2000). Global production capability of urea is now approximately 70 million metric tons year^{-1}.

Although urea fertilizer is commonly assumed to be retained in soils, there is growing evidence of urea transport to sensitive coastal waters (e.g. Glibert et al. 2005a). There is also mounting evidence that urea differentially stimulates the growth of some types of phytoplankton in coastal waters and that it may, under some conditions, promote a shift in phytoplankton species to organisms that are more noxious to the ecosystem and to human health (e.g. Berg et al. 1997, 2003; Gobler et al. 2002; Glibert et al. 2001, 2004b, 2005b). Here we show the extent of recent changes in urea consumption and production globally and its contribution to dissolved nitrogen in some coastal waters. We also substantiate the linkage between coastal urea enrichment and compositional changes in microbial communities leading to species that are more deleterious to the environment.

Global production and consumption

Commercial urea production began in the 1920s with the development of the Haber-Bosch process (Smil 2001). Urea is produced by reacting carbon dioxide with anhydrous ammonia under pressure at high temperatures. The molten

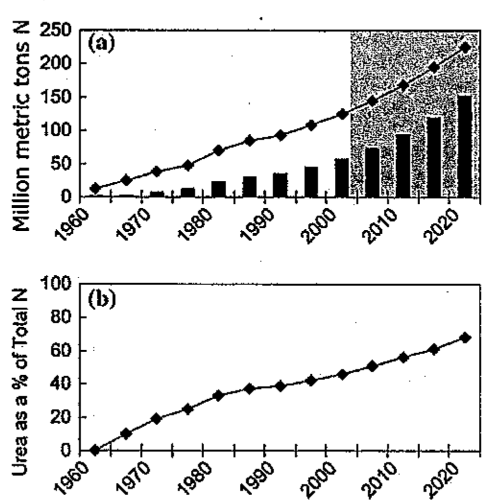

Figure 1. (a) The change in world consumption (million metric tons of N) of total synthetic nitrogen fertilizers (solid line) and urea consumption (solid bars) since 1960. The data through 1990 are from Constant and Sheldrik (1992); data for 1990–2000 are from the Global Fertilizer Industry (FAO 2001) data base; and for 2005–2020 (shown as the shaded region) are calculated assuming an annual increase of 3% in total consumption and 5% in the fraction that is urea. (b) Same data as in panel (a) with the fraction that is urea displayed as a percentage of the total nitrogen fertilizer.

mixture is then further processed into granules or other forms. Urea production is energy intensive. Most commonly, it is produced using natural gas, so the major producing regions are those where natural gas is abundant. Several leading manufacturing countries for urea are Russia, Canada, and Saudi Arabia, but other Middle East producers, including Iran and Iraq are (or were before the Gulf Wars) significant. In the US, urea production facilities are located mainly in the Gulf of Mexico states.

Production of urea has at least doubled every decade since 1980 in the Middle East (Hamdi and Ashkar 1999), increasing from 2 million metric tons year^{-1} in 1980 to 10 million metric tons year^{-1} in 2000. Further expansion of production is anticipated in the coming years in Kuwait, Qatar, Egypt, Oman and Iran (Prud'homme 2002, 2003, 2004). From the mid-1970s to the early 1990s, Russia (USSR) erected at least 40 new ammonia and urea production facilities (Constant and Sheldrick 1992). Production of urea in China tripled from 1989 to 1999 (International Raw Material 2000). Dramatic increases in global production have also occurred in many countries since 2000, with several Latin American countries increasing production by more than 25% (Prud'homme 2002).

As late as the 1960s, urea represented only about 5% of world nitrogen fertilizer use (FAO 2001; Smil 2001; Figure 1b). However, urea usage escalated in the 1980s, such that it represented about 40% of global nitrogen fertilizer by the early 1990s (Smil 2001), and soon thereafter urea surpassed ammonium nitrate as the most common nitrogen fertilizer (Overdahl et al. 1991). It is now estimated that urea represents > 50% of world nitrogen fertilizer (Figure 1b). Assuming urea consumption continues at 5% year^{-1}, as projected for many parts of the world (e.g. http://nation-com.pk/daily/dec-2004/3/bnews5.php and www.the-innovation.group.com/ChemProfiles/Urea.htm), urea consumption may reach 70% of total nitrogen use by the end of the next decade (Figure 1b): this is a dramatic global change in the composition of nitrogen applied to land throughout the globe. Such projections depend on global commodity markets, construction of new plants, and other factors that are difficult to project, but most of this increase is expected to occur in developing countries, particularly in Asia and Latin America (Constant and Sheldrick 1992).

China and India together account for about half of the global consumption (Soh 2001), and have at least doubled their consumption of urea in the past decade (Roy 2001). In India, Bangladesh and Pakistan, urea fertilizer has been heavily subsidized (as much as 50% of the cost of production) leading to its widespread use and over-application (e.g. Ayala 2002). The US and Canada now represent about 20% of the global urea market, with urea constituting about 30% of US synthetic nitrogen fertilizer usage. Consumption is increasing even in regions where land applications of nitrogen have heretofore been low. The rural Canadian provinces of Manitoba, Saskatchewan and Alberta, for example, are now the regions where over 70% of Canada's urea is consumed. Urea is the only form of fertilizer used in British Columbia forests (www.for.gov.bc). In Latin America, consumption of urea has fluctuated more than in Asia during the past decade due to various economic crises and unstable political environments, leading to fluctuating incentives and subsidies (Matthews and Hammond 1999). This global trend in increased urea consumption represents both a net increase in total nitrogen applied, as well as a shift from the use of nitrate or anhydrous ammonium to urea. These increases parallel the increases in the production of both cereal and meat (associated with increasing human population) that have occurred globally in the past several decades (Matthews and Hammond 1999).

Urea is used in the production of virtually all crops from corn to Christmas trees, sugar cane to sweet potatoes, and vegetables to vineyards. Urea is preferable to nitrate for growing rice in flooded soils (Soh 2001), and thus the Far East and the Mid-East are major consumers of urea. In coated form, urea becomes a slow-release fertilizer and this is one of the most popular forms for applications to lawns, golf courses, and parks, as well as many crops (Overdahl et al. 1991).

The global shift toward the use of urea fertilizer stems from several advantages it has over other fertilizer forms. It is less explosive than ammonium and nitrate when stored, it can be applied as a liquid or solid, and it is more stable and cost effective to transport than other forms of reactive nitrogen. The increasing production of 'granular' urea has contributed to its widespread use, as this is safe and easy to transport. Urea also contains twice the nitrogen of ammonium sulfate, making application rates per unit of fertilizer less costly for individual farmers. With the growth of large, industrial farms, the economics and safety of urea transport and storage are thus major factors in the shift away from ammonium nitrate.

Range of global uses of urea

While more than 75% of manufactured urea is consumed as nitrogen fertilizer (e.g. Rabchevsky 1996), there are other significant uses of urea, which also are increasing globally. These non-fertilizer uses can be categorized according to their potential pollution impact: those that involve direct applications of urea to land and sea, and those that involve the use of urea in manufacturing. The direct applications are of greatest environmental concern. One such use is as a feed additive for ruminants, used to stimulate gut microbial flora. This application represents about 10% of non-fertilizer usage (Constant and Shedrick 1992). Urea can be added directly to feed, such as in urea-treated wheat or rice straw (Noi et al. 2001; Celik et al. 2003), or mixed with molasses ('urea–molasses licks' or 'urea multi-nutrient blocks') for sheep, cattle, water buffalo, and horses (Tiwari et al. 1990; Sansoucy 1995; Salman 1996; Celik et al. 2003). Urea may also be used as a fertilizer of the grasslands on which cattle or sheep may graze.

Another direct application of urea to land is as urea-based herbicides or pesticides (sulfonyl urea pesticides). In this case, urea is chemically synthesized with a poison or inhibitor. Sulfonyl urea is one of the preferred herbicides for broadleaf and grassy weeds. It is also commonly used in non-agricultural situations, such as to control weeds in railroad and electric utility rights of way (Flogel 1998). Urea-based herbicides potentially have a large impact by both increasing urea inputs and reducing the potential for local uptake.

Urea has long been used as a de-icer. Commercial airports and airfields are the largest consumers of these de-icing materials (Stefi and George 1992), although recommendations are now in place to reduce its usage in the US and elsewhere (Jones 1997) because of its recognized contribution to water pollution (e.g. US EPA 1986). Even with such reductions, it is still the de-icer of choice under some weather conditions. It is also used fairly extensively for domestic ice-melting applications (e.g. roads and sidewalks). Urea may also be spread on agricultural crops to prevent frost when temperatures drop to a level that may cause crop damage, and commercial formulations of urea are available for this purpose.

Urea is also used in some direct applications to seawater. It is used in the growing world aquaculture industry. In intensive shrimp culture, for example, ponds may be fertilized with urea and superphosphate to initiate an algal bloom that eventually serves as food for the commercial resource (Landesman 1994). A significant proportion of such nutrients are subsequently discharged to local waters with pond effluent (Boyd and Musing 1992), as only a small fraction of added nutrients ultimately winds up in marketable product (Burford and Glibert 1999).

Urea may also be spread on coastal oil spills, to stimulate the growth of natural bacteria populations which break down the oil (Prince et al. 2003); it was widely used, for example, during the Exxon Valdez spill (Prince et al. 2003), and has been used in numerous other spills since. For the Exxon Valdez spill, fertilizer applications continued for years following the initial crisis, and this approach was estimated to have enhanced the degradation of the oil by 2–5-fold (Prince et al. 2003). Recommended protocols for future oil spills call for maintenance of 100 μM-N throughout the oil clean-up period (Prince et al. 2003).

In addition to the direct applications of urea to land and sea, urea is used in many other applications, including manufacture of a wide range of common materials such as urea formaldehyde and plastics. This use represents about 50% of the non-fertilizer urea (Constant and Sheldrick 1992). Urea is also an additive in fire retardant paints, tobacco products, and in some wines. In the cosmetics industry, urea is an ingredient in moisturizing creams. There are numerous uses of urea in holistic medicine therapies. One application currently being considered which would greatly expand the global use of urea is as a reductant in catalytic and non-catalytic reduction of combustion products in vehicles (Jackson et al. 2001; Fable et al. 2002).

Urea in sewage and excretory products

In addition to agriculture and the anthropogenic uses described above, there are other pathways by which urea reaches both the land and aquatic environments. An important one is sewage, as urea is the major nitrogen component of urine. The extent to which this source of nitrogen is released to the environment depends on the state of the sewage treatment plant, the effectiveness of its mineralization and nitrification processes and the degree of nitrogen removal (Maurer et al. 2003). Urea is also one of the major nitrogen excretory products of dairy cattle, sheep and many other large animals (Livingston et al. 1962). Sheep that have been supplemented with urea–molasses licks have a higher excretion rate of urea than those that have not received such supplements (Nuwanyakpa and Butterworth 1986). Therefore, large animal operations located near waterways may be a source of urea to surface waters. Non-ruminants animals are also a source of this nitrogen nutrient. Uric acid is the primary nitrogen form released by poultry, and the first decomposition product of uric acid is urea. The time scale of conversion from uric acid to urea depends on the microbial activity of the poultry litter and its moisture content (Gordillo and Cabrera 1997). Poultry manure is a common fertilizer.

Natural and anthropogenic enrichment of urea in coastal waters

In order to assess urea enrichment of coastal waters, it is necessary to differentiate between *in situ* production and anthropogenic inputs. Within the water column itself, urea is known to be produced *in situ* from zooplankton excretion (Corner and Newell 1967; Mayzaud 1973; Bidigare 1983; Miller and Glibert 1998), fish excretion (McCarthy and Kamykowski 1972; Wright et al. 1995; Wood et al. 1998; Chadwick and Wright 1999; Walsh et al. 2000), bacterial regeneration (Mitamura and Saijo 1980; Cho and Azam 1995; Cho et al. 1996), and from release from sediments (Lomstein et al. 1989; Lund and Blackburn 1989; Therkildsen et al. 1996). While measurements of *in situ* urea production are relatively few for coastal waters, these rates are generally lower than the rates of *in situ* ammonium production, and are also generally too low to sustain the high concentrations of urea found in many coastal waters (Hansell and Goering 1989; Lomas et al. 2002). In Chesapeake Bay, annual average rates of urea regeneration are <1 μM-N h^{-1} (Lomas et al. 2002), and on the western English Channel rates of urea regeneration by plankton have been measured in the range of 0.6–20.6 nM-N h^{-1}(L'Helguen et al. 2005).

Anthropogenic sources of urea can be characterized as those associated with urea production and transport, and those associated with use of the product. During the industrial production process itself, both urea and ammonium may be released to surface waters and to the atmosphere, but such release depends on the age and quality of the manufacturing plant. Although few, there have been catastrophic spills of urea during transport and distribution, including a 12,500 tonne spill of granular urea in Alaska (Fable et al. 2002), and the grounding of a bulk carrier in New Zealand with 9500 tonnes of urea (Maritime Safety Authority of New Zealand 2003).

More generally, anthropogenic urea can reach coastal waters where agriculture or animal operations are located near streams, tributaries, rivers or estuaries. It has long been assumed that nitrogen in the form of urea applied to soils will be consumed by crops, rapidly oxidized to nitrate, or will volatilize to the atmosphere as ammonia, and thus will not contribute to coastal pollution or eutrophication as urea (Meisinger and Randall 1991). However, relatively few studies have directly measured the fate of urea in agricultural applications (but see Moe et al. 1968; Dunigan et al. 1976; DeDatta et al. 1989). Urea is readily hydrolyzed to ammonium carbonate by the enzyme urease. The rate of hydrolysis to ammonium and loss from volatilization in the form of ammonia depends on the timing of application, weather, soil temperature and pH and other factors (Khakural and Alva 1995; Wali et al. 2003). These losses may exceed 20%, even 40% depending on pH (Figure 2). Urea itself has also been found in atmospheric precipitation, in concentrations that can match those of nitrate (e.g. Timperley et al. 1985). Once urea has been hydrolyzed it can be subsequently nitrified and leached from agricultural soils to surface and ground waters. While these are probably the largest fluxes of fertilizer nitrogen, there are several reasons to suspect direct runoff of urea may be significant in systems with local waterways. First, urease inhibitors are increasingly being added to urea fertilizer to slow the transformation of amide nitrogen to ammonium hydroxide and ammonium (Marking 1995; Kiss and Simihalan 2001). The use of urease inhibitors delays the hydrolysis of urea for up to several weeks, and thus increases the likelihood that runoff or overland transport will contain urea and not its decomposition products (Prakash et al. 1999). In fact, urease inhibitors are being explored for cattle and swine manure, in order to reduce ammonia emissions and odors from feedlots (Hardlin 1998). Second, in many regions, no-till agricultural practices are encouraged to minimize soil erosion. Consequently, surface applied fertilizers are more likely to leave agricultural fields via overland flow than is the case when fertilizers are injected into the soil. In irrigated agriculture, urea is often applied just before irrigation, thus providing a window of time for urea runoff losses, depending on soil type and condition. Lastly, urea is often applied when rainfall is anticipated. This further increases the likelihood that some urea will be carried into local surface waters. While in total quantity, overland and runoff losses of urea may not be large (it is commonly estimated that 3–5% of surface applied urea may be lost via runoff), the contribution may, nevertheless, be significant to a receiving water body.

Urea concentrations and contribution to total organic nitrogen in receiving waters

Urea is not typically measured in either oceanographic surveys or in pollution monitoring. Some older data exist, and a few newer monitoring programs are beginning to incorporate this variable (Table 1). Several examples demonstrate that high concentrations often are coincident with fertilization or other agricultural activities. In Chesapeake Bay, where urea has been monitored in the tributaries for 5 years, concentrations of urea exceeding 10 μM-N have been

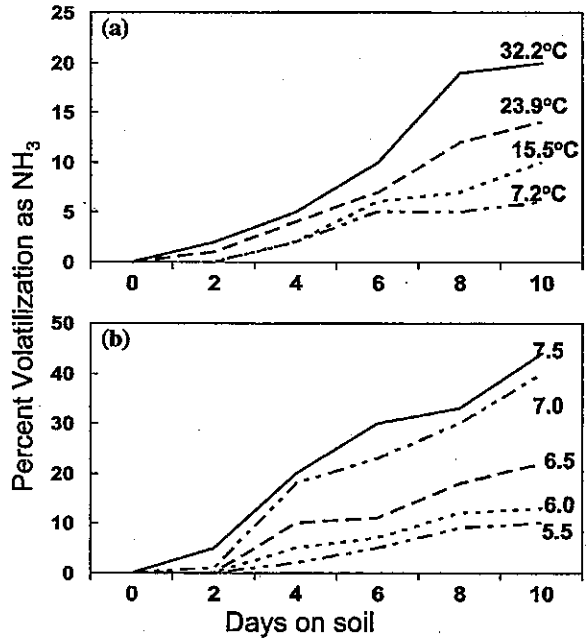

Figure 2. The percent of surface-applied urea fertilizer to soils that volatilizes as ammonia as a function of days on soil. (a) Response pattern with variable soil temperatures; (b) response pattern with variable soil pH. Data derived from North Dakota State University Extension Service (http://www.ag.ndsu.nodak.edu/aginfo/procrop/fer/ureavo05.htm).

observed frequently, generally in late spring when urea or poultry manure is applied to winter wheat and corn (Figure 3a; Glibert et al. 2001, 2005a). These levels are 50-fold higher than average urea concentrations in surface waters of Chesapeake Bay (Lomas et al. 2002). In Mexico's Yaqui Valley, which is intensively fertilizer with urea (~250 kg N ha^{-1}; Naylor et al. 2001), up to 20–40% of the nitrogen is lost in surface runoff, much of it occurring within a few days of peak irrigation (Beman et al. 2005). Irrigation and fertilization events commonly occur in December, and significantly elevated urea concentrations, from 13 to 43 µM-N, were found in six stations post-fertilization, compared to values < 10 µM-N from the same stations from non-fertilization (March), and pre-fertilization (early November) periods (Figure 3b – from J. Harrison unpub.). In yet another example (Heil and Glibert, unpub. data), urea concentrations were mapped on the Western Florida Shelf during two seasons near the mouths of the Shark and Caloosahatchee Rivers which drain significant agricultural lands in sugarcane production: the first time period was during the low flow, dry season, and the second time was 1 week after the passage of Hurricane Charley through this region in 2004. Concentrations of urea are generally low,

Table 1. Range of concentrations (μM-N) of urea from some coastal and estuarine sites reported in the literature.

Location	Range of concentration	Reference
Savannah R., Georgia	0.59–8.89	Remsen 1971
Ogeechee R., Georgia	1.26–4.89	Remsen 1971
Great South Bay, New York	0.6–9.4	Kaufman et al. 1983
Mankyung and Dongjin River estuary, Korea	0.6–4.3	Cho et al. 1996
Oslofjord, Norway	0.1–10.0	Kristiansen 1983
Chesapeake Bay, mainstem	<0.01–8.16	Lomas et al. 2002
Florida Bay, Florida	0.36–1.7	Glibert et al. 2004
Coastal Bays, Maryland	<0.01–14.4	Glibert et al. 2005a
Kings Creek, Chesapeake Bay, Maryland	0.3–24.2	Glibert et al. 2005a
Chicamicomico R., Chesapeake Bay, Maryland	1.0–23.4	Glibert et al. 2005a
Baltic Sea	0.09–6.91	Stepanauskas et al. 2002
Knysna Estuary, South Africa	0.4–5.8	Switzer, unpub data

<0.5 μM, during the dry season when gated discharge through the Caloosahatchee River and normal flows through the Shark River are both low (Figure 4a). Concentrations were significantly greater over the entire region following hurricane flooding, with elevated urea patches adjacent to the mouths of both the Shark and Caloosahatchee Rivers (Figure 4b). Localized reduced urea concentration near-shore following the hurricane coincide with areas of high chlorophyll *a* concentrations that developed with this nutrient pulse (data not shown). Lastly, in the Krysna Estuary of South Africa, where the catchment is used for cattle farming and also heavily fertilized with urea, concentrations of urea were found to double from winter to summer, and to increase 4-fold following a spring storm event (T. Switzer, unpub. data). These findings show that the sources of urea in these sensitive ecosystems cannot solely be *in situ* microbial regeneration; anthropogenic urea is reaching the water column.

Another indicator of the potential for anthropogenic sources to be significant contributors of urea to local waters is the contribution of urea to total dissolved organic nitrogen (DON). DON is now recognized to be a dynamic component of the nitrogen pool in aquatic systems (Seitzinger et al. 2002a, b; Stepanauskas et al. 2002; Berman and Bronk 2003), but urea has heretofore generally been thought of as a minor constituent. In the few cases where it has been measured, urea can make up a significant portion of the DON pool. Urea concentrations as a percent of total DON have recently been measured over various time scales in several estuaries: Chesapeake Bay, Florida Bay, Moreton Bay, Australia, and the Baltic Sea. These results reveal that urea, while typically representing only ~5% on average of the DON pool, can exceed 40% (Figure 5). In fact, some of the highest percentages of urea in the DON pool come from data from the Chesapeake Bay and demonstrate that even when urea concentrations are low (<1 μM-N), their relative contributions to the DON pool can be very high, suggesting a high degree of bioavailability of many fractions of DON in this system.

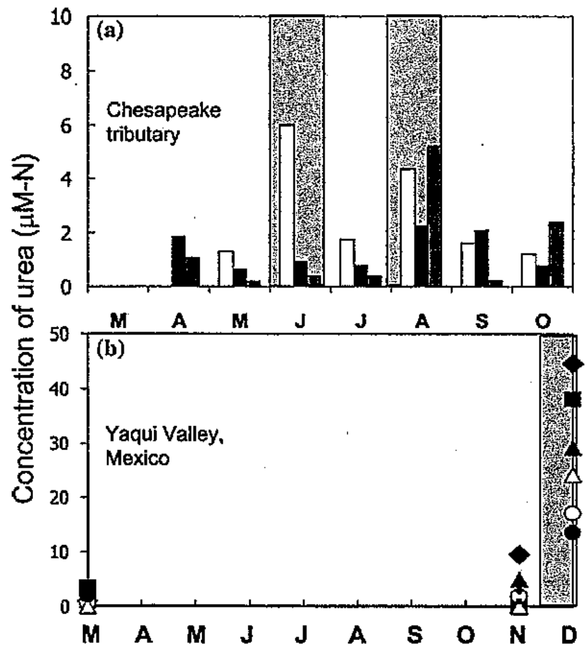

Figure 3. (a) Concentrations of urea (µM-N) in one tributary of Chesapeake Bay (Chicamacomico River) as a function of month of the year for three years (1999–2001); and (b) Concentrations of urea (µM-N) in six stations of the receiving waters of the Yaqui Valley, Mexico, as a function of month of the year for 2001. In both panels the major period of urea fertilization is shown by gray shading.

Urea uptake by phytoplankton

Urea is not environmentally inert in aquatic systems. With concentrations that often exceed 1 µM-N, urea can be a significant nitrogen source for phytoplankton. Phytoplankton groups differ in their requirements for, and in their ability to utilize, both inorganic and organic forms of nitrogen. Within the cell, the enzyme urease breaks urea down into carbon dioxide and ammonium for assimilation into amino acids and proteins (Paul 1983). The extent to which any nutrient form is used, however, depends not only on physiological ability of the cells to use specific substrates, but also on the physiological state (nutrient status, growth rate, temperature and other conditions for growth) of the cells at the time of nutrient supply.

Urea is a significant contributor to the total nitrogen used by phytoplankton in estuarine and coastal waters (McCarthy 1972; Harvey and Caperon 1976; McCarthy et al. 1977; Furnas 1983; Kaufman et al. 1983; Harrison et al. 1985; Glibert et al. 1991). Kudela and Cochlan (2000), in reviewing the range of

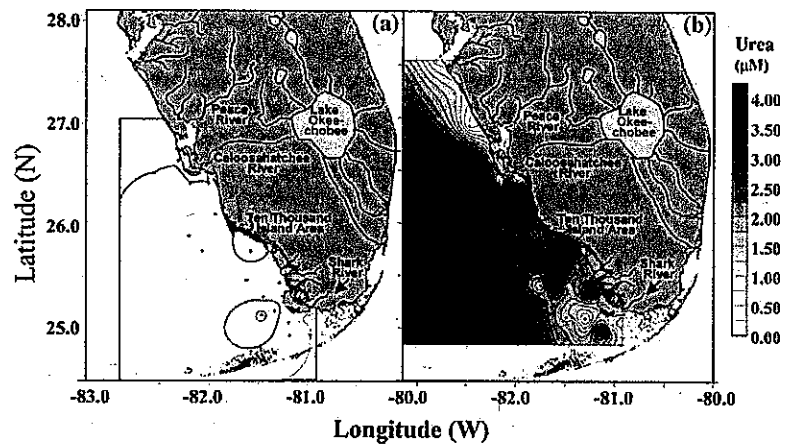

Figure 4. Contour plots of urea concentration on the southwest Florida Shelf during (a) the dry season (May 2003) and (b) one week following Hurricane Charley (August 2004).

literature values for urea uptake as a percentage of total nitrogen uptake, found for that urea can contribute up to 56% of the total nitrogen taken up in ocean regions (e.g. NE Subarctic Pacific; Varela and Harrison 1999), and that it commonly constitutes more than 50% of the total nitrogen taken up in coastal and estuarine regions (e.g. Oslofjord, Norway, Kristiansen 1983; Narragansett Bay, Furnas 1983; Chesapeake Bay, Glibert et al. 1991; Tasman Sea, New Zealand, Chang et al. 1995; and Gulf of Bothnia, Sweden, Cochlan

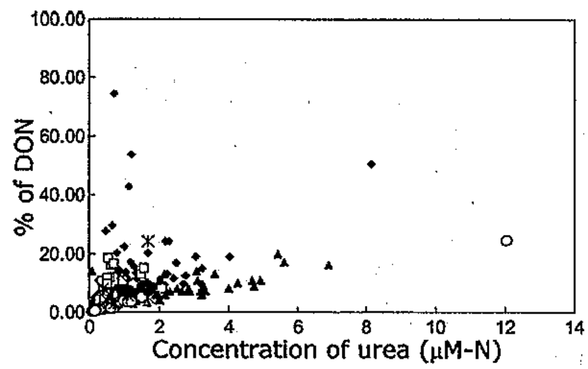

Figure 5. Relationship between total dissolved organic nitrogen as urea and urea concentration for various rivers and tributaries of the world's oceans. Open symbols represent data from Moreton Bay, Australia (squares), and Florida Bay (triangles); closed diamonds are data from Chesapeake Bay and its tributaries (from Glibert et al. 2004a, b), and closed triangles are data from the Baltic Sea (from Stepanauskas et al. 2002). The open circle is data from Maryland Coastal Bays.

and Wikner 1993). Furthermore, in the subartic Pacific, netplankton (1–200 μm) were found to have higher nitrogen-specific uptake rates for urea than nanoplankton (<10 μm; Kokkinakis and Wheeler 1988), a result of higher cell-specific demand by the phytoplankton relative to the bacteria. Further reviews by Bronk (2002) and Berman and Bronk (2003) support this contention. Urea has been shown to serve as the primary source of nitrogen for many phytoplankton species in the field and in the laboratory (Thomas 1968; Carpenter et al. 1972; Antia and Landymore 1975; Bekheet and Syrett 1977; Oliveira and Antia 1986; Gu et al. 1997; Kudela and Cochlan 2000).

Of particular interest is the fact that many regions of the world where both total nitrogen use has increased, and where the urea dominates the agricultural applications of nitrogen, are also regions that have experienced increasing frequency and extent of harmful algal blooms (HABs). HABs are those proliferations of algae that can cause fish and shellfish kills, produce toxins harmful to human health, and develop biomass accumulations that can alter ecosystems in other deleterious ways (Hallegraeff 1993; GEOHAB 2001). The most common HABs are caused by either dinoflagellates or cyanobacteria, although not all dinoflagellates or cyanobacteria are harmful, and not all HABs are made up of these species groups.

Throughout much of the world, the number, intensity, and toxic nature of dinoflagellate algal blooms have increased dramatically in the past few decades (Smayda 1990; Hallegraeff 1993; Anderson et al. 2002) but this is especially pronounced throughout Southeast Asia (GEOHAB 2001; Anderson et al. 2002; Glibert et al. 2005c). China, for example, is experiencing more dinoflagellate blooms of longer duration, and of wider geographic coverage, than a decade ago (Qi et al. 1993; Zhang 1994; Anderson et al. 2002). In the Gulf of California, the coastal waters of Mexico are also experiencing greater numbers and frequencies of algal blooms than a decade ago (Sierra Beltran et al. 2005). Global eutrophication is now recognized to be one of the important factors contributing to habitat change and to the geographical and temporal expansion of these blooms (Smayda 1990; Hallegraeff 1993; Nixon 1995; Anderson et al. 2002; Trainer et al. 2003; Glibert et al. 2005b).

Available data permit a global comparison of the changes in urea consumption and one significant type of harmful dinoflagellate bloom over the past several decades (Figure 6). In this comparison, the change in urea consumption by country over the past 30 years was compared with the change in the number of recorded observations of outbreaks of those species that are responsible for paralytic shellfish poisoning (PSP). PSP is a toxin syndrome associated with the consumption of toxic shellfish exposed to saxitoxin-containing dinoflagellates, including *Pyrodinium bahamense* var. *compressum*, *Alexandrium* spp. and *Gymnodinium catenatum*. This comparison demonstrates that many of the regions of the world that have substantially increased urea consumption are also those regions of the world where increased number of recorded PSP events have

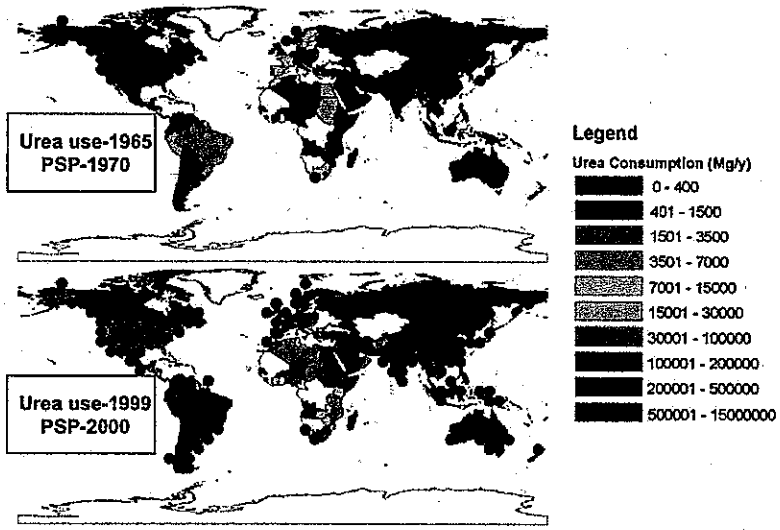

Figure 6. Global distribution of the consumption of urea fertilizer, in metric tons per year by country, in 1960 (upper panel) and in 1999 (lower panel), based on data from the Global Fertilizer Industry data base (FAO 2001), and the global change in recorded observations of dinoflagellates contributing to paralytic shellfish poisoning (PSP) or documented cases of PSP from 1970 (upper panel) to 2000 (lower panel) (modified from GEOHAB 2001). The PSP observations are shown as small circles superimposed on the base map of changes in global urea use by country from the time interval from 1965 (upper panel) to 1999 (lower panel). Note that these estimates of urea consumption do not include uses other than fertilizer.

occurred. The increases are of particular note for Asia, Europe and the US coasts. It should also be recognized that some regions of the world receiving significant applications of urea (e.g. Brazil, and the east African nations) are most likely significantly under-sampled with respect to HABs, and thus the relationship for these regions of the world remains a question. While the distributions of these bloom-forming species may be related to multiple factors, such as physical dynamics, temperature, salinity, total community composition, nutrient availability and composition can and does influence their distribution (Glibert et al. 2005b). The potential for PSP-producing HABs to be related to nutrient loading is underscored by the recent observation of Trainer et al. (2003) who found for Puget Sound that the maximum levels of recorded PSP toxin were strongly correlated with the increase in human population over the past several decades, and they attributed this relationship to increasing eutrophication from sewage. From measurements of activity of the enzyme urease, urea has been suggested to be important in the nutrition of the PSP-associated dinoflagellate *Alexandrium fundyense* (Dyhrman and Anderson 2003).

The correlation of increasing numbers of HABs occurring in regions receiving increasing agricultural urea runoff is supported by the physiological capability for urea uptake by many HAB species. Several specific examples illustrate that urea may contribute disproportionately to the proliferation of some dinoflagellates and cyanobacteria (Figure 7). In the subtropical waters of Moreton Bay, Australia, the percent contribution of urea to total nitrogen uptake was found to be highly related to the percent of the algal community that was comprised of dinoflagellates when all sampled stations from a western to eastern bay transect of the bay from 3 seasons of the year are compared (R^2 = 0.76; Figure 7a; Glibert and Heil unpub. data). Urea uptake in this system was proportionately greatest during austral spring when it represented more than 30% of total nitrogen uptake (Glibert et al. in press). In a large red tide of the dinoflagellate *Lingulodinium polyedrum* off the Baja Peninsula, Mexico, urea was not only used preferentially to the other nitrogen forms, it constituted the major form of nitrogen supporting the bloom (Kudela and Cochlan 2000). Results re-analyzed from that bloom show that the percent contribution of urea to the total nitrogen pool also predicted the concentration of dinoflagellates (based on chlorophyll *c* concentrations) with an R^2 of 0.77, while the percent contribution of nitrate was a poor predictor. Blooms of the dinoflagellate *Prorocentrum minimum* have been observed to follow short term increases in urea in Chesapeake Bay tributaries following a heavy rainfall and fertilizer application (Glibert et al. 2001), and during one *P. minimum* bloom in North Carolina, urea contributed up to 35% of the total nitrogen demand of the bloom (Fan et al. 2003). Urease activity in *P. minimum* has also been found to equal the nitrogen demand of the cells (Fan et al. 2003). Toxic *Pfiesteria piscicida*, the dinoflagellate associated with fish kills along the eastern seaboard of the US, has been shown to use urea even though the bulk of its nutrition is obtained from feeding on other microbes (Lewitus et al. 1999). In Chesapeake Bay, the presence of *P. piscicida* in the sediment has been shown to be directly correlated (R^2 = 0.94) with the mean concentration of urea in the water column (Glibert et al. 2004a). For the dinoflagellate *Alexandrium catenella*, the uptake rate of urea has been found to be considerable greater than that of

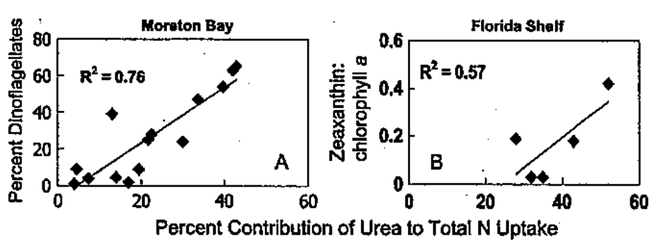

Figure 7. Relationship between the percent contribution of urea to total nitrogen uptake (as measured using stable isotope tracer techniques) and the response of two harmful algal bloom species groups. In panel A is shown the relationship for dinoflagellates in Moreton Bay, Australia (determined by direct enumeration). In panel B is shown the relationship for cyanobacteria on the southwestern Florida Shelf (determined by the ratio of zeaxanthin: chlorophyll *a*).

nitrate at all concentration levels, and to be faster than that of ammonium uptake at concentrations above 10 μg at N l^{-1} (Collos et al. 2004).

For *Alexandrium tamarense*, the availability of urea has also been related to toxin content of the cells: the toxin content for urea-grown cells was higher than that of nitrate-grown cells, but not as high as cells grown on ammonium (Leong et al. 2004), and the biosynthesis of toxin when grown on urea appears to differ from that which occurs under nitrate or ammonium growth conditions. For another dinoflagellate, *Karenia brevis*, increases in toxin content, up to 6-fold, under urea growth have also been observed compared to controls without urea enrichment (Shimizu et al. 1993). For the toxic diatom *Pseudo-nitzschia* sp., increases in toxicity in both laboratory cultures and natural field assemblages have also been found for cells growing on urea compared to those growing on ammonium or nitrate (Armstrong and Kudela 2003; Cochlan et al. 2005; Kudela et al. 2005).

In the case of some recently reported cyanobacterial blooms, similar relationships have been observed. In Florida Bay and on the southwest Florida shelf, the fraction of the algal community composed of cyanobacteria has been shown to be positively correlated with the fraction of nitrogen uptake from urea (R^2 = 0.48 to 0.55; Figure 7b), and negatively correlated with the fraction of nitrogen uptake from nitrate (R^2 = −0.46 to −0.55; Glibert et al. 2004b). Results from the Gulf of Riga, Baltic Sea, also indicate that the percent of urea taken up was a far better predictor of the cyanobacterial contribution to the total plankton assemblage than was nitrate, and that other forms of organic nitrogen also predicted cyanobacterial and dinoflagellate abundance with $R^2 > 0.8$ (Berg et al. 2003). Culture studies have also reported urea to be important in the growth of cyanobacteria. For example, *Aphanizomenon ovalisporum* and *Trichodesmium theibautii* have been shown to grow faster on urea than on other nitrogen sources (Berman and Chava 1999; Mulholland et al. 1999).

Similar patterns are also beginning to emerge from some other classes of algae that are also considered harmful. For the species that causes brown tides off of Long Island, New York, the pelagophyte *Aureococcus anophagefferen*, urea has been shown to be an excellent nitrogen source for growth and a preferred nitrogen source in natural blooms (Lomas et al. 1996; Berg et al. 1997; Gobler et al. 2002). Furthermore, in mesocosm experiments, enrichments with urea stimulated growth of *A. anophagefferns* but inorganic nitrogen enrichments did not (Kana et al. 2004). The fish-killing rhaphidophyte *Chattonella* cf. *verriculosa* grows far better on urea or ammonium compared to nitrate, and natural outbreaks have confirmed higher concentrations of these nitrogen forms compared to nitrate (Tomas 2005).

The frequency of reports that urea is used preferentially by many HAB species, and can result in disproportionate community dominance of some HAB species, has thus grown in recent years. The quality of the nutrient supply has a direct impact on the rate of uptake, and ultimately on the relative composition of the plankton community, but this impact is also dependent on the prevailing environmental conditions, such as temperature, salinity, or abundance of other nutrients, and plankton composition at the time of nutrient delivery. Our understanding of the potential for urea, or any form of nutrient, to affect phytoplankton abundance, growth, or community composition, requires a fundamental understanding of physiological differences within and between species groups. This understanding is growing, but is still rudimentary, not only for urea but for many other organic substrates as well.

Implications and future trends

Urea now represents a significant anthropogenic nitrogen form, and one which likely will be used at escalating rates for years to come throughout the globe. This review has shown that: (1) global rates of urea fertilizer usage have increased rapidly over the past several decades, so that more urea is now used than any other nitrogen fertilizer; (2) unhydrolyzed urea can be lost to surface runoff; (3) urea concentrations in receiving estuaries and coastal waters can be significantly enhanced by land-based inputs; (4) urea can constitute a significant fraction of the total DON pool in some coastal waters; and (5) urea may contribute disproportionately to nitrogen nutrition of some harmful and nuisance phytoplankton groups. The latter contention is supported by the demonstrated ability of harmful and nuisance algae to use urea and by the emerging correlations between HAB formation and either the ambient urea concentration or the proportion that urea contributes to their nutrition. However, demonstrating a causal link between urea inputs and HABs will require future work. To better understand the connection between urea and its coastal impacts we must begin to understand the significance of the global shift to urea fertilizers in a comprehensive fashion, integrating the study of agricultural soil urea nitrogen transformations with the study of biogeochemical fate of urea–nitrogen in local waters, and the role of urea in the physiological ecology and successional patterns of aquatic microbial communities.

The world's human population is expected to continue to increase by 1–2% year^{-1} (Cohen 2003). Current projections are that cereal and meat production will increase by about 10–20% by the year 2010, but global fertilizer use may increase another 50% in the same decade (Matthews and Hammond 1999). Given the current rate at which urea production facilities are being constructed, the enrichment of the globe with urea will only escalate. Most of these increases are on track to occur in parts of the world that are already saturated with nitrogen and frequently plagued by harmful blooms.

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THE MARINE LABORATORY
University of Miami

54-14

Final Report

June, 1954

A PRELIMINARY SURVEY OF THE EFFECTS OF RELEASING WATER FROM LAKE OKEECHOBEE THROUGH THE ST. LUCIE & CALOOSAHATCHEE ESTUARIES

to

Corps of Engineers, U. S. Army

Contract No. DA-08-123-ENG-1376

by

James F. Murdock

Coral Gables,
Florida

F. G. Walton Smith
Director

ML 7745

TABLE OF CONTENTS

SUMMARY

1. The results and conclusions here reported are based upon a preliminary survey of the periodic release of water from Lake Okeechobee through the Caloosahatchee River and the St. Lucie Canal and its effects upon the marine life of the estuaries.

2. Stations are listed and observations presented, with notes on conditions encountered. Anecdotal evidence is included which notes some of the complaints lodged by people in these areas.

3. The release of lake water westward through the Caloosahatchee River is considered in Section (A) while the eastward discharge through the St. Lucie Canal is considered in Section (B).

SECTION (A): Caloosahatchee River

1. Evidence is presented that the release of water from the lake caused changes in the salinity, oxygen content, hydrogen ion concentration and turbidity of the estuarine waters. Oxygen content and hydrogen ion concentration changes are of minor importance.

2. These conditions are sufficiently severe during conditions at or near maximum release to cause temporary movements of marine life from the lower river, the southern part of Matlacha Pass, and sections of San Carlos Bay. These conditions are also severe enough to cause the death of some forms unable to move from these areas.

3. The sports fishery is hampered in the areas mention in (2). This is minimized by the fact that anglers may make good catches by traveling short distances into areas adjacent to those mentioned.

4. Businesses engaged in renting boats and selling live bait to the sport fisherman on the lower river and at Punta Rassa suffer. Changing water conditions, due to the water releases, cause them to lose their live bait at times.

5. Commercial fishermen using hook and line are forced to travel out of the area mentioned in (2) to make good catches during conditions of maximum or near maximum water release.

6. Commercial crabbers appear to be affected by the water releases which force them to travel further in order to make their catches. This fishery is at present being studied by this laboratory under an agreement with the State Board of Conservation.

7. The scallop fishery is not directly affected by the water releases.

8. The major commercial net fisheries are not affected to any degree by the water releases.

9. The offshore charter boat fishery is not affected by the water releases.

10. Sediments are being deposited in the Caloosahatchee River but do not affect to any degree the fisheries of the estuary.

11. The continuing high rate of water release from the Caloosahatchee River may be a contributing cause of Red Tide outbreaks. On the other hand, since Red Tide outbreaks show a general correlation with the cumulative monthly rainfall of the peninsula, it is probable that the

contributions of the Peace River and other drainage systems are sufficiently greater that a reduction of flow in the Caloosahatchee would have little, if any, effect upon the probability of Red Tide outbreaks.

12. Large numbers of water hyacinths create unfavorable conditions.

13. Complaining parties in this area are unaware of the seriousness of the situation at St. Lucie Inlet and are under the impression that they are receiving the bulk of the water releases. It is recommended that they be informed of the actual circumstances.

14. It is also recommended that control measures be taken to minimize the water hyacinth damage.

<u>SECTION (B):</u> St. Lucie Inlet

1. Evidence is presented that the release of water from the lake caused changes in the salinity, oxygen content, hydrogen ion concentration and turbidity of the estuarine waters. Oxygen content and hydrogen ion concentration change are of minor importance.

2. Sediments are being deposited in the estuary due to water releases.

3. Other tributaries entering the estuary are contributing factors to the conditions described in (1) and (2).

4. The damage to navigation, boating, and recreation caused by the sediments is the most serious problem. The permanent ecological effects of the sediments also present a serious problem which cannot be properly assessed without more detailed studies.

5. The severe and rapid changes in salinity which occur as a result of lake water releases cause immediate harm to the sports fishery in the river and to some extent in the estuary.

6. An examination of the commercial fish landings of Martin County and a comparison of these landings with adjacent counties indicates that the water releases have not significantly affected commercial fish landings in Martin County. Although the salinity changes in the estuary certainly influence the commercial fisheries, the net effect is apparently small.

7. A small crab fishery carried on in this area is probably influenced to some extent by the water releases, in particular by the salinity changes.

8. The offshore charter boat fishery is not significantly affected except that at times of high water release they may travel further to make their catch.

9. Since it is absolutely necessary to release certain volumes of water through the St. Lucie inlet the only possible means of alleviating the ill effects is to reduce the rate of flow and to increase its duration. This might be expected to limit the range of sediment transport and to bring about some improvement in the salinity characteristics of the area. It is, therefore., recommended that a careful study be made of these possibilities, as well as of the general nature of the ecological effects of the silt and the permanent effects of the salinity changes. Since the release of water might well be continued for a considerable number of years, and since many of the effects are relatively permanent it is considered of great importance that these effects be determined as fully as possible. In this way, the continuing effects of sediment may be estimated and an attempt made to forecast their long range effects on the ecology and fisheries of the St. Lucie.

ANECDOTAL EVIDENCE

Name:	Mr. and Mrs. Ainsworth
Location:	Fort Myers Beach
Occupation:	Operate a tackle and live bait shop at Snug Harbor; they also have boat docks and are agents for charter boat fishermen.
Statement:	The opening of the locks does not affect their business. They feel that they are far enough away from the influence of any of the water coming from the Caloosahatchee river. They are, however, affected by outbreaks of Red Tide and wonder if that is caused by the quantities of river water entering the gulf.

Name:	Captain Walter Bostick
Location:	Fort Myers Beach
Occupation	Charter boat captain operating out of Snug Harbor
Statement:	He says that he is unaffected.

Name:	Mr. Peed
Location:	Fort Myers Beach
Occupation	Manager of the Bonita Fish Company
Statement:	His fishermen do not complain to him about the conditions and he thinks he is unaffected.

Name:	Mr. Snodgrass
Location:	Fort Myers Beach
Occupation	Manager of the Dixie Fish Company
Statement:	Same as Mr. Peed

Name:	S. C. Williams and C. R. Collier
Location:	Punta Rassa
Occupation	They rent boats and sell live bait to sport fishermen. They also are purchasing agents for a wholesale fish company.
Statement:	They complain that when the locks are open the water by their place becomes fresh instead of its normally brackish condition. They have their live bait tanks set up using a continual flow of this water. When the water becomes fresh they lose their bait which consists of minnows and shrimp, The only way they can keep bait is in the open gulf water. They have had a loss of several hundred dollars worth of bait during 1951 and 1952. They further complain that the trout fishing about two and one half miles north of their camp in the Caloosahatchee River is good except when the locks are open. They also remark about a dark green moss which fouls up the nets of the commercial fishermen during late summer. On July 30, 1953 they lost all their live bait. Prior to this date they were not having any trouble keeping fish and shrimp alive in the tanks.

Name :	Mel and Thelma Waite
Location:	Iona Cove
Occupation:	Operate a fish camp and have docks and a marine way for hauling and repair work. They also sell live bait to fishermen.
Statement:	They complain that they lose their live bait, which consists of minnows and shrimp, when the locks are open. The opening of the locks also causes the fresh water to kill the oysters in Iona Cove and on the bars in the mouth of the Caloosahatchee River. They say these oysters are at times gathered commercially by fishermen from Sarasota. They also complain that the East Coast politicians use their influence to have all the water from Lake Okeechobee

emptied out on the West Coast and have none on the East Coast. Their estimated loss for 1952 was about five hundred dollars.

Name:	Mr. Thomas Smoot
Location:	Fort Myers
Occupation	Owner and operator of the South Fish Company, a wholesale fish company. They own several smaller houses in this area.
Statement:	He does not think the opening of the locks affects his business which is concerned with the commercial fisheries in this areas.

Name:	Mr. Guy H. Gourley
Location:	St. James City, Pine Island
Occupation	Retired
Statement:	He knows little about any damage being done in this area because of the locks being open.

Name:	P.A. Barnhill
Location:	St. James City, Pine Island
Occupation	Operator of a boat rental and live bait business at St. James City. He is also a commercial fisherman. In September 1953 he leased out his rental and bait business and now devotes all his time to commercial fishing.
Statement:	He doesn't think the opening of the locks hurts his business. He says that mullet fishing in September 1953 has been very good. During the early part of the month of September 1953 they were shut off on mullet several times. Two men caught 2,000 lbs of mullet and trout during two days in September 1953.

Name:	Harrison and Samuel Woodring
Location:	Sanibel Island
Occupation:	Commercial Fishermen
Statement:	They do not have much to complain about except that the water gets dirty when the locks are open. They do not know how much this hurts the trout fishing.

Name:	J. B. De Shazo
Location:	Fort Myers
Occupation:	Crabber
Statement:	They do not complain but remark that with all the rain at this time of the year they have to move further down the river, toward the mouth, in order to catch their crabs. As of the first of September 1953 they were doing their crabbing near Shell Point on the Caloosahatchee River and for a little way up the river.

Name:	J.W. Airriwood
Location:	Lives aboard his cruiser, he sometimes ties up at St. James City
Occupation:	Commercial fisherman
Statement:	He has noticed the change in the color of the water when the locks are open but does not think this affects the mullet which are the principal fish.

Name:	Manuel Tomilson
Location:	St. James City, Pine Island
Occupation:	Commercial Fisherman and construction worker
Statement:	His mullet catches nave been good throughout September however his wife has complained that the dirty water has affected her trout fishing adversely.

Name:	Clyde Dampier
Location:	St. James City, Pine Island.

Occupation: Manager of a commercial fish wholesale house
Statement: They have bean landing plenty of mullet at his fish house.

Name: Mr. L.C. Piner
Location: Pine Island
Occupation: Owner and operator of a wholesale scallop and crab house.
Statement: He does not think the opening of the locks hurts his business.

Name: James K. Keene
Location: Pine Island
Occupation: Operates a wholesale fish house on Pine Island
Statement: Mr. Keene states that during the winter the water of Matlacha Pass is usually very clear. This he opines is not the most favorable condition for fishing. During the spring the water becomes less transparent and with some runoff from the land of fresh water the conditions of fishing are at their best. The fish seem to swarm toward the area of brackish water. However as more fresh water is poured from the rivers the salt water species are driven further out to seaward. and the fishermen have to travel further to make their catch, At this time many fresh water species appear in what is normally a salt water environment. They are eventually killed as the water becomes more saline. He concludes that the opening of the locks on the river causes an abnormal freshening of the water which is detrimental to the fisheries.

Name: Mr. Daniel Jursik
Location: Fort Myers
Occupation: Owner and operator of Daniels Seafood Company, dealers in crabs and scallops.
Statement: During February 1952 this company reported that 2670 shedding crabs they were holding were killed by fresh water when the Army Engineers opened the locks to lower the water in Lake Okeechobee. At this time of year, September 1953 his men have to go further down the river toward its mouth before they can catch any crabs. A few months before this they were catching crabs a few miles further up the river.

Name: Frank Richards
Location: Punta Rassa
Occupation: Fisherman
Statement: He caught 146 lb. of trout on September 5, 1953 over at the St. James cutoff by St. James City. The trout move around; usually he does not have to go across the bay but that is where the trout are now.

Numerous people complained of the water hyacinths in the river during the spring of 1954.

DISCUSSION

TEMPERATURES

The temperatures recorded from this area were those which might be expected at the time of observations. Observed temperatures were in many instances above 30 °C. These high temperatures were due to seasonal climatic changes and not caused by the release of water from Lake Okeechobee.

HYDROGEN ION CONCENTRATION (pH)

The pH of the water in tile Caloosahatchee River and its tributaries is lower than the pH of the water in the estuary, or in the Gulf of Mexico, or in Lake Okeechobee. When the rate of flow of the river is increased by rainfall or of the release of water from the lake the net effect, as affects the hydrogen ion concentration, is a lowering of the pH in the estuary.

At various locations in the estuary the pH range was from 8.3 to 8.7 before the water releases. During the time that water was being released the pH range was from 7.6 to 8.3. In most cases the pH was lowered a small amount due to the water releases but still remained above 8.0. A pH of 7.2 was measured in the upper river both before and during the time that water was being released. Near the mouth of the river the lowest pH measured during the that water was being released was 7.8, in Matlacha Pass during this period the lowest pH measured was 7.6. In other areas the effect was not large or critical.

DISSOLVED OXYGEN

Dissolved oxygen values taken before and during the release of water from Lake Okeechobee show that the effect of the water release is to lower the dissolved oxygen content of water in the estuary. This effect is most pronounced in Matlacha Pass where dissolved oxygen values from 68.8% to 117.5% saturation were recorded on July 22, before the release of water from Lake Okeechobee; on September 3-11 during the period when water was being released from the lake, the dissolved oxygen values in this area ranged from 26.2% to 59.91% saturation. In other areas the effect is noticeable but not large or critical. In the river there were only small differences in the dissolved oxygen measurements made before and during the periods of water releases. Lower values were obtained upriver both before and during the period of water releases.

SALINITY AND TIDAL EFFECTS

Changes in the conditions measured in the estuary were closely linked With the opening of the locks which released water from Lake Okeechobee through the Caloosahatchee River. The magnitude of the charges in the different areas was Proportional to the amount of river water which reached the various locations in the estuary.

Seasonal climatic changes contribute to some of these differences, however, it is believed that at the time of sampling the water being released from the lake was mainly responsible.

The river water, which includes water being released from the lake, is easily distinguished from the ocean or estuarine water. It is characterized by its freshness, low pH, low oxygen content and visibly by its color.

When the flow of the river was increased by the release of lake water the incoming tide did not penetrate as far up the river. The effect was to change the river, from near its mouth to Fort

Myers, from an estuarine to a riparian situation. It is believed that this change would occur although to a lesser extent, as a result of the increased amount of rainfall during the autumn.

In San Carlos Bay and the approach to Pine Island Sound the effects of the greater volume of river water, which enters this area when the locks are open, were more noticeable in the eastern part of the bay. At Punta Rassa the salinity was measured during a tidal cycle before the locks were opened. Near high water the surface salinity was 31.2°/oo, the bottom salinity was 32.5°/oo. Near low water the surface salinity was 20.0°/oo and the bottom salinity was 24.8°/oo. During the period that the locks were open the salinities measured at this station were 27.6°/oo at the surface and 27.8°/oo on the bottom at high water. At law water the surface salinity was 7.9°/oo and the bottom salinity was 12.6°/oo.

The following conditions cause changes to occur in the Matlacha Pass area from McCardle Island south to Merwin Key. As the tide floods at Shell Point the direction of flow of the water emptying from the river is diverted to the westward. During periods when the looks are not open, or when the rate of flow is low, the volume of water that flows westward across the flats toward Pine Island is small. The volume of water leaving the river is great when large amounts of water are released from the lake or during times of flood. This water flows into the northeastern part of San Carlos Bay on the ebb tide. On the incoming flood tide part of the river water is diverted to flow in the direction of Pine Island covering the intervening flats with river water. The full flood tide then forces this water back in Matlacha Pass. These effects are felt in Matlacha Pass as far north as McCardle Island. To the north of this point the tide comes in through Charlotte Harbor unless this situation is changed by unusual conditions of wind and weather.

The salinity of the Matlacha Pass area did not vary greatly during the tidal cycles. Salinities from 20.3°/oo to 21.6°/oo were recorded in this area during a tidal cycle before the locks were open. Salinities measured during the period that the locks were open measured form 3.7°/oo to 6.3°/oo. This drop in salinity is severe enough to cause the species of fish which prefer a more saline habitat to temporarily leave this area. It is also severe enough to cause the death of forms unable to migrate from this area. Oysters, on bars in Matlacha Pass, did survive during these conditions.

The area around St. James Point on Pine Island is not seriously affected by the increase in the river flow when large amounts of water are released from the lake or during times of flood. At these times the greatest difference occurs in the salinity of the surface water. Measurements of the surface salinity before the locks were opened were from 28.2°/oo to 29.3°/oo during the tidal cycle. During the Period that the locks were open the surface salinities measured from 13.5°/oo to 17.4°/oo. Bottom salinities measured from 28.3°/oo to 29.3°/oo before the locks were open and from 25.1°/oo to 28.9°/oo when the locks were open. This condition is not critical.

SEDIMENTS

All of the sediment samples collected from the Fort Myers area consisted mainly of black organic ooze. A small amount of plant fibers and detritus was found in Sample #1 taken from the upper river at Olga. A small amount of shell fragments was found in the samples taken from the estuary. None of the samples contained any amount of quartz.

Sample #1, taken at the bridge at Olga during the month of August, 1953 contained the greatest amount of sediment. It appears that greater amounts of organic ooze are deposited in the river than in the estuary. The sediment transported beyond the mouth of the river was widely dispersed and was not deposited in any amount critical to the fisheries in the area investigated,

Deposition of sediments in the river and navigation channels is a damage being caused by water release which does not directly affect the fisheries of this area.

FISHERIES

Only a part of the commercial and sport fishing carried out in Lee County occurs in waters which are directly affected by the releases of water from Lake Okeechobee. No statistics are available which could validly be employed to evaluate the effects of the water releases upon this part of the Lee County Fishery .

The commercial net fishermen active in the area affected by the water releases do not complain of direct damages for these reasons:

(1) They are not solely dependent upon the area affected by the water releases from which to make their catch.

(2) Areas not directly affected by the water releases are readily accessible to them.

(3) The areas affected by the water releases are not the major fishing grounds.

(4) Good catches of mullet are made in areas affected by the water releases.

(5) Fishing is generally good during the autumn when the mullet runs occur. Because of economic factors the fishermen often are forced to cease fishing. Production is not a problem during this season. This is coincidental with the major portion of the water releases. (This statement is not meant to imply that the water releases benefit the fishery.)

Commercial fishermen using trolling gear do fish the area affected by the water releases. The species fished is the sea trout. They cannot successfully fish this species near the mouth of the Caloosahatchee River or in the southern half of Matlacha Pass when the flow of water from the river is great enough to so reduce the salinity that this species of fish moves from this area. They cannot successfully catch this species when using surface trolling rigs in the vicinity of St. James City when a surface layer of discolored water of low salinity is present. Sea trout are caught commercially at this time in the vicinity of St. James City in water not directly affected by the lake water releases. The effect, therefore, upon the fishermen is that they must travel further in order to make a successful catch.

Crabbers fishing the Caloosahatchee River claim to be similarly affected when lake water releases decrease the salinity in the Caloosahatchee River near Fort Myers, During the autumn season they have to travel further toward the mouth of the river for their catch. This is coincident with lake water releases but is also coincident with the rainy season and the time of the year when the blue crab may normally be migrating from this area. At present an investigation of this fishery is being conducted by this laboratory under an agreement with the State Board Of Conservation.

The scallop fishery located in Pine Island Sound is not directly affected by lake water releases.

The sport fishermen in this area have ready access to many areas not directly affected by the lake water releases. Sport fishermen who could not easily reach areas unaffected by the water releases may have reason for complaint if the outflow of fresh water has driven the fish from the locations easily accessible to them.

The offshore charter boat fishery is not affected by the water releases.

Damages might justly be claimed. by the owners of boat rental and live bait dealers in the area near the mouth of the river. Excessive fresh water outflow from the river drives the fish from their vicinity and also is at times responsible for killing their live bait.

HYACINTHS

Large numbers of water hyacinths are brought down by the river. Their presence, floating in the river, decomposing along the shores or forming dense growths in protected coves, is objectionable. This is particularly true near the city of Fort Myers where accumulations of hyacinths seriously hinder small boat movements.

RED TIDE

The phenomena causing the most damage to west coast interests during the past few years has been the "Red Tide". At present a study is being made by this laboratory of the factors which might operate to bring about a "Red Tide". It is suspected that these factors would be more likely to be found originating from inshore than from offshore waters. The alteration of the natural drainage features of south and central Florida by the work carried on by the U. S. Army Engineers is one of the, factors being investigated. The data collected and analyzed to date does not eliminate the possibility that a continuing high rate of water release may be a contributory cause of Red Tide outbreaks. On the other hands since Red Tide outbreaks show a general correlation with the cumulative monthly rainfall of the peninsula, it is probable that the contributions of the Peace River and other drainage systems are sufficiently greater that a reduction of flow in the Caloosahatchee River would have little if any effect upon the probability of a Red Tide outbreak.

CONCLUSIONS AND RECOMMENDATIONS

In view of the nature of the overall problem concerning the South and Central Florida Flood Control Program it is concluded that the damage resulting from the release of lake water through the Caloosahatchee River is small,

The lower river and estuary are affected by the water releases. Such changes which do occur are not believed to be serious and would occur during periods of heavy run-offs independent of lake water releases.

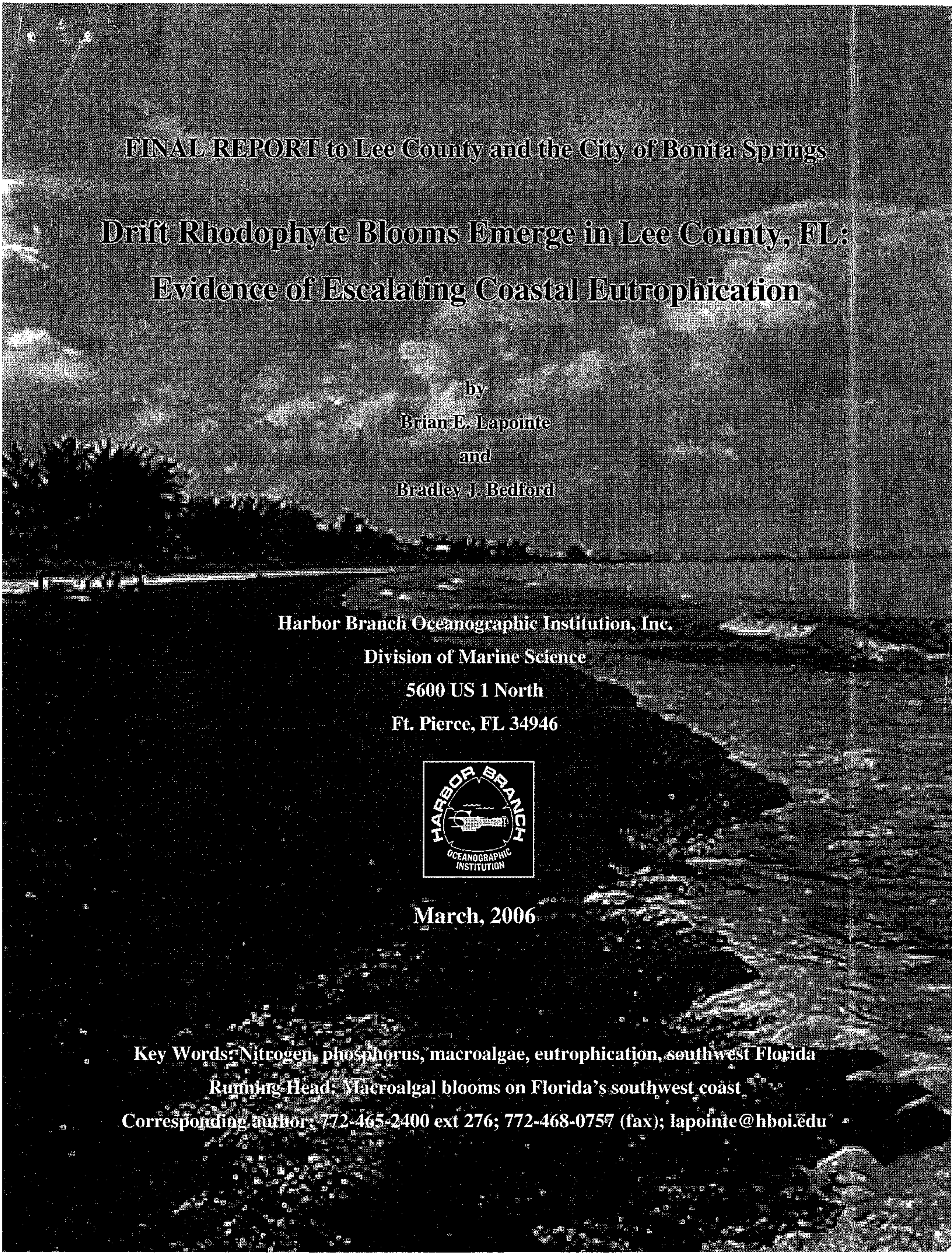
Fishing interests do not suffer any considerable damage with the possible exception of the crab fishery in "he lower river and a few fishing camps near the mouth of the river. Si-nee this laboratory is at present studying the crab fishery of the state under an agreement with the State Board of Conservation, it has been recommended that particular attention be paid to this area to determine the effects of water releases upon the crab fishery in the lower Caloosahatchee River.

Large numbers of water hyacinths float down river. After long periods of water release many become trapped in enclosed areas dry docks and impair the movements of small craft.

Sediments are being deposited in the river. The extent of the damage from these sediments is not known) however, no serious harm is being done to the fisheries of the estuary by these sediments.

Complaining parties in this area are unaware of the seriousness of the situation at St. Lucie Inlet and are under the impression that they are receiving the bulk of the water releases. It is recommended that they be informed of the actual circumstances.

It is also recommended that control measures be taken to minimize the water hyacinth damage.



FINAL REPORT to Lee County and the City of Bonita Springs

Drift Rhodophyte Blooms Emerge in Lee County, FL: Evidence of Escalating Coastal Eutrophication

by

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Executive Summary

Macroalgal blooms have increased globally in recent decades as a result of increased nutrient enrichment and eutrophication of coastal waters. In Lee County, FL, this problem reached a critical stage in 2003 and 2004 when massive drift rhodophyte blooms washed ashore between Sanibel Island and Bonita Springs, making beaches unsuitable for recreation and requiring an expensive removal program. To better understand the ecology of these blooms, water quality and macroalgae sampling was conducted in early August 2004 prior to hurricane Charley and again in late October following several months of heavy discharges from the Caloosahatchee River. During both samplings, water and macroalgae were collected along a gradient extending from the Caloosahatchee River to natural and artificial reefs some 26 km from shore.

Concentrations of dissolved nutrient pools ($DIN = NH_4^+ + NO_3^- + NO_2^-$, TDN, TDP) were generally high throughout the study area with significantly enriched (~ 10-fold) concentrations in the Caloosahatchee River. The mean DIN concentrations increased from the Ortona Lock (< 18 μM) to the Franklin Lock (23-28 μM) in the Caloosahatchee River during both samplings, indicating significant enrichment within the basin. The mean concentrations of NH_4^+ and SRP at the coastal reefs increased six-fold ($\leq$ 0.20 to 1.31 μM) and three-fold (0.30 to 0.92 μM), respectively, between August and October following increased freshwater discharges. The mean C:N ratios of macroalgae at the reefs were relatively low and similar between August and October (13.9 vs. 13.5). The mean C:P and N:P ratios were also low and indicative of N-limitation, and decreased significantly (386 to 242 and 27.4 to 17.5, respectively) between August and October. The $\delta^{15}N$ values of macroalgae increased from the Ortona Lock (+ 8-9 ‰) to the Franklin Lock (+ 12-15 ‰) during both samplings and were within the range reported for

sewage nitrogen; these values decreased with increasing distance from shore to ~ + 3.0 ‰ at the most offshore reef site. Macroalgae (*Gracilaria*, *Hypnea, Botryocladia, Eucheuma, Sargassum*) collected in July 2004 from Bonita Springs Beach and Sanibel Island had mean $\delta^{15}N$ values > + 6.0 ‰, similar to values measured in macroalgae from shallow inshore reefs and within the range of sewage nitrogen. However, mean $\delta^{15}N$ values of coastal macroalgae decreased from August (+ 5.84 ‰) to October (+ 3.89 ‰) with increased discharges from the Caloosahatchee River, suggesting an increased contribution of N from rainfall and agricultural sources with lower $\delta^{15}N$ values (< + 3 ‰) in the wet season. These results suggest that improved management of freshwater releases from Lake Okeechobee, combined with nutrient removal strategies for sewage within the Caloosahatchee River drainage basin, could help mitigate the development of these macroalgal HABs in the future.

1. Introduction

Point-source and non-point source enrichment of nitrogen (N) and phosphorus (P) is now recognized as the most serious pollution problem facing coastal waters worldwide (GESAMP, 1990; NRC, 2000; Howarth et al., 2000). In the United States, scientists and policymakers recognize that a wide range of problems plaguing nearshore waters can be tied, directly or indirectly, to nutrient over-enrichment (Pew Oceans Commission, 2003; U.S. Commission on Ocean Policy, 2004). Nutrient pollution is the common thread that links an array of problems including eutrophication, harmful algal blooms (HABs), bio-invasions, fish kills, shellfish poisonings, loss of seagrass and kelp beds, coral reef die-off, emerging marine diseases, and marine mammal and seabird deaths (Howarth et al., 2000; Lapointe et al., 2004; Lapointe et al., 2005).

The development of macroalgal HABs is a predictable ecological response to increased nutrient loading in shallow bays, estuaries, and coastal waters (Morand and Briand, 1996; Lapointe et al., 1994; Valiela et al., 1997). Unlike toxic phytoplankton HABs such as red tides, macroalgal HABs lack direct chemical toxicity but typically have a broader range of ecological impacts. The effects of macroalgal blooms are largely indirect, multi-faceted, and of longer duration than toxic phytoplankton HABs. Excessive biomass of macroalgae can cause hypoxia, anoxia, and die-off of seagrasses and other benthic biota (Lapointe et al., 1994; Valiela et al., 1997), thereby reducing habitat for desirable and economically important fisheries. In oligotrophic subtropical and tropical waters, nutrient-enriched macroalgal blooms can alter food web dynamics by increasing the abundance of grazers in seagrass (McGlathery, 1995) and coral reef ecosystems (Lapointe and Thacker, 2002). Increasingly, macroalgal blooms foul beaches and shorelines important to local tourist economies and require ever more expensive biomass removal programs (Morand and Briand, 1996; Lapointe and Thacker, 2002).

Land-based nutrient discharges to bays and coastal waters along southwest Florida have long been linked to the development of macroalgae and phytoplankton blooms. Sewage-driven eutrophication in Tampa Bay during the 1960's, 1970's, and 1980's led to drift macroalgal blooms that included the rhodophyte *Gracilaria* and chlorophyte *Ulva* (Humm, 1973; Guist and Humm, 1976). In Hillsboro Bay, a subdivision of Tampa Bay, drift macroalgal HABs with biomass levels > 600 g dry wt/m^2 developed in the early 1980's, which included the rhodophytes *Gracilaria, Spyridia, Hypnea,* and *Agardhiella*, and the chlorophytes *Ulva* and *Caulerpa* (Avery, 1997). Following considerable seagrass loss in Hillsboro Bay by the late 1970's, N removal from the local wastewater treatment plant was initiated in 1979, and by 1994 drift macroalgae had decreased by > 90% while seagrass cover increased from 0.2 ha in 1986 to over 28 ha in 1995 (Avery, 1997). In coastal waters of southwest Florida, Ketchum and Keen (1947) correlated red tide blooms off Sarasota, FL, with unusually high P concentrations in the water column and suggested "the excessive nutrient content may be the result of terrigenous contamination or fertilization of the waters." Slobodkin (1953) reported that the red tide outbreaks off southwest Florida may be intiated by the development of a stratified water mass characterized by reduced salinity and elevated nutrients resulting from discharges of the combined Charlotte Harbor – Caloosahatchee River drainage basins.

Recent increases in nutrient loading associated with expanding urbanization of the watershed and discharges from the Peace and Caloosahatchee rivers could be linked to emerging blooms of benthic macroalgae in estuaries and coastal waters of Lee County, FL (Fig. 1). McPherson and Miller (1990) noted that projected increases in nitrogen loadings from the Peace

River basin would favor undesirable increases in phytoplankton and benthic algae in the Charlotte Harbor estuarine system. An analysis of monitoring data for the Caloosahatchee River indicated that water quality in the downstream estuary changes as a function of total discharge and water source (river basin, Lake Okeechobee; Doering and Chamberlain, 1999). While these assessments were limited to the estuarine regions of the Peace and Caloosahatchee rivers, the combined flows and nutrient loads associated with these discharges have the potential to impact coastal waters for considerable distances distances from shore (> 50 km; Yang et al., 1999). Accordingly, increased land-based nutrient pollution could be influencing coastal waters off southwest Florida and may help explain the unprecedented accumulation of drift rhodophytes that fouled coastal beaches between Sanibel Island and Bonita Springs in 2003/2004 (Fig 2 A, B, E). The excessive biomass of these rhodophytes caused odor problems and greatly diminished the use of the beaches by tourists. Concerns of the local governments of Lee County and the City of Bonita Springs prompted the present investigation in order to determine if these macroalgal HABs could be linked to increasing land-based nutrient pollution as in Tampa Bay and other parts of the world (Morand and Briand, 1996; Valiela et al., 1997; NRC, 2000).

Several approaches can be used to assess the spatial extent and degree of land-based nutrient enrichment in coastal waters of Lee County. One traditional method involves measurements of salinity and concentrations of dissolved inorganic nitrogen (DIN = $NH_4^+ + NO_3^- + NO_2^-$) and soluble reactive phosphorus (SRP) in water samples along inshore to
Am Nitrate Nitrite
offshore gradients. If nutrient concentrations of lower-salinity inshore waters are higher than that of higher-salinity offshore waters, then a land-based source of nutrients is indicated (Ketchum, 1967). A more specific approach involves the measurement of stable nitrogen isotope ratios in macroalgae that can be used to "fingerprint" the source of N when the various N sources

are known (Heaton, 1986; Owens, 1987). Attached macroalgae have a distinct advantage over free-floating phytoplankton as nutrient indicators because they provide a long-term integration of the aqueous N signal for a particular location (Lapointe et al., 2004). Enrichment of $\delta^{15}N$in aquatic systems can result from N transformations that occur prior to, during, or following the treatment and discharge of sewage. Volatilization of ammonia and isotopic fractionation by microbes during nitrification and denitrification produce residual DIN with elevated $\delta^{15}N$ values of + 6 ‰ to + 22 ‰ (Heaton, 1986; Lindau et al., 1989). This range includes secondarily treated discharges from sewage outfalls (Hoch et al., 1995; Table 1) as well as shallow (< 10 m) groundwaters contaminated by septic tanks in south Florida (Lapointe and Krupa, 1995 a, b; Table 1). In comparison, N derived from rainfall, fertilizers and organic peat associated with stormwater runoff from agricultural areas have $\delta^{15}N$ values ranging from -3 ‰ to + 3 ‰ (Heaton, 1986; Paerl and Fogel, 1994; Table 1) and can therefore be effectively discriminated from the higher sewage N signature.

We hypothesized that, if land-based anthropogenic N sources such as sewage was the primary DIN source supporting macroalgal HABs in Lee County's coastal waters, then the highest $\delta^{15}N$ values would occur in macroalgae from the Caloosahatchee River, beaches, and shallow coastal reefs most influenced by land-based discharges. Macroalgae that rely on natural nitrogen fixation have low $\delta^{15}N$ values of ~ 0 ‰ (France et al., 1998; Table 1) in contrast to those using sewage N, which become increasingly enriched in $\delta^{15}N$ with increasing sewage N contributions over a range from + 3 ‰ to + 16 ‰ (Lapointe, 1997; Costanzo et al., 2001). Globally, many case studies have used $\delta^{15}N$ as a tool to discriminate between natural and anthropogenic N sources supporting macroalgal growth (Lapointe, 1997; France et al., 1998; McClelland and Valiela, 1998; Costanzo et al., 2001; Wayland and Hobson, 2001; Umezawa et al., 2002; Gartner et al., 2002; Barile, 2004; Savage and Elmgren, 2004; Lapointe et al., 2004). Several studies have successfully utilized $\delta^{15}N$ values in macroalgae and reef corals to assess the spatial extent of land-based N enrichment along gradients into the coastal ocean, on scales from several kilometers (Umezawa et al., 2002; Lapointe et al., 2004; Lapointe et al., 2005b), to nearly forty kilometers across the Great Barrier Reef lagoon (Sammarco et al., 1999).

We also predicted that "wet versus dry" seasonality could significantly affect the degree and relative importance of various sources of land-based N enrichment. In the Florida Keys, local N loadings from sewage were relatively constant compared to the large non-point source agricultural N loads that were transported into coastal waters during wet years when large water releases from the Everglades occurred (Lapointe et al., 2004). We initiated our study in Lee County in early August 2004, prior to landfall of three hurricanes that struck Florida in August and September, 2004. Because historically significant amounts of rainfall resulted from the overlapping paths of hurricanes Charley, Frances, and Jeanne in the Kissimmee River drainage basin north of Lake Okeechobee (South Florida Water Management District, rainfall data), we had an opportunity to test this hypothesis by re-sampling in late October of 2004.

2. Materials and methods

2.1. Sample collection and analysis

Samples of the water column and attached macroalgae and/or seagrasses were collected August 8-10 (dry season) and October 28-29 (wet season), 2004, along an onshore to offshore gradient extending from the Caloosahatchee River into coastal waters of Lee County, FL (Fig. 1). Nine fixed stations sampled in both August and October included the Ortona and Franklin locks on the Caloosahatchee River; seagrass beds in San Carlos Bay and S. Charlotte Harbor; a shallow, natural, nearshore reef off Boca Grande, known locally as the 17th Street Reef (4 m depth); the Belton-Johnson Reef (10 m), an artificial reef; Blanda's Reef (14 m), an artificial reef; ARC Reef (19 m,), an artificial reef; and North Deep Ledge (20 m), a natural ledge and farthest station from shore (26 km; Fig. 1). In August, two additional stations (Peace and Imperial rivers) were sampled for water column nutrients, and macroalgal tissue was collected for $\delta^{15}N$ analysis from beaches at Bonita Springs, Fort Myers, Sanibel, and Captiva. In addition, dried rhodophytes collected from stranded material on Bonita Beach in late July, 2004 (Table 2; Fig. 2B) were analyzed for $\delta^{15}N$.

At each of 11 sites in August and 9 sites in October, replicate samples (n = 2) of near-bottom water were collected into clean, 250 ml HDPE bottles and held on ice in a cooler until processing. In the lab, 100 ml sample aliquots were filtered via syringe through 0.45 μm Whatman GF/F filters into clean, 150 ml HDPE bottles and frozen. The samples were subsequently analyzed for NH_4^+-N, $NO_3^- + NO_2^-$-N and PO_4^{3-}-P (SRP) at the Nutrient Analytical Services Laboratory, Chesapeake Biological Laboratory, Center for Environmental and Estuarine Studies, University of Maryland, Solomons, MD (NASL). A Technicon Auto-Analyzer II was used for determination of nitrate (NO_3^-) and soluble reactive phosphate (SRP), and a Technicon TRAACS 800 was used for analysis of ammonium (NH_4^+) and nitrite (NO_2^-). Detection limits were 0.20 μM for NH_4^+, 0.01 μM for $NO_3^- + NO_2^-$, 0.01 μM for NO_2^-, and 0.02 μM for SRP (D'Elia et al., 1997). We used the *f*-ratio ($NO_3^- / (NO_3^- + NH_4^+)$) to gauge the relative importance of NO_3^- versus NH_4^+ as a DIN source (McCarthy et al. 1975; Harrison et al., 1987) to macroalgae at the study sites. Samples collected in October were also analyzed for total dissolved nitrogen (TDN) and total dissolved phosphorus (TDP) at NASL, using a Technicon Auto-Analyzer II with detection limits of 1.43 μM for TDN, and 0.03μM for TDP (D'Elia et al., 1997), and were used to calculate dissolved organic nitrogen (DON = TDN – DIN) and dissolved organic phosphorus (DOP = TDP – SRP).

(Sol. react. Phos)

Samples of macroalgae and/or seagrasses were collected at the nine stations in August and October by SCUBA or snorkeling (Table 2). Rhodophytes were collected at the five coastal reef sites (17th St. Reef, Culvert Reef, Blanda's Reef, ARC Reef, and N. Deep Ledge); the seagrass *Thalassia testudinum* was collected at S. Charlotte Harbor and San Carlos Bay; and the chlorophyte *Cladophora* sp. and the cyanophyte *Lyngbya* sp. were collected at Ortona and Franklin locks (Table 2). Field samples were stored in plastic, zipper-lock, storage bags and held on ice in a cooler until processing. In the lab, composite samples (thalli from 5-8 different plants of each species) of macroalgae were sorted, cleaned of visible epiphytes and sediments, identified (Dawes, 1974; Littler and Littler, 2000), and rinsed briefly (3-5 sec) in deionized water to remove salt and debris. The cleaned, composite samples were dried in a Fisher Scientific Isotemp™ oven at 60 °C for 48 h and then ground to a fine powder using a mortar and pestle. Samples of the dried, powdered macroalgae were stored in plastic screwtop vials and placed in a dessicator until analysis for C:N:P contents (molar ratios) at NASL. Percent C and N were measured on an Exeter Analytical, Inc (EAI) CE-440 Elemental Analyzer and percent P was measured following the methodology of Asplia et. al. (1976) using a Technicon Autoanalyzer II with a IBM compatible Labtronics Inc. DP500 software data collection system (D'Elia et al., 1997). All samples were also analyzed for $\delta^{15}N$ (n = 2 analytical replicates per sample) with a Carlo-Erba N/A 1500 Elemental Analyzer and a VG Isomass mass spectrometer using Dumas combustion, at Isotope Services, Inc., Los Alamos, NM. The standard used for stable nitrogen isotope analysis was N_2 in air. $\delta^{15}N$ values (‰) were calculated using

$[(R_{Sample}/R_{Standard})-1]*10^3$; where R = $^{15}N/^{14}N$.

2.2. Statistical analysis

Data were tested for normality using the Shapiro-Wilk test (W statistic), and for homoscedasticity using Levene's test of equality of error variances. Normally distributed datasets were compared using the Generalized Linear Model (GLM, Type III sum of squares) procedure in SPSS 11.0 for Mac. Data not normally distributed were compared using either the Kruskal-Wallis H test (three or more groups), or the Mann-Whitney U test (two groups). Post hoc comparisons were made using Tukey's HSD test.

Sites where water samples were collected in August only (Imperial and Peace rivers) were not included in overall (August and October) water column nutrient statistics. However, data analyzed to compare seasonal differences (August vs. October) included all sites sampled. In order to assess water column charcteristics in the vicinity of the coastal macroalgal blooms, a subset of coastal water samples (San Carlos Bay, S. Charlotte Harbor, 17th St. Reef, Belton-Johnson Reef, Blanda's Reef, ARC Reef, and N. Deep Ledge) from August and October were tested for significant effects of season. For all analyses, differences were considered significant at $p \leq 0.05$.

3. Results

3.1. Taxonomic Composition of the Macroalgal Blooms

The drift macroalgal community that washed ashore on Bonita Springs beach in July and August 2004 was dominated by rhodophytes (Table 2). Species identified from the beach collections included *Botryocladia occidentalis, Eucheuma isiforme* var. *denudatum, Gracilaria cervicornis, Gracilaria tikvahiae, Agardhiella subulata,* and *Hypnea musciformis.* In August, the pelagic phaeophyte *Sargassum fluitans* was also collected from Ft. Myers Beach, Sanibel Island, and Captiva Island.

The rhodophytes from the beach strandings were found to be abundant on the natural and artificial reefs in coastal waters off Lee County (Table 2). In both August and October, *Botryocladia occidentalis* was collected from all five reef sites. Other rhodophytes collected from the reefs included *Agardhiella subulata, Eucheuma isiforme* var. *denudatum, Gracilaria cervicornis, Gracilaria tikvahiae, Hypnea musciformis,* and *Rhodymenia divaricata.*

3.2. Dissolved nutrient concentrations, *f*-ratios, DIN/SRP ratios, and salinity

Overall NH_4^+ concentrations varied significantly with location ($F = 89.882$, $p < 0.001$, GLM), season ($p < 0.001$, Mann-Whitney) and the location-season interaction ($F = 50.164$, $p < 0.001$, GLM), averaging 1.74 ± 3.66 µM ($n = 22$) in August and 2.48 ± 2.59 µM ($n = 18$) in October. Concentrations were significantly higher in the rivers, with maximum values of 12.70 µM at the Imperial River (August) and 8.30 µM at Franklin Lock (October). In August, values ≤ 0.21 µM (detection limit) were measured at all bay and coastal reef sites whereas in October values were > 0.55 µM at all sites (Fig. 3). At the five coastal reef sites, mean NH_4^+ concentrations increased from ≤ 0.21 µM ($n = 14$) in August to 1.31 ± 1.08 µM ($n = 14$) in October (Table 3) with a highly significant effect of season ($F = 715.765$, $p < 0.001$, GLM).

NO_3^- concentrations varied significantly with location ($F = 1644.205$, $p < 0.001$, GLM) and location-season interaction ($F = 354.582$, $p < 0.001$, GLM), averaging 5.62 ± 9.29 µM ($n = 22$) in August and 3.92 ± 5.70 µM ($n = 18$) in October. High concentrations occurred in the rivers, with maximum values at the Franklin Lock in both August (26.15 µM) and October (14.35 µM); minimum values occurred at the bay and coastal sites, with minimums of 0.49 µM at S. Charlotte Harbor and Belton-Johnson Reef (August) and 0.27 µM at 17th St. Reef

(October). At the coastal reef sites, the mean NO_3^- concentrations were similar in August (0.91 ± 0.72 μM, n = 14) and October (0.97 ± 0.69 μM, n = 14; Table 3).

Overall, DIN concentrations varied significantly with location (F = 169.055, p < 0.001, GLM), season (p = 0.034, Mann-Whitney), and location-season interaction (F = 133.093, p < 0.001, GLM), averaging 7.36 ± 10.61 μM (n = 22) in August and decreasing to 6.40 ± 8.09 μM (n = 18) in October. The highest DIN concentrations occurred in the rivers, with the maximum value at the Franklin Lock in August (27.70 μM) and October (22.65 μM); the lowest levels occurred at the bay and coastal reef sites, with minimum values of 0.69 μM at S. Charlotte Harbor and Belton-Johnson Reef in August and 0.83 μM at 17th St. Reef in October (Fig. 3). On the coastal reefs, mean DIN concentrations increased significantly (F = 66.322, p < 0.001, GLM) from August (1.11 ± 0.72 μM, n = 14) to October (2.29 ± 1.57 μM, n = 14; Table 3).

Overall, the f-ratio varied with location (F = 11.822, p < 0.001, GLM), season (p < 0.001, Mann-Whitney), and location-season interaction (F = 7.702, p < 0.001, GLM) with a higher mean value in August (0.75 ± 0.19, n = 22) compared to October (0.48 ± 0.17, n = 18). In August, the f-ratios were statistically similar among sites (maximum of 0.94 at Franklin Lock) except the Imperial River (p ≤ 0.015, THSD) where the minimum (0.27) occurred. In October, the maximum values occurred in the rivers (Ortona, 0.75) and the minimum at the offshore ARC Reef (0.32, Fig. 3). The f-ratios for the coastal reef sites averaged 0.77 ± 0.11 (n = 14) in August and decreased significantly (F = 168.32, p = 0.006, GLM) to 0.41 ± 0.14 (n = 14) in October (Table 3).

SRP concentrations varied with location (F = 195.032, p < 0.001, GLM), season (p = 0.011, Mann-Whitney), and the location-season interaction (F = 119.383, p <0.001, GLM), averaging 2.01 ± 4.96 μM (n = 22) in August and 1.04 ± 1.08 μM (n = 18) in October. In

August, the maximum concentrations occurred in the Peace River (16.80 μM), which was significantly ($p < 0.001$, THSD) higher than all other sites, and the minimum concentrations (0.14 μM) occurred at San Carlos Bay (Fig. 4). In October, the maximum SRP concentrations (3.74 μM) occurred at S. Charlotte Harbor downstream of the Peace River (which was not sampled) with lower values at the coastal reefs (minimum 0.19 μM at N. Deep Ledge) (Fig. 4). Mean SRP concentrations at the coastal reefs were significantly ($F = 289.115$, $p < 0.001$, GLM) lower in August (0.30 ± 0.18 μM, $n = 14$) than in October (0.92 ± 1.20 μM, $n = 14$; Table 3).

The DIN/SRP ratio varied significantly with location ($F = 25.510$, $p < 0.001$, GLM), averaging 11.25 ± 19.51 ($n = 22$) in August and 6.92 ± 4.95 ($n = 18$) in October. The highest DIN/SRP ratio in August was in the Imperial River (68.30) compared to the Franklin Lock (14.86) in October. The lowest DIN/SRP ratios in August (1.32) and October (0.29) both occurred at S. Charlotte Harbor (Fig. 4). At the coastal reef sites, the DIN/SRP ratios were similar in August (4.77 ± 3.10, $n = 14$) and October (4.88 ± 3.41, $n = 14$; Table 3).

Total dissolved N and P were measured only during the October sampling, when both TDN ($F = 430.949$, $p < 0.001$, GLM) and TDP ($F = 437.560$, $p < 0.001$, GLM) varied with location. TDN averaged 35.8 ± 30.8 μM and concentrations in the Caloosahatchee River (70.9 μM at Franklin Lock) were significantly ($p < 0.001$, THSD) higher than all other sites; the bays were significantly ($p \leq 0.016$, THSD) higher than coastal reef sites, and the minimum value (11.07 μM) occurred at N. Deep Ledge (Fig. 5). TDP averaged 1.57 ± 1.42 μM and concentrations were significantly elevated in the rivers and S. Charlotte Harbor ($p < 0.001$, THSD) compared to all other sites, with the highest value at S. Charlotte Harbor (5.16 μM) and the lowest at N. Deep Ledge (0.37 μM, Fig. 5).

High P in Peace R.

In October, DON ($F = 255.172$, $p < 0.001$, GLM) and DOP ($F = 30.976$, $p < 0.001$, GLM) varied significantly with location. DON dominated the TDN pool (averaged 29.4 ± 23.1 μM) with the highest concentrations in the rivers (70.92 μM maximum at Franklin Lock), which were significantly ($p < 0.001$, THSD) higher than all other sites. Lower values occurred in the bays, which were significantly ($p < 0.001$, THSD) higher than the coastal reef sites where the minimum of 9.69 μM occurred at N. Deep Ledge (Fig. 5). In contrast, DOP comprised a relatively minor portion of the TDP pool, averaging 0.53 ± 0.36 μM. The highest DOP concentrations were in S. Charlotte Harbor (1.42 μM), which was was the only site significantly ($p < 0.001$, THSD) different than the other sites; the lowest value (0.18 μM) occurred at N. Deep Ledge (Fig. 5).

Salinities ranged from 0.3 ‰ at the Ortona and Franklin locks in both August and October to 37.3 ‰ offshore at N. Deep Ledge and 37.0 ‰ at ARC Reef in August. During both samplings, a lower salinity surface layer (buoyant plume) occurred at our most offshore stations, especially ARC Reef. In August, the surface layer had a salinity of 32 ‰ compared to a near-bottom salinity of 37 ‰. Stratification was also observed in October at ARC Reef, where a lower-salinity (34.8 ‰), highly colored surface layer extended to a depth of ~ 12 m over the clearer, higher salinity (36.0 ‰) bottom layer (12-19 m depth).

3.3. C:N:P analysis of macroalgae

Overall, there were no significant effects of location or season on C:N ratios of macroalgae and seagrasses, which averaged 13.2 ± 3.0 ($n = 20$) in August and 12.9 ± 3.5 ($n = 15$) in October. The lowest C:N ratios occurred at Franklin Lock in August (9.0) and October (8.7);

the highest ratios were recorded at the coastal reef sites N. Deep Ledge in August (36.6) and Belton-Johnson Reef in October (15.3) (Fig. 6).

C:P ratios varied significantly with season ($F = 4.268$, $p = 0.053$, GLM), averaging 343 ± 197 (n = 20) in August and 236 ± 132 (n = 15) in October. The lowest C:P ratios were 170 at Franklin Lock in August and 139 at N. Deep Ledge in October when a buoyant darkwater surface layer was evident 26 km from the coast (Fig. 6). At the coastal reef sites, seasonal differences were significant ($F = 6.141$, $p = 0.024$, GLM), with the August mean (386 ± 198, n = 16) higher than October (17.5 ± 6.7, n = 13) (Table 4).

There was significant ($F = 4.868$, $p = 0.040$, GLM) seasonal variation in N:P ratios, with a higher mean in August (25.4 ± 11.0, n = 20) than October (18.1 ± 6.4, n = 15). The lowest N:P ratios occurred at Ortona Lock (15.8 in August) and S. Charlotte Harbor (12.8 in October); the highest ratios were at N. Deep Ledge (42.4, August) and Belton-Johnson Reef (24.3, October) (Fig. 6). On the coastal reefs, N:P ratios decreased significantly ($F = 8.979$, $p = 0.008$, GLM), from 27.4 ± 11.4 (n = 16) in August, to 17.5 ± 6.7 (n = 13) in October (Table 4).

3.4. Stable nitrogen isotopes in macroalgae

Overall, $\delta^{15}N$ values in macroalgae and seagrasses varied significantly with location ($F = 50.118$, $p < 0.001$, GLM), season ($F = 12.746$, $p = 0.001$, GLM) and the location-season interaction ($F = 5.280$, $p < 0.001$, GLM), with a higher mean in August (+ 6.2 ± 2.3 ‰, n = 46) than October (+ 4.7 ± 3.1 ‰, n = 34) and values generally decreasing with increasing distance from shore. In both August and October, $\delta^{15}N$ values at Franklin Lock were significantly ($p \leq 0.001$, THSD) higher than all other stations except Ortona Lock, with values of + 11.8 ‰ and + 15.6 ‰, respectively (Fig. 7A). Blanda's Reef had the lowest values: + 3.2 ‰ in August and +

3.0 ‰ in October (Fig. 7A). At the coastal reef sites $\delta^{15}N$ in macroalgae decreased significantly, from + 5.84 ± 1.37 ‰ (n = 32) in August to + 3.89 ± 0.96 ‰ (n = 26) in October (Table 4).

The $\delta^{15}N$ values of macroalgae (phaeophytes and rhodophytes, Fig. 7B) collected from Lee County beaches in August 2004 did not vary significantly with location (p = 0.264, Kruskal-Wallis) and values ranged from a high of + 7.1 ‰ at Fort Myers Beach to a low of + 5.7 ‰ at Bonita Springs Beach, with an overall mean of + 6.1 ± 1.3 ‰ (n = 14). Samples of the rhodophyte *Hypnea musciformis* (Fig. 7B) collected from drift accumulations on Bonita Springs Beach were enriched (+ 8.0 ± 0.55) compared to samples of the same species collected at 17th St. Reef (+ 7.19 ± 0.15) and N. Deep Ledge (+ 5.12 ± 0.08).

4. **Discussion**

Results of this study support the hypothesis that the drift rhodophyte blooms that have developed in Lee County's coastal waters in recent years are linked to increasing land-based nutrient enrichment, especially N. Although similar drift macroalgal blooms have developed in shallow seagrass meadows in Tampa Bay (Humm, 1973; Guist and Humm, 1976 ; Avery, 1997), the Indian River Lagoon (Virnstein and Carbonara, 1985), coral reefs off southeast Florida (Lapointe et al. 2005 a,b), and the Florida Keys (Lapointe et al., 1994; Lapointe et al., 2004), the blooms of these particular rhodophytes in Lee County are the first to be reported for shallow coastal waters along barrier beaches of southwest Florida (Fig. 2 E). Our results documented that significant N and P enrichment extended at least 26 km from shore in fall of 2004, supporting previous suggestions that river discharges can cause large-scale enrichment of coastal waters off southwest Florida (Slobodkin, 1953; Yang et al., 1999). Considering that these macroalgal HAB phenomena are symptomatic of cultural eutrophication in shallow, coastal waters of south Florida (Humm, 1973; Lapointe and Ryther, 1979), the large scale and economic impact of these blooms demand serious concern by water and resource managers for protection of this popular tourist destination.

4.1 Taxonomic composition and ecology of blooms

The drift rhodophyte community that washed ashore on Bonita Springs Beach in July 2004, prior to hurricane Charley, was dominated by the genera *Gracilara, Hypnea*, and *Agardhiella*. Humm (1973) noted that rhodophytes dominated (51%) the benthic macroalgal communities in the eastern Gulf of Mexico, compared chlorophytes (31%) and phaeophytes (18%). We found a diverse rhodophyte community to be common on natural and artificial reefs throughout the study area prior to hurricane Charley, indicating that "seed" populations for these blooms are present in local waters.

The abundance of macroalgae in the eastern Gulf of Mexico is limited by the scarcity of suitable rocky substrata (Humm, 1973). Most of the intertidal zone and coastal waters are unconsolidated sediments that will not support the establishment of most macroalgae. Where limestone reef outcrops or other suitable benthic substrata are available, the rhodophytes begin growing as attached plants and can become the dominant biotic cover of inshore reefs and suitable soft bottom communities when nutrient availability is adequate (see Fig. 2C). Under nutrient enriched conditions, some of these rhodophytes are capable of very rapid growth and bloom formation. For example, *Gracilaria tikvahiae*, which was abundant in the Bonita Springs Beach bloom and coastal waters in Lee County, can double its biomass in < 3 days when irradiance, temperature, and nutrients are not limiting (Lapointe et al., 1984). As the rhodophytes grow, waves and currents detach larger plants that continue to grow as unattached (drift) populations. Irradiance is a critical factor regulating growth rate of *G. tikvahiae*, which can utilize nearly full, natural irradiance levels (Lapointe et al., 1984). The irradiance we measured on the bottom at the offshore reefs in 10-20 m water depths was < 30 μmol photons m^{-2} sec^{-1}, very low values that would result in severe light-limitation for *G. tikvahiae* at 20-30 °C (Lapointe et al., 1984). Hence, the reflective sand bottom in shallow, nearshore coastal waters of Lee County would provide the higher irradiance levels (> 400 μmol photons m^{-2} sec^{-1}) needed to generate these blooms (Fig. 2E).

The tissue C:N data show that the rhodophytes in coastal waters of Lee County are generally enriched in N (a low C:N ratio) compared to macroalgae on reefs in southeast Florida and the wider Caribbean (Fig. 8). The mean C:N ratio of the rhodophytes was ~ 13.7, a value that can support maximum growth rates in *Gracilaria tikvahiae*. For example, growth rates as high as 0.37 doublings d^{-1} (a biomass doubling every 2.5 days) were observed in *G. foliifera* var. *angustissima* (= *G. tikvahiae*) growing under full, natural irradiance at a C:N ratio of 13.4; lower growth rates of 0.2 doublings d^{-1} occurred when these plants were grown under lower irradiance and a lower C:N ratio of 8.56 (Lapointe, 1981). Under such light-limited conditions, *G. tikvahiae* increases its characteristic protein pigment, phycoerythrin, which decreases the C:N ratio and provides a N storage pool that can support growth when N availability decreases (Lapointe, 1981; Lapointe and Ryther, 1979). Because of this physiological profile, *G. tikvahiae* and other rhodophytes are well adapted to assimilate and store pulses of DIN in coastal waters associated with stormwater runoff and discharges from the DIN-enriched waters of the Caloosahatchee and Peace rivers.

The low C:P and N:P ratios of the rhodophytes in Lee County further indicate a high degree of P enrichment compared to macroalgae from southeast Florida and the wider Caribbean region (Fig. 8). Although relatively high C:P (622) and N:P (42.4) ratios occurred in August at the most offshore station (N. Deep Ledge), these ratios decreased significantly with increased runoff following hurricanes Charley, Frances, and Jeanne, and were generally low, averaging 314 and 22.5, respectively, in the coastal waters during the study. These C:P and N:P ratios are much lower than the means of 976 and 43.4 reported for carbonate-rich waters of the Caribbean where macroalgal growth is strongly limited by P (Lapointe et al., 1992). In experimental field studies in the Lower Florida Keys in 1983, *G. tikvahiae* experienced severe P limitation when very high C:P (892-2,816) and N:P (73-250) ratios developed in ambient seawater of Pine Channel (Lapointe, 1987). The low SRP concentrations (< 0.1 μM) in the Florida Keys obviously preclude *G. tikvahiae* from forming blooms in that location, in contrast to Lee County where much higher SRP concentrations (0.30-0.92 μM) support low C:P and N:P ratios and result in N limitation of growth. The low mean C:P (314) and N:P (22.5) ratios in rhodophytes from Lee County are indicative of N rather than P limitation of growth (Lapointe et al. 1992).

The phaeophyte *Sargassum fluitans* also washed ashore on Lee County beaches in summer 2004. Populations of pelagic *Sargassum* (*S. natans, S. fluitans*) have been present for centuries and are continually transported by winds and surface currents between the Caribbean Sea, the Gulf of Mexico and the western North Atlantic Ocean. During this large-scale circulation, these pelagic oceanic populations frequently encounter relatively nutrient enriched neritic waters where the C:N, C:P, and N:P ratios decrease while productivity and growth rate increase. For example, the C:N, C:P, and N:P ratios of *Sargassum natans* decreased significantly from mean values of 49.4, 877, and 18.1 in the Sargasso Sea, to 27.9, 347, and 10.2 in neritic waters off the southeastern U.S. coastline (Lapointe, 1995). Such nutrient enrichment in coastal waters, coupled with strong onshore winds, can bring excessive biomass of Sargassum ashore and cause a variety of problems. Along the Florida panhandle and Texas coastlines, strandings of pelagic *Sargassum* have become a major problem for beach tourism in recent years (Lapointe, 1995). At the nuclear power plant in Crystal River, FL, a massive influx of *Sargassum* in 1990 caused a blockage in the cooling system, forcing a system shutdown (Rogers, 1991).

4.2. Land-based sources of nutrient enrichment

Multiple lines of evidence support the hypothesis that discharges from the Caloosahatchee River and other land-based sources can provide nutrients to blooms of red drift macroalgae (and phytoplankton) for considerable distances from shore. The evidence includes significant enrichment of DIN, SRP, TDN, and TDP in fresh waters of the Caloosahatchee and Peace Rivers relative to coastal waters of the study area. Following increased discharges from these rivers after hurricanes Charley, Frances, and Jeanne, we observed a six-fold increase in NH_4^+ ($\leq$ 0.20 vs. 1.31 μM) and a three-fold increase in SRP (0.30 vs. 0.92 μM) to ~ 26 km from shore.

The increasing importance of NH_4^+ relative to NO_3^- with increasing land-based runoff to Lee County's coastal waters is apparent from the significant decrease in the f-ratio between our dry (August) and wet (October) samplings. Although the f-ratio was historically used by oceanographers to gauge the relative importance of upwelled NO_3^- to phytoplankton growth (Harrison et al., 1987), our previous research in the Florida Keys (Lapointe et al., 2004) and in Lee County during this study demonstrate the utility of this ratio in assessing land-based discharges of NH_4^+. Concentrations of NO_3^- in Lee County's coastal waters were statistically similar (~ 0.9 μM) in August and October, compared to the six-fold increase (0.20 vs. 1.31 μM) in NH_4^+ concentrations that resulted in the decreased f-ratio. This NH_4^+ concentration is high for coastal waters and two-fold greater than the concentration needed to support maximum growth rates of *Karenia brevis* (Steidinger et al., 1998), as well as the rhodophytes *Neoagardhiella bayleii* and *Gracilaria tikvahiae* (DeBoer et al., 1978). Considering that NH_4^+ is the preferred N source for growth of *K. brevis* (Steidinger et al., 1998) and the rhodophytes *N. bayleii* and *G. tikvahiae* (DeBoer et al., 1978), it is not surprising that blooms of these species can follow seasonal increases in land-based runoff and NH_4^+ enrichment of coastal waters following the onset of the wet season in Lee County.

Although considerable nutrient loadings from the Caloosahatchee River discharges are linked to water releases from Lake Okeechobee, a comparison of the $\delta^{15}N$ values of macroalgae along the Caloosahatchee River provide evidence of significant N enrichment from within the basin itself. The algal tissue $\delta^{15}N$ values increased westward from the Ortona (+ 8-9 ‰) to Franklin locks (+16 ‰) along the Caloosahatchee River, indicating significant localized N enrichment. This $\delta^{15}N$ enrichment correlated with increased DIN concentrations between these two structures, a phenomenon that is also apparent in the nutrient monitoring data collected by the South Florida Water Management District (SFWMD, DBHYDRO). The $\delta^{15}N$ values at the Franklin Lock are at the high end of the sewage nitrogen range (Heaton, 1986; Lapointe, 1997; Costanzo et al., 2001) and suggest significant sewage N enrichment of the Caloosahatchee River from the surrounding basin. Doering and Chamberlain (1999) analyzed the importance of source (Lake Okeechobee vs. Caloosahatchee River basin) to the quality of freshwater discharges to Caloosahatchee estuary and found that nutrient concentrations (except ammonia) and color in the estuary were higher when the basin rather than Lake Okeechobee was the source. Downstream of the Franklin Lock, ~ 20 million gallons per day (MGD) of sewage effluent receiving advanced wastewater treatment (AWT; DIN and SRP concentrations of ~ 214 μM and 32 μM, respectively) is discharged directly into the Caloosahatchee estuary upstream of San Carlos Bay (Florida Department of Environmental Protection, personal communication).

The $\delta^{15}N$ values in macroalgae from Lee County's beaches and coastal reefs indicate that land-based N-enrichment affects the water column for considerable distances from shore. Compared to the Caloosahatchee River, lower $\delta^{15}N$ values of ~ + 6 ‰ occurred in drift macroalgae on Lee County's beaches, values within the range reported for macroalgae enriched with sewage N (Costanzo et al., 2001; Lapointe et al., 2004). The $\delta^{15}N$ values of macroalgae decreased with increasing distance from shore, but remained at or above + 3 ‰ (the low end of the sewage range) at N. Deep Ledge, the most offshore station some 26 km offshore Sanibel Island. Although these high $\delta^{15}N$ values in macroalgae of the Caloosahatchee River and downstream receiving waters suggest the importance of surface water transport of wastewater N, submarine groundwater discharge in the study area could be of the same magnitude as the river discharges (Miller et al., 1990) and may therefore be an important route for the transport of sewage N from septic tanks and/or injection wells to coastal waters. The significant N enrichment of the water column to at least 26 km from shore would be available to support growth of not only macroalgae, but phytoplankton as well. Blooms of the red tide dinoflagellate, *Karenia brevis*, develop along this coastline at similar distances from shore (Tester and Steidinger, 1997).

The present study cannot resolve the relative importance of specific sourcs of sewage N enrichment, although multiple sources on the southwest Florida watershed could contribute. Historically, the Caloosahatchee River was not connected to Lake Okeechobee and canal projects were developed in the early 1880's to lower the water level in Lake Okeechobee.

This resulted in "new" nutrient sources from Lake Okeechobee, which receives drainage from the Kissimmee River basin, the Everglades Agricultural Area, and the St. Lucie drainage basin to the east when that water is backpumped into Lake Okeechobee (Steinman et al., 2002). Accordingly, runoff from dairy and cattle farms in the Kissimmee basin, domestic treated sewage that is discharged into surface waters or re-used in agricultural areas, and septic tank discharges from throughout this region could all contribute to the sewage $\delta^{15}N$ signature we observed at both the Ortona and Franklin locks on the Caloosahatchee River.

However, the significant reduction in $\delta^{15}N$ values of the coastal macroalgae from August (+ 5.84 ‰) to October (+ 3.89 ‰) may reflect an increased contribution of N from rainfall and agricultural N sources following the high Lake Okeechobee discharges and the 2004 hurricanes (Fig. 9). The $\delta^{15}N$ values of N in rainfall, organic peat, and fertilizers used on sugarcane and citrus farms in south Florida have $\delta^{15}N$ values in the range -3 to + 3 ‰ (Table 1). Hence, periods of peak discharge from Lake Okeechobee, such as those between August and October 2004, would result in increased N (especially ammonia) contributions from these sources that would lower the $\delta^{15}N$ signature of macroalgae in downstream coastal waters. In the Lower Florida Keys, elevated $\delta^{15}N$ values of macroalgae reflect sewage N sources from local sources in the Keys during drought periods when little agricultural runoff of N from the Everglades occurs. In wet years, however, increased stormwater runoff from agricultural areas lowers the $\delta^{15}N$ values of macroalgae to values similar to the source signatures of fertilizers and peat (Lapointe et al., 2004).

The three-fold increase in SRP concentrations between August and September throughout the study area also indicate widespread P enrichment from land-based runoff. The SRP concentrations were highest in the Peace River (~ 17 μM) and downstream waters of S. Charlotte

Harbor (3.7 μM) during our study, supporting previous conclusions of the importance of this river as a P source (McPherson and Miller, 1990). SRP concentrations in rivers along the southwest coast of Florida are substantially higher than in most North American rivers (Lovejoy et al., 1990; Flannery et al., 1991) and correlate with the natural phosphatic rock formations in this region (Kaufman, 1969). The greatest contribution of SRP to these waters is a direct result of anthropogenic pollution (Odum, 1953), particularly the phosphate mining industry (Task Group Report, 1967). These large P burdens make the Alafia, Peace, and Fenholloway rivers the greatest P carriers in all of Florida (LaRock and Bittacker, 1973). Runoff from the Peace River following Hurricane Charley would contribute to our observed increase in mean SRP concentrations in coastal waters from 0.30 μM in early August to 0.92 μM in October, respectively. These represent very high SRP concentrations (which dominated the TDP pool) as only ~ 0.1 μM is required to satisfy growth demands of macroalgae (Lapointe, 1997) and the red tide dinoflagellate, *Karenia brevis* (Wilson and Ray, 1958).

4.3. Understanding and managing macroalgal blooms in Lee County's coastal waters

The development of macroalgal blooms in coastal waters of southern Lee County and accumulation on adjacent beaches is dependant on local hydrodynamic and meteorological factors, including antecedent events. Discharges from the Caloosahatchee River deliver not only nutrients from Lake Okeechobee and basin sources, but also estuarine nutrient loads associated with municipal sewage outfalls in Ft. Myers that are discharged into the estuary. Although the initial beach accumulation of red drift macroalgae in August 2003 followed major discharges (> 12,000 cfs) and nutrient loading from the Caloosahatchee River (Fig. 9), the massive biomass involved would require a considerable time period for development prior to stranding. In addition to nutrients, light is a critical factor in the development of benthic macroalgal HABs and increased light attenuation follows major freshwater discharges as a result of the high color (dissolved humic compounds) content of the fresh water and increased chlorophyll *a* that develops downstream of the discharges (Doering and Chamberlain, 1999). Considering the importance of light to the growth of these rhodophytes, the development of benthic macroalgal HABs might be favored during periods of low or moderate flows from the Caloosahatchee River, which occurred during and following the 2000/2001 drought (Fig. 9) in South Florida (Abtew et al., 2002). On Florida's east coast, invasive blooms of *Codium isthmocladum* first developed during the drought years of 1989-1990 with subsequent blooms of *Caulerpa brachypus* forma *parvifolia* occurring during the 2000/2001 drought (Lapointe et al., 2005). Periods following peak flows and nutrient loads from the Caloosahatchee River and other land-based sources would favor phytoplankton rather than macroalgal blooms (Valiela et al., 1997), and the blooms of rhodophytes that occurred in 2003 and early 2004 have not re-emerged with the increased discharges following the 2004 hurricanes (Fig. 9). However, an intense *Karenia brevis* bloom persisted in southwest Florida throughout 2005, which led to a 2,100 square mile hypoxic dead zone and the death of 79 manatees (Rothschild, 2005).

Increasing urbanization of southwest Florida, combined with pulsed water releases from the Caloosahatchee River, could make protected bays and shallow, nearshore waters of southern Lee County more prone to the development of rhodophyte blooms. The inshore bays (Estero Bay, San Carlos Bay) and shallow coastal waters off southern Lee County are directly impacted by the Caloosahatchee River plume. Although the shallow waters between Ft. Myers Beach and Bonita Springs are dominated by soft bottom sediments not conducive to growth of attached rhodophytes, surveys of this area indicated extensive populations of *Gracilaria tikvahiae*, *Agardhiella subulata*, and *Hypnea* sp. growing attached to the tubes of the polychaete worm

Chaetopterus cf. variopedatus (Fig. 2D). This large, tubiculous, suspension feeding polychaete plays an important role in nutrient cycling and benthic-pelagic coupling in lower Chesapeake Bay (Thompson and Schaffner, 2001) and could provide not only suitable substrate, but also recycled nutrients that may enhance the growth of rhodophytes attached to their tubes. Strong winds, currents, and tides eventually detach the macroalgae from the benthos and deposit the biomass on beaches (Fig. 2 A,B, and E), where odor and aesthetic problems diminish the use of the beaches by residents and tourists alike.

Excessive biomass of macroalgae can have major impacts on coastal economies through loss of tourism and increased costs associated with beach cleanup programs. Along Maui's Kihei coast, Hawaii, USA, over $20 million (U.S.) a year in tourism revenues and property values have been lost as a result of macroalgal blooms (*www.hawaii.edu/ssri/hcri/ev/kihei_coast.htm*). In Maui County, some $250,000 (U.S.) is spent annually by condominium owners to remove excessive seaweed biomass from the beaches. In the Peel Inlet, Australia, removal of seaweeds cost $160,000 (U.S.) annually for 13,000 m^3 of macroalgae (Atkins et al., 1993). In France, the cost exceeded 3.6 million francs for 90,000 m^3 of "green tides" removed from the Brittany coastline in 1992 (CEVA, 1993). In Lee County, seaweed removal programs for the beaches were historically nominal but increased dramatically, to $260,503 for the fiscal year 2003/2004, with the onset of the red drift macroalgal blooms (U.S.; Lee County Visitor and Convention Bureau; Fig. 10). Following the termination of these blooms by hurricane Charley, beach cleanup costs decreased in 2005 (Fig. 10).

Because the physical harvesting of macroalgae is costly and often insufficient to control macroalgal blooms, water quality restoration is usually necessary (Morand and Briand, 1996). The recent emergence of the red drift macroalgal HABs in Lee County suggests that nutrient loading to these inshore waters is increasing. Data generated from ongoing and new water quality monitoring programs could be used to develop a conceptual model for the influence of various land-based nutrient sources, including discharges from the Peace and Caloosahatchee rivers, on the development of phytoplankton and macroalgal HABs. Such a model could help visualize how biological, chemical, physical, and meteorological factors interact to produce these blooms. For example, biomass of *Ulva* and *Gracilaria* in the Venice Lagoon, Italy, has become so large that it can regulate seasonal nutrient cycles through growth and decomposition, thereby controlling the seasonal development of phytoplankton blooms (Sfriso et al., 1992). In Lee County, nutrient uptake by extensive blooms of rhodophytes could play an increasing role in regulating nutrient cycles and seasonal phytoplankton blooms, including blooms of *Karenia brevis*. Studies in the Bachimen Sea, China, showed that *Gracilaria tenuistipitata* depressed red tide blooms (Tang et al., 2003), suggesting that nutrient competition and/or allelopathy by rhodophytes may provide a means to mitigate red tides.

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Figure Legend

Fig. 1. A map of the Lee County, FL area showing station locations for the 2004 study: Ortona Lock (ORT) and Franklin Lock (FRK) on the Caloosahatchee River, Peace River (PCR), Imperial River (IMP), San Carlos Bay (SCB), S. Charlotte Harbor (SCH), 17th Street Reef (NSL), N. Deep Ledge (NDL), ARC Reef (ARC), Blanda's Reef (BLD), and Belton-Johnson Culvert Reef (CLV).

Fig. 2. Red drift macroalgae in coastal waters of Lee County, FL: A.) rhodophytes, Bonita Springs Beach, January, 2004; B.) rhodophytes, Bonita Springs Beach, July, 2004; C.) rhodophytes, 17th Street Reef, August, 2004; D.) worm tube with attached rhodophyte, Bonita Springs Beach, August, 2005; E.) rhodophytes in shallow water along beaches in southern Lee County.

Fig. 3. Mean concentrations (μM, ± 1 SD, n = 2) of water column dissolved inorganic nitrogen (DIN), ammonium (NH_4^+), nitrate (NO_3^-) and f-ratios (NO_3^-:DIN) in August and October 2004 at sampling stations in Lee County, FL.

Fig. 4. Mean water column SRP concentrations (μM, ± 1 SD, n = 2) and DIN:SRP ratios in August and October 2004 at sampling stations in Lee County, FL.

Fig. 5. Mean water column TDN and TDP concentrations (μM, ± 1 SD, n = 2), with relative contributions of organic and inorganic forms, in August and October at sampling stations in Lee County, FL.

Fig. 6. Mean tissue C:N, C:P, and N:P molar ratios (± 1 SD, n = 1-8) in macroalgae collected August and October 2004 at sampling stations in Lee County, FL.

Fig. 7. A.) Mean tissue $\delta^{15}N$ (‰, ± 1 SD, n = 2-8) of macroalgae collected in August and October 2004 at sampling stations in Lee County, FL and B.) from Bonita Springs Beach in July and August 2004, including a comparison among beach and reef samples of the rhodophyte *Hypnea musciformis*.

Fig. 8. A comparison of mean tissue C:N, C:P, and N:P molar ratios (± 1 SD, n = 3-6) in macroalgae from Lee County, FL during this study with macroalgae from southeast Florida (Lapointe et al. 2005), Jamaica and the Bahamas (Lapointe et al. 1992).

Fig. 9. Monthly mean flow rates (cubic feet per second, cfs) at Franklin Locks on the Caloosahatchee River, FL in 2003-2004. Arrows indicate beach drift algae events.

Fig. 10. Beach clean-up costs in Lee County, FL, 1997-2005 ($ U.S.).

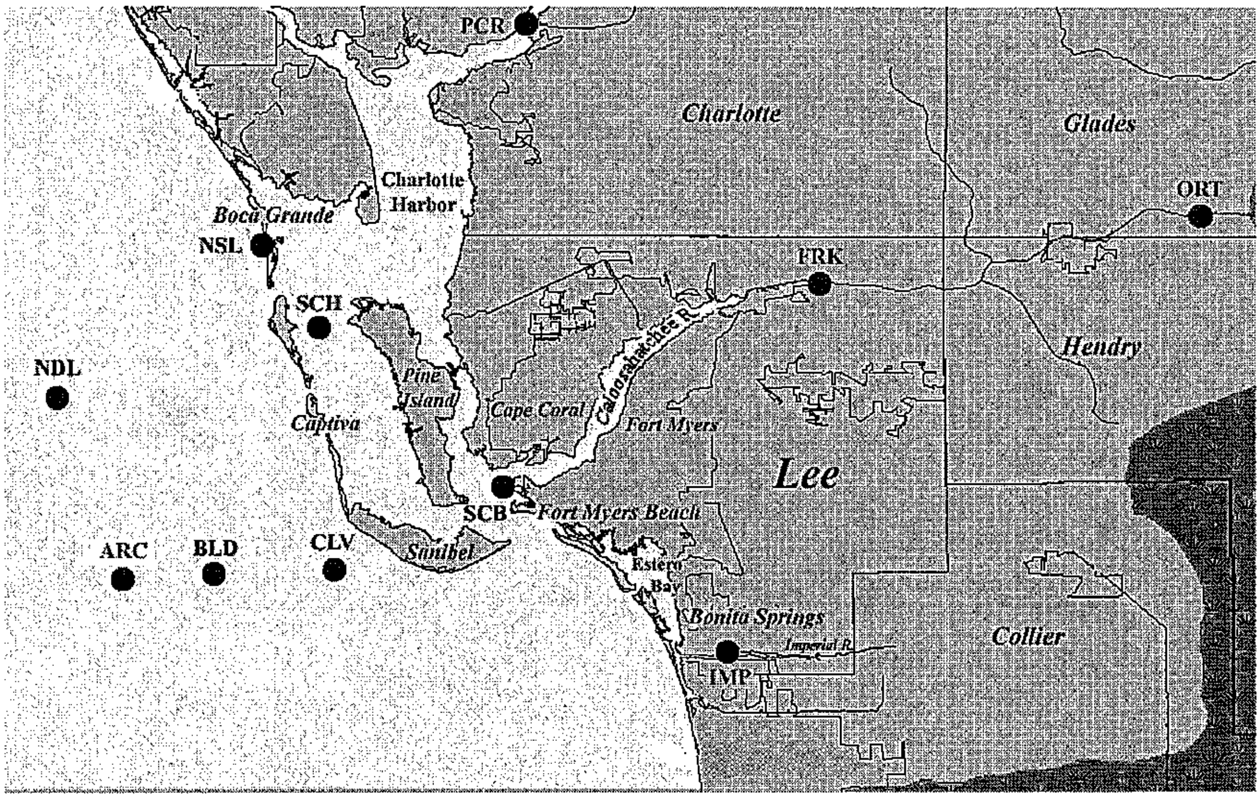

PCR
Charlotte
Glades
Charlotte
Harbor
Boca Grande
NSL
ORT
FRK
SCH
Caloosahatchee R.
Hendry
NDL
Pine
Island
Cape Coral
Captiva
Fort Myers
Lee
SCB
Fort Myers Beach
ARC
BLD
CLV
Sanibel
Estero
Bay
Bonita Springs
Imperial R.
Collier
IMP

Fig. 1

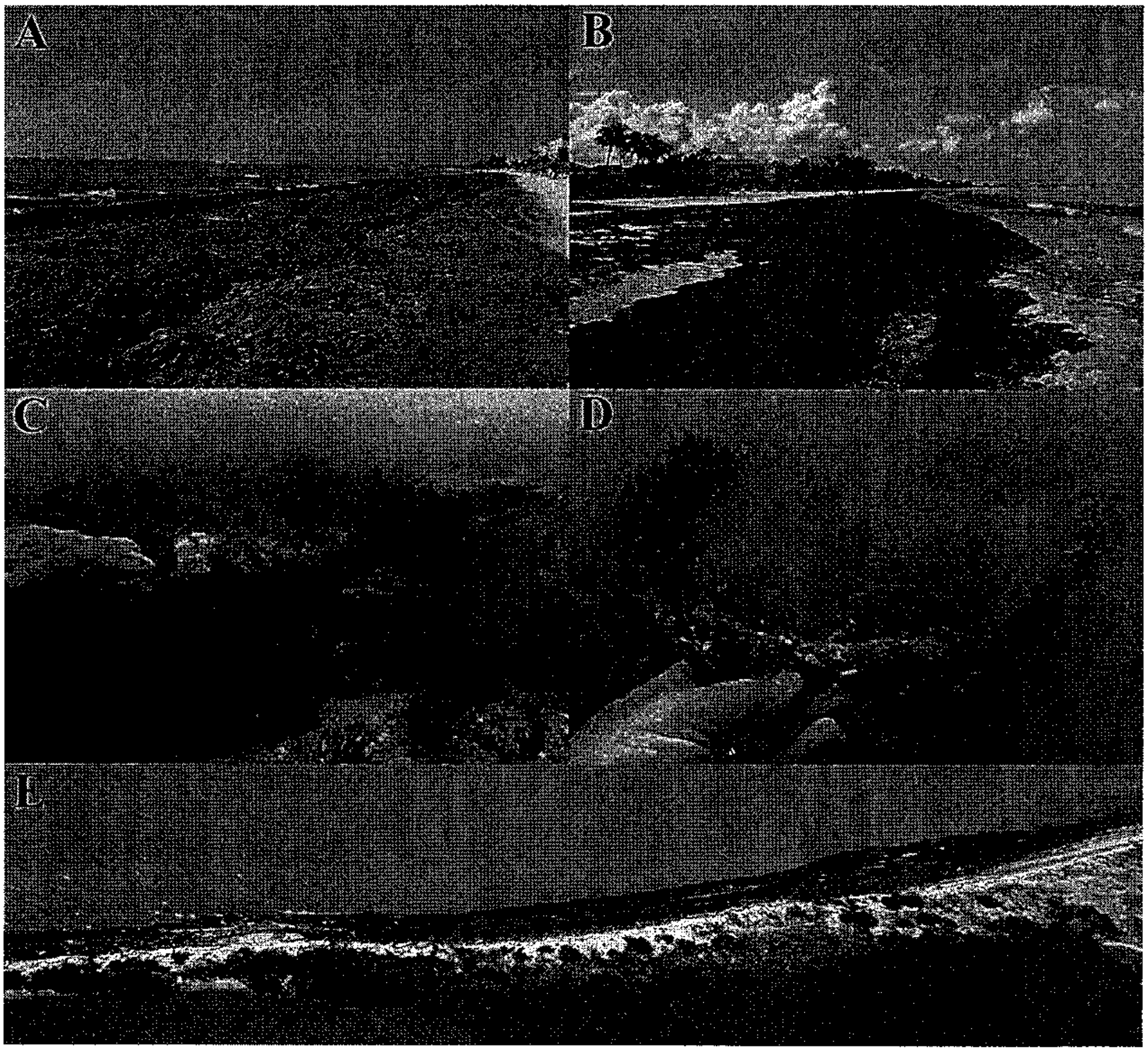
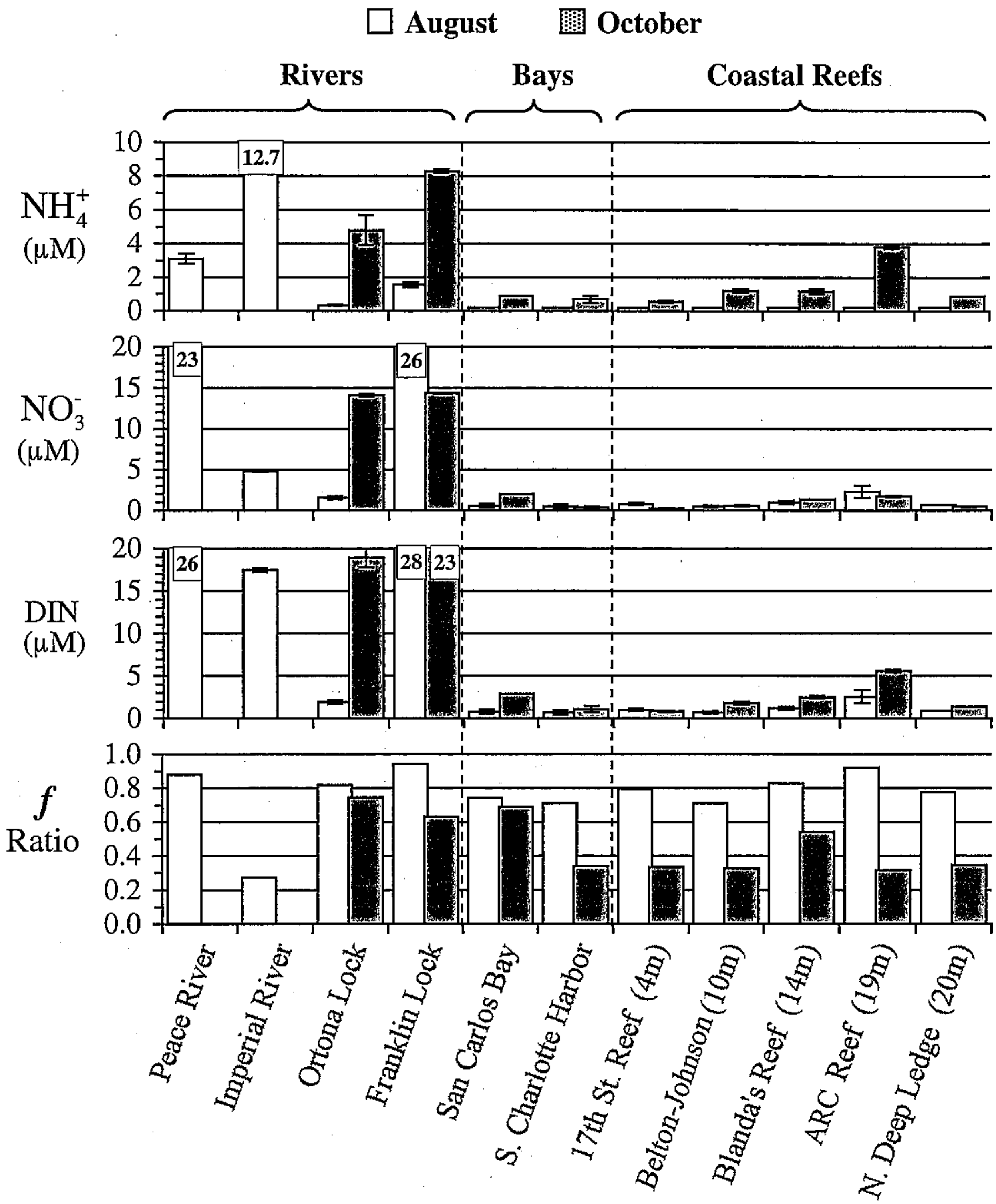


Fig. 2



August
October
Rivers
Bays
Coastal Reefs
NH4+ (μM)
NO3- (μM)
DIN (μM)
f Ratio
12.7
23
26
26
28
23
Peace River
Imperial River
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harbor
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)

Fig. 3

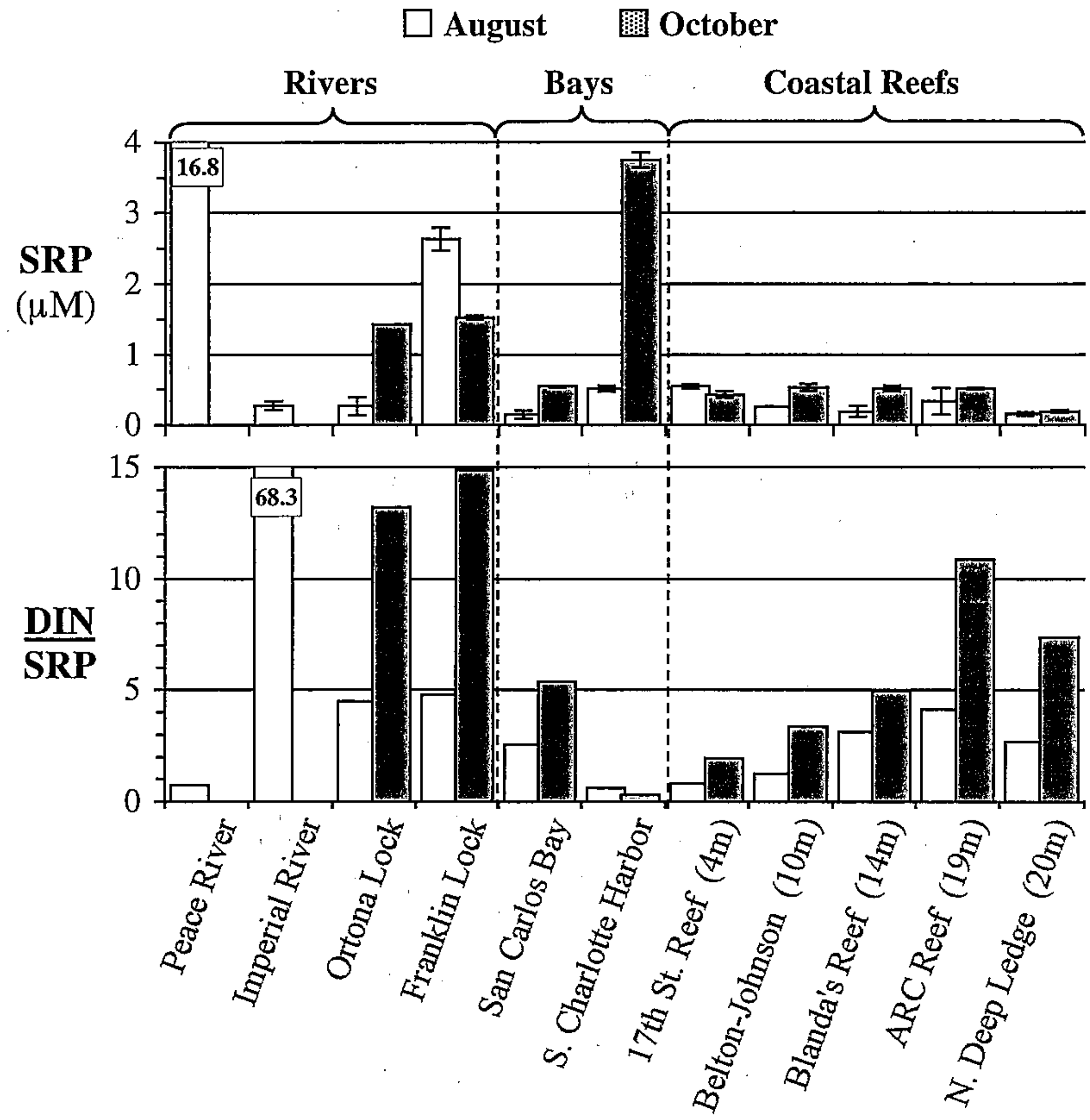
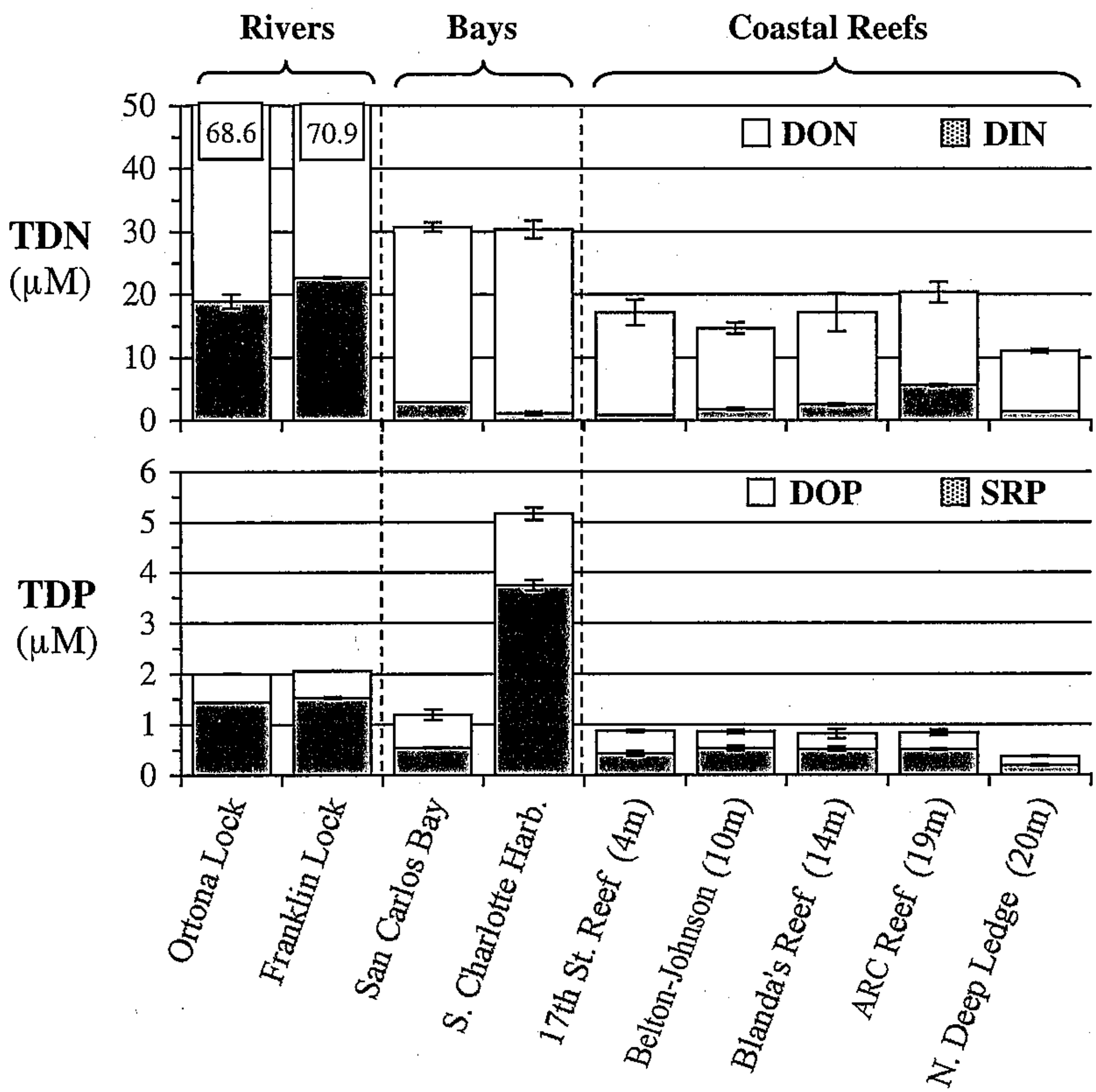

August
October
Rivers
Bays
Coastal Reefs
SRP (μM)
4
3
2
1
0
16.8
15
10
5
0
DIN / SRP
68.3
Peace River
Imperial River
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harbor
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)

Fig. 4



Rivers
Bays
Coastal Reefs
TDN
(µM)
68.6
70.9
DON
DIN
TDP
(µM)
DOP
SRP
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harb.
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)

Fig. 5

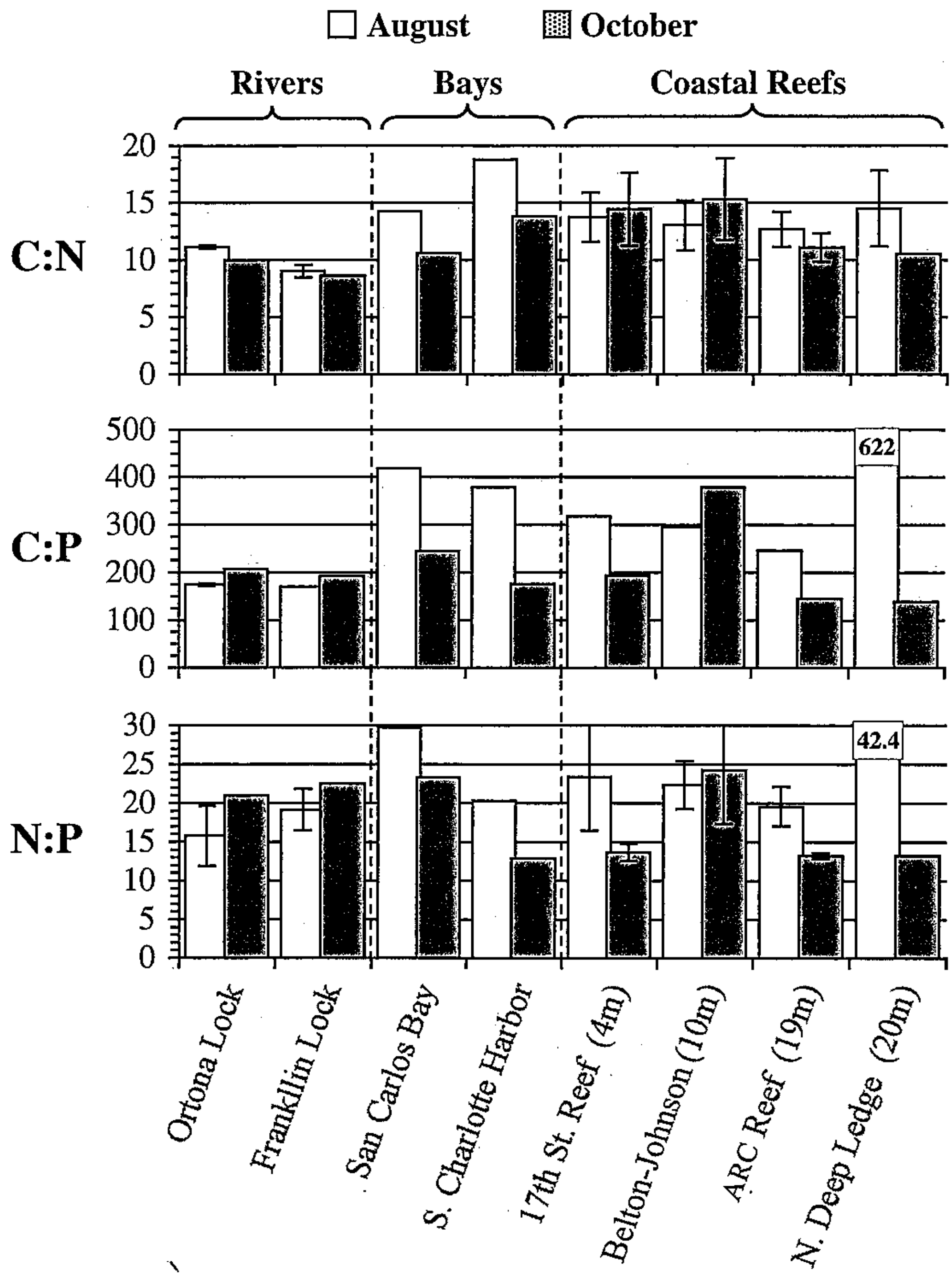


Fig. 6

mean tissue molar ratios in macroalgae

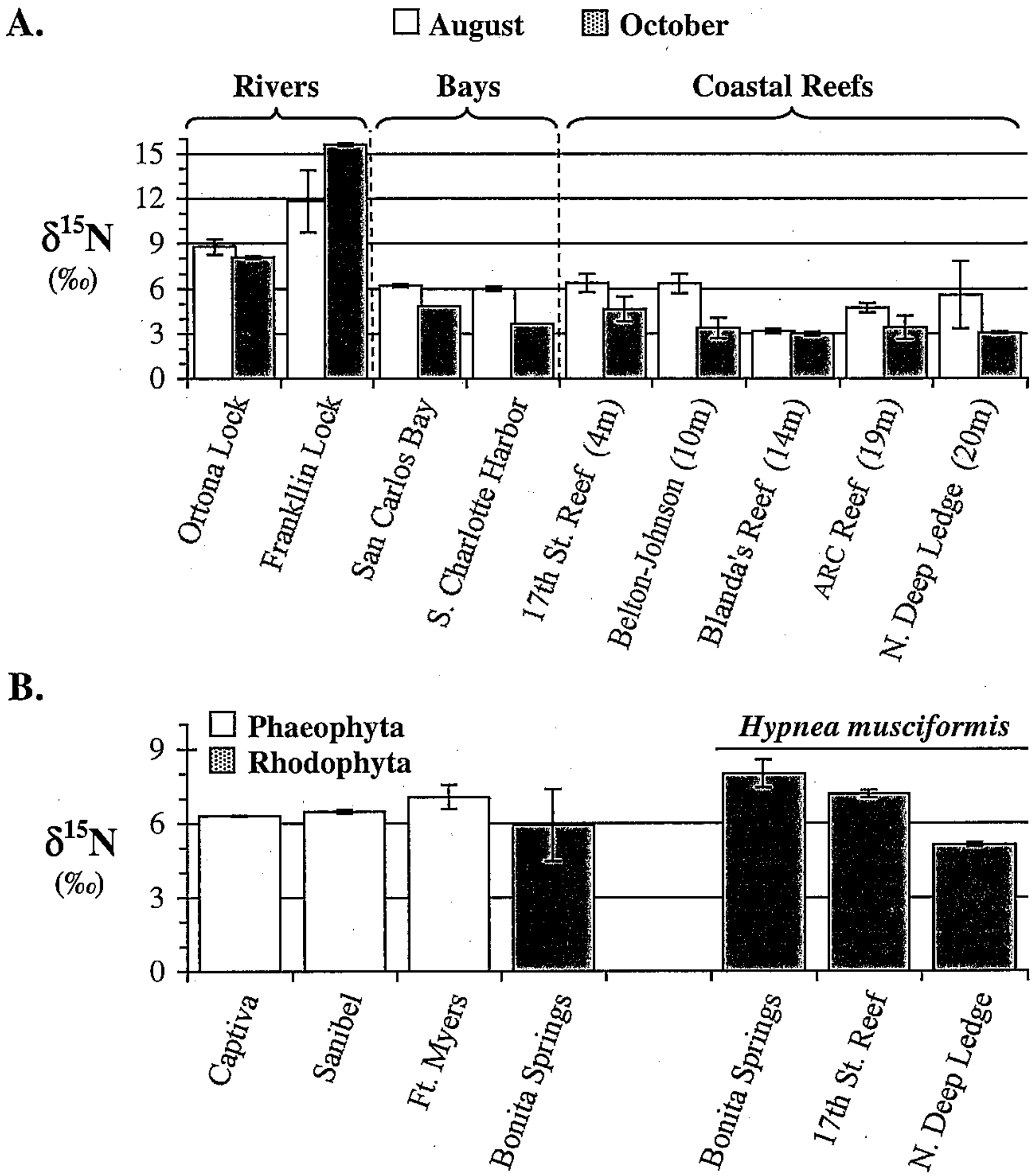
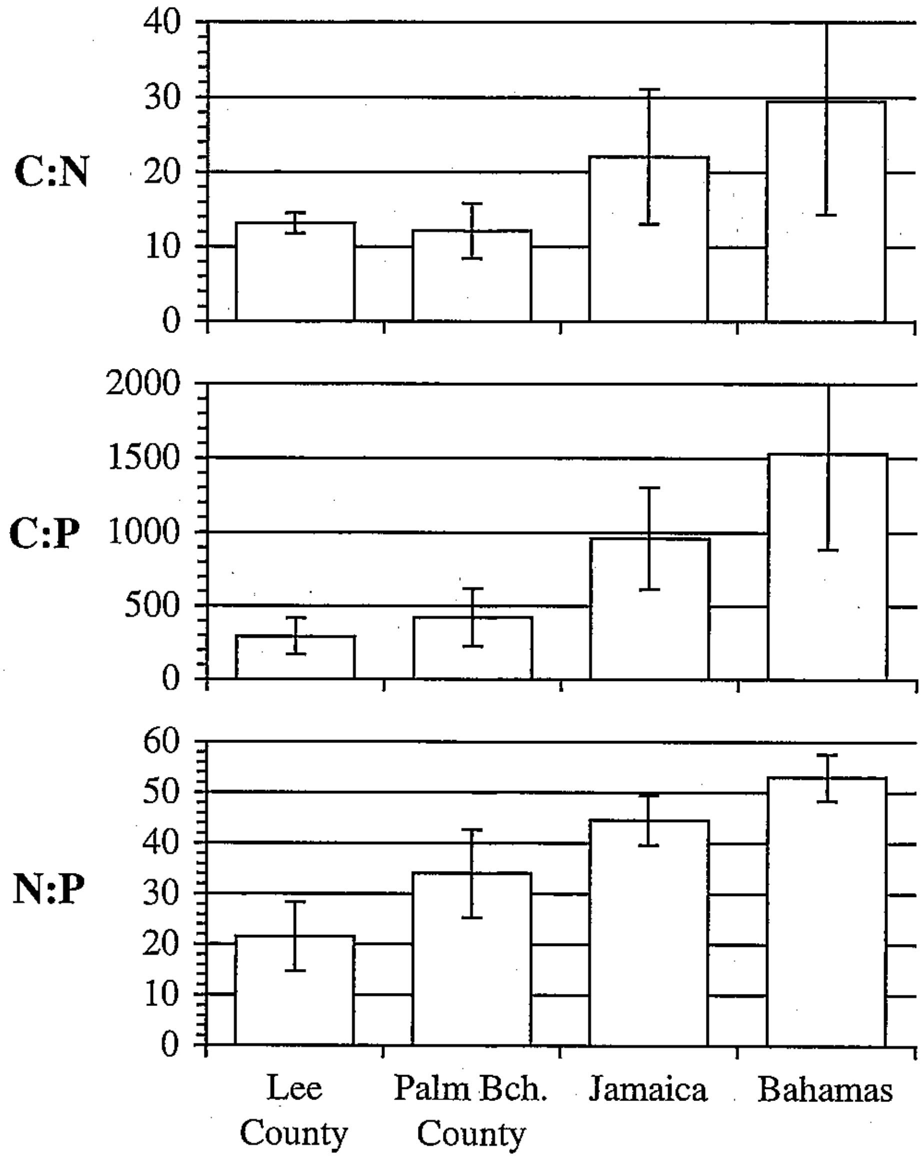
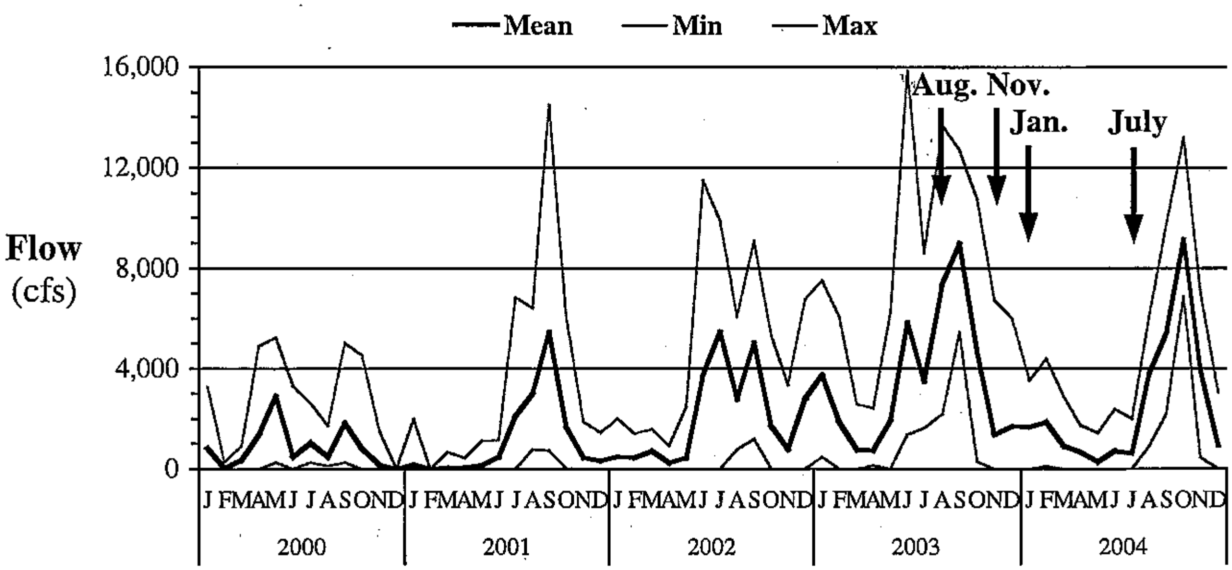

A.
August
October
Rivers
Bays
Coastal Reefs
15
12
9
6
3
0
δ15N
(‰)
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harbor
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)
B.
Phaeophyta
Rhodophyta
Hypnea musciformis
9
6
3
0
δ15N
(‰)
Captiva
Sanibel
Ft. Myers
Bonita Springs
Bonita Springs
17th St. Reef
N. Deep Ledge

Fig. 7



Shows
N Limitation

Fig. 8



Arrows indicate Drift algae events

Fig. 9

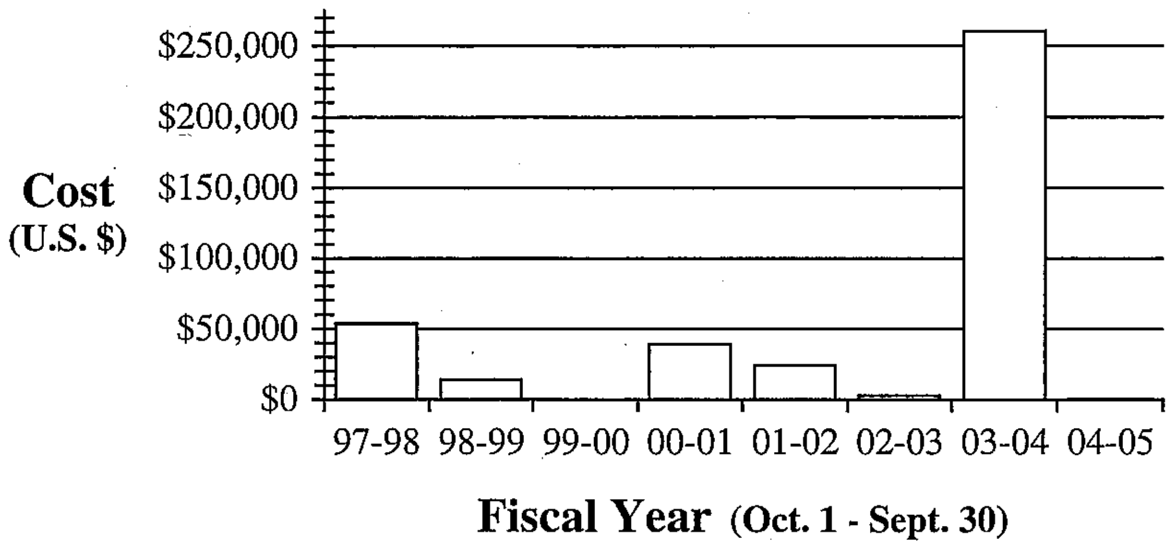

Cost
(U.S. $)
$250,000
$200,000
$150,000
$100,000
$50,000
$0
97-98 98-99 99-00 00-01 01-02 02-03 03-04 04-05
Fiscal Year (Oct. 1 - Sept. 30)

Fig. 10

Table 1. Source $\delta^{15}N$ values.

Source & Location	$\delta^{15}N$ (‰)	Reference
Ocean Sewage Outfall -		
N. Broward County	+8.6	Hoch et al., 1995
Septic Tank Effluent -		
Jupiter Creek Monitor Well #4	+7.3	Lapointe and Krupa, 1995a
Jupiter Creek Monitor Well #5	+19.5	"
Tequesta Monitor Well #6	+4.6	Lapointe and Krupa, 1995b
Tequesta Monitor Well #10	+11.8	"
Upwelled Nitrate -		
North Atlantic Ocean	+4.8	Sigman et al., 2000
Inorganic Fertilizer	0 - +3.0	Owens, 1987
Peat	0 - +3.0	Heaton, 1986
Atmospheric Ammonia	-3.13	Paerl and Fogel, 1994
Atmospheric Nitrate	+1.0	"

Table 2. Stations, depths, and species collected for analysis from study sites in Lee County, FL, USA in July (J), August (A), and October (O) of 2004.

Species \ Site, Depth	ORT <1 m	FRK <1 m	SCB 1 m	SCH 1 m	NSL 3 m	CLV 10 m	BLD 14 m	ARC 19 m	NDL 20 m	BSB Bch.	FMB Bch.	SAN Bch.	CAP Bch.
Rhodopyta	-	-	-	-	-	-	-	-	-	-	-	-	-
Agardhiella subulata						*O*				*J*			
Botryocladia occidentalis					*A O*	*A O*	*A O*	*A O*	*A O*	*J*			
Euchuma isiforme var. *denudatum*					*O*	*O*	*A O*			*J*			
Gracilaria cervicornis					*A O*	*A*	*A*	*A*	*A*	*J*			
Gracilaria mammalaris					*A O*								
Gracilaria tikvahiae										*J*			
Hypnea musciformis					*A*					*A*			
Rhodymenia divaricata						*A O*		*A O*	*A*				
Phaeophyta	-	-	-	-	-	-	-	-	-	-	-	-	-
Sargassum fluitans											*A*	*A*	*A*
Chlorophyta	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladophora sp.	*A O*	*A O*											
Cyanophyta													
Lyngbya sp.	*A*	*A*											
Angiosperma	-	-	-	-	-	-	-	-	-	-	-	-	-
Thalassia testudinum			*A O*	*A O*									

CLADOPHORA NOT PRESENT ~~PRESENT~~ IN SCB, BUT PRESENT @ ORTONA + FRANKLIN LOCKS DURING STUDY (AUG + OCT 2004)

Table 3. Water column nutrient concentrations at study sites in Lee County, FL, USA in August and October of 2004. Values represent means ± 1 S.D.

	n	Ammonium (μM)	Nitrate+Nitrite (μM)	DIN (μM)	*f* -Ratio (NO3+2) / DIN	SRP (μM)	DIN / SRP Ratio
August	14	0.20 ± 0.00	0.91 ± 0.72	1.11 ± 0.72	0.77 ± 0.11	0.30 ± 0.18	6.88 ± 2.35
October	14	1.31 ± 1.08	0.97 ± 0.69	2.29 ± 1.57	0.41 ± 0.14	0.92 ± 1.20	4.96 ± 0.99

Table 4. Tissue C:N, C:P, and N:P molar ratios and ¶15N in macroalgae from coastal study sites in Lee County, FL, USA in August and October 2004. Values represent means ± 1 S.D.

	C:N Ratio	C:P Ratio	N:P Ratio	¶15N (ä)
August	13.93 ± 2.78 (n=16)	386.3 ± 198.0 (n=16)	27.43 ± 11.40 (n=16)	5.84 ± 1.37 (n=32)
October	13.54 ± 3.43 (n=13)	242.0 ± 142.1 (n=13)	17.51 ± 6.74 (n=13)	3.89 ± 0.96 (n=26)

PHASE II FINAL REPORT

Harmful Algal Blooms in Coastal Waters of Lee County, FL: Bloom Dynamics and Identification of Land-Based Nutrient Sources

Prepared by:

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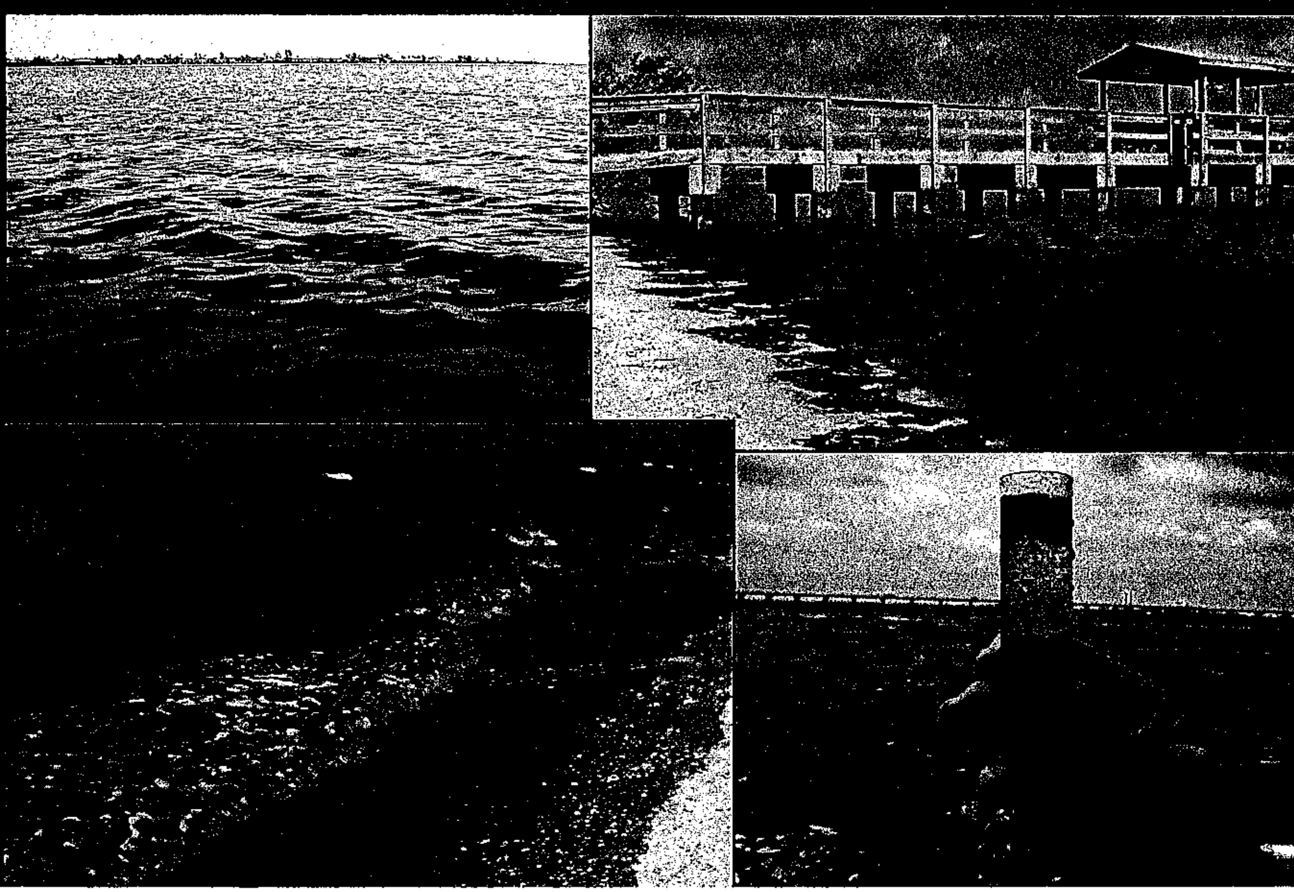
June 2006



Background

Harmful Algal Blooms (HABs) have increased in their frequency of occurrence and spatial extent over recent decades throughout coastal waters of the world. HABs include both toxic phytoplankton species, such as red tides (*Karenia brevis*), as well as excessive biomass of macroalgae, or seaweeds. There is general agreement among scientists that increasing runoff of nutrient pollution from land-based sources is a major cause of the global increase in HABs (Glibert et al. 2005). The strength of the causal relationship and the ultimate source of the nutrients is highly variable and somewhat unique to each location, season, and HAB species.

During our Phase I studies evidence was presented indicating a link between the increasing intensity and duration of HABs and increasing land-based nutrient pollution from southwest Florida. In the case of red tide (*Karenia brevis*), an analysis of existing data (cell counts) from the 1950's and 1990's showed that these blooms have intensified an average of 15-fold since the 1950's, occur primarily in nearshore (not offshore) waters, and that the duration of the blooms has increased (Brand and Compton, in press). Newly acquired evidence from Lee County's coastal waters has indicated that the red drift macroalgal blooms that plagued area beaches in 2003 and 2004 are a recent phenomenon and indicative of increasing land-based nutrient pollution (Lapointe and Bedford, in press).

The Phase I macroalgal HAB study used tissue $\delta^{15}N$ analysis to identify potential land-based nitrogen sources supporting these blooms. Analysis of macroalgae from area beaches for $\delta^{15}N$ revealed values of + 5 to + 8 ‰, which closely matches the source values of wastewater nitrogen (Lapointe and Bedford, in press). Although local sewage sources along area beaches and municipal outfalls may contribute to this sewage signal, macroalgae from the Caloosahatchee River showed the highest $\delta^{15}N$ values (+ 8 ‰ to + 15 ‰), which suggest the importance of the river discharges during high flow periods in transporting wastewater nitrogen loads from eastern areas of Lee County, Glades County, and Lake Okeechobee, into coastal waters of Lee County.

The limited scope of our Phase I study would not allow us to resolve the relative importance of local nitrogen inputs from Lee County versus far-field sources from Caloosahatchee River discharges. Accordingly, we performed a Phase II program following months of high Caloosahatchee flows in August and September 2005 to develop a long-term water quality monitoring in collaboration with Lee County staff. A primary goal of the Phase II program was to identify what aspects of a long-term water quality monitoring program could be performed by Lee County staff compared to more specialized services required from expert outside consultants.

Materials and Methods

The Phase II research performed in August and September 2005 included examination of existing data files that began in Phase I of this research. We continued to examine hard scientific data collected from published scientific papers, unpublished scientific manuscripts, government reports, digital libraries, and websites. Existing data from satellite imagery and aerial photography was also used. Personnel at organizations such as University of South Florida, Florida Gulf Coast University, Florida International University, Mote Marine Laboratory, county environmental laboratories, the Conservancy of Southwest Florida, Sierra Club, and other non-governmental organizations were considered for information that could be useful in testing the hypotheses

The water quality sampling design for Phase II involved three basic approaches: 1) collection of water samples along a gradient from various freshwater sources to offshore stations for analysis of a variety of water quality published values for nutrient sources (agricultural canal discharges, sewage outfalls, stormwater outfalls, rainfall).

I. *Water Sampling and Analysis*: In collaboration with Lee County staff, water samples were collected in August and September from stations along Lee County's beaches, through San Carlos Bay, Pine Island Sound, Charlotte Harbor, Estero Bay, and to offshore areas. The water samples were analyzed by the Lee County Environmental Laboratory for salinity and nutrients (ammonium, nitrate, nitrite, orthophosphate, total dissolved nitrogen, total dissolved phosphorus). The water samples were also analyzed for phytoplankton composition and abundance, presence and abundance of toxic algae, turbidity, organics, and nutrient bioavailability by Larry Brand at RSMAS, University of Miami, Virginia Key, FL.

II. *Distribution and Abundance of Macroalgal Blooms*: Sampling stations for long-term monitoring of macroalgal biomass on beaches were established in collaboration with Lee County staff and other key contacts A network of seven sites spanning Lee County's shoreline (Fig. 1) were sampled for water quality paramters (salinity and nutrients) and biomass of macroalgae using quadrats placed along replicate belt transects. Macroalgal samples were sorted, identified, wet weighed, and dried in a Fisher Isotemp lab oven to establish a wet weight-to-dry weight conversion factor. Biomass was quantified as grams dry weight per square meter (g/m^2). Digital photographic images were also collected at the stations to provide digital data for percent cove: determinations using the randomized point-count method.

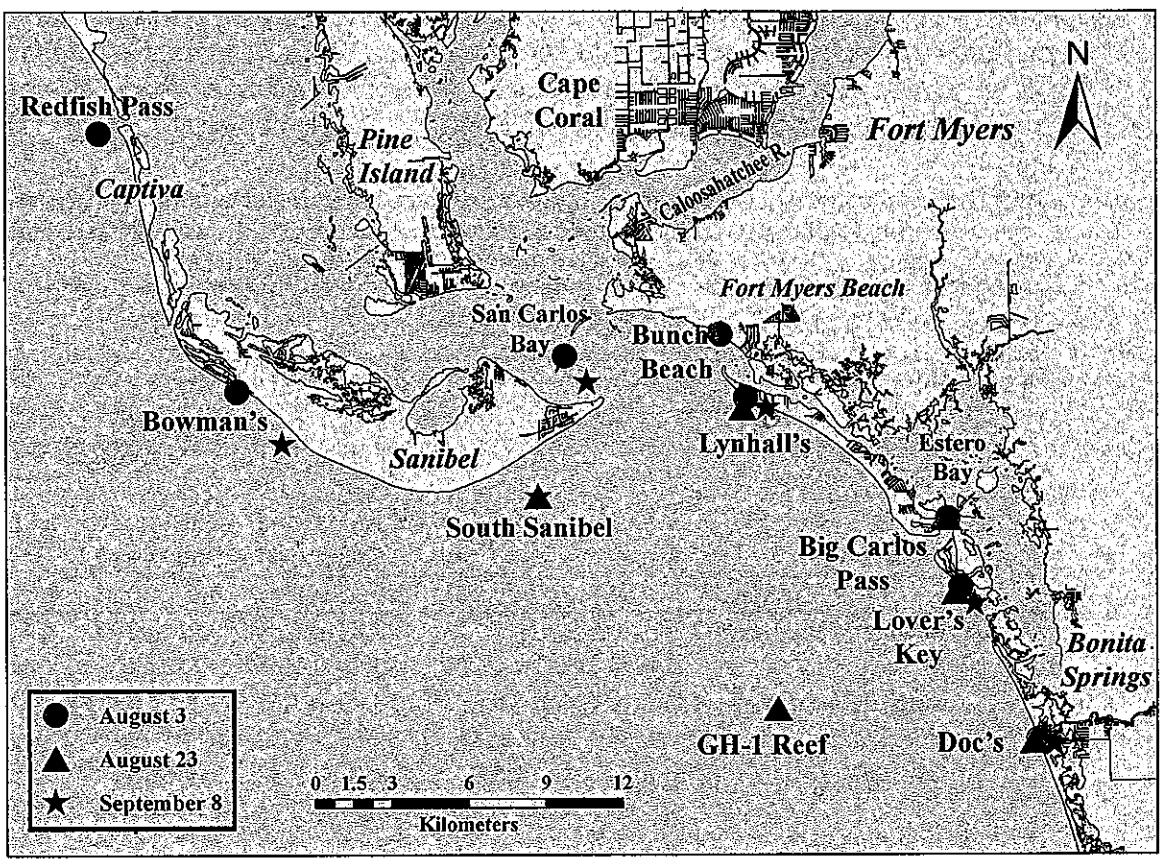


Figure 1. Map of the Lee County area showing sites sampled in August and September 2006

Digital aerial photography was also used to identify HABs in Lee County's coastal waters. On September 8th and 14th, 2005, we used a small aircraft flying at 500-1,000 ft to obtain digital photographic images of nearshore waters and beaches. These photos provided a planar section of coastline that can be used like a GIS image for overlay of important environmental parameters. The digital images were used to distinguish color

III. *$\delta^{15}N$ and C:N:P Analysis of Macroalgae and Toxic HABs*: Samples of macroalgae from the seven monitoring stations described above (II) were processed and analyzed for $\delta^{15}N$ values and C:N:P ratios as in the Phase I program. In addition, samples of *Karenia brevis* and *Microcystis aeruginosa* blooms were collected from offshore southern Sanibel Island and the Caloosahatchee River estuary, respectively, for $\delta^{15}N$ analysis. These phytoplankton were filtered onto GF/F filters, dried in a lab oven, and analyzed for $\delta^{15}N$ values.

Results and Discussion

I. Water Sampling and Analysis: Water samples for phytoplankton and nutrients were collected in August and September 2005 by Lee County staff from their routine monitoring stations. Subsamples of these collections, as well as additional samples from May to July 2005 and from October 2005 onward, have been analyzed by Larry Brand for phytoplankton variables. These results and a discussion of the data are provided in Appendix of this report.

Water samples were also collected at the beach sites for salinity and nutrient analysis on August 3rd, August 23rd, and September 8th. The August samples were analyzed by the Lee County Environmental Lab for ammonium, nitrate, total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), and the TDN:TDP molar ratio. Concentrations of ammonium and nitrate were below detection limits for these analyses (0.93 µM for ammonium, 0.71 µM for nitrate) at the beach sites on August 3rd (Table 1). On August 23rd, four of eight samples were below detection limits for ammonium and all samples were below detection limits for nitrate (Table 1). The September 8th samples were analyzed by the

Table 1. Water column concentrations (µM) of ammonium, nitrate, soluble reactive phosphorus (SRP), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP), and TDN:TDP molar ratios in samples collected August and September 2005 in Lee County, FL, USA.

Date	Site Name	Ammonium (µM)*	Nitrate (µM)*	TDN (µM)	SRP (µM)*	TDP (µM)*	TDN:TDP Ratio (M)
8/3/05	Bowman's Beach	*< 0.93*	*< 0.71*	28.91 ± 7.57	0.47 ± 0.02	*< 0.65*	44.8
	Sanibel Causeway	*< 0.93*	*< 0.71*	46.05 ± 1.51	0.98 ± 0.02	1.29 ± 0.00	35.7
	Bunche Beach	*< 0.93*	*< 0.71*	51.05 ± 1.51	0.71 ± 0.00	0.97 ± 0.00	52.7
	Lynhall's Beach	*< 0.93*	*< 0.71*	49.26 ± 6.06	0.69 ± 0.02	0.97 ± 0.00	50.9
	Lover's Key Beach	*< 0.93*	*< 0.71*	49.62 ± 4.54	0.36 ± 0.05	0.81 ± 0.23	64.9
	Doc's Beach	*< 0.93*	*< 0.71*	39.98 ± 4.04	0.42 ± 0.05	*< 0.65*	61.9
	8/3/05 Mean	*< 0.93*	*< 0.71*	44.15 ± 8.45	0.61 ± 0.24	1.01 ± 0.2	51.80
8/23/05	Bowman's Nearshore	1.14 ± 0.20	*< 0.71*	47.83 ± 1.01	0.21 ± 0.11	*< 0.65*	74.1
		< 0.93	*< 0.71*	53.90 ± 13.63	*< 0.13*	*< 0.65*	83.5
	Lynhall's Nearshore	1.00 ± 0.10	*< 0.71*	53.90 ± 7.57	0.47 ± 0.07	*< 0.65*	83.5
		< 0.93	*< 0.71*	34.63 ± 2.52	0.44 ± 0.02	*< 0.65*	53.6
	Lover's Nearshore	*< 0.93*	*< 0.71*	31.06 ± 3.53	*< 0.13*	*< 0.65*	48.1
		< 0.93	*< 0.71*	32.84 ± 3.03	0.87 ± 0.73	1.02 ± 0.53	38.1
	Doc's Nearshore	0.96 ± 0.05	*< 0.71*	34.98 ± 2.02	0.37 ± 0.02	*< 0.65*	54.2
		3.68 ± 0.15	*< 0.71*	34.27 ± 4.04	1.69 ± 0.34	1.94 ± 0.00	17.7
	8/23/05 Mean	1.70 ± 1.32	*< 0.71*	40.43 ± 9.74	0.68 ± 0.53	1.48 ± 0.46	56.60
9/8/05	Bowman's Nearshore	*< 0.21*	0.30 ± 0.03	23.00 ± 0.10	0.25 ± 0.00	1.02 ± 0.08	22.6
	San Carlos Bay	0.25 ± 0.05	2.40 ± 0.01	48.36 ± 0.21	1.34 ± 0.03	2.08 ± 0.08	23.3
	Lynhall's Nearshore	*< 0.21*	0.47 ± 0.06	33.72 ± 1.11	0.68 ± 0.01	1.48 ± 0.23	23.1
	Doc's Nearshore	*< 0.21*	0.44 ± 0.04	29.04 ± 0.05	0.23 ± 0.01	0.92 ± 0.01	31.6
	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Nutrient Analytical Services Lab at the Chesapeake Biological Lab, Solomons, MD, using more sensitive analytical methods. Despite much lower detection limits for ammonium (0.21 µM vs. 0.93 µM), concentrations of this nutrient were still undetectable at four of the five beach sites (Table 1), indicating the rapid assimilation of this preferred nitrogen form by nitrogen-limited algal blooms in the coastal waters. However, concentrations of nitrate were all above the detection limit (0.10 µM), with the highest concentration (2.40 µM) occuring in the relatively low salinity waters of San Carlos Bay. Regression analyses of SRP, TDN and TDP concentrations in surface waters versus salinity in all three samplings were all significant ($P < 0.05$; Fig. 2), indicating that nutrient enrichment of coastal waters was a result of freshwater discharges from land.

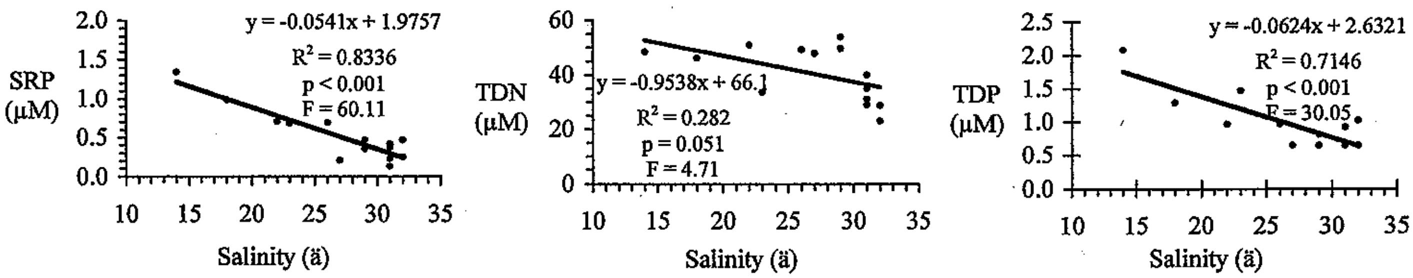


Figure 2. Regressions of soluble reactive phosphorus (SRP), total dissolved nitrogen (TDN), and total dissolved phosphorus (TDP) versus salinity for surface water samples collected in August and September 2005, Lee County, FL, USA.

The TDN:TDP ratio varied between 8.5 and 83.5, with the lowest value associated with a red tide bloom in 30 ‰ salinity water off southern Sanibel Island on September 8th (Fig. 3). These results support the observations of Ketchum and Keen (1947) and Slobodkin (1953) that the nearshore red tides on Florida's southwest coast are associated with high phosphorus coastal waters associated with fresh water runoff of the Peace and Caloosahatchee rivers.

II. *Distribution and Abundance of Macroalgal Blooms*: Biomass of macroalgae collected from seven beach sites on August 3, 2005 are shown in Table 2. At Doc's, Lover's Key, and Lynhall's, a variety of macroalgae were present at biomass levels up to ~ 30 g dry weight / m^2. Although this was a relatively low level of biomass compared to red drift bloom events in 2003 and 2004, many of the same rhodophyte bloom species occurred in August 2005 (e.g. *Hypnea spinella*, *Agardhiella subulata*, *Gracilaria tikvahiae*, *Acanthophora spicifera*). In addition, blooms of chlorophytes that are well known nutrient indicators species also occurred on beaches in southern Lee County during the present study. These included blooms of *Enteromorpha* sp. at Doc's and *Ulva lactuca* (Sea Lettuce) at Lynhall's.

Figure 3. Image of red tide sampling off southern Sanibel Island, September 8, 2005.

Nearshore biomass of macroalgae was estimated along underwater transects at Doc's, Lover's Key, and Lynhall's on August 23rd. Collections by divers indicated that ~ 7-9 g dry weight / m^2 occurred on these soft bottom communities at this time (Table 2). These are very low levels of benthic macroalgae and incapable of supporting the massive red drift blooms that occurred in 2003 and 2005.

The low levels of macroalgal biomass in August 2005 are clearly related to the highly turbid conditions and low levels of downwelling light in Lee County's coastal waters at this time. Water sampling at the beach sites in August indicated relatively low salinities (18-32 ‰), largely a result of large discharges from the Caloosahatchee River (Franklin Lock) that occurred during this period (Table 3). These low salinities corresponded with high concentrations of chlorophyll *a* (2.6-16.7 µg/l) in August, as well as high turbidity (Secchi depths < 1.8 m) in August/September (Table 3). Stratification of the water column was apparent in the

Table 2. Algal biomass (g / m^2) and percent cover on beaches and in nearshore waters at sampling sites in August 2005, Lee County, FL, USA, .

Location	Species	% of Site Total	Beach Drift Biomass Wet Weight (g / m^2)	Beach Drift Biomass Dry Weight (g / m^2)	Beach Drift Zone Width (m)	Beachfront Biomass Dry Weight (g / m)	Beach Drift Zone % Cover	Nearshore Biomass Wet Weight (g / m^2)	Nearshore Biomass Dry Weight (g / m^2)	Nearshore % Cover
Doc's	*Hypnea spinella*	79.85	71.00	9.23		9.23				
	Enteromorpha sp.	15.97	14.20	1.99		1.99				
	Thalassia testudinum	2.50	2.22	0.51		0.51				
	Agardhiella subulata	1.12	1.00	0.12		0.12				
	Gracilaria tikvahiae	0.56	0.50	0.06		0.06				
	Doc's Total:	100	88.92	11.91	1	11.91	1.5	75	9	13
Lover's Key	*Thalassia testudinum*	9.15	87.67	20.16		80.65				
	Halodule wrightii	1.91	18.33	7.15		28.60				
	Gracilaria tikvahiae	1.58	15.11	1.81		7.25				
	Acanthophora spicifera	0.27	2.56	0.31		1.23				
	Hypnea spinella	0.08	0.78	0.10		0.40				
	Lover's Total:	100	124.44	29.53	4	118.14	14.2	58	7	6
Lynhall's	*Ulva lactuca*	44.95	23.22	6.27		100.32				
	Gracilaria tikvahiae	40.43	20.89	2.51		40.11				
	Gracilaria cervicornis	5.16	2.67	0.32		5.12				
	Hypnea spinella	4.09	2.11	0.27		4.39				
	Acanthophora spicifera	2.37	1.22	0.15		2.35				
	Thalassia testudinum	1.51	0.78	0.18		2.86				
	Halymenia floresia	1.51	0.78	0.09		1.49				
	Lynhall's Total:	100	51.67	9.79	16	156.64	12.8	-	-	-
Bunche	*Thalassia testudinum*	100	43.89	10.09	4	40.38	1.2	-	-	-
San. Causeway	*Thalassia testudinum*	100	94.44	21.72	4	86.89	19.8	-	-	-
Bowman's	*Thalassia testudinum*	100	27.56	6.34	2	12.68	3.0	-	-	-
Captiva	*Thalassia testudinum*	100	126.56	29.11	7	203.75	20.2	-	-	-

Table 3. Site locations, field data--temperature (ūC), salinity (ä), pH, Secchi depth (m)--and water column chlorophyll *a* (µg/l) and phaeophytin (µg/l) concentrations during August and September 2005 samplings, Lee County, FL, USA.

Date	ūLatitude	ūLongitude	Site Name	Temp. (ūC)		Salinity (ä)		pH		D.O. (ä)		Secchi Depth (m)	Chl a (µg/l)	Phaeo-phytin (µg/l)
				S	B	S	B	S	B	S	B			
8/3/05	26.4692667	-82.0285167	Sanibel Causeway	31.8	-	18	-	8.0	-	9.2	-	-	16.6	1.9
	26.4759833	-81.9674333	Bunche Beach	32.5	-	22	-	8.0	-	8.2	-	-	7.7	2.2
	26.4535667	-81.9579667	Lynhall's Beach	31.7	-	26	-	7.9	-	7.8	-	-	7.5	2.9
	26.3859000	-81.8754667	Lover's Key Beach	31.1	-	29	-	7.8	-	7.1	-	-	3.1	2.7
	26.3315167	-81.8463000	Doc's Beach	31.2	-	31	-	7.8	-	5.9	-	-	4.0	2.4
	26.4587000	-82.1574500	Bowman's Beach	32.0	-	32	-	7.9	-	6.1	-	-	2.7	1.5
8/23/05	26.44979	-81.95906	Lynhall's Nearshore	31.2	31.2	29	29	7.9	7.9	5.0	4.9	-	14.9	7.7
	26.38391	-81.87747	Lover's Nearshore	31.8	32.3	31	31	8.1	8.0	6.2	4.7	1.8	6.9	3.2
	26.33080	-81.84799	Doc's Nearshore	31.9	32.5	31	32	8.1	7.9	5.6	2.4	-	4.0	3.8
	24.42000	-82.04000	Bowman's Nearshore	32.1	31.2	27	28	7.8	7.9	5.8	6.1	-	21.8	9.1
9/8/05	26.46000	-82.02000	San Carlos Bay	29.7	29.5	14	22	8.2	8.0	6.8	6.2	1.1	9.0	6.9
	26.43000	-81.95000	Lynhall's Nearshore	29.5	29.9	23	26	8.0	8.0	6.2	6.7	1.4	7.3	3.0
	26.38000	-81.87000	Lover's Nearshore	29.8	30.0	30	31	7.9	7.9	4.9	3.6	1.6	-	-
	26.33000	-81.84000	Doc's Nearshore	29.6	29.8	31	32	7.0	7.6	3.4	0.7	1.5	12.9	3.8
	26.42000	-82.04000	Bowman's Nearshore	29.4	29.4	32	32	8.1	8.1	7.0	6.7	0.3	12.9	3.2

September 7th (Fig. 4). This aerial survey also revealed patches of discolored water indicative of *Karenia brevis* off Sanibel Island (Fig. 5), as well as blooms of *Microcystis aeruginosa* in the Caloosahatchee River anc downstream estuary adjacent to Ft. Myers (Fig. 6).


Figure 4. Aerial photo showing Caloosahatchee River plume flowing southward along Fort Myers Beach, September 7, 2005.


Figure 5. Aerial photo of discolored water indicative of a red tide (*Karenia brevis*) bloom off Sanibel Island, September 7, 2005


Figure 6. Aerial photo of the *Microcystis aeruginosa* bloom in the Caloosahatchee estuary, September 7, 2005.

To develop a digital imaging system for the measurement of areal coverage by macroalgal blooms in shallow coastal waters and beaches, we have obtained spectral reflectance data on species of benthic algae growing in the shallow waters off Lee County. The optical instrumentation for this measurement is shown below (Fig. 7). Fiber optic light pipes focus on the alga specimens (c) and reflected and incident light enters at an angl of 40 degrees into the spectrometer (a). The measurements are referenced against a white standard of 98 % reflectance (d). Examples of the spectral data measured using specimens collected off Lee County on September 8th include *Agardhiell subulata, Botryocladia occidentalis, Gracilaria blodgetii, Gracilaria tikvahiae*, and *Rhodymenia divaricata* (Fig. 8A-E). These species form a composite of the biomass that bloomed in the shallow waters off Bonita Springs Beach ir July 2004.

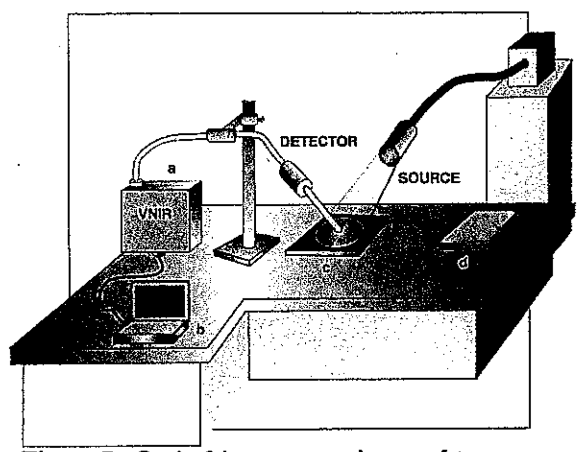


Figure 7. Optical instrumentation used to measure reflectance spectra of macroalgal and toxic phyto-plankton HABs in Lee County coastal waters.

Two regions of these spectra are important in making estimates of area coverage. Between 500 nm and 700 nm the reflectance is relatively constant for these species. This is because of the combined absorption of light at these wavelengths by chlorophylls and chromo-proteins. The reflectance from 700 nm to 750 nm increases markedly to a plateau at 900 nm in all species. Although the overall albedo differs from species to species, the relationship between the two spectral regions is relatively constant. This allows discrimation between algal substances versus reflection and absorption by water covering the benthic substrate. We have not made extensive measurements of the reflection from dry sand beaches in Lee County, but the few measurements we have made indicate that it is 80-90%. We have modeled the changes in reflectance with water depth covering the algal sand bottom (Fig. 9). Figure 9A shows the spectral transmission of light through one meter of water and the spectral reflectance of typical algae. The product of

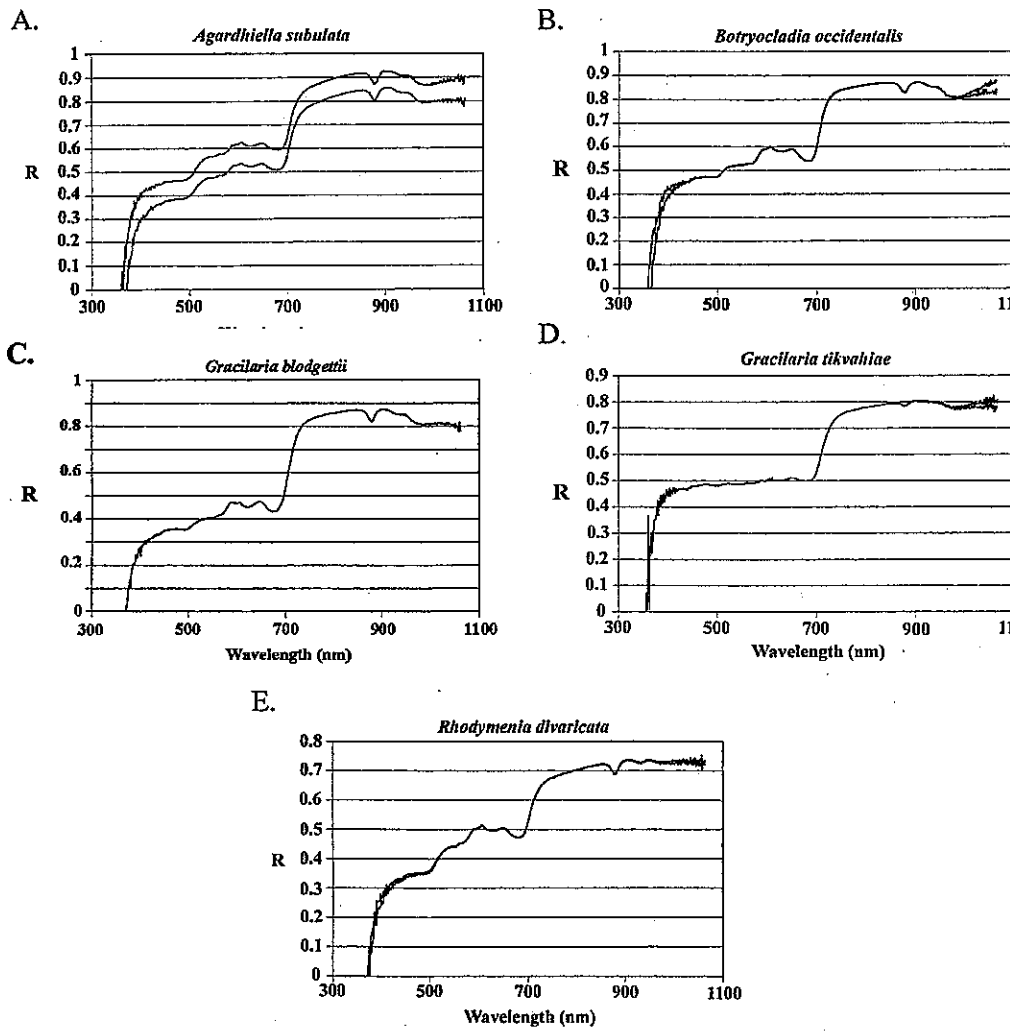


Figure 8. Reflectance spectra of red macroalgae from Lee County, FL, USA, showing reflectance spike above 700 nm. Species shown: A) *Agardhiella subulata*; B) *Botryocladia occidentalis*; C) *Gracilaria blodgettii*; D) *Gracilaria tikvahiae*; E) *Rhodymenia divaricata.*

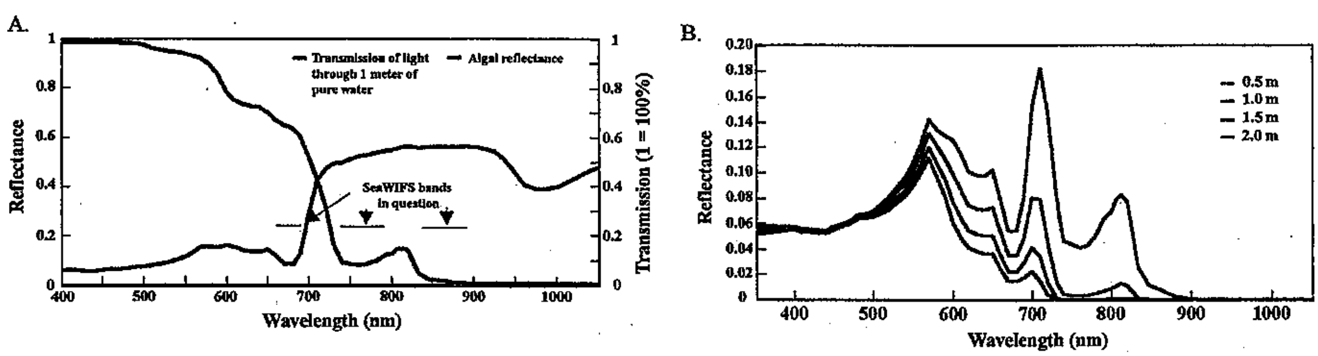
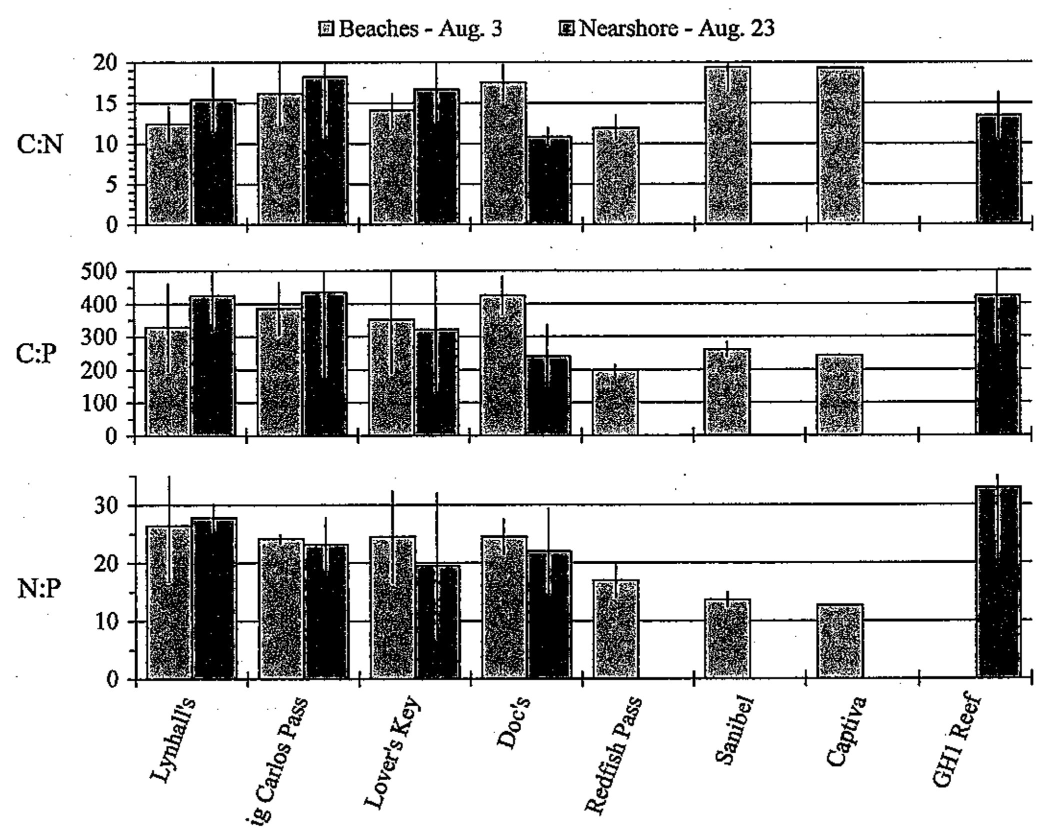


Figure 9. Model of how macroalgal reflectance may be used to monitor HABs in Lee County coastal waters: A) Spectral reflectance and transmission of light through 1 meter of pure water (in red) and macroalgal average (in black); B) Graph showing the product of the two plots in panel 'A' at depths of 0.5, 1.0, 1.5, and 2.0 meters.

III. *$\delta^{15}N$ and C:N:P Analysis of Macroalgae and Toxic HABs*: The C:N:P ratios in macroalgae collected from the seven beach sites on August 3rd were relatively low, indicating a high degree of both N and P enrichment. Along the beach gradient, the C:P and N:P values at Sanibel and Captiva islands were low compared to beaches in southern Lee County (Table 4, Fig. 10). Macroalgal C:P and N:P ratios from Sanibel and Captiva

Table 4. Percent carbon, nitrogen and phosphorus; C:N, C:P and N:P molar ratios, and $\delta^{15}N$ values in macroalgae collected August 3, 2005 from beaches in Lee County, FL, USA.

Date	Location	Species	¶15N (ä, n=2)	Carbon (% ± 1 SD)	Nitrogen (% ± 1 SD)	Phosphorus (% ± 1 SD)	C:N Ratio (M)	C:P Ratio (M)	N:P Ratio (M)
8/3/05	Lynhall's	*Gracilaria tikvahiae*	6.96 ± 0.11	28.6	2.8	0.32	12.0	233	19.5
		Halymenia floresia	5.71 ± 0.10	15.2	1.5	0.19	11.5	201	17.7
		Hypnea spinella	9.96 ± 0.10	28.2	2.1	0.15	15.5	468	30.5
		Ulva lactuca	9.40 ± 0.08	25.1	2.7	0.16	10.9	414	38.1
		Lynhall's Mean	8.01 ± 1.86	24.3 ± 6.2	2.3 ± 0.6	0.20 ± 0.08	12.5 ± 2.0	329 ± 132	26.5 ± 9.6
	Big Carlos Pass	*Gracilaria tikvahiae*	9.87 ± 0.08	24.8	1.5	0.14	18.8	441	23.6
		Acanthophora spicifera	8.42 ± 0.19	18.2	1.6	0.14	13.5	330	24.7
		Big Carlos Mean	9.14 ± 0.85	21.5 ± 4.7	1.6 ± 0.0	0.14 ± 0.00	16.2 ± 3.8	385 ± 78	24.1 ± 0.8
	Lover's Key	*Agardhiella subulata*	9.84 ± 0.04	19.3	1.4	0.09	16.4	530	32.6
		Gracilaria tikvahiae	9.22 ± 0.01	21.6	1.9	0.18	13.3	314	23.8
		Hypnea spinella	9.63 ± 0.17	18.4	1.7	0.22	12.6	212	17.0
		Lover's Key Mean	9.56 ± 0.29	19.8 ± 1.7	1.7 ± 0.3	0.16 ± 0.07	14.1 ± 2.0	352 ± 162	24.5 ± 7.8
	Doc's	*Agardhiella subulata*	9.92 ± 0.35	26.0	1.8	0.14	16.9	469	28.0
		Hypnea spinella	10.71 ± 0.16	21.2	1.6	0.15	15.7	359	23.0
		Enteromorpha intestinalis	10.29 ± 0.14	16.8	1.0	0.10	19.9	446	22.5
		Doc's Mean	10.31 ± 0.40	21.3 ± 4.6	1.4 ± 0.4	0.13 ± 0.03	17.5 ± 2.2	424 ± 58	24.5 ± 3.0
	Redfish Pass	*Ceramium nitens*	9.34 ± 0.00	16.9	1.7	0.23	11.3	186	16.6
		Dictyota sp.	8.84 ± 0.33	15.1	1.3	0.20	13.6	195	14.4
		Acanthophora spicifera	9.03 ± 0.17	16.0	1.7	0.19	10.9	216	20.1
		Redfish Pass Mean	9.07 ± 0.28	16.0 ± 0.9	1.6 ± 0.3	0.21 ± 0.02	11.9 ± 1.5	199 ± 16	17.0 ± 2.8
	Sanibel	*Cladophora* sp.	9.15 ± 0.00	15.2	0.8	0.14	22.1	287	13.1
		Halymenia floresia	8.81 ± 0.14	21.2	1.3	0.22	19.6	248	12.8
		Hypnea spinella	10.28 ± 0.35	22.9	1.6	0.24	16.4	247	15.1
		Sanibel Mean	9.41 ± 0.71	19.8 ± 4.0	1.2 ± 0.4	0.20 ± 0.05	19.4 ± 2.8	261 ± 23	13.7 ± 1.3
	Captiva	*Halymenia floresia*	5.34 ± 0.16	22.4	1.4	0.24	19.3	243	12.7
		Grand Mean	8.98 ± 1.47	20.7 ± 4.4	1.6 ± 0.5	0.18 ± 0.05	15.3 ± 3.5	318 ± 112	21.4 ± 7.2

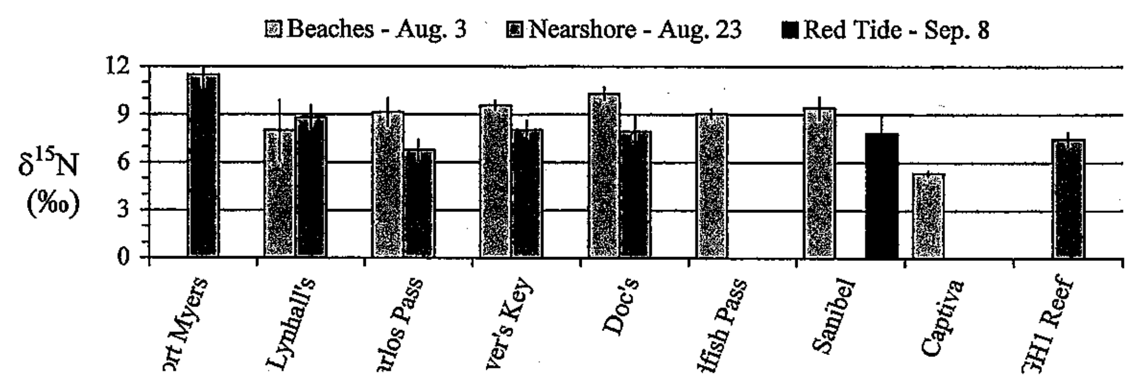


In comparison, there was no significant spatial trend in C:N ratios, which averaged 15.3 ± 3.5 in the macroalgae at the seven beach sites.

The $\delta^{15}N$ value of macroalgae from the seven beach sites averaged + 8.98 ± 1.47 ‰, a relatively high value, well within the range reported for sewage nitrogen. The lowest $\delta^{15}N$ value (+ 5.34 ‰) occurred at Captiva; the highest was occurred at Doc's (+ 10.31 ± 0.40; Table 4). Macroalgae, collected from nearshore waters off four beaches and from an offshore artificial reef (GH1 Reef) in Lee County on August 23rd, again showed relatively low C:N:P values, indicating a high degree of nutrient enrichment (Table 5, Fig. 11).

Table 5. Tissue percent carbon, nitrogen and phosphorus; C:N, C:P and N:P molar ratios; and $\delta^{15}N$ in macroalgae collected from nearshore sites in Lee County, FL, USA, on August 23 and September 8, 2005.

Date	Location	Species	¶15N (ä, n=2)	Carbon (% ± 1 SD)	Nitrogen (% ± 1 SD)	Phosphorus (% ± 1 SD)	C:N Ratio (M)	C:P Ratio (M)	N:P Ratio (M)
8/23/05	Fort Myers	*Microcytis aeruginosa*	12.28 ± 0.04						
		Microcytis aeruginosa	10.72 ± 0.43						
		Fort Myers Mean	11.50 ± 0.93	-	-	-	-	-	-
	Lynhall's	*Gracilaria tikvahiae*	9.66 ± 0.13	25.0	2.0	0.18	14.4	352	24.6
		Halymenia floresia	7.92 ± 0.00	23.2	1.3	0.10	21.2	586	27.8
		Hypnea spinella	9.30 ± 0.10	25.3	2.2	0.18	13.3	370	28.2
		Ulva lactuca	8.48 ± 0.01	20.2	1.8	0.13	12.9	390	30.5
		Lynhall's Mean	8.84 ± 0.73	23.4 ± 2.3	1.83 ± 0.4	0.15 ± 0.04	15.4 ± 3.9	424 ± 108	27.8 ± 2.4
	Estero Bay	*Acanthophora spicifera*	6.22 ± 0.16	17.3	1.6	0.17	12.9	254	19.8
		Gracilaria tikvahiae	7.36 ± 0.06	24.7	1.2	0.10	23.5	617	26.4
		Estero Bay Mean	6.79 ± 0.67	21.0 ± 5.2	1.39 ± 0.2	0.14 ± 0.05	18.2 ± 7.5	435 ± 257	23.1 ± 4.6
	Lover's Key	*Acanthophora spicifera*	7.48 ± 0.20	14.8	1.2	0.20	13.9	186	13.5
		Caulerpa sertularioides	7.40 ± 0.00	30.3	2.5	0.13	14.4	580	40.6
		Agardhiella subulata	8.58 ± 0.28	18.9	1.0	0.11	22.9	449	19.8
		Gracilaria tikvahiae	8.70 ± 0.01	18.3	1.1	0.17	18.7	278	15.0
		Hypnea spinella	8.16 ± 0.13	12.6	1.1	0.28	13.6	115	8.5
		Lover's Key Mean	8.06 ± 0.58	19.0 ± 6.8	1.37 ± 0.6	0.18 ± 0.07	16.7 ± 4.0	321 ± 191	19.5 ± 12.5
	Doc's	*Agardhiella subulata*	7.62 ± 0.16	18.9	1.9	0.14	11.5	348	30.4
		Gracilaria tikvahiae	9.07 ± 0.07	18.2	1.9	0.23	11.4	202	17.8
		Hypnea spinella	7.14 ± 0.25	14.6	1.8	0.22	9.6	169	17.8
		Doc's Mean	7.94 ± 0.91	17.2 ± 2.3	1.84 ± 0.1	0.20 ± 0.05	10.8 ± 1.1	239 ± 95.1	22.0 ± 7.3
	GH1 Reef	*Bryopsis pennata*	7.82 ± 0.06	20.4	2.3	0.16	10.2	324	31.9
		Caulerpa mexicana	7.18 ± 0.11	30.6	2.6	0.13	13.5	613	45.8
		Codium carolinianum	7.95 ± 0.04	17.1	1.5	0.09	12.9	467	36.4
		Sargassum hystrix	7.03 ± 0.33	22.3	1.5	0.20	17.1	290	17.1
		GH1 Reef Mean	7.49 ± 0.44	22.6 ± 5.7	2.01 ± 0.6	0.15 ± 0.04	13.4 ± 2.8	423 ± 148	32.8 ± 12.0
		8/23/06 Mean	8.30 ± 1.40	20.7 ± 5.1	1.70 ± 0.5	0.16 ± 0.05	14.9 ± 4.1	366 ± 158	25.1 ± 9.9
9/8/05	Sanibel Red Tide	*Karenia brevis*	7.22 ± 0.64						
		Karenia brevis	8.24 ± 0.91						
		Karenia brevis	8.04 ± 2.04						
		Sanibel Red Tide Mean	7.83 ± 1.14	-	-	-	-	-	-



The expansive blooms of *Microcystis aeruginosa* that occurred in the Caloosahatchee estuary at Ft. Myers in August 2005 had very high $\delta^{15}N$ values averaging + 11.50 ± 0.93 ‰ (Fig. 11, Table 5). These high $\delta^{15}N$ values are typical of sewage effluent and closely match the $\delta^{15}N$ values of macroalgae sampled in the Caloosahatchee River at the Franklin Lock in 2004 (Lapointe and Bedford, in press). The dense red tide sampled on September 8th off southern Sanibel Island had an average $\delta^{15}N$ value of + 7.83 ± 1.14 ‰, which is also within the range of sewage nitrogen. These high $\delta^{15}N$ values in *Karenia brevis* and *Microcystis aeruginosa* provide strong evidence that these blooms were supported by land-based nitrogen discharges, particularly the massive releases from Lake Okeechobee and the Caloosahatchee River that occurred in 2004/2005 following hurricanes Charley, Frances, and Jeanne. These $\delta^{15}N$ data do not support the hypothesis that the red tide off Sanibel Island was supported by nitrogen fixation from the cyanobacterium *Trichodesmium* as suggested by Lenes et al. (2001), which would have produced much lower $\delta^{15}N$ values of ~ 0 ‰ to +1 ‰ (Heaton 1986; Owens 1987).

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Gymnodinium breve red tide blooms: Initiation, transport, and consequences of surface circulation

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Abstract

From its source waters in the Gulf of Mexico the red tide dinoflagellate, *Gymnodinium breve* is moved throughout its oceanic range by major currents and eddy systems. The continental shelf off the west coast of Florida experiences frequent *G. breve* blooms (in 21 of the last 22 years) where the spatially explicit phases of *G. breve* blooms are closely coupled to physical processes. Bloom initiation occurs offshore and in association with shoreward movements of the Loop Current or spinoff eddies. A midshelf front maintained by seasonal wind reversals along the Florida west coast may serve as a growth and accumulation region for *G. breve* blooms and contribute to the reinoculation of nearshore waters. Local eddy circulation in the northeastern Gulf of Mexico and in the Dry Tortugas affects the retention and coastal distribution of blooms while the Florida Current and Gulf Stream transport cells out of the Gulf of Mexico and into the U.S. South Atlantic Bight. The causes of bloom dissipation are not well known but mixing or disruption of the water mass supporting *G. breve* cells, especially in combination with declining water temperatures, are important factors.

Much of what is known about the distribution of the toxic dinoflagellate *Gymnodinium breve* Davis [=*Ptychodiscus brevis* (Davis) Steidinger] is explained by oceanic circulation patterns. *G. breve* cells are positively phototactic (or negatively geotactic) (Steidinger 1975; Heil 1986) and can concentrate in the upper water column during the day. There they behave like surface drifters, only smaller writ. The resident population is in the Gulf of Mexico and *G. breve* is transported throughout its range by the Gulf Loop Current, the Florida Current, and the Gulf Stream, with the warmth of the Gulf Stream fostering this subtropical species as it moves north of 31°N. *G. breve* has been recorded throughout the U.S. South Atlantic Bight (Tester et al. 1993) and beyond.

G. breve rarely occurs in shelf waters north of Cape Hatteras, North Carolina (Marshall 1982; *see also* Churchill and Cornillon 1991), but the Gulf Stream may carry it farther (*see* Fraga and Sanchez 1985). A drift bottle released in an October 1966 study off the central west Florida shelf was recovered in the Outer Hebrides a little over a year later; another released in February 1967 reached Belgium in 187 d (averaging >50 km d^{-1}) (Williams et al. 1977). So it seems likely that long before A.D. 1497, when Vespucci, credited with being the first European to explore the Gulf of Mexico, sailed out of the gulf in the direction of the "maestrale" for 870 leagues to Cape Hatteras and then turned eastward toward Bermuda before returning to Spain (Galtsoff 1954), *G. breve* had made a similar voyage.

The reports of discolored water and effects of phycotoxins in tropical Atlantic waters were recognized and recorded in ships' logs by 1530–1550 (Martyr 1912). As early as 1844 popular accounts of *G. breve* blooms were linked with noxious "gases" and massive fish kills along the west coast of Florida (Feinstein et al. 1955). Prophetically, in that same year an intensive study of ocean currents was begun by Maury (1859). Data on ocean circulation, physical processes, and the distribution and biology of *G. breve* would accumulate for more than a century before this information would be coupled, the consequences appreciated, and a model conceptualized to help focus research efforts.

Range

Although Lackey (1956) reported *G. breve* from Trinidad in the southern Caribbean basin (cell counts were not verified), there were no recorded cases of neurotoxic shellfish poisoning reported (S. Hall pers. comm.), and there have been no subsequent observations of *G. breve* anywhere in the Caribbean. Early interest in the circulation of the Caribbean, though, stemmed from its role as the source region for water flowing into the Gulf of Mexico. In this semi-enclosed basin the eastern gulf is characterized by anticyclonic circulation and is dominated by two currents. The Yucatán Current (75 cm s^{-1}), entering between the Yucatán Peninsula and Cuba, becomes the Loop Current as it extends northward into the gulf and returns southward along the west Florida

Acknowledgments

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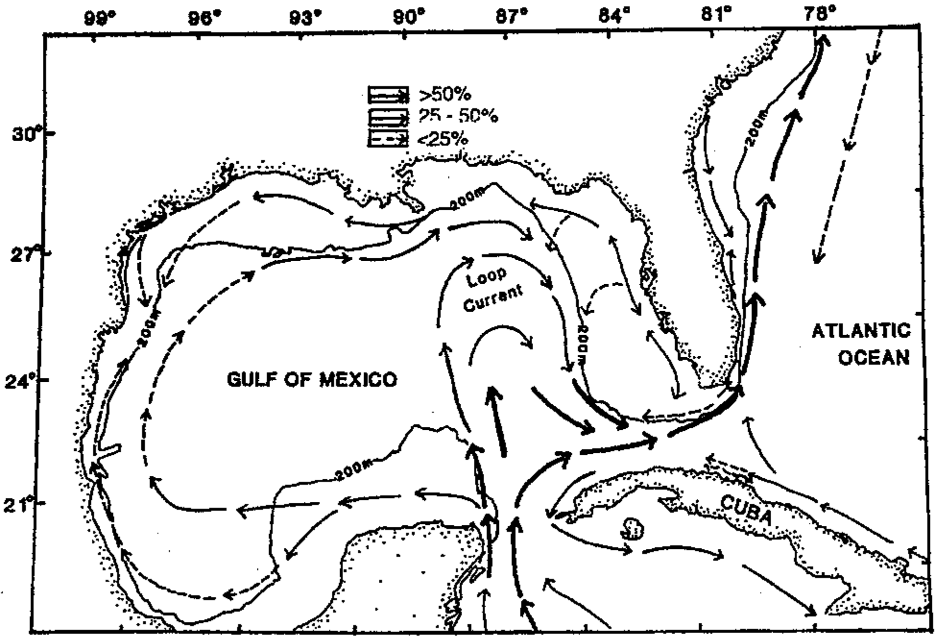

Fig. 1. Generalized surface circulation of the Gulf of Mexico. Arrows denote steadiness of current drift. (Redrawn from UNEP/CEPAL Caribbean Environment Program, Project 1037.)

continental shelf. It exits the gulf between the Dry Tortugas and Cuba where it is known as the Florida Current (165 cm s^{-1}) (*see* Hofmann and Worley 1986) (Fig. 1). The extent of northward penetration of the Loop Current (Maul 1977; Vukovich et al. 1979), its spinoff eddies (Dietrich and Lin 1994; Sturges 1994), and its intrusions onto the west Florida continental shelf vary seasonally (Huh et al. 1981) and greatly affect the potential of bloom initiation, transport, and retention (Haddad and Carder 1979; Haddad 1982; Lee et al. 1994). Rotating eddies can be shed from the Loop Current and propagate westward across the gulf (Liepper et al. 1972; Maul and Vukovich 1993). Cross-basin surface transport also has been documented in drift-bottle studies (Williams et al. 1977). Summer–fall bottle releases from the west Florida shelf frequently were recovered from Texas beaches (Matagorda to Brownsville) to Vera Cruz, Mexico. The general circulation patterns of the south central and western Gulf of Mexico are clockwise but the velocities are less intense (15–25 cm s^{-1}). The only exceptions to this general clockwise pattern are the cyclonic flows in the extreme northeastern and northwestern areas of the gulf (Molinari 1980; Vastano et al. 1995)—regions where elevated background concentrations of *G. breve* cells (>100 cells $liter^{-1}$) have been noted (Geesey and Tester 1993).

Throughout the Gulf of Mexico and the U.S. South Atlantic Bight, *G. breve* is found in background concentrations (1–1,000 cells $liter^{-1}$) except in areas off the Texas coast and the west Florida coast where local circulation may play a role (Fig. 2; *see* Geesey and Tester 1993; Tester et al. 1993). Although *G. breve* blooms have occurred in many different areas in the Gulf of Mexico, from Yucatán in the south (Graham 1954), to the lower Laguna Madre, in the Mexican state of Tamaulipas in the western gulf (Gunter 1952; Wilson and Ray 1956) to Freeport, Texas (Burr 1945; Trebatoski 1988), and around the northern gulf coast, they are most frequent along the west coast of Florida. Blooms there are especially frequent from Clearwater to Sanibel Island (Joyce and Roberts 1975; K. A. Steidinger and B. S. Roberts unpubl.), occurring in 21 of the last 22 years. These blooms on the southwest Florida shelf serve as a source for cells inoculating the U.S. South Atlantic Bight (Murphy et al. 1975; Steidinger et al. 1995; Tester et al. 1991).

Bloom initiation

The regions of the Gulf of Mexico that experience blooms of *G. breve* lasting more than 2 months include the west Florida shelf (Clearwater to Sanibel Island), the Campeche Bay between Rio Ciatzacoalcos and Rio Grijalva (Smithson. Inst. 1971), and the Texas coast between Port Arthur and Galveston Bay. All have common features conducive to the formation of blooms. Each of these areas is adjacent to a continental shelf break where it intersects with the permanent seasonal thermocline (Fig. 3). The isothermal water on the outer shelf results in a minimum bottom temperature of 20°C in areas off Texas and west Florida (NOAA 1985) and Campeche Banks. Consequently these areas may provide an important winter refuge for *G. breve.* These same areas also experience either persistent, intermittent, or event-related slope-shelf upwelling. This is best known for the west Florida shelf where blooms can occur any time of the year but are typical in late summer and fall when >70% of the outbreaks have begun. Bloom concentrations first appear offshore (Dragovich and Kelly 1966; Steidinger 1975; Steidinger and Haddad 1981) and are associated with the fronts caused by the onshore–offshore meanders of the Loop Current water along the outer southwest Florida shelf. Water on

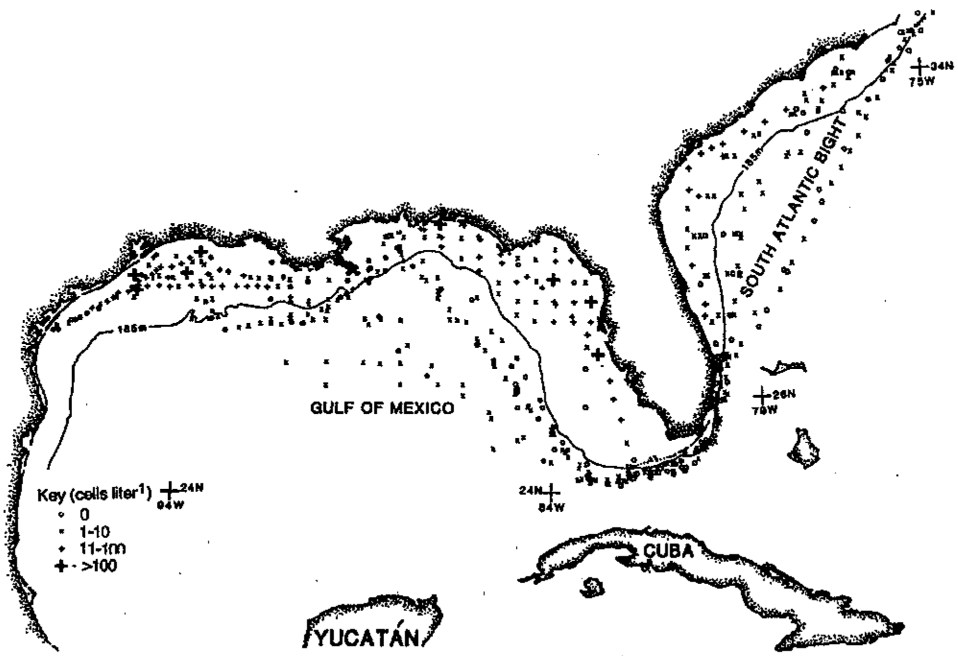

Fig. 2. *Gymnodinium breve* nonbloom, background concentrations in cells $liter^{-1}$. Samples were taken during 1989–1991 by ships of opportunity (after Geesey and Tester 1993; Tester et al. 1993).

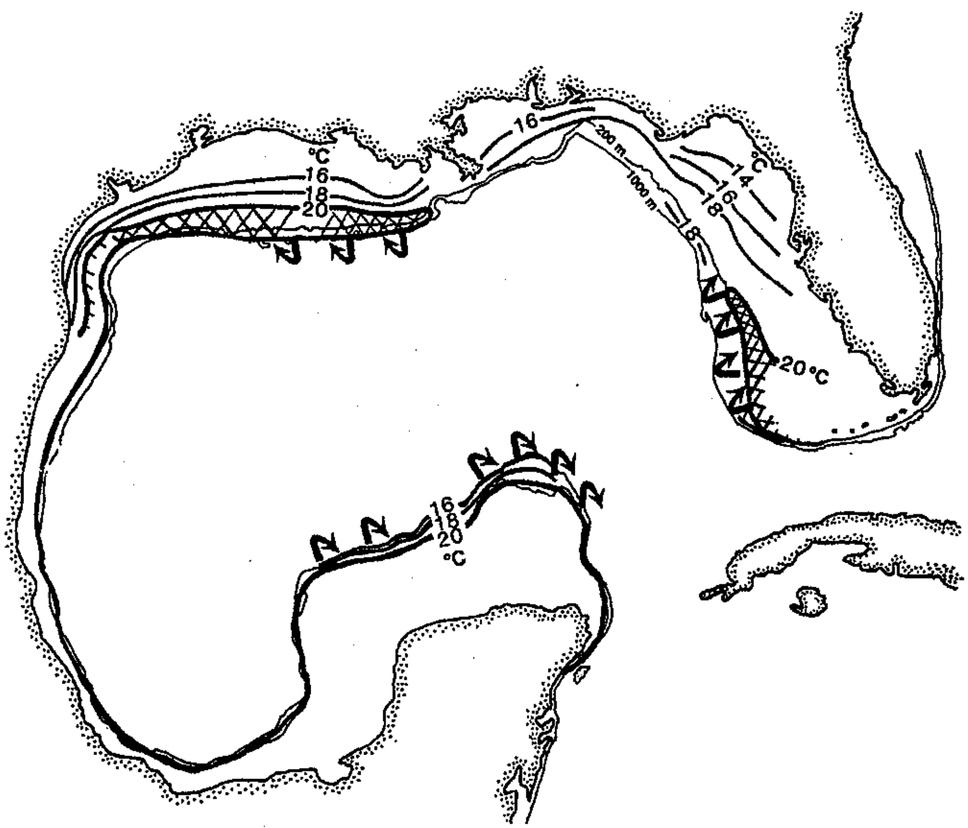

Fig. 3. Winter bottom-water temperatures on the continental shelf of the Gulf of Mexico basin (redrawn from NOAA 1985). Regions of persistent upwelling off the southwest Florida shelf, Texas-Louisiana coast, and the Yucatán Peninsula are indicated by the arrows.

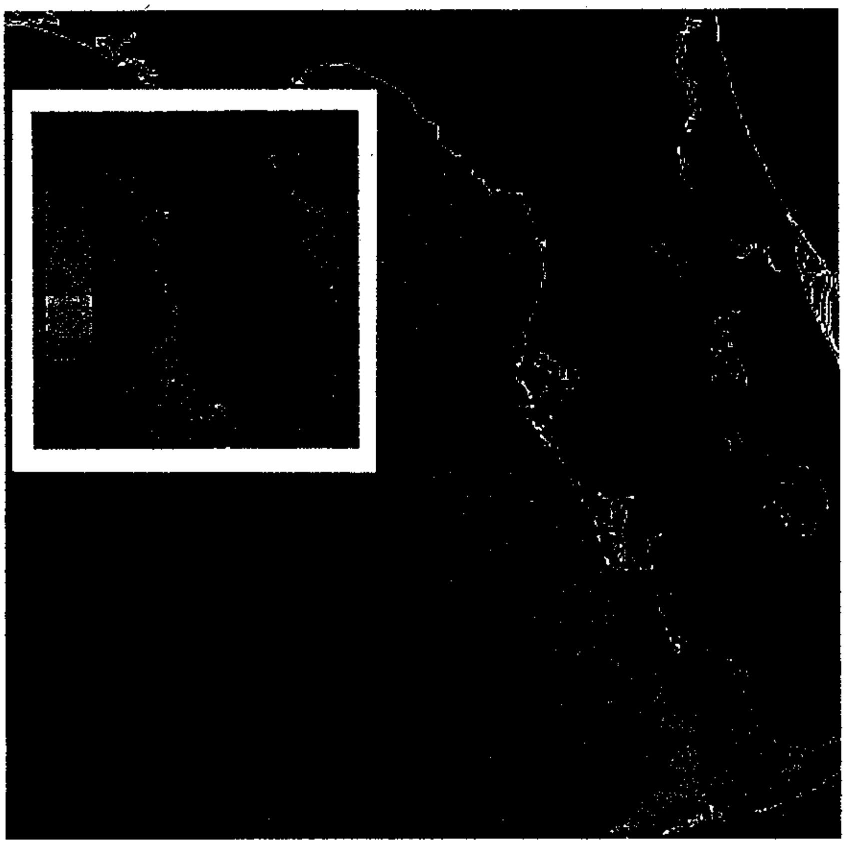

Fig. 4. CZCS image, 14 November 1978, providing an estimate of chlorophyll *a* in μg liter^{-1} (inset) during a *Gymnodinium breve* bloom off the west Florida coast from south of Tampa Bay to the Florida Keys. When processed at a higher resolution, chlorophyll *a* is detectable at *G. breve* cell concentrations that are not visible to the human eye (i.e. Stump Pass, top arrow, 6.7×10^4 cells liter^{-1}; Doctor-Gordon Passes, bottom arrow, 4.6×10^5 cells liter^{-1}).

the leading edge of an eddy or meander is generally sinking and that on the trailing edge is rising, until the feature experiences bottom drag (Dietrich and Lin 1994) and forms a midshelf front.

Fronts represent a dynamic area of nutrient regimes and light conditions which can favor accumulation and growth (<1 div. d^{-1}, often 0.2–0.5 div. d^{-1}) of dinoflagellates. Bloom species such as *G. breve* and *Gyrodinium* cf. *aureolum* (European waters) are well adapted to such environments and can grow throughout the euphotic zone. They have a high photosynthetic capacity at low light and are light-adapted at varying intensities (Shanley 1985; Garcia and Purdie 1992) although photoinhibition thresholds are species-specific. Once growth occurs, it takes 2–8 weeks to develop into a bloom of fish-killing proportions ($1–2.5\times10^5$ cells liter^{-1}) depending on physical, chemical, and biological conditions.

Some species such as *G. breve, G.* cf. *aureolum,* and *Lingulodinium polyedrum* have growth and competitive exclusion strategies that can lead to almost monospecific surface blooms of these species (as biomass) (Steidinger and Vargo 1988; Morin et al. 1989). Such blooms (*G. breve, G.* cf. *aureolum*) can cover a surface area of up to $1.4–3.0\times10^4$ km^2 (Steidinger and Joyce 1973; Holligan 1985; Vargo et al. 1987) and although biomass concentration is patchy, chlorophyll *a* values from >2 to >100 mg m^{-3} make the resultant discolored surface water detectable by color sensors onboard satellites (Fig. 4). In the case of *G. breve* the CZCS sensor detected chlorophyll *a* from cells at densities one–two orders of magnitude less (10^4–10^5) than are present when discolored water is detectable by the human eye (>10^6) (K. Haddad and K. Steidinger pers. comm.).

Both *G. breve* and *G.* cf. *aureolum* discolor surface waters and are phototactic; in daylight hours cells are at or near the surface; at night they are dispersed (Holligan 1985; Heil 1986; Geesey and Tester 1993). In addition to their ability to exploit light regimes, both species have advantages in nutrient dynamics. Both assimilate nitrogen at low light and are able to utilize organic as well as inorganic nutrients (Vargo and Shanley 1985; Steidinger and Vargo 1988; Dahl and Tangen 1993; Shimizu et al 1995). When *G. breve* blooms have been tracked, the zone of initiation (cell numbers >1,000 liter^{-1}) develops from 18 to 74 km offshore (Steidinger and Haddad 1981) and the strongest evidence for this lies in the cell distribution along cross-shelf transects sam-

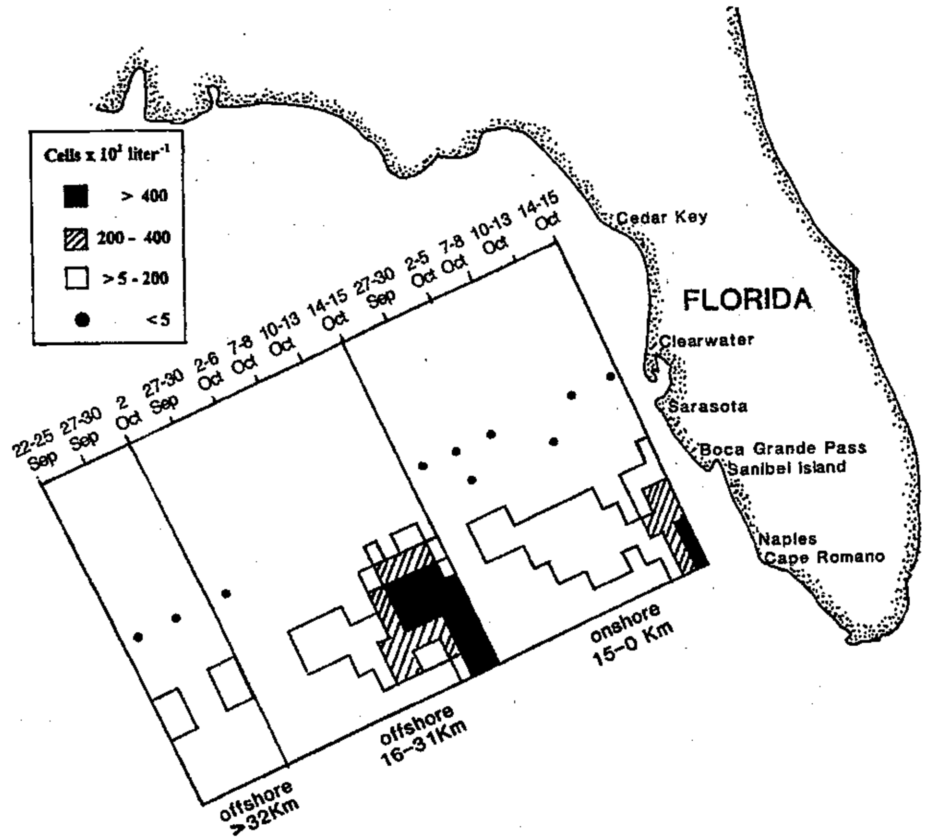

Fig. 5. Spatial and temporal distribution of *Gymnodinium breve* cell abundance along the west Florida coast during a late summer–fall 1976 bloom.

pled by personnel from the Florida Marine Research Institute (FMRI) and Mote Marine Laboratory.

The first example is taken from transects sampled during a late summer bloom in 1976. A series of stations from the inlets or nearshore to 32–70 km offshore was made between 22 September and 15 October. Concentrations above background were first noted offshore between Sarasota and Boca Grande Pass in late September (Fig. 5). During the following week in the same area, cell concentrations increased and then generally spread south. No nearshore or inlet samples during this time were either positive for *G. breve* or above background until 2 weeks later. Data from north of Boca Grande Pass are representative of the cell distributions from transects run perpendicular to shore (Fig. 6). Typically the cells are moved from the midshelf to onshore and then, under the influence of the wind and(or) alongshore currents, move up or down the coast (Fig 5). From 7 to 11 October there were still high numbers (>1–6×10^5 cells liter^{-1}) of *G. breve* 3–25 km offshore north of Boca Grande Pass. The bloom had moved south and was parallel to the coast with 10–100-fold lower cell concentrations onshore than offshore. By 13–14 October the bloom was centered south of Boca Grande Pass and had intensified. Counts offshore of Sanibel Island were 1–1.5×10^6 cells liter^{-1}; counts nearshore ranged from 1.5 to 70×10^3 cells liter^{-1}. Farther south at Naples there were no cells in the 25-km station, but nearer shore cells were noted. After 15 October the inshore passes between Clearwater and Naples had <1,000 cells liter^{-1} and sampling was suspended.

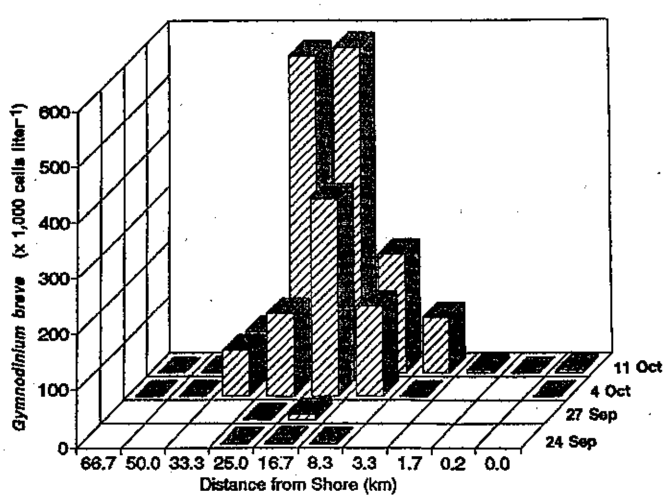

Fig. 6. Distribution and abundance of *Gymnodinium breve* cells along cross-shelf transects north of Boca Grande Pass to >66 km offshore taken between 24 September and 11 October 1976.

A similar pattern of bloom development and movement is evident from blooms in November–December 1979 and Sep-

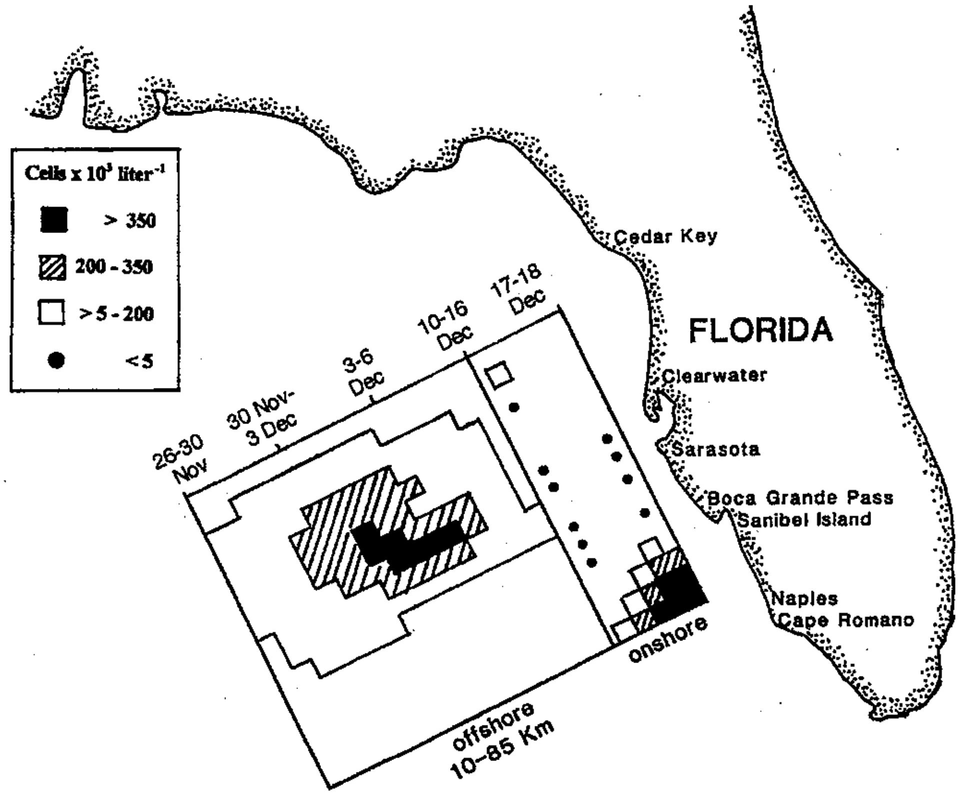

Fig. 7. Spatial and temporal distribution of *Gymnodinium breve* cell abundance along the west Florida coast during late fall 1979.

tember–November 1985 (FMRI data). The 1979 bloom was first reported 130 km northwest of Clearwater and the earliest cell counts from the Clearwater and Cedar Key areas (26–30 November) indicated that it was a large bloom (Fig. 7). Note however, there were no cells or very low counts (0–2,000 cells $liter^{-1}$) onshore until 10–11 December, when offshore numbers were dropping and the bloom seemed to have moved south 100–120 km and onshore. The third example is from a 1985 bloom which was first sampled 16 km off Cedar Key and southward (10^4–10^5 cells $liter^{-1}$) on 10 September (Fig. 8). Again the passes and nearshore were free of *G. breve* cells until more than a month later. The alongshore (south) and onshore movement of the bloom is evident; the offshore stations between Clearwater and Sarasota were cell-free during the first sampling period, but 1–2 weeks later there were up to 10^3–10^4 cells $liter^{-1}$. Within 4–5 weeks between 10^5 and 10^6 $liter^{-1}$ were observed onshore and south of Sarasota and Boca Grande Pass (4 November).

Bloom transport

There is evidence that some blooms can be maintained within the midshelf zone and continually inoculate the nearshore waters or recur in a "high occurrence zone" from Clearwater to Sanibel Island (Steidinger and Roberts unpubl.). One possible mechanism for this is the circulation pattern reported by Weisberg et al. (1996). They describe seasonal wind reversal, (northeast–southwest flow) on the midshelf that result in zero mean flows both in the alongshore and crossshore directions during a 16-month period. However, the monthly means can be relatively large, and Weisberg et al. suggested the maximum values have a baroclinic origin via a thermal wind relationship. Recent research on the west Florida shelf circulation describes two basic patterns, a summer pattern (April–September) and a winter pattern (October–March) characterized by a semipermanent anticyclonic eddy (Weisberg et al. 1996) on the northwestern Florida shelf in the Apalachee Bay–Middle Grounds area (H. Yang and R. Weisberg pers. comm.) This feature dominates the northeastern shelf onshore of the 50-m isobath (Yang and Weisberg pers. comm.) and may be responsible for the entrainment and transport of cells northward to the Florida panhandle. Haddad (1982) recorded an example of a red tide preceded by the shoreward advection of a bottom thermocline between 10 August and 3 September 1978 when the bloom surfaced at 19 km from shore. Similar transport along a thermal gradient may explain the spring–summer bloom of 1995 when a *G. breve* red tide apparently moved north up to Cedar Key and then onto the Florida panhandle 55–110 km offshore and subsequently inoculated inshore waters (FMRI unpubl. data).

From Tampa Bay south small-scale eddy features (<100 km; Maul 1977; Hela et al. 1955) or filaments (R. Stumpf pers. comm.) may also play a role in the translocation of offshore blooms. Frontal eddies (Loop Current water) and

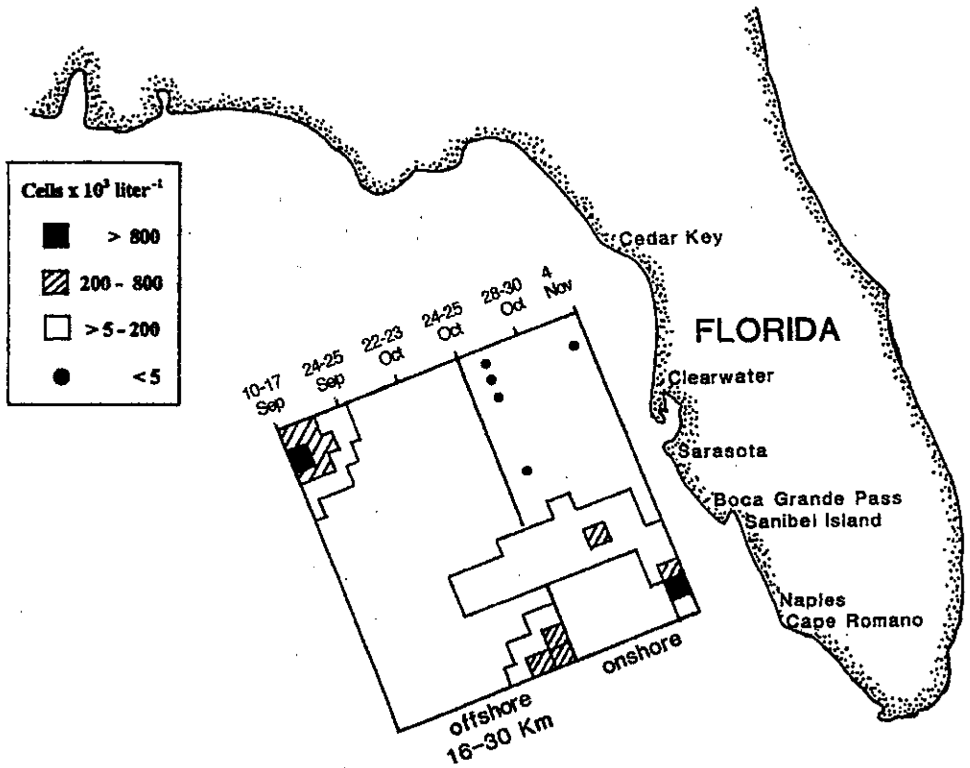

Fig. 8. Spatial and temporal distribution of *Gymnodinium breve* cell abundance along the west Florida coast during a late summer–fall bloom in 1985.

on–offshore meanders of the Loop Current move southward along the outer southwest Florida shelf (every 2–14 d) (Paluszkiewicz et al. 1983), and there is evidence for a southward mean flow over the shelf when the Loop Current is at the shelf edge (Sturges and Evans 1983). The annual cycle of wind stress, northward during summer and southward in fall, is responsible for the persistent upwelling (summer) or downwelling (fall) found over the west Florida shelf (Lee and Williams 1988) and may concentrate or disperse blooms depending on the site and timing of the bloom.

Another recently described eddy system operative between the Tortugas and the upper keys is dependent on a well-developed Loop Current and the consequent offshore position of the Florida Current. The Tortugas Gyre is a cyclonic recirculating feature (100–180 km) with a duration of 40–108 d that has a strong influence on the transport and retention of zooplankton and larval fish in the lower Florida Keys (Lee et al. 1994). In the intervals between gyre recirculation periods there are episodes (20–30 d) of intense eastward flow (Lee et al. 1994). This feature may provide insight into the distribution and transport of *G. breve* from the west coast of Florida to the Atlantic in 1994–1995 (T. Lee pers. comm.). The bloom started in September 1994, between Tampa Bay and Sanibel Island off the west coast of Florida. In January and February 1995, extensive fish kills were reported in >5,000 km² of open water westward from the Florida mainland to the Dry Tortugas; a sample with 1.5×10^5 cells liter^{-1} was counted from Sanibel on 18 January. In February, coincident with fish kills off the southwest Florida coast, a sample from 12 km off Duck Key (14 February 1995) contained 9.6×10^6 cells liter^{-1} (Fig. 9). Concern about the possibility of *G. breve* transport to the Atlantic prompted sampling off West Palm Beach from September 1994 through early March 1995. Cell counts at West Palm Beach were only 0–6 cells liter^{-1} from September to December 1994 but from 17 to 24 February 1995, as the Gulf Stream impinged on the West Palm Beach sampling site and formed a meander, *G. breve* cell densities increased to $\sim2\times10^4$ cells liter^{-1} (Fig. 10) (Steidinger et al. 1995). As the Gulf Stream moved offshore, away from the sampling area, cell numbers decreased (27 February–3 March). From 3 to 7 March 1995, samples from the Occulina Reef National Park (~27°53′N, 79°58′W) off Cape Canaveral, north of the West Palm Beach site contained 0–80 cells liter^{-1}, but the Gulf Stream did not impinge on the reef during the 4-d sampling period. Fourteen days after the Gulf Stream meander migrated past West Palm Beach, *G. breve* cells were found in 10 of 12 samples from the outer shelf of Onslow Bay, North Carolina (33°51′N, 76°53′W, 23.4°), >1,000 km downstream. Although the cell counts were low (≤5 cells liter^{-1}) the presence of *G. breve* in >80% of the samples is unusual in early March. Fortunately, the dire oceanic menace (as depicted by the *Miami Herald* on 22 February 1995) following the course of the Gulf Stream was exaggerated. In early March the inner shelf water of Onslow Bay is too cold (<12°C) to support the growth of *G. breve* and wind mixing prevented water-column stabilization conducive to bloom development.

Prior to 1969, *G. breve* had not been recorded in the U.S.

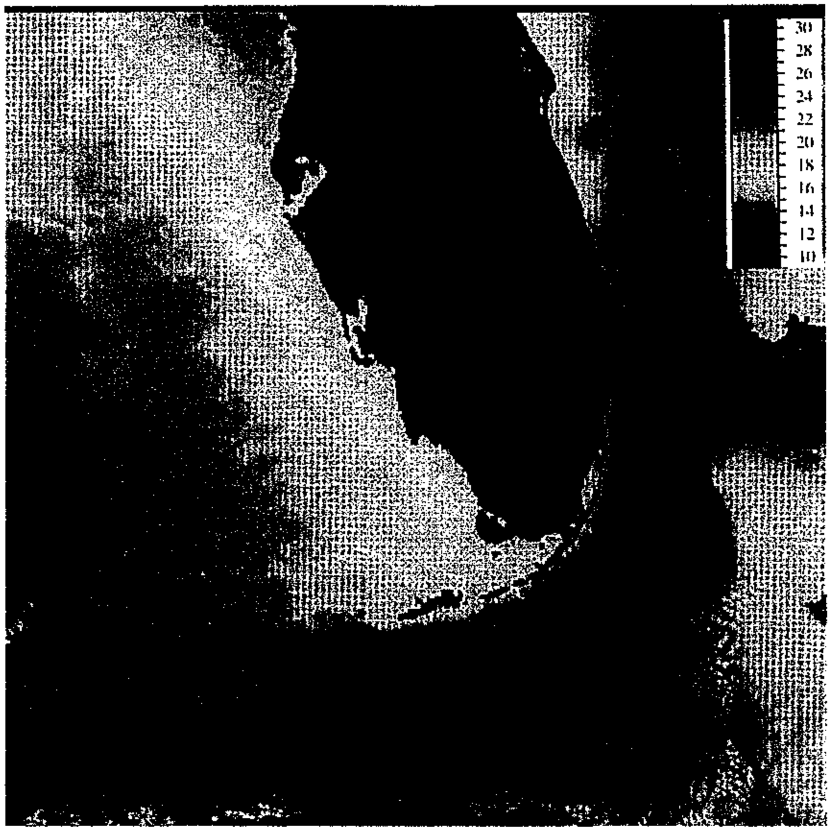

Fig. 9. 3 February 1995 sea-surface temperature image (NOAA-14) (scale is in °C) showing an intrusion of the Loop Current water (≥23°C) onto the southwest Florida continental shelf. Between 10 February and 19 February 1995 warm water bathed the region from Sanibel Island to the Dry Tortugas and Florida Bay warmed from 17–18°C to >22°C. Extensive fish kills were reported in more than 5,000 km² of open water and *Gymnodinium breve* cell counts 12 km off Duck Key (arrow) on 14 February 1995 were 9.6×10^6 cells liter^{-1} and associated with the intrusion of warm water.

South Atlantic Bight, but Lackey (1969) found one cell in an unpreserved sample taken from Boca Raton during a water-quality study. Not until autumns 1972, 1976, and 1977 after the typical manifestations of *G. breve* blooms (e.g. eye and respiratory irritation, fish mortality) were described by beachgoers from Miami to Palm Beach (Murphy et al. 1975; Roberts 1979), did we understand that blooms—even short-lived ones (±1 month)—could occur outside the Gulf of Mexico basin. These first blooms recorded in the U.S. South Atlantic Bight were restricted in area and intensity. No cells were found as far north as Cape Canaveral, and the counts were neither high nor persistent ($2–100 \times 10^4$ cells liter^{-1}). The events were considered the result of concentration and transport of cells to the east coast by unusual Loop Current patterns (Murphy et al. 1975).

The seasonality of the west Florida shelf circulation and wind fields also contributes to the likelihood of shelf water being advected into the Florida Current for transport to the U.S. South Atlantic Bight (Williams et al. 1977). Late summer–autumn blooms have the greatest potential for transport to the Atlantic coast because summer transport rates are the highest and "detrainment" is greatest in fall due to low, inconsistent transport (Maul and Bravo 1989). The three areas of detrainment identified by Maul and Bravo (1989) as likely areas for receiving flotsam and jetsam are southeast of Cape Canaveral, east of St. Augustine, and southeast of Onslow Bay. *G. breve* was to prove itself as an apt surface-drifter and a good test of their ideas.

Cells from a May–October 1980 west Florida shelf bloom were transported farther than any recorded up to that time. Gulf Stream Frontal Analyses (composite GOES satellite imagery) confirmed a warm-water intrusion 7–10 November off Jacksonville (Fig. 11) and by 14 November local Jacksonville residents were suffering sore throats and watery eyes; by 25–28 November *G. breve* counts were 6.7×10^5 cells liter^{-1} and the bloom had spread >100 km south to Daytona where beachgoers were affected by exposure to the surf (FMRI data). Cells were found off Cape Canaveral (Melbourne) on 5 December and between Jacksonville and Cape Canaveral meanders of warm water shoreward of the western edge of the Gulf Stream were evident in GOES imagery of 8 December 1980 (not shown).

The 1980 east coast *G. breve* red tide demonstrated that Gulf Stream meanders off Jacksonville could inoculate in-

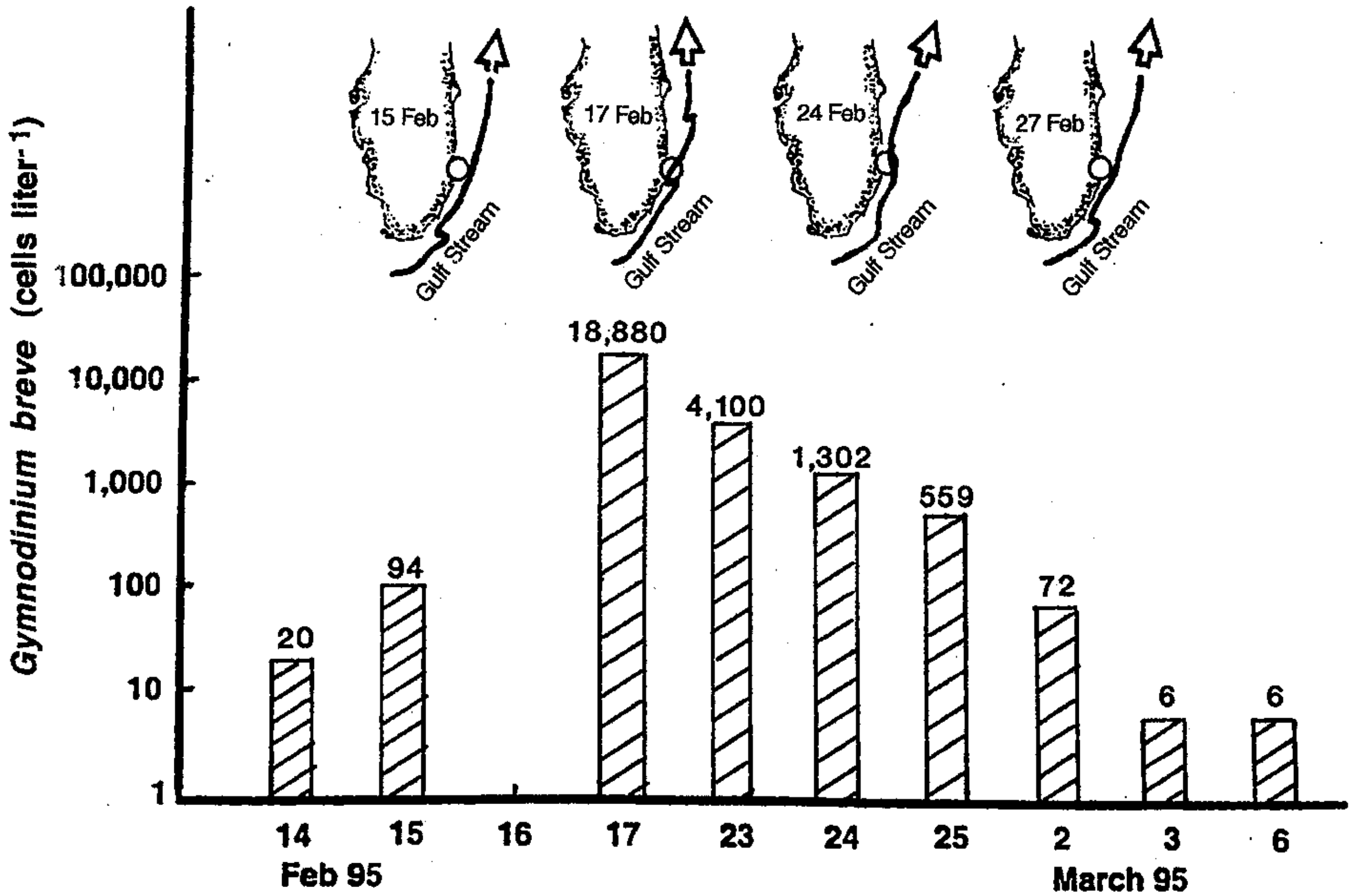

Fig. 10. *Gymnodinium breve* cell counts near West Palm Beach, FL in relation to the position of the Gulf Stream. When the western front of the Gulf Stream was closer to the nearshore sampling site the cell counts were 1–18.8$\times10^3$ cells liter^{-1}. When the Gulf Stream was seaward of the sampling site *G. breve* cell concentrations were <100 cells liter^{-1} (after Steidinger et al. 1995). Cape Canaveral is the cape immediately north of West Palm Beach (O).

shore areas and be transported by countercurrents south along the coast beyond Cape Canaveral. In 1983, another transport occurred concurrently as a meander of the Gulf Stream formed south of Jacksonville on 10 October (S. Baig pers. comm.). In the area from Daytona to below Cape Canaveral (Volusia and Brevard Counties) all three signs of a *G. breve* red tide were evident (i.e. human respiratory irritation, fish kills, and discolored water). The cell counts were much higher than for previous east Florida shelf blooms (5.5$\times10^6$ cells liter^{-1}, 10 October). The following day cell counts were 1$\times10^7$ cells liter^{-1}; during the next 10 d, red tide affected areas immediately south of Cape Canaveral (Patrick Air Force Base, Cocoa Beach, and Melbourne). By 28 October, it had moved 55 km south of Cape Canaveral (Sebastian Inlet) and remained there until 4 November. By 23 November, the red tide had dissipated and shellfish harvesting areas were opened.

Prior to that east coast event, a well-developed red tide was detected on the west coast on 6 October. Patches of dead fish and surface-water discoloration (indicative of cell counts $\geq$1$\times10^6$ cells liter^{-1}) were reported from Sarasota to Venice from shore to 15 km offshore. Inshore *G. breve* concentrations were 4.5$\times10^5$ cells liter^{-1} and beachgoers were experiencing respiratory irritation. Cell counts from 7 October were 3$\times10^6$ cells liter^{-1} 9 km off Captiva Island in the Charlotte Harbor area. This is the classic source area for transport of red tides from the west coast to the east coast of Florida. Because it takes 2–8 weeks for a red tide to develop concentrations of $\pm$2.5$\times10^5$ cells liter^{-1} offshore, this west Florida bloom was the likely source for cells inoculating the Jacksonville area.

Gulf Stream transport also was implicated in an unusual *G. breve* fall and winter (1987–1988) bloom along the coast of North Carolina which continued for 4–5 months (Tester et al. 1991). Thirty days before this bloom there was a late summer bloom off the southwest coast of Florida. The coupling of these two events is supported by transport time of an Argos-tracked surface drifter (60 km d^{-1}) making the same passage in ~20 d (Ortner et al. 1995) and the drift bottles recovered from Wrightsville Beach, North Carolina, between 31 and 100 d after their release off the west Florida shelf (Williams et al. 1977). The continental shelf between Cape Hatteras and Cape Lookout where this bloom occurred is the narrowest of any in the U.S. South Atlantic Bight north of the Miami area and is frequently overwashed by meanders of Gulf Stream water, some of which nearly reach the barrier

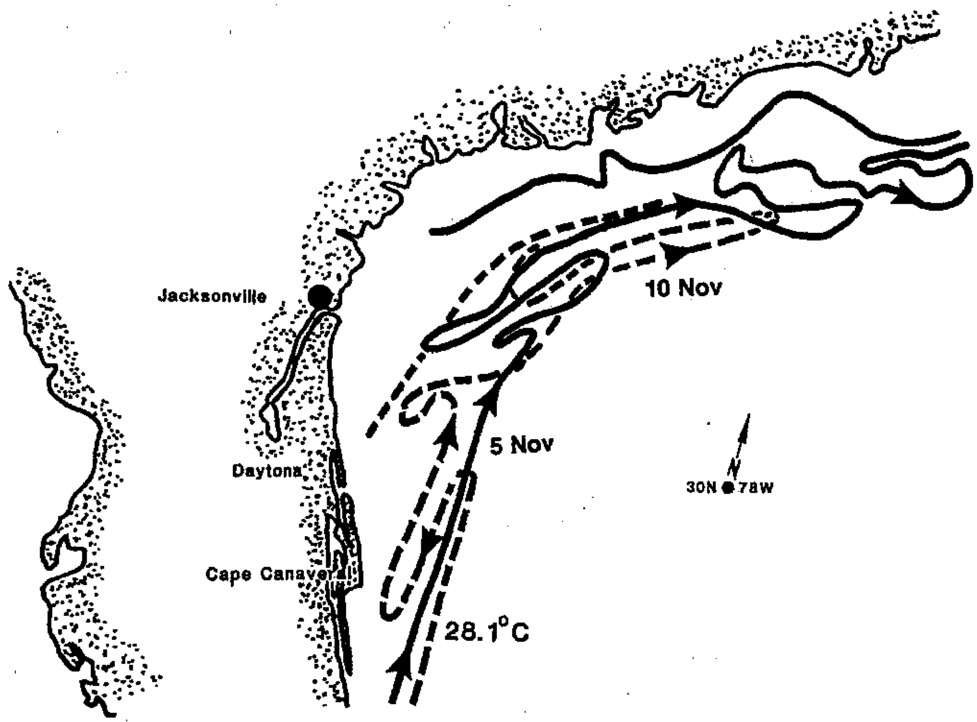

Fig. 11. Shoreward intrusions of Gulf Stream water onto the continental shelf off Jacksonville on 5 (solid line) and 10 (dashed line) November 1980. Note the filaments of water stranded shoreward of the intrusions. [Redrawn from Gulf Stream Frontal Analyses (GOES sea surface temperature) S. Baig, NOAA.]

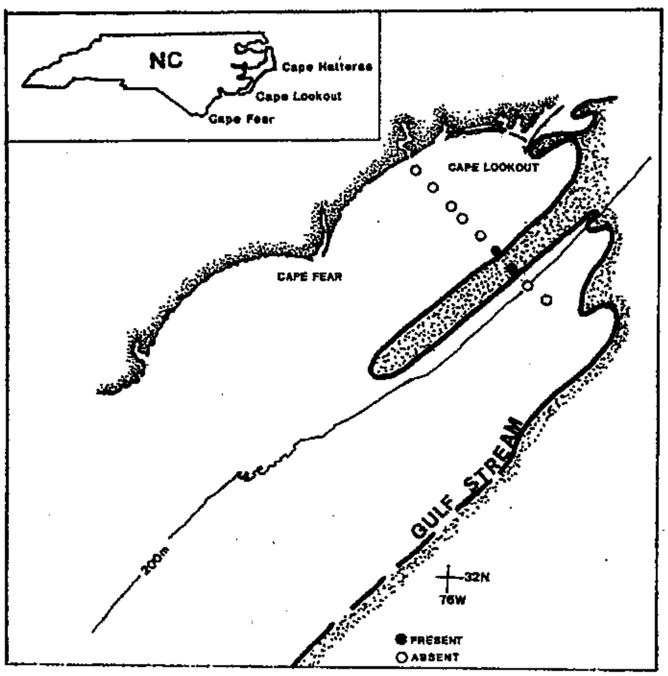

Fig. 12. Association of *Gymnodinium breve* cells with Gulf Stream water in Onslow Bay between Cape Lookout and Cape Fear during winter. In a February 1991 cross-shelf transect of nine stations, *G. breve* cells were found only at the two stations most closely associated with the Gulf Stream meander. Water temperatures in the Gulf Stream meander were ~22°C; temperatures of the shelf water did not exceed 14°C.

islands (Bane et al. 1981; Yoder et al. 1985). These meanders serve as nutrient pumps introducing new nitrogen from strata beneath the Gulf Stream (Lee et al. 1991). After a meander passes, parts of the filament may remain on the shelf for as long as a week before dispersing or rejoining the stream (FRED Group 1989). The longevity (>19 d) of the Gulf Stream filament stranded on the continental shelf off North Carolina in late fall 1987 was credited with sustaining this unique *G. breve* bloom (Tester et al. 1991).

Dissipation

Significant questions remained in the aftermath of the North Carolina bloom that caused the closure of major shellfish harvesting areas for an entire season and had an estimated cost of $25 million (Tester and Fowler 1990). Samples from ships of opportunity were used to determine nonbloom, background levels of *G. breve* for the northern and eastern Gulf of Mexico, the Florida Strait, and the entire U.S. South Atlantic Bight including the Gulf Stream and western Sargasso Sea (Fig. 2). *G. breve* has a continuous distribution throughout this range but in winter its occurrence in nearshore waters of the U.S. South Atlantic Bight is closely associated with Gulf Stream meanders overriding the shelf (Tester et al. 1993). Perhaps the best example of this dependency is from a cross-shelf sampling transect in Onslow Bay (between Cape Lookout and Cape Fear) in February 1991. This transect bisected a Gulf Stream meander and *G. breve* cells were found only in the meander and at its shoreward edge (Fig. 12). Field studies of Rounsefell and Nelson

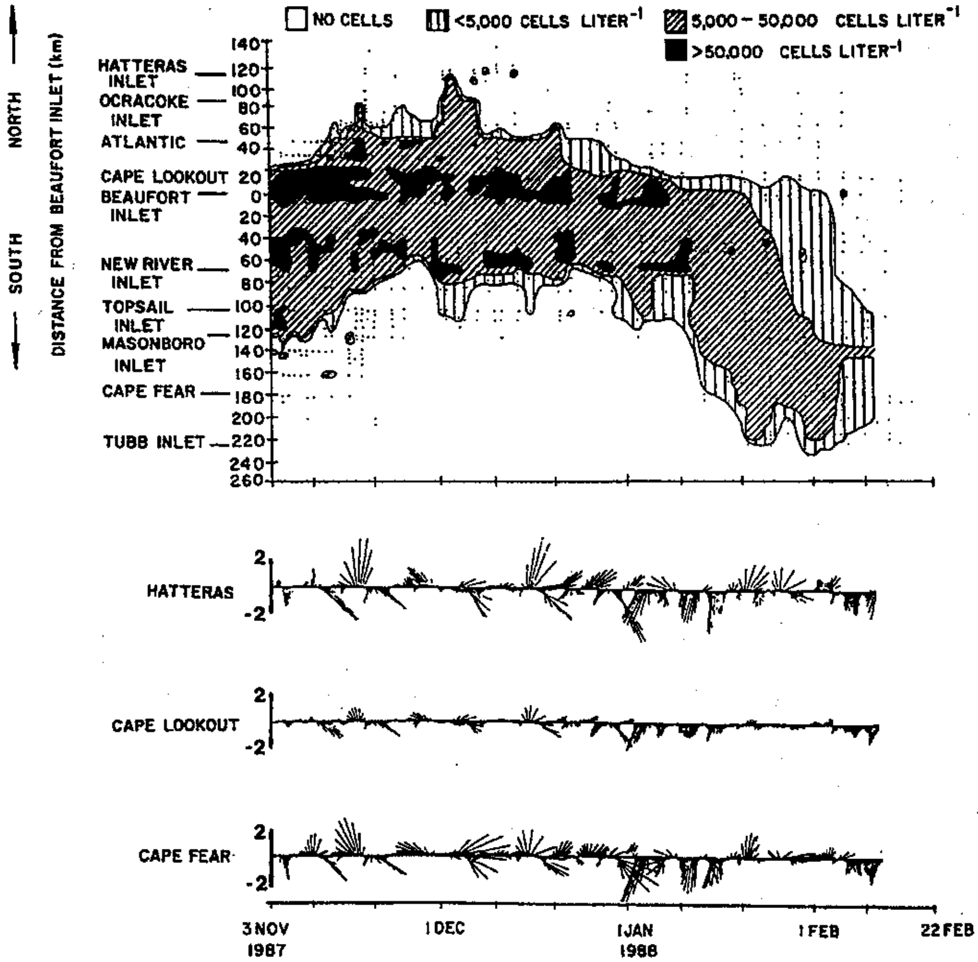

Fig. 13. Above—distribution and concentrations of *Gymnodinium breve* cells along the coast of North Carolina between 2 November 1987 and 22 February 1988. Below—wind stress (dyne cm^{-2}) measured at the Cape Hatteras, Cape Lookout, and Cape Fear C-MAN stations (after Tester et al. 1991).

(1966) indicated *G. breve* thrives between 16 and 27°C with only a few cells surviving 7–9.9°C (Aldrich 1959). Theoretically the lower thermal tolerance of this species is a major factor restricting bloom formation in the U.S. South Atlantic Bight. There is no permanent thermocline near the continental shelf edge and in winter nearshore bottom-water temperatures may be <9°C when inundated by Virginia coastal water (~5°C) (Stefánsson et al. 1971).

Dissipation or termination of blooms can occur when the offshore bloom component is entrained and transported out of the area or when the integrity of the water mass is weakened by mixing and dilution. Both declining water temperature and increasing wind stress contributed to the dissipation of the 1987–1988 *G. breve* bloom off North–South Carolina. From early November to late December 1987 most of the cells from this bloom moved back and forth within Onslow Bay depending on wind direction (Fig. 13). After nearshore water temperatures dropped (≤10°C) and the first winter storm (31 December 1987) was followed by intermittent but strong southward winds (1–16 January 1988), cell numbers decreased and the bloom was blown out of Onslow Bay, around Cape Fear to the south. Samples from 5 to 30 km off Little River Inlet to Myrtle Beach, South Carolina, from 6 to 7 February 1988 contained from 2–11×10³ cells liter⁻¹. The last samples from nearshore waters of North Carolina containing *G. breve* were collected on 11 February, and the bloom dissipated off Myrtle Beach by late February 1988 (Tester et al. 1991).

Conclusions

G. breve blooms are neritic phenomena. They have a successful survival strategy in the Gulf of Mexico ecosystem where they can be found from the central basin to nearshore waters (salinity >24‰). The bloom model that is most consistent with observations made during the last 80–100 yr starts with an offshore bloom initiation in late summer or fall in conjunction with a Gulf Loop intrusion on the outer continental shelf. Following cross-shelf transport, largely influenced by winds and wind-induced upwelling or downwelling, cells concentrate and grow at a region approximating the midshelf front. If cross-shelf transport mechanisms continue to operate on the bloom, cells concentrate in nearshore waters where movement is governed by winds and alongshore currents.

G. breve is found in low concentrations (<1,000 cells liter^{-1}) in the Florida Current–Gulf Stream throughout the year. During blooms cell concentrations of $>2\times10^4$ cells liter^{-1} become entrained in the Florida Current and transported to the Atlantic. Gulf Stream meanders are known to deliver the cells into nearshore waters. Small-scale eddy features like the Tortugas Gyre are very productive regions for phytoplankton and may prove to be so for *G. breve* as well. Strengthened transport through the Florida Strait at the dissipation of the Tortugas Gyre suggests an explanation for the infrequent, high cell counts in the Atlantic.

This conceptual model provides a framework to help define spatial and temporal scales, processes, timing, and linkages vital to hypothesis testing. It is essential that our understanding of the prerequisites for each bloom phase (e.g. initiation, growth, maintenance, and dissipation) be as complete as possible. We know little about factors that affect the intensity of *G. breve* blooms. It is critical that surface circulation be coupled with a depth component and the model expanded to three dimensions. It is equally important to understand what factors contribute to the reintroduction of cells into coastal waters—a major concern during prolonged blooms. Increased access to archived wind and temperature data combined with cell counts from "bloom logs" will aid in retrospective analyses of blooms in greater detail. The advent of online, real-time environmental data and the prospect of new ocean color sensors may allow enough predictive capability that bloom conditions can be detected early enough to allow for focused research efforts and provide reliable information to the public.

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Review

Literature review of Florida red tide: implications for human health effects

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Abstract

Florida red tides are a natural phenomenon caused by dense aggregations of single cell or several species of unicellular organisms. Patches of discolored water, dead or dying fish, and respiratory irritants in the air often characterize these algal blooms. In humans, two distinct clinical entities, depending on the route of exposure, are associated with exposure to the Florida red tide toxins (particularly the brevetoxins). With the ingestion of brevetoxin-contaminated shellfish, neurotoxic shellfish poisoning (NSP) presents as a milder gastroenteritis with neurologic symptoms compared with other marine toxin diseases such as paralytic shellfish poisoning (PSP) or ciguatera fish poisoning. With the inhalation of the aerosolized red tide toxins (especially the brevetoxins) from the sea spray, respiratory irritation and possibly other health effects are reported in both humans and other mammals [Nat. Toxins Drugs (1995) 141; Fleming, L.E., Baden, D.G., 1988. Neurotoxic shellfish poisoning: public health and human health effects. White Paper for the Proceedings of the Texas Conference on Neurotoxic Shellfish Poisoning. In: Proceedings of the Texas NSP Conference, Corpus Christi, TX, pp. 27–34; Travel Med, 2 (10) (1998b) 1; Travel Med. 3 (10) (1999a) 1; Toxins Pathol. 26 (2) (1998) 276; J. Allergy Clin. Immunol. 69 (1982) 418; Arch. Intern. Med. 149 (1989) 1735; Toxicon 24 (1986) 955; Florida Med. J. 60 (11) (1773) 27; J. Nat. Toxins 4 (1995) 181; J. Nat. Toxins 4 (1995) 181; Sci. Am. 271 (4) (1994) 62].

This paper reviews the literature on the known and possible human health effects of exposure to the Florida red tides and their toxins. The review includes discussion of the red tide organisms and their toxins, as well as the effects of these toxins on both wild and laboratory animals as they relate to possible human health effects and exposures.

Keywords: Florida red tide; Red tide; Neurotoxic shellfish poisoning; NSP; Brevetoxins; Harmful algal bloom; HAB; *Karenia brevis*; Shellfish poisoning; Respiratory irritation; Marine toxin diseases

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1. Background

Toxic red tides have been observed in Florida since the 1840s. Since that time, multiple episodes with significant fish kills, as well as cases of NSP have been reported from the Gulf of Mexico (including the east coast of Mexico), the east coast of Florida, and up to the North Carolina coast; toxic blooms occur almost annually on the west coast of Florida. Recently, these and other red tides appear to be increasing in incidence, duration and geographic spread (Viviani, 1992; Smayda and White, 1990; Van Dolah, 2000; Tester et al., 1991; Tester and Steidinger, 1997). Anthropogenic influences such as nutrient run-off inducing red tide blooms and the transport of dinoflagellate cysts in ballast water of ships have been suggested as possible causes. However, these red tides in Florida occurred even before significant pollution and development by human populations: during 1844–1971, red tides and their sequellae were noted along the west coast of Florida at least 24 times before the major industrial and agricultural development of that area. Alternative explanations (such as the effects of changing ocean temperatures, currents and weather patterns associated with global warming, as well as atmospheric transport of Sahara dust) are being investigated (Tester and Steidinger, 1997; Tester et al., 1991; Viviani, 1992; Tibbetts, 1998; Morris et al., 1991; Ishida et al., 1996; Anderson, 1994; Sierra-Beltran et al., 1998; Cortes-Altamirano et al., 1995; Tommasi, 1983; Epstein et al., 1994; NRC, 1999; Epstein, 1998; Steidinger and Ingle, 1972; Kin-Chung and Hodgkiss, 1991; Smayda and White, 1990; Walsh and Steidinger, 2001).

Recent prolonged red tides in the Gulf of Mexico have been associated with significant environmental, human health, and economic impacts. Beaches in Texas and shellfish beds from Florida to Mexico have been closed. Significant die-offs of fish, endangered manatees, and double-crested cormorants, as well as reported adverse human health effects, have resulted annually secondary to the red tide toxin exposure along the coastline of the Gulf of Mexico (Bossart et al., 1998; Hopkins et al., 1997; Kreuder et al., 1998; Trainer and Baden, 1999).

1.1. Organisms

The dinoflagellates are ancient, single-celled, eukaryotic organisms that can exist in benthic, parasitic, symbiotic, and free-living forms; ocean currents can transport the latter easily. Many of the dinoflagellates include in their life cycle at least one resting form or cyst. The cysts may serve as the seeds for the red tides because they are the renewal of the motile phase of the dinoflagellate when the environmental conditions are appropriate; the motile forms create the blooms and the natural toxins (Anderson, 1994; De M Sampayo, 1997; Baden et al., 1995; Baden, 1983).

The classic causative organism of Florida red tides is *Karenia brevis* (formerly known as *Gymnodinium breve* and *Ptychodiscus brevis*). *K. brevis* is a dinoflagellate restricted to the Gulf of Mexico and the Caribbean, but has been carried by ocean currents around Florida and up the east coast of the United States as far as North Carolina. Other species producing the same or similar toxins occur throughout the world, particularly in New Zealand (Ishida et al., 1996; MacLean, 1979; Hermes 1984; Chang, 1998; Temple, 1995; Morohashi et al., 1999; Anderson, 1994; Sierra-Beltran et al., 1998; Cortes-Altamirano et al., 1995; Tommasi, 1983; Horstman et al., 1991; Khan et al., 1997; Steidinger, 1983). *K. brevis* usually blooms in the late summer and autumn, almost every year off the west coast of Florida, causing massive fish and bird kills.

The *K. brevis* organism is relatively fragile, because it is unarmored. Therefore, particularly in wave action along beaches, the organism is easily broken open, releasing the toxins. During an active in-shore red tide, the aerosol of contaminated salt spray will contain the toxins and organism fragments, both in the droplets and attached to salt particles; these can be carried inland depending on wind and other environmental conditions (Pierce, 1986; Pierce et al., 1989, 1990; Sakamoto et al., 1987; Music et al., 1973; Backer et al., 2003; Horstman et al., 1991; ILO, 1984).

1.2. Toxins

Associated with these algal bloom episodes of *K. brevis*, a variety of phytoplankton-related natural toxins have been identified. There are reportedly hemolytic components and even cardiotoxic anti-cholinesterase phosphorus-containing compounds (Mazumder et al., 1997), however the most important group is the neurotoxic brevetoxins (*Ptychodiscus brevis* toxin, i.e. PbTx). As a group, the brevetoxins are lipid soluble, cyclic polyethers with molecular weights around 900. Over nine different brevetoxins have been isolated in sea water blooms and *K. brevis* cultures, as well as multiple analogs and derivatives from the metabolism of shellfish and other organisms (Morohashi et al., 1999; Baden and Trainer, 1993; Baden et al., 1995; Mazumder et al., 1997; Mattei et al., 1999; Pierce and Kirkpatrick, 2001). In red tides, the major brevetoxin produced by concentration is PbTx-2, as well as lesser amounts of PbTx-1 and PbTx-3 (Baden, 1989; Pierce et al., 1992).

As with many of the known marine toxins, the brevetoxins are tasteless, odorless, and heat and acid stable. These toxins cannot be easily detected, nor removed by food preparation procedures (Baden and Mende, 1982; Baden and Trainer, 1993; Baden et al., 1995; Sakamoto et al., 1987).

These brevetoxins are depolarizing substances that open voltage gated sodium (Na^+) ion channels in cell membranes, leading to uncontrolled Na^+ influx into the cell (Baden, 1983; Purkerson et al., 1999). This alters the membrane properties of excitable cell types in ways that enhance the inward flow of Na^+ ions into the cell; this current can be blocked by external application of tetrodotoxin, an Na^+ ion channel blocker (Gallagher and Shinnick-Gallagher, 1980; Baden, 1983; Halstead, 1988; Poli et al., 1986; Viviani, 1992; Trainer et al., 1991; Jeglitsch et al., 1998). Recent work by Purkerson et al. (1999) and others using electrophysiology studies of single sodium channel of rat central nervous system cells suggest that PBTx-3 may cause hyper excitability as well as inhibitory effects in the intact brain (Apland et al., 1993; Templeton et al., 1989a,b). As a consequence of their lipid solubility, these toxins are expected to easily pass through cell membranes including the blood brain barrier, as well as buccal mucosa and skin (Mehta et al., 1991; Kemppainen et al., 1991; Apland et al., 1993).

The massive fish kills associated with Florida red tides result from the neurotoxin exposure, with possible contribution of the hemolytic fraction. In particular, PbTx-3 is believed to be responsible for the respiratory irritation associated with toxin inhalation (Baden and Mende, 1982; Baden et al., 1982). The brevetoxins ionically depolarize nerve cells and lead to the characteristic disruptions of respiratory and cardiac function known as neurotoxic shellfish poisoning (NSP). When Borison et al. (1985) and Koley et al. (1995) studied brevetoxin in cats, they concluded that brevetoxin exerts its major toxic effects on circulation and respiration through reflex and central actions, largely sparing peripheral motor mechanisms. These toxins are also directly cardiotoxic and hepatotoxic in various in vitro and in vivo systems (Templeton et al., 1989a,b; Rodriguez-Rodriguez and Maldonado, 1996; Bossart et al., 1998; Rogers et al., 1984).

The respiratory problems associated with the inhalation of aerosolized Florida red tide toxins are believed to result from the opening of sodium channels of nerve cell membranes by the brevetoxins (Baden and Mende, 1982; Baden and Trainer, 1993; Asai et al., 1982; Borison et al., 1980; Franz and LeClaire, 1989; Baden, 1989). These effects can be blocked by atropine (muscarinic blocker) as well as tetrodotoxin (sodium channel blocker), but not by the interruption of vagal nerve stimulation or by diaphragm dissection in experimental animals (Baden and Mende, 1982; Gallagher and Shinnick-Gallagher, 1980; Asai et al., 1982; Trainer et al., 1991; Baden, 1989; Tsai et al., 1991; Watanabe et al., 1988). In isolated canine tracheal smooth muscle, neostigmine, an acetylcholinesterase inhibitor, potentiated the brevetoxin-induced contraction; mepyramine, phentolamine, methysergide, and chlorisondamine did not effect the contraction (Asai et al., 1982). In isolated human bronchial smooth muscle, Shimoda et al. (1988) found similar results as well as attenuation by verapamil (calcium and sodium channel blocker). Therefore, brevetoxin produces contraction of the lower airway smooth muscle by stimulation of the cholinergic nerve fiber sodium channels with acetylcholine release. However, additional pathways may be important for brevetoxin's physiologic effects. For example, in the rat vas deferens, Sakamoto et al. (1985) found that brevetoxin stimulated sodium channels on adrenergic nerve fibers, releasing norepinephrine from the nerve endings.

In addition, there appears to be a role for mast cells in the brevetoxin-associated respiratory effects. Watanabe et al. (1988) noted that brevetoxin can combine with a separate site on the h gates of the sodium channel, causing the release of neurotransmitters from autonomic nerve endings. In particular, this can release acetylcholine, leading to smooth tracheal muscle contraction, as well as massive mast cell degranulation. The mast cell contribution to the adverse airway effects of brevetoxin is supported by studies in a sheep model of asthma. In this model, aerosolized brevetoxin causes bronchoconstriction that can be blocked by the mast cell stabilizing agent cromolyn and the histamine H1 antagonist chlorpheniramine (Singer et al., 1998; Abraham and Baden, 2001). Thus, in addition to the direct neural component, brevetoxin appears to induce the release of histamine from mast cells and the combination of these actions results in adverse airway effects. Furthermore, because brevetoxin exposure by the respiratory route results in systemic distribution of brevetoxin, the initial bronchoconstriction may only be part of the overall consequences associated with toxin inhalation, including the central nervous system (Benson et al., 1999; Apland et al., 1993).

Computer modeling suggests that brevetoxin is a possible enzymatic binding inhibitor of cysteine cathepsins. Cathepsins are powerful lysosomal proteinases and epitope presenting enzymes, found within cytosol or lysosomes of macrophages cells, lymphoid tissues and other cells (Bossart et al., 1998; Sudarsanam et al., 1992). Bossart et al. (1998) postulated that the effects of aerosolized brevetoxins may be chronic not just acute. These chronic effects would begin with the initial phagocytosis by macrophages, inhibition of cathepsins, and apoptosis of these cells, followed by the phagocytosis of the debris by new macrophages, ultimately resulting in chronic neuro-intoxication, hemolytic anemia, and/or immunologic compromise.

Brevetoxins undergo biotransformation in rodents and fish (Poli et al., 1990a,b; Kennedy et al., 1992). In fish, the brevetoxins induce both cytochrome P4501A, and glutathione *S*-transferase with a variety of pathways for metabolism (Washburn et al., 1994, 1996). On the basis of evaluations of PbTx-3 on the sodium channels of rat sensory neurons, Jeglitsch et al. (1998) suggested that PbTx-3 metabolites may be more potent than PbTx-3 parent compound in affecting sodium channels. Work by Poli et al. (2000) evaluating metabolites in both the urine of three persons suffering from NSP and from the contaminated shellfish supported this conclusion; the authors suggested that these toxic metabolites from both the shellfish and the humans may be an additional cause of NSP and should be taken into account during regulatory testing.

1.3. Animals

The major seafoods contaminated by brevetoxins are shellfish, although no definitive evidence exists of any health effects to the shellfish, with possible exception of scallops (Cummins et al., 1971; Sakamoto et al., 1987; Steidinger and Ingle, 1972; Summerson and Peterson, 1990; Ellis, 1985).

Fish, birds, and mammals are susceptible to the brevetoxins. In the mosquito fish (*Bambusia affinis*) bioassay, the LD50 is reported at 0.011 μg/l (0.005–0.023) while with Japanese madaka (*Oryzias latipes*) the LC50 was reported to be 0.015–25 μg/ml (Bossart et al., 1998; Forrester et al., 1977; Geraci, 1989; O'Shea et al., 1991; Laverty, 1993; Trainer and Baden, 1999; Anderson, 1994; Sierra-Beltran et al., 1998; Cortes-Altamirano et al., 1995; Ellis, 1985; ILO, 1984; Poli, 1988). Fish kills associated with these red tides have been estimated up to 100 tonnes of fish per day during an active red tide. The fish are killed apparently through lack of muscle coordination and paralysis, convulsions, and death by respiratory failure. In the toadfish model, Kennedy et al. (1992) found that radiolabeled PbTx-3 was rapidly distributed within 1 h of intravenous administration (40.2% muscle, 18.5% intestine, and 12.4% liver); after 96 h, levels in the liver remained constant, but those in bile, kidney, and skin increased, with a variety of metabolites detected. Birds die acutely with neurologic and hematologic effects.

With respect to mammals, the mouse LD50 is 0.170 mg/kg body weight (0.15–0.27) intraperitoneally, 0.094 mg/kg body weight intravenously and 0.520 mg/kg body weight orally (Baden, 1983; Baden et al., 1995; ILO, 1984). Franz and LeClaire (1989) reported respiratory failure in less than 30 min in guinea pigs exposed intravenously to 0.016 ng/kg PbTx-3. With intravenous administration of PbTx-3 in rats, Poli et al. (1990a,b) found that approximately 90% was cleared within 1 min from the circulation. Furthermore, radiolabeling distributed to the skeletal muscle (70%), liver (19%), and intestine (8%) with little activity found in the heart, kidneys, lungs, spleen, testes, or brain. Elimination over a 24-h period was primarily through the feces. The parent compound was present in the skeletal muscle, but several metabolites of PbTx-3 excreted in the bile were found in the feces. Cattet and Geraci (1993) orally administered sublethal doses (18.6 μg/kg) of PbTx-3 in rats, and found wide distribution to all organs, with the highest concentrations in the liver up to 8 days after exposure. Ingested PbTx-3 was eliminated approximately equally in urine and feces.

To evaluate brevetoxin toxicokinetics from acute exposure up to 7 days, Benson et al. (1999) exposed 12-week-old male F344/Crl BR rats to a single exposure of 6.6 μg/kg PbTx-3 through intratracheal instillation. More than 80% of the PbTx-3 was rapidly cleared from the lung and distributed by the blood throughout the body, particularly the skeletal muscle, intestines, and liver with low but constant amounts present in blood, brain, and fat. Approximately 20% of the toxin was retained in the lung, liver, and kidneys for up to 7 days. The majority of the PbTx-3 was excreted within 48 h after exposure, with twice as much excreted in the feces than in the urine. The authors concluded that potential health effects associated with inhaled brevetoxins may extend beyond the reportedly transient respiratory irritation reported by humans exposed to Florida red tide brevetoxin aerosol.

Wells et al. (1984) reported increased airway resistance in six unanaethestized female Hartley guinea pigs when brevetoxin was inhaled as an aerosol or applied to the nares as nose drops, compared with cross over exposure to methacholine with and without pretreatment with atropine. Furthermore, the authors reported that the animals were significantly less responsive to brevetoxin with pretreatment by atropine or by diphenhydramine, although no observable effects on the sneezing, drooling, and defecation of the animals with pretreatment. In the unanaesthestized asthmatic sheep, picogram doses of PbTx-3 can cause a significant and rapid increase in respiratory resistance (200–300× baseline); as noted above, this brevetoxin-induced bronchospasm can be effectively blocked by the mast cell stabilizing agent cromolyn and the histamine H1 antagonist chlorpheniramine (Singer et al., 1998; Abraham and Baden, 2001). Thus in the lung, brevetoxin appears to be a potent respiratory toxin involving both cholinergic and histamine-related mechanisms.

Multiple die-offs of marine mammals have been reported in association with Florida red tide and brevetoxins (Geraci, 1989; O'Shea et al., 1991; Bossart et al., 1998). In 1996, a prolonged Florida red tide in the Gulf of Mexico resulted in the documented deaths of 149 endangered Florida manatees (Bossart et al., 1998; Trainer and Baden, 1999). The brevetoxin exposure of the manatees appears to have been prolonged inhalation of the red tide toxin aerosol and/or ingestion of contaminated seawater over several weeks. This manatee die-off investigation revealed severe catarrhal rhinitis, pulmonary hemorrhage and edema, and non-suppurative leptomeningitis, as well as possible chronic hemolytic anemia with multi-organ hemosiderosis and evidence of neurotoxicity (particularly cerebellar) in the dead manatees. Therefore, the respiratory tract, liver, kidneys, and brains of the manatees were primary brevetoxin targets, and the brevetoxin exposures and effects were believed to be chronic rather than acute. PbTx-3 and its metabolites were identified by a immunohistochemical stain using a polyclonal primary antibody to brevetoxin to be stored in the lung and other organs in alveolar macrophages and in the brain within lymphocytes and microglial cells. Immunohistochemical staining with interleukin-1-beta converting enzyme showed positive staining with a cellular trophism similar to the brevetoxin antibody staining, suggesting that brevetoxin may initiate apoptosis and/or release inflammatory mediators that culminate in fatal toxic shock. Additional studies demonstrated that brevetoxin binds to isolated nerve preparations from manatee brain with a similar affinity as that reported for terrestrial mammals (Trainer and Baden, 1999), as well as causing significant liver damage in in vitro mouse liver studies (Rodriguez-Rodriguez and Maldonado, 1996).

2. Humans

The two known forms of red tide toxins-associated clinical entities in humans first characterized in Florida are an acute gastroenteritis with neurologic symptoms after ingestion of contaminated shellfish (i.e. NSP) and an apparently reversible upper respiratory syndrome after the inhalation of the aerosols of the dinoflagellate and their toxins (i.e. aerosolized red tide toxins respiratory irritation) (Asai et al., 1982; Baden et al., 1995; Fleming and Baden, 1988; Fleming and Easom, 1998;

Fleming et al., 1999, 2001; Morris et al., 1991; Music et al., 1973; Baden et al., 1982; Poli et al., 2000).

2.1. Ingestion of brevetoxin

Neurotoxic shellfish poisoning can be viewed clinically as a milder form of paralytic shellfish poisoning (PSP) or ciguatera fish poisoning. In human cases of NSP, the brevetoxin concentrations present in contaminated clams have been reported to be 30–118 mouse units (MU)/100 g (78–120 μg/mg). Poli et al. (2000) reported on the measurement of brevetoxin in urine from three persons who suffered from severe NSP after eating contaminated shellfish from Florida; the urine brevetoxin levels ranged from 42 to 117 ng/ml by RIA analysis on admission to the emergency department. As a comparison, in PSP fatal paralysis can occur with as little as 1 mg of saxitoxin, while picogram levels of ciguatoxin in ciguatera fish poisoning have been reported to make adult humans severely ill. The shellfish reported to be associated with NSP when contaminated with brevetoxin include oysters, clams, coquinas, and other filter feeders (Keynes, 1979; Baden et al., 1995; ILO, 1984; Hughes and Merson, 1976; ILO, 1984; Poli et al., 2000).

NSP typically causes gastrointestinal symptoms of nausea, diarrhea, and abdominal pain, as well as the neurologic symptoms primarily consisting of paresthesias similar to those seen with ciguatera fish poisoning (including reports of circumoral parathesiae and hot/cold temperature reversal), beginning within minutes to 3 h after ingestion. Cerebellar symptoms such as vertigo and incoordination also reportedly occur. In severe cases, bradycardia, headache, dilated pupils, convulsions, and the subsequent need for respiratory support have been reported. Death from NSP (rather than from PSP or ciguatera) is rare. Reportedly, symptoms resolve within a few days after exposure, however, no studies have been reported evaluating possible chronic health effects after acute NSP (Morse, 1977; Sakamoto et al., 1987; Baden et al., 1995; Fleming et al., 1995, 2001; Morris et al., 1991; McFarren et al., 1965; Viviani, 1992; Hughes and Merson, 1976; Noble, 1990; Martin et al., 1996; Music et al., 1973; Hopkins et al., 1997; ILO, 1984; Rheinstein, 1993; Dembert et al., 1981).

Morris et al. (1991) reported on an outbreak of NSP secondary to a red tide of *K. brevis* (then known as *P. brevis*) in October 1987 along the North Carolina coast. Ultimately, over 48 persons were diagnosed with NSP following consumption of cooked and raw oysters at 20 different meals. Acutely, 23% of the cases reported gastrointestinal and 39% reported neurologic symptoms. These symptoms were described as having a rapid onset (median incubation of 3 h), mild, and of short duration (maximum malaise and vertigo up to 72 h with median duration of 17 h). Ultimately, 94% had multiple symptoms, and 71% had more than one neurologic symptom. Although no deaths or respiratory distress occurred, one woman was admitted to the intensive care unit because of severe neurologic symptoms. The illness attack rate increased significantly in association with the number of oysters eaten. Of note, 56% of the cases occurred before the first closure of affected shellfish waters to harvesting in early November; North Carolina had no red tide monitoring program at that time.

2.2. Inhalation of aerosolized brevetoxin

Few reports have been published about human exposure and health effects associated with exposure to aerosolized red tide toxins in humans. The exposure usually occurs on or near beaches with an active red tide bloom. Onshore winds and breaking surf result in the release of the toxins into the water and into the onshore aerosol (Pierce, 1986; Pierce et al., 1989, 1990, 2001; Sakamoto et al., 1987; Music et al., 1973; Backer et al., 2003; Horstman et al., 1991; ILO, 1984). After initial reports in Florida and Texas, Woodcock (1948) reported respiratory irritation during a severe red tide on the west coast of Florida in 1947. When seawater containing the red tide organisms was sprayed as an aerosol into the nose and throat of volunteers, coughing and a burning sensation similar to that experienced on the beaches were reported (Woodcock, 1948). Pierce et al. (1989, 1990) simulated the red tide toxin aerosol in the laboratory by bubbling air through seawater cultures of lysed *K. brevis* cells; they recorded toxin enrichment in the aerosol of 5–50 times the concentration of original concentrations in the seawater. Collection of marine aerosol along the Gulf coast of Florida and the North Carolina Atlantic coast during natural red tide blooms showed that the aerosolized toxins were the same as those in the water and as those resulting from the *K. brevis* culture experiments (Pierce et al., 1989, 1990).

Inhalation of aerosolized red tide toxins reportedly results in conjunctival irritation, copious catarrhal exudates, rhinorrhea, nonproductive cough, and bronchoconstriction (Music et al., 1973; Asai et al., 1982, 1984; Franz and LeClaire, 1989; Eastaugh and Shepard, 1989; Pierce, 1986; Temple, 1995; Sakamoto et al., 1987; Baden et al., 1982; Davis, 1994; Ahles, 1974; Hughes and Merson, 1976; Tommasi, 1983; Hopkins et al., 1997; ILO, 1984; Dembert et al., 1981; Cummins et al., 1971). Some people also report other symptoms such as dizziness, tunnel vision, and skin rashes. In the normal population, the irritation and bronchoconstriction are usually rapidly reversible by leaving the beach area or entering an air-conditioned area (Steidinger and Baden, 1984; Baden, 1983).

However, people with asthma are apparently particularly susceptible; Asai et al. (1982) found that 80% of 15 asthmatic patients exposed to red tide aerosol at the beach complained of asthma attacks. Further studies by the same investigators (Watanabe et al., 1988) using human bronchial smooth muscle tissue from 12 non-asthmatic persons, all with a smoking history, showed similar results to canine smooth muscle studies: brevetoxins caused contraction with a threshold of 0.1 μg/ml with peak response at 12.0 μg/ml (EC50 = 1.24 μg/ml); this response was blocked by verapamil, atropine and tetrodotoxin, and it was potentiated by neostigmine. The possibility of susceptibility of asthmatics to the brevetoxins is corroborated by recent investigations with an asthmatic sheep model evaluating the exposure of aerosolized red tide toxins discussed above (Singer et al., 1998; Abraham and Baden, 2001). Furthermore, there are anecdotal reports of prolonged pulmonary symptoms even after exposure has ceased, especially in susceptible populations such as the elderly or people with chronic lung disease.

Reportedly, aerosolized red tide toxins respiratory irritation is associated only with significant Florida red tide blooms (including significant fish kills with dead fish on the beaches) within a few feet of the breaking surf of an active bloom. However, exposure to aerosolized red tide toxins can cause respiratory irritation, even in non-asthmatics and without obvious fish kills or high dinoflagellate cell counts in the seawater within a few feet of the seashore (K. Steidinger, Florida Department of Environmental Protection, verbal communication). This may be due to the concentration of the brevetoxins in the aerosol of sea spray generated by waves hitting the shore during a red tide (Pierce et al., 1989, 1990; Music et al., 1973; Cummins et al., 1971). How far inshore this red tide toxins aerosol will travel, especially given strong offshore winds during a red tide bloom, is not known.

Cummins et al. (1971) sampled water and bivalves during a red tide along the west coast of Florida in September 1967. In addition to identifying *K. brevis* in the water samples and showing toxicity in the mouse bioassay with shellfish samples, the investigators reported burning of the eyes and respiratory irritation during the course of sampling. These symptoms increased as investigators approached the surf zone and were associated with organisms in the water. The investigators reported similar symptoms when they received an inadvertent inhalation exposure from an aerosol of *K. brevis* organism cultures being aerated in the laboratory during oyster intoxication studies.

Music et al. (1973) reported on a November 1972 *K. brevis* red tide on the east coast of Florida, after currents and weather patterns had carried an existing red tide from the usual epicenter of west coast of Florida. This red tide coupled with strong easterly onshore winds resulted in multiple reports of symptoms to the Palm Beach Health Department; the reports came from people on the beach (swimmers, workers, lifeguards), as well as from persons living on or near the beach throughout Palm Beach County. Symptoms reported included acute eye and nose irritation (e.g. profuse watery eyes, copious rhinorrhea with burning of the eyes and nose), non-productive cough, and respiratory distress similar to that associated with the Florida west coast red tide. The symptoms were described as having a sudden onset, i.e. occurring as soon as people got near the beach areas or were exposed to the onshore winds in their homes. The symptoms reportedly resolved upon leaving the beach or wind exposure, although less rapidly for those who were exposed for a longer time. Exposure to air-conditioning in homes or cars seemed to improve the symptoms more rapidly. Persons on boats or long piers not exposed to breaking surf with onshore winds did not report any symptoms. All reports of symptoms stopped when the winds changed direction.

Hopkins et al. (1997) briefly reported on a prolonged Florida red tide with confirmed *K. brevis* identification along the west coast of Florida from December 1995 to May 1996. The Lee County Health Department conducted a mailed survey of 1100 residents and long-term visitors in areas adjacent to beaches. There were 416 (39%) responses, with most respondents reported symptoms (although the authors point out that response to the survey encouraged report from symptomatic persons). Eye and respiratory irritation were associated with the amount of time spent at the beach, but more serious conditions (i.e. bronchitis, pneumonia, and various neurologic problems) were not. Six persons were hospitalized for illnesses they attributed to red tide exposure (although no definite diagnoses by physicians were reported).

Kirkpatrick et al. (2001) conducted a similar pilot study in 1999 using scientists on *K. brevis* red tide research cruises as volunteer study subjects. Air and water samples were analyzed for brevetoxins and personal interviews and pulmonary function tests were conducted daily. On one day of the research cruise when seas and winds were higher than on other days and cell counts were up to 8 million cells/l, two scientists reported shortness of breath and/or difficulty taking a deep breath. At that same time, both had a decrease in pulmonary function. Although the pulmonary function decrease was not clinically significant, it is worth noting because neither scientist had any history of lung disease, both were young (30 years old), and neither were smokers.

In a pilot study of aerosolized red tide, Backer et al. (2003) measured the levels of brevetoxins in air and water samples and conducted personal interviews and pulmonary function tests on people before and after visiting Florida beaches during *K. brevis* red tide events. One hundred twenty-nine people participated in the study, which was conducted during two separate red tide events in the west and east coasts of Florida. During these episodes, *K. brevis* and brevetoxins were measured in the seawater, as well as brevetoxins in environmental and personal air sampling. Exposure was categorized into three levels: little or no exposure, moderate exposure, and high exposure. Lower respiratory symptoms (e.g. wheezing) were reported by 8% of unexposed, 11% of moderately exposed, and 28% of highly exposed people. A detectable inflammatory response to the inhaled toxins was observed in over 33% of the people examined after they visited the beach. During the moderate and high exposure study periods, people were exposed to up to 36 or 80 ng/m^3, respectively, of brevetoxin in the air. If an average adult breathes in about 25 l of air per minute for light exercise, then the authors estimated that people visiting the beaches during the pilot study inhaled between 54 and 120 ng brevetoxin each hour, or an inhaled dose of between 0.77 and 1.71 ng/kg (assuming an average weight of 70 kg) each hour. No clinically significant changes occurred in pulmonary function test results; however, the study population was small. The authors plan to further investigate the human health impact of inhaled brevetoxins in future epidemiologic studies.

Red tide events in the Gulf of Mexico are usually reported from along the western coast of Florida and can occur nearly annually (Kusek et al., 1999). Red tides along the Texas coast are much less frequent (Villareal et al., 2001). Cheng et al. (submitted) reported a red tide episode in the Gulf of Mexico near Corpus Christi, Texas, in October 2000. At Marine Science Institute (MSI) and Texas State Aquarium (TSA), airborne brevetoxin concentrations between 1.6 and 6.7 ng/m^3 were reported, along with a few reports of upper respiratory symptoms (throat irritation, nasal irritation, and itchy skin) and no reports of lower respiratory symptoms. Although the number of workers was too small for statistical analysis, the reported symptoms were consistent with no/low exposure at the MSI and detectable exposures at the TSA. This suggests that at lower environmental concentrations of about 2–7 ng/m^3, exposure to brevetoxin could result in upper respiratory symptoms. This lower level of airborne brevetoxin concentrations could be detected because of a more sensitive LC/MS technique. The brevetoxin particle size distribution with the impactor samplers, the first time that particle size of brevetoxin was reported. The MMAD was between 7 and 9 μm (a range of 3–20 μm), a relatively large size for inhaled ambient particles. Fine particles below 2.5 μm were not detected. Inhaled particles of this size would be deposited in the upper respiratory tract (nasal, oral, and pharyngeal area) (ICRP, 1994; Yeh et al., 1996), and subsequent respiratory irritation could result from the presence of the particles themselves or from toxins associated with the particles. Inhaled particles also deposited on the face and exposed skin causing the skin to itch.

Whether the inhalation of aerosolized brevetoxins can result in other systemic health effects (such as affecting the neurologic or immunologic systems) and in chronic effects is not known. The manatee evidence and other laboratory animal studies suggest that this possibility should be explored further (Fleming et al., 1995, 2001; Bossart et al., 1998; Benson et al., 1999).

2.3. *Diagnosis*

In general, NSP is a rare event in the United States. This is due in part to the extensive monitoring of shellfish beds for toxins and organisms in areas where red tide is endemic, resulting in shellfish bed closure if either is elevated. If shellfish are not available for testing, Florida red tide toxins-associated human diseases is diagnosed primarily on recognition of the clinical scenario of persons becoming ill with gastrointestinal and neurologic symptoms after eating shellfish or with acute respiratory symptoms after inhaling aerosols associated with exposure to Florida red tide toxins.

The primary toxicity testing methods for contaminated shellfish currently is the US Food and Drug Administration (FDA) approved mouse bioassay. Several chemical, pharmacologic, and immunologic techniques, and the in vitro neuroblastoma cytotoxicity assay are available. In spite of specific strengths, each of these methodologies suffers limitations (Hannah et al., 1996). The mouse bioassay in particular gives false positives and does not conclusively prove the presence of a particular toxin (Kerr et al., 1999).

Recent promising brevetoxin research includes: HPLC, HPLC–MS, and micellar electrokinetic capillary chromatography/laser induced fluorescence detection methodologies for the identification of the *K. brevis* toxins, as well as an experimental ELISA test using antibodies to brevetoxin, radioimmunoassay, a cell-based assay with tritium labeled PbTx-3 and rat brain synaptosomes, a sodium channel specific neuroblastoma cytotoxicity assay, and a neurophysiologic method using in vitro rate hippocampal slices (Templeton et al., 1988; Melinek et al., 1994; Fairey et al., 1997; Hua et al., 1995; Ishida et al., 1996; Whitney et al., 1997; Poli et al., 1995; Naar et al., 2002; Trainer et al., 1991; Hannah et al., 1996; Dickey et al., 1999; Kerr et al., 1999; Poli et al., 1990b; Shea, 1997; Garthwaite et al., 1996; Manger et al., 1995; Van Dolah et al., 1994). In particular, the brevetoxin ELISA (based on goat anti-brevetoxin) is currently being applied experimentally to detect brevetoxin in: contaminated seawater, air, and contaminated shellfish (Naar et al., 2002). Although water sampling for both the dinoflagellates and the toxins has been performed for many years, red tide toxins air monitoring is presently experimental. Air monitoring could provide qualitative and quantitative time- and geographic-based data.

Work with Florida manatees (apparently killed by the inhalation of the red tide toxins) has led to the development of a qualitative immunohistochemical stain for the Florida red tide toxins found within the macrophages and lymphocytes in nasal mucosa, lung, and other tissues (Bossart et al., 1998). This staining technique has also been used to look for toxins in the tissues of marine birds exposed to red tide toxins (Jessup et al., 1998; Kreuder et al., 1998). This biomarker could be used as both an indicator of exposure and effect. On the basis of recent research in a sheep animal model using a modified immunocytochemical technique on the bronchial lavage specimens of animals exposed to aerosolized red tide toxins, this biomarker holds promise as a diagnostic and prognostic tool. Initial work shows that the immunocytochemical staining of throat and nasal swab specimens reflect the bronchial lavage results, thus allowing for a more human-applicable biomarker.

Currently, no tests are available for measuring the brevetoxins in human fluids, although the work of Poli et al. (2000) measuring brevetoxin and its metabolites in urine using HPLC–MS and other methods, as well as the new brevetoxin ELISA of Naar et al. (2002) are promising.

2.4. *Treatment and prevention*

Treatment for shellfish poisoning is supportive (i.e. fluid replacement and respiratory support if necessary). In PSP, emesis may not occur, hence gastric lavage is commonly used. Ciguatera fish poisoning caused by the natural marine toxin, ciguatoxin, was shown in a clinical trial to respond to the early administration of intravenous mannitol within 72 h (Palafox et al., 1988; Fleming et al., 1997; Blythe et al., 2001). Because brevetoxin and ciguatera are similar structurally, intravenous mannitol might be efficacious in treating early NSP (Mattei et al., 1999).

Recent efforts have been directed in experimental animals toward developing specific monoclonal antibodies and antidotes against brevetoxin (Templeton et al., 1989a,b). Furthermore, Templeton et al. (1989a) and Poli et al. (1990b) indicated that in rats pretreated with an infusion of anti-brevetoxin IgG, nearly all the neurologic symptoms were blocked. Additionally, Purkerson-Parker et al. (2000) identified brevetoxin derivatives that actually inhibit brevetoxin activity in electrophysiologic experiments. Initial data suggest that one of these derivatives, β-naphthoyl-PbTx-3 can inhibit increases in pulmonary resistance in asthmatic sheep caused by aerosols of *K. brevis* cultures as well as aerosols of pure PbTx-2 and PbTx-3.

In the case of aerosolized red tide toxins respiratory irritation, the use of particle filter masks may prevent or diminish the symptoms, and retreating to air-conditioned environment reportedly will provide relief from the airborne irritation (Watanabe et al., 1988; Woodcock, 1948; Music et al., 1973; Backer et al., 2003). Brevetoxin-induced bronchospasm in asthmatic sheep and other animal models exposed to aerosolized red tide toxins can be effectively blocked by the mast cell stabilizing agent cromolyn and the histamine H1 antagonist chlorpheniramine, as well as by the muscarinic blocker atropine, the beta-2-agonists, the calcium channel blocker verapamil, and the sodium channel blocker tetrodotoxin (Baden and Mende, 1982; Gallagher and Shinnick-Gallagher, 1980; Asai et al., 1982; Trainer et al., 1991; Singer et al., 1998; Watanabe et al., 1988). In the future, some of these medications may be used to treat, and if used prophylactically, even to prevent the bronchoconstrictive response. These medications may be useful for people with asthma and for other susceptible persons exposed to aerosolized red tide toxins.

In the laboratory, *C. virginica* oysters accumulated *K. brevis* in less than 4 h in the presence of less than 5000 cells/ml of *K. brevis*; the oysters will then naturally "detoxify" 60% of the toxins in 36 h when placed in *K. brevis* free water. There is substantial variability between species of the potency of depuration, even under laboratory conditions. Canning does not decrease the brevetoxin concentration in bivalves. Commercial bivalves are reportedly safe to eat 1–2 months after the termination of single bloom episode (Baden, 1983; Viviani, 1992; Steidinger and Ingle, 1972). Successful ozone-assisted depuration of red tide contaminated shellfish, both killing the organism and inactivating the toxin, have been reported; depuration with ultraviolet light and chlorination have proven unsuccessful (Baden et al., 1995; Blogoslawski et al., 1975; Fletcher et al., 1998; Roderick, 1997).

Poli (1988) reviewed laboratory procedures for the detoxification of equipment and waste contaminated with brevetoxins PbTx-2 and PbTx-3. In particular, laboratory equipment can be safely decontaminated using a dilute 0.1 N NaOH solution for at least 10 min, and disposable waste can be either soaked in the NaOH solution before disposal or burned in an incinerator with a combustion chamber of at least 500 °C; steam autoclaving is not a viable method of decontamination. Workers should be protected from dermal, oral, and inhalation exposures to brevetoxins.

2.5. Monitoring and surveillance

The most effective way to prevent adverse health effects to humans from the red tides is to prevent exposure to the toxins and organisms. In the case of NSP, this means monitoring shellfish beds for organisms and toxins and closing shellfish beds to harvest when specified levels are detected. For the aerosolized red tide respiratory irritation, water and air monitoring could detect high levels in the air, and warning notices can be posted along affected coastal areas for susceptible subpopulations. Surveillance and reporting of red tide disease in humans, other mammals, and animals are important for early warning, prevention, and further understanding of these diseases. In addition, education and outreach programs to healthcare providers, workers involved in the seafood and tourism industries, and the general public are important components of successful monitoring and surveillance programs (Fleming et al., 1995).

Since the mid-1970s, the Florida Department of Agriculture and Consumer Services (DACS) has conducted a monitoring program of shellfish beds in the Gulf of Mexico. Beds are closed when the level of *K. brevis* exceed 5000 cells/l near or in harvesting areas. The areas remain closed until at least 2 weeks after a drop in cell counts below the action level and mouse bioassay results in shellfish below 20 MU/100 g (Viviani, 1992; Park, 1995; Baden et al., 1995). No regulatory limit exists for brevetoxin in the seawater. The regulatory limit for shellfish is 20 MU/100 g of shellfish meat, which is equivalent to 80 μg brevetoxin/100 g of shellfish meat (Subcommittee, 1970; Dickey et al., 1999).

The standardized mouse bioassay is used to test specimens for neurotoxicity. The bioassay is based on the time until death of mice injected intraperitoneally with crude toxin residues extracted from shellfish. Relative toxicity is expressed in mouse units. One mouse unit is the amount of crude toxin residue that will on average kill 50% of test mice in 930 min. Although any detectable level of toxin per 100 g of shellfish tissue is considered potentially unsafe for human consumption, in practice a residue toxicity >20 MU was adopted as the guidance level for the prohibition of shellfish harvesting (Morris et al., 1991; Dickey et al., 1999).

These monitoring programs should prevent ingestion NSP related to contaminated shellfish consumption in most of the Florida human population but not in areas where red tide is not an annual event or where monitoring programs do not exist (e.g. North Carolina). Furthermore, such monitoring programs do not prevent the respiratory irritation associated with exposure to aerosolized red tide toxins, although they could serve as early warning devices. In Florida, where the red tides occur almost yearly, beaches are not closed to recreational or occupational activities even during active near-shore blooms.

Marine toxin diseases such as NSP are believed to be significantly underreported. This is due to the public and medical misconception that all food poisoning events result mainly from microbial contamination; furthermore, many healthcare providers even in endemic areas do not realize that cases of marine toxin disease are required to be reported to the public health authorities. Thus, in the case of ciguatera fish poisoning, the CDC has estimated that only 2–10% of cases are actually reported in the United States, even in endemic areas such as south Florida (Sierra-Beltran et al., 1998; Cortes-Altamirano et al., 1995; Fleming et al., 1995, 2001; Ahmed, 1993; McKee et al., 2000). In 1999, the Florida Department of Health added NSP to its list of reportable diseases; however, aerosolized red tide toxins respiratory irritation is not reportable.

The Florida Poison Information Center at the University of Miami initiated a toll-free 24-h per day Marine and Freshwater Toxin Hotline (1-888-232-8635) in 1997 to increase reporting of marine and freshwater-related illness, including the marine toxin-associated diseases such as NSP and aerosolized red tide toxin irritation. The Poison Information Center passes on any cases of reportable illnesses by to the Florida Department of Health for official reporting purposes. Efforts are ongoing to increase knowledge and reporting of these illnesses by healthcare providers and public health officials. These include a video conference on the human health effects of marine toxins in Florida in June 1999, with a video and educational materials by the NIEHS Marine and Freshwater Water Biomedical Sciences Center at the University of Miami through funding from CDC, the Florida Department of Health, and the Area Health Education Coalition (AHEC) (Fleming et al., 1998, 1999).

2.6. Economic impact

The economic impact of all the harmful algal blooms is difficult to quantify. This is due in part to their unreported and unrecognized costs, including public health, seafood industry and tourism (Anderson et al., 2000; Martin and Martin, 1976). In the case of *K. brevis*, economic costs are associated with closure of shellfish beds (as well as possible depressed commerce in shellfish, even after the beds are re-opened, because of worried public perception), the public health and medical costs of NSP and the aerosolized red tide toxin respiratory irritation response, the impact on tourism and related activities from the presence of active red tides in recreational areas, the impact on marine mammals (including endangered animals) and other animals, and the disposal of literally millions of tons of dead fish on beaches and in canals and rivers. For example, in 1971, St. Petersburg, Florida, officials estimated that it cost US$ 155,763 to remove 2367 tonnes of fish from their beaches and canals (Steidinger and Ingle, 1972). With regards to potential fisheries impact, Sierra-Beltran et al. (1998) reported that the shellfish beds are closed to harvest because of active red tide contamination along the eastern coast of Mexico on an average 60 days per year. The 1987 closure of shellfish beds in North Carolina for an entire season due to *K. brevis* cost an estimated US$ 25 million, without taking into account the NSP public health investigation and other intangibles (Tester and Steidinger, 1997).

Anderson et al. (2000) estimated the annual economic impact for all the harmful algal blooms (including *K. brevis* red tides) for the United States. For 1987–1992 in 2000 dollars, the average 15 year capitalized impacts were US$ 449,291,987, with an annual average of US$ 49 million per year; of these impacts, 45% were attributed to public health costs, 37% to commercial fishery costs and losses, 13% to recreation and tourism, and 4% to monitoring and management. The authors believe that these estimates were highly conservative because of low monitoring, reporting and data collection of harmful algal bloom events and impacts.

2.7. Identified research areas

Inexpensive, reliable, and easily accessible testing for the brevetoxins in multiple media (sea water, air, shellfish, and biologic fluids) are essential for the understanding of the human health effects of Florida red tide and its toxins. No established biomarkers of exposure and effect for either of the Florida red tide toxins-associated conditions in humans. Little information is available on appropriate treatment and prevention methodologies particularly of the respiratory irritation illness.

The exact composition, including droplet size, of the red tide brevetoxin aerosol is unknown. It is not known how far inshore this red tide toxins aerosol will travel, especially given strong offshore winds during a red tide bloom. Although water has been sampled for both the dinoflagellates and the toxins for many years, red tide toxins air monitoring is not widely conducted. Expanded air monitoring could provide qualitative and quantitative time- and geographic-based data.

Published literature and formal epidemiologic studies are scarce on the human health effects of the diseases, either ingestion NSP or inhalation aerosolized red tide toxins respiratory irritation. Both NSP and aerosolized red tide toxin respiratory irritation are likely to be under-reported and under-diagnosed. No population-based statistics exist for the incidence of NSP or aerosolized red tide toxins respiratory irritation, even in endemic areas. Whether inhalation of aerosolized brevetoxins can result in other systemic health effects (such as neurologic or immunologic), and in chronic effects is unknown. The manatee evidence, as well as other laboratory animal studies, suggests that this possibility should be explored further. These effects should be considered particularly in possibly sensitive subpopulations.

Finally, education and outreach programs to healthcare providers, workers involved in the seafood and tourism industries, and the general public are important components of successful monitoring and surveillance programs (Fleming et al., 1995; Fleming and Baden, 1988; Fleming and Easom, 1998; Fleming et al., 1999; Fleming, 2000; Anderson et al., 1993, 2000; Steidinger et al., 1999; NRC, 1999; Ahmed, 1993; Pierce, 1986; Kin-Chung and Hodgkiss, 1991; Smayda and White, 1990; Martin and Taft, 1998; ILO, 1984).

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GEOPHYSICAL RESEARCH LETTERS, VOL. 33, L11601, doi:10.1029/2005GL025449, 2006

- nutrient Budget for Red tide

Hurricanes, submarine groundwater discharge, and Florida's red tides

Chuanmin Hu,[1] Frank E. Muller-Karger,[1] and Peter W. Swarzenski[2]

Received 9 December 2005; revised 19 April 2006; accepted 24 April 2006; published 1 June 2006.

[1] A *Karenia brevis* Harmful Algal Bloom affected coastal waters shallower than 50 m off west-central Florida from January 2005 through January 2006, showing a sustained anomaly of ~1 mg chlorophyll m^{-3} over an area of up to 67,500 km^2. Red tides occur in the same area (approximately 26–29°N, 82–83°W) almost every year, but the intense 2005 bloom led to a widespread hypoxic zone (dissolved oxygen <2 mg L^{-1}) that caused mortalities of benthic communities, fish, turtles, birds, and marine mammals. Runoff alone provided insufficient nitrogen to support this bloom. We pose the hypothesis that submarine groundwater discharge (SGD) provides the missing nutrients, and indeed can trigger and support the recurrent red tides off west-central Florida. SGD inputs of dissolved inorganic nitrogen (DIN) in Tampa Bay alone are ~35% of that discharged by all central Florida rivers draining west combined. We propose that the unusual number of hurricanes in 2004 resulted in high runoff, and in higher than normal SGD emerging along the west Florida coast throughout 2005, initiating and fueling the persistent HAB. This mechanism may also explain recurrent red tides in other coastal regions of the Gulf of Mexico. **Citation:** Hu, C., F. E. Muller-Karger, and P. W. Swarzenski (2006), Hurricanes, submarine groundwater discharge, and Florida's red tides, *Geophys. Res. Lett.*, *33*, L11601, doi:10.1029/2005GL025449.

1. Introduction

[2] Harmful algal blooms (HABs, or red tides) on the west Florida shelf (WFS) are primarily caused by the toxic species *Karenia brevis*. This species can produce brevetoxins that accumulate in bivalves, cause mortalities of marine organisms, and lead to irritation of the eye and respiratory systems of animals including humans. The earliest documented red tide on the WFS dates to 1854 [*Ingersoll*, 1882], but over the past 120 years there are numerous reports of such events off the same west-central Florida area (approximately 26–29°N, 82–83°W). They occur almost every year between August and March, but also at other times [*Feinstein et al.*, 1955; *Tester and Steidinger*, 1997].

[3] For over a hundred years, scientists have puzzled about the source of the nutrients that initiate and maintain such extensive, toxic blooms in this specific confined area. Much informal discussion has centered on the role of fresh water discharge from either local rivers or eastward dispersal of Mississippi River water [*Feinstein et al.*, 1955; *U.S. Bureau of Commercial Fisheries*, 1958, available at http://www.floridamarine.org/features/view_article.asp?id=2853]. The more recent Ecology of HABs (EcoHAB) program (1998–2001) provided insights into the nutrient dynamics of red tides [*Walsh and Steidinger*, 2004], suggesting that there is phosphorus and nitrogen deficiency from estuarine fluxes [*Vargo et al.*, 2004] (G. A. Vargo et al., Nutrient availability in support of *Karenia brevis* blooms on the central West Florida Shelf: What keeps *Karenia* blooming?, submitted to *Cont. Shelf. Res.*, 2006).

[4] The following complicated hypothesis was proposed by EcoHAB researchers to explain the initiation and maintenance of *K. brevis* blooms under nitrogen limitation [*Lenes et al.*, 2001; *Walsh and Steidinger*, 2001; *Walsh et al.*, 2003]: Phosphorus-rich river water is delivered to the coast, where *Trichodesmium* blooms are stimulated by deposition of iron-rich Saharan dust, fixing nitrogen. These blooms decompose upon sinking, releasing dissolved organic nitrogen and stimulating a toxic dinoflagellate seed population located near the bottom. Coastal upwelling moves this population onshore in the bottom Ekman layer, toward coastal regions rich in colored dissolved organic matter (CDOM) where light-inhibition is alleviated. Small *K. brevis* blooms would use dead fish as a supplementary nutrient source and swim toward the surface using positive phototaxis, and further protect themselves from light-inhibition by self-shading.

[5] This sequence of events, which was proposed to repeatedly lead to the unfortunate outcome of HABs only in a restricted area off west-central Florida (or immediately off Texas, according to the authors), has not been independently validated. It seems unlikely that the extensive Saharan dust deposition throughout the tropical and subtropical Atlantic, the Caribbean, and the Gulf of Mexico would have such consequences only in this small area.

[6] In January 2005, a red tide started off west central Florida that lasted through early January 2006. In July and August 2005, this event caused hypoxic ("dead") zones off west-central Florida and within Tampa Bay, Sarasota Bay, and Charlotte Harbor. Benthic communities, fish, turtles, birds, manatees and other marine mammals suffered extensive mortality. The event is hard to explain with the "dust" hypothesis, and it has sparked citizen activism and speculation as to the role of nutrient inputs from agriculture and phosphate mines, and possible links to global warming.

[7] Were environmental factors different in 2004–2005 compared to other years? Here we examine the origin, intensification, and longevity of this bloom and focus on submarine groundwater discharge (SGD) as a

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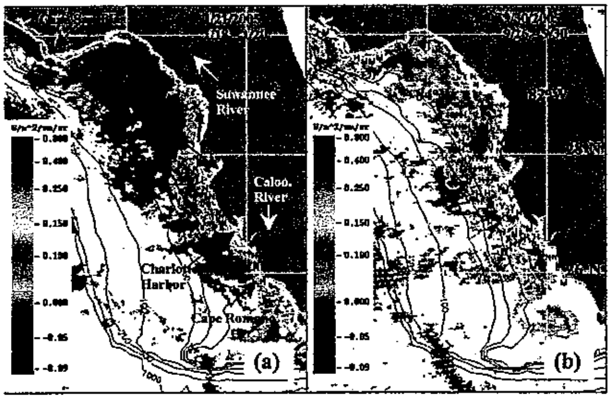

Figure 1. MODIS FLH images show a *K. brevis* red tide in shallow (<50 m) regions of WFS. The second date on each figure indicates the *in situ* sample collection time. Letters represent different *K. brevis* concentrations in cells L^{-1} as follows: N – below detection limit; P – present ($<10^3$); L – low (10^3 to 10^4); M – medium (10^4 to 10^5); H – high (10^5 to 10^6); V – very high ($>10^6$). Overlaid are bathymetric contours (30 to 1000 m), and cruise tracks for May 1999 and April 2000 (red line from Tampa Bay to 84°W, average surface salinity was 35.9 to 36.4) and for April 2005 (red line running WSW from Tampa Bay to 30 m water depth, surface salinity was 32.3 to 35.4). The January 2005 cruise found salinity between 35.1 and 35.7 within the red tide patch (letters H and V). Caloosahatchee was abbreviated to "Caloo."

potential source of nutrients that has been previously ignored.

2. Data and Methods

[8] *K. brevis* cell counts from routine surveys were conducted by the Florida Fish and Wildlife Research Institute (FWRI). Meteorological, river flow, and limited nutrient concentration observations were obtained from the National Hurricane Center and the National Weather Service, the Florida Weather Service, the U.S. Geological Survey (USGS), and the Southwest Florida Water Management District (SFWMD). Limited ground-water nutrient data were collected by the USGS. Daily sea surface temperature (SST), reflectance (SSR), and fluorescence line height (FLH) observations were obtained from AVHRR, SeaWiFS, and MODIS satellite imagery [*Hu et al.*, 2005] to help assess the spatial extent of *K. brevis* blooms.

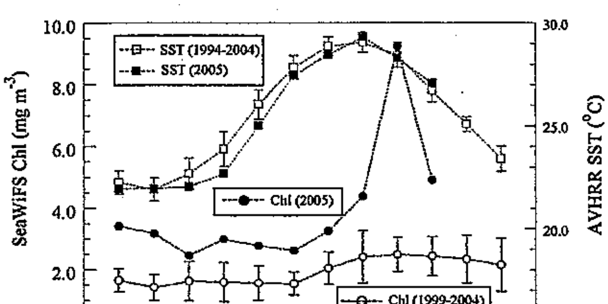

Figure 2. Average chlorophyll-*a* concentration (Chl) derived from high-resolution SeaWiFS satellite data (OC4v4 algorithm) for the <50 deep coastal waters off western Florida, from Cape San Blas to Cape Romano (area ~67500 km^2) between 1999 and 2005. Also plotted is the average SST for 0–30 m in the same area.

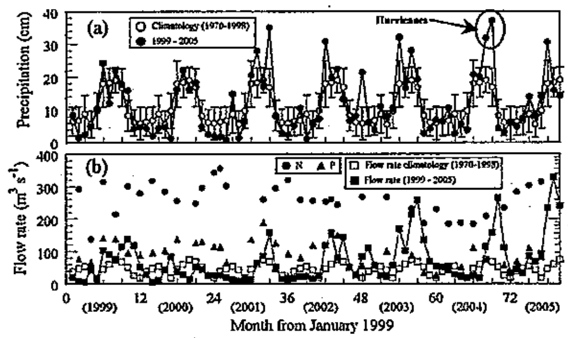

Figure 3. (a) Monthly precipitation for central Florida (data source: NWS); (b) Flow rate and nutrient concentrations of the Caloosahatchee River (source: SFWMD). N here represents the sum of NO_2 + NO_3 and P stands for PO_4.

3. Results, Discussion, and Conclusion

3.1. 2005 Red Tide Episode

[9] Blooms detected on 19 December 2004 off Tampa Bay in SeaWiFS and MODIS images contained *Heterosigma,* which can cause fish kills but is not harmful to humans. On 28 and 29 December, MODIS FLH images revealed a bloom covering ~1100 km^2 immediately off Tampa Bay. By 21 January 2005, the patch had grown to ~7140 km^2 (Figure 1a). A field survey on 19 January revealed high (10^5–10^6 cells L^{-1}) to very high ($>10^6$ cells L^{-1}) *K. brevis* concentrations near the 30–40 m isobath. Nil to low *K. brevis* counts were observed near the coast (Figure 1a).

[10] Over subsequent months, *K. brevis* patches were observed along the coast and within the estuaries from Tampa Bay to Charlotte Harbor. The red tide intensified between August and October 2005, occupying the entire inner shelf (<50 m; Figure 1b) in late September. The chlorophyll anomaly of 2005 was sustained (Figure 2) and persisted through January 2006.

[11] The "dust" hypothesis does not explain the timing, extent and longevity of the 2005 red tide. The 2005 SeaWiFS and MODIS images reveal small *Trichodesmium* surface slicks near the red tide of 2005. However, we have not identified any out-of-season, significant, or long-lasting dust events in 2005. The SeaWiFS aerosol optical thickness was low throughout the year.

[12] Satellite-derived SST anomalies showed cooler inner shelf waters by 0.5–1.0°C between March and May 2005 relative to the previous ten-year monthly climatology (Figure 2). This suggests that upwelling of colder waters occurred immediately at the coast in early 2005. The entire

Table 1. Flow Rate and Nutrient Concentration of Major Central Florida Rivers That Discharge Into the Gulf of Mexico (1997–2004)[a]

River	Flow Rate, $m^3\ s^{-1}$	$NO_2 + NO_3$ µM Flux[b]	NH_4, µM Flux[b]	PO_4, µM Flux[b]	DON, µM Flux[b]
Suwannee	232 (188)	47.9 (22.1)		2.7 (1.2)	35.3 (22.8)
		0.96 (0.62)		0.53 (0.047)	0.91 (0.97)
Caloo.	76 (72)	22.1 (12.9)	4.0 (3.0)	3.1 (1.5)	84.7 (16.1)
		0.15 (0.23)	0.028 (0.033)	0.019 (0.018)	0.51 (0.50)
Peace	36 (46)	N/A	N/A	N/A	N/A
Alafia[c]	10 (12)	25.7	4.3	N/A	48.6
		0.03	0.005		0.06

[a]Numbers in parenthesis are standard deviations. Data from SFWMD and EPA.
[b]Flux is in 10^6 moles day^{-1} (second number set for each river).
[c]Alafia nutrient data are from limited sampling results in 1991 by the USGS; numbers in parentheses are standard deviations.

shelf showed normal or above average SSTs approximately between June and October. Surface drifters released by NOAA/AOML near the southwest Florida coast during the first half of 2005 showed very slow (<5 cm s^{-1}) southward drift along the coast. After June 2005, inner shelf drifters showed slow motion to the north, parallel to the coast, suggesting that downwelling took place during the second half of 2005. During this period, the red tide intensified and expanded over the entire inner shelf, even as direct and strong mixing was effected by hurricanes *Dennis* (9–10 July 2005) and *Katrina* (24–29 August 2005).

3.2. River Nutrients and HABs in Coastal Florida Waters

[13] Rainfall over Florida between October 2004 and February 2005 was comparable to or below typical climatological values. However, in August and September 2004, Florida experienced four hurricanes (Charley, Frances, Ivan, and Jeanne) and some of the highest precipitation since 1970 (>38 cm in a month; Figure 3). This led to high discharge by Florida rivers into early 2005. The Caloosahatchee River, altered since the 1880's and with flow progressively more regulated since the 1930's, showed increasing flow since 1999 (Figure 3b). The Suwannee, Peace, and Alafia Rivers also showed high flow in 2005 (data not shown). This in part explains the lower coastal and inner shelf salinities detected in winter 2005 surveys relative to recent years (Figure 1a).

[14] A moderate *K. brevis* population (3×10^5 cell L^{-1}, or ~3 mg Chl m^{-3}) requires 0.056–0.267 µM day^{-1} dissolved inorganic nitrogen (DIN) and 0.002–0.012 µM day^{-1} phosphorus (DIP) to sustain a ~0.2 division day^{-1} growth rate [*Vargo et al.*, 2004]. Therefore, 3 mg m^{-3} (Figure 2) within a 5 m surface layer of ~67500 km^2 require ~13.5×10^6 moles DIN and 2.25×10^6 moles DIP day^{-1}. Major rivers supply an annual average of about 1.14×10^6 moles DIN and 0.55×10^6 moles DIP day^{-1} (Table 1). Small rivers and non-point coastal runoff may contribute an additional amount equivalent to about half of these fluxes. These estimates include wastewater contributions. Therefore, a total of ~1.71×10^6 moles DIN and 0.83×10^6 moles DIP day^{-1} are normally delivered by surface runoff to west-central Florida's estuaries and coast. Dissolved organic nitrogen (DON) from these sources may be 50–100% higher, yet how much of DON is biologically available is unknown (typically between 10–70%) [*Kroeger et al.*, 2006]. Discharge by the major rivers was 30–100% higher after fall 2004, but riverine nutrient concentrations were only 5–20% above normal values. Clearly, rivers are an important nutrient source to coastal blooms, yet even the higher 2004–2005 surface discharges provided barely sufficient DIP and between three and five times less DIN than required to maintain the 2004–2005 bloom. Similarly, the intense blooms were likely not fueled by nutrient recycling (G. A. Vargo et al., Nutrient availability in support of *Karenia brevis* blooms on the central West Florida Shelf: What keeps *Karenia* blooming?, submitted to *Cont. Shelf. Res.*, 2006). Over the course of 2005, diffusion, mixing, advection and sinking of the nutrients and particles would have diluted the nutrients and dissipated the bloom.

3.3. Submarine Groundwater Discharge (SGD)

[15] Groundwater has long been identified as a nutrient source to estuarine and coastal waters [*D'Elia et al.*, 1981; *Dowling et al.*, 2004; *Paytan et al.*, 2006]. Florida has 27 of the USA's 78 first order springs (64 million gallons per day), with the three largest land-based springs located near

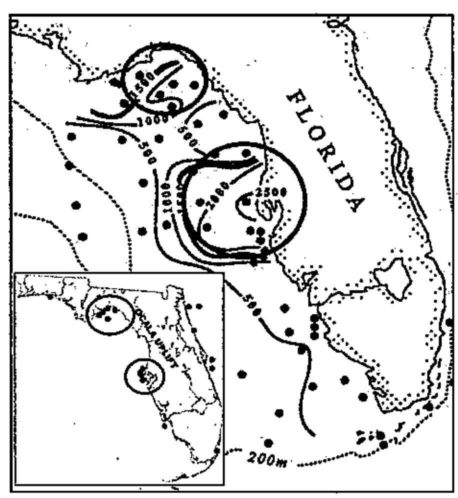

Figure 4. Near-bottom ^{222}Rn (dpm 1000 L^{-1}) from *Fanning et al.* [1987], with dots showing station locations. The inset shows locations of submarine springs identified by *Rosenau et al.* [1977].

Table 2. Nutrient Fluxes From Several Sources

Nutrient Source	PO_4	$NO_2 + NO_3$	NH_4	DON
Tampa Bay SGD, 10^{-6} moles m^{-2} d^{-1}[a]	27.7	0.3	694.7	218.6
Tampa Bay SGD, moles d^{-1}	2.9×10^4	2.9×10^2	7.2×10^5	2.3×10^5
Tampa Bay rivers, μM[b]	3.1	10.6	3.8	47.0
Tampa Bay rivers, moles d^{-1}	1.4×10^4	4.6×10^4	1.7×10^4	2.1×10^5
All west-coast rivers for north and central FL, moles d^{-1}[c]	0.83×10^6	1.71×10^6		2.45×10^6

[a]SGD data from *Swarzenski et al.*, [2006]. The total area of Tampa Bay is ~1031 km^2.
[b]Based on the USGS data of annual nutrient load from seven major rivers to Tampa Bay. The average total river discharge to Tampa Bay is ~50.7 m^3 s^{-1} [*Yassuda*, 1996].
[c]See text for details.

the west Florida coast (Figure 4) [*Rosenau et al.*, 1977]. Indeed, many large submarine springs are located off west-central and northern Florida where red tides also occur, but the link between SGD nutrient inputs and red tides has not been addressed.

[16] Despite a study in the Florida Keys [*Lapointe et al.*, 1990], nutrient fluxes from coastal ground water discharges in relation with red tides have received little attention in Florida. *Fanning et al.* [1987] observed elevated ^{222}Rn activities in bottom waters immediately off Tampa Bay, and *Cable et al.* [1996] demonstrated the utility of this isotope as a groundwater tracer. *Cunningham et al.* [2001] examined the hydrogeologic framework that leads to SGD off Charlotte Harbor. SGD nutrients may be enriched over natural levels by septic tank effluents.

[17] We pose the following hypothesis: the nitrogen demand of the 2005 red tide was satisfied by the elevated runoff and SGD caused by the high precipitation associated with the 2004 hurricanes. Coastal nutrient budgets need to account for benthic fluxes across leaky coastal margins [*Swarzenski and Kindinger*, 2003; *Dowling et al.*, 2004]. SGD DIN and DIP fluxes within Tampa Bay far exceed those from local rivers, and DON fluxes from the two sources are also comparable (Table 2) [*Swarzenski et al.*, 2006]. Tampa Bay SGD alone provides nearly 35% as much DIN as all north and central Florida rivers draining toward the Gulf of Mexico combined.

[18] We propose that the nitrogen inputs to the inner shelf off west-central Florida from these SGD may exceed those from riverine and atmospheric sources [e.g., *Swarzenski et al.*, 2001; *Kim and Swarzenski*, 2006], such as observed in other coastal areas [*Moore et al.*, 2002]. Further possible evidence of SGD is the cooling anomaly of inner shelf waters in early 2005 (Figure 2). Coastal SGD may delay and modulate the input derived from precipitation. SGD-derived nutrients may trigger and sustain algal blooms, and likely overwhelm any aeolian-derived nutrient and iron contributions to Florida coastal waters.

[19] Future studies of this region need to test this alternative to the "dust" hypothesis. Since SGD take place around the Gulf of Mexico where red tides occur, this process should be quantified in a systematic manner, for example, by pinpointing the locations of submarine springs off west-central Florida and quantifying their volume flow and nutrient flux.

[20] **Acknowledgments.** This work was supported by NASA (NNS04AB59G and NAG5-10557), the NOAA Coastal Ocean Program (NA04NOS4780022), and the US Office of Naval Research (N00014-02-1-0972 SEACOOS program). PWS was supported by the USGS Coastal Marine Geology Program. We thank Dr. Gabriel Vargo (USF) for his review of the nutrient budgets, David English and James Ivey for their help in obtaining field observations. We are indebted to several Federal and state agencies, including FWRI, SWFWMD, USGS, EPA, NWS, NHC, and NOAA/AOML for sharing their data. We thank the reviewers for their critical yet constructive comments.

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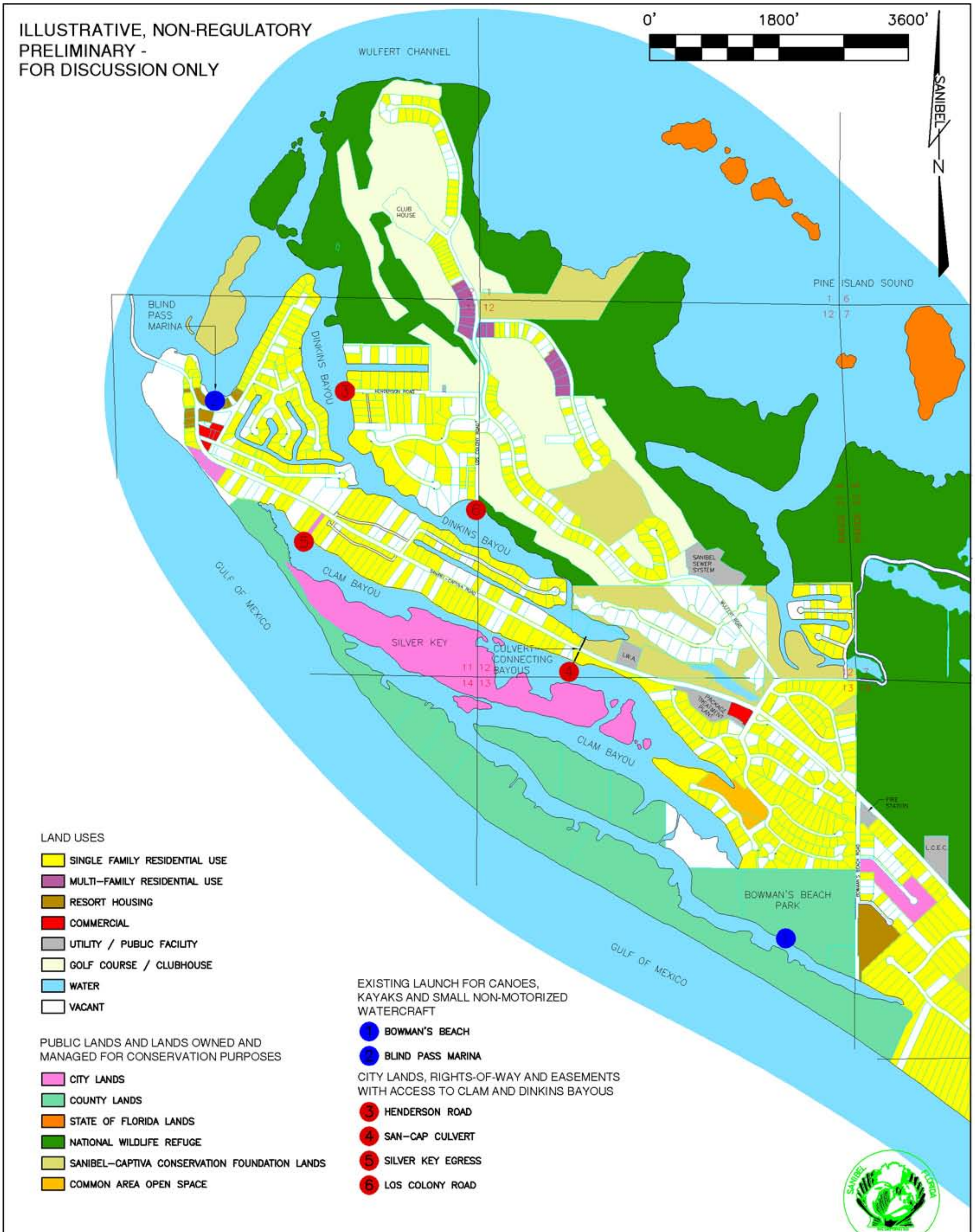
10. OLD BUSINESS

d. Staff Report regarding parking alternatives for Clam/Dinkins Bayou

ATTACHED IS THE MAP OF INVENTORY AND ANALYSIS OF PUBLIC ACCESSES TO DINKINS AND CLAM BAYOUS



INVENTORY AND ANALYSIS OF PUBLIC ACCESSES TO
DINKINS AND CLAM BAYOUS

15. CITY MANAGER'S REPORT

a. Informational Items
   1. Composite Report from Business Roundtable Discussion Groups and next steps

ATTACHED IS THE COMPOSITE REPORT

City of Sanibel

Planning Department

MEMORANDUM

DATE: August 9, 2006

TO: Judie Zimomra, City Manager

FROM: Robert J. Duffy, AICP, Planning Director

SUBJECT: **Locally Owned Business Initiative - Business Roundtables**
- **Report 1: Composite Report from Discussion Groups**
- **Report 2: Preliminary Outline of Potential Next Steps**

Enclosed for your review and consideration are the following two reports based on the three Business Roundtables held on June 23, 24 and 26, 2006.

Report 1: Composite Report from Business Roundtable Discussion Groups

The report outlines specific issues and ideas expressed by the 15 discussion groups for each of the following three questions.

Question 1: What are the most significant forces or issues, both on and off-island, impacting local businesses?

Question 2: What specific steps can the City take to assist locally owned businesses?

Question 3: How can communication be improved between local businesses, residents and the City?

The issues and ideas reported for questions 1 and 2 have been grouped into the following general subject areas: Market; Transportation; Communication and Participation; Regulations and Fees; Environment; Redevelopment, Planning and Design; Licensing; Code Enforcement; Media; Economy and Work Force; City Policies and Services; and Infrastructure.

The report also identifies the number of discussion groups that defined a particular issue or idea.

Report 2: Potential Next Steps

The report further consolidates the general subject areas and the underlying range of key issues and ideas. The report also advances a preliminary outline of next steps or strategies that the City is either currently pursuing or could initiate to address not only the key ideas or issues expressed during the Roundtables but also as identified by the recent Resident Survey and through the joint City Council and Planning Commission public work sessions associated with redevelopment. The report is structured as a series of worksheets to facilitate review and revisions.

Please contact me if you would like to discuss the enclosed reports.

City of Sanibel
Locally Owned Business Initiative

Preliminary

BUSINESS ROUNDTABLES
POTENTIAL NEXT STEPS

Submitted To

CITY COUNCIL

By

PLANNING DEPARTMENT

August 15, 2006

L:rjd:sbr-ReportCoverPage

City of Sanibel

Locally Owned Business Initiative

Preliminary for Discussion Only

BUSINESS ROUNDTABLES

Summary of Key Issues and Potential Next Steps

August 15, 2006

ECONOMY AND WORK FORCE WORK SHEET:

Key Issues	Potential Next Steps
1. Cost of tolls and transponder.	• City to participate in Lee County Value Pricing Study to examine lowering tolls prior to A.M. and P.M. Peak periods.
2. Attracting and retaining work force due to housing costs.	• City Council to continue to work in partnership with CHR to expand supply of Below Market Rate Housing.
3. Concerns with Formula Retail Impacts.	• Planning Commission to submit revised Commercial District regulations to City Council in October, 2006.
4. Occupancy of resort properties.	• City to undertake update of Sanibel Environmentally Based Market, Economic and Land Use Analysis. • Planning Department to complete inventory and analysis of resort properties.

City of Sanibel
Locally Owned Business Initiative

Preliminary for Discussion Only

BUSINESS ROUNDTABLES

Summary of Key Issues and Potential Next Steps

August 15, 2006

ENVIRONMENT WORK SHEET:

Key Issues	Potential Next Steps
1. Beach conditions—need proactive partnership between City and property owners.	• City Council to convene Beach Carrying Capacity Consortium that will involve business and property owners.
2. Water quality.	• City Council's highest priority will continue to be efforts to address water quality issues.

L:RJD:RoundtableKeyIssuesandPotentialNextStepsenvironment

City of Sanibel

Locally Owned Business Initiative

Preliminary for Discussion Only

BUSINESS ROUNDTABLES

Summary of Key Issues and Potential Next Steps

August 15, 2006

TRANSPORTATION and INFRASTRUCTURE WORK SHEET:

Key Issues	Potential Next Steps
1. Encourage reasonable and frequent public transportation and a potential island circulator. City to promote alternative forms of travel.	• City application, in partnership with Lee Tran and Ding Darling National Wildlife Refuge, pending with U.S. DOT FTA to plan for alternative forms of transportation service on island.
2. Provide coupon book/reduced tolls/transponder/debit card for visitors and workers.	• City to participate in Lee County Value Pricing Study to examine lowering tolls prior to A.M. and PM. Peak periods.
3. Improve traffic management and control.	• Transportation planner, in conjunction with Department of Public Works and Police Department, to examine and recommend traffic management and design strategies at critical intersections.
4. Provide public parking.	• As part of Town Center District Plan, examine alternative shared/public parking strategies.
5. Remove delineators.	• Implement Periwinkle Way Shared Use Path redesign plan.
6. Bike paths must be improved – safety conflicts.	• Complete updated Shared Use Path Master Plan. • Define alternative funding strategy for improvement and maintenance of Shard Use Path system.

7. Improve cell phone and Wi-Fi coverage.	• MIS and Planning Department to research strategies communities are pursuing to introduce Wi-Fi.

City of Sanibel
Locally Owned Business Initiative

Preliminary for Discussion Only

BUSINESS ROUNDTABLES

Summary of Key Issues and Potential Next Steps

August 15, 2006

REDEVELOPMENT, PLANNING AND DESIGN WORK SHEET:

Key Issues	Potential Next Steps
1. Commercial redevelopment—upgrade dated properties. Design commercial buildings to reflect "Island Character". Exterior appearance of buildings.	• Redevelopment Work Program approved by City Council. Town Center District Plan to address regulatory and financial strategies to support short and long term redevelopment, redesign and improvement of commercial district properties and environment.
2. Periwinkle Way tree canopy.	• City of Sanibel and Periwinkle Partnership completing final phase of Periwinkle Way Master Plan. Second phase to be completed in FY 06-07.

City of Sanibel

Locally Owned Business Initiative

Preliminary for Discussion Only

BUSINESS ROUNDTABLES

Summary of Key Issues and Potential Next Steps

August 15, 2006

MARKET WORK SHEET:

Key Issues	Potential Next Steps
1. Definition of market(s). Market(s) changing. Competition from other destinations and changes in visitor demographics	• City to undertake update of Sanibel Environmentally Based Market, Economic and Land Use Analysis. • City Council to convene local businesses as part of focus groups to assist with preparation of Economic and Market Analysis update.

City of Sanibel

Locally Owned Business Initiative

Preliminary for Discussion Only

BUSINESS ROUNDTABLES

Summary of Key Issues and Potential Next Steps

August 15, 2006

COMMUNICATION AND PARTICIPATION WORK SHEET:

Key Issues	Potential Next Steps
1. Improve City's Web Site	• MIS Department proceeding with redesign of City's web site. • City Council to convene business focus group to review preliminary web site design and service.
2. Improve communications with businesses.	• City, on an annual or semi-annual basis, will provide Welcome to Sanibel-Orientation Program for newly licensed businesses.
3. Hold additional Round Tables or business forums/meetings. Report actions on results of Roundtables.	• City Council, on a quarterly basis, to report progress on implementing "next steps" as part of a regularly scheduled meeting that will also provide a public forum for ongoing dialogue with local businesses.

City of Sanibel

Locally Owned Business Initiative

Preliminary for Discussion Only

BUSINESS ROUNDTABLES

Summary of Key Issues and Potential Next Steps

August 15, 2006

REGULATIONS, FEES, LICENSING, CODE ENFORCEMENT AND PERMITTING SERVICE WORK SHEET:

Key Issues	Potential Next Steps
1. City Permit Fees, particularly sign fees.	• City Council to review all permit and sign fees.
2. Restrictions on outdoor dining.	• City Council to consider adoption of outdoor dining regulations on August 15, 2006.
3. Local government regulations.	• City Council to recommend that Permitting Process Review Subcommittee of Planning Commission to conduct further review Land Development Code regulations, processes and procedures.
4. More education on codes and regulations. No heavy handed code enforcement.	• Planning Director to report to City Council on current, pending and potential Code Enforcement operations.
5. Licensing for resort property managers not located on-site.	• City Manager, City Attorney and Planning Director to review current licensing procedures and prepare recommendations for City Council consideration.
. 6. Enforcement of occupational licenses.	• City Manager, Director of Finance and Planning Director to review current licensing procedures and prepare recommendations for City Council consideration.

7. Unlicensed Contractors. Provide clear description of types of licensed contractors.	• Building Department and Contractor Review Board to review current licensing procedures and make recommendations to City Council.
8. Timely response to correspondence.	• City Manager to review policies and procedures.
9. Special events licensing.	• City Manager has convened interdepartmental work group to review and recommend revisions to City Council.
10. Planning Department more accessible, responsive and proactive.	• Planning Department to introduce and improve the following during FY06-07: - Planner of the Day to be assigned to respond to requests and inquiries. - On-Line access to Planner of the Day. - Revise Planning Department web page. - Expanded and improved scheduling of meetings with Planning staff. - On-Line meeting scheduling. - 24 hour telephone Access line to Planning Department. - Revised web page to consolidate and streamline access to all Planning Commission, Planning and Code Enforcement functions. - Guide to Land Development Code and Permitting to be produced. - As part of HTE permit management system upgrade, development and building permit applications to be reviewed and possibly consolidated as part of a comprehensive or master permit.

City of Sanibel
Locally Owned Business Initiative

COMPOSITE REPORT FROM BUSINESS ROUNDTABLE DISCUSSION GROUPS

Submitted To

CITY COUNCIL

By

PLANNING DEPARTMENT

August 15, 2006

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City of Sanibel

Locally Owned Business Initiative

BUSINESS ROUNDTABLES - June 23, 24, and 26, 2006

Composite Report from Discussion Groups

Question: 1. **What are the most significant forces or issues, both on and off island, impacting local businesses?** **Issues:**	**No. of Discussion Groups that Reported on Issue (1-15)**
Market –	
Competition from other destinations and changes in visitor demographics and perceptions.	**5**
Lack of favorable, interesting and memorable experiences to generate repeat visitors.	**4**
Visitors must feel welcome. Recognize contribution of visitors.	**3**
Definition of market(s) we want to attract is not clear. Market(s) changing.	**2**
Recognize tourism drives business.	**2**
Difficulty in attracting off-season guests.	**1**
Sanibel is over priced. Lack of short term rentals.	**1**
Lack of marketing unique businesses.	**1**
No cooperative intra-business advertising.	**1**
Market shifting to sophisticated and younger visitors.	**1**
Lack of short-term home/condo rentals.	**1**
Transportation –	
Seasonal traffic congestion and traffic management at Lindgren intersection.	**5**
Provide public transportation to alleviate traffic problems, including possible shuttle for off island employees.	**4**

Causeway construction.	**2**
Need more public parking at reasonable costs including off island parking for employees.	**2**
Training, communication and coordination of traffic control officers.	**2**
Lack of Punta Rassa turn.	**1**
Delineators on Periwinkle.	**1**
Bike and auto safety conflicts.	**1**
J. N. Ding Darling/CROW/etc. generates vehicular traffic.	**1**
Better separation of shared use paths.	**1**
Need overnight parking location for trucks and other large vehicles.	**1**
Communication and Participation –	
Design, Content and Coverage of City's web site.	**3**
Bring together community resources to "fix" problems. Rely more on local talent and resources.	**2**
Absentee owners "do not have a voice".	**1**
Regulations and Fees –	
Local government regulations too restrictive and costly. Streamline. Provide flexibility, particularly sign code.	**6**
City permit fee structure, particularly sign and building permits	**3**
Restrictions on outdoor dining.	**1**
Regulations limiting shared office space too restrictive.	**1**
Environment –	
Beach conditions and clean up - need proactive partnership between City and property owners.	**6**
Water quality due to Lake Okeechobee releases.	**6**
Weather/hurricane patterns.	**2**
Red tide.	**1**

Concern about opening Blind Pass.	1
Redevelopment, Planning and Design –	
Commercial redevelopment – upgrade dated properties and adopt revised regulations to support small businesses.	5
Design of commercial buildings should be improved to reflect "Island Character". Greater flexibility with signage colors and appearance.	4
Sign proliferation.	1
East End of Sanibel – Old Town is changing.	1
Restore tree canopy on Periwinkle Way.	1
Exterior appearance of businesses—too many bright painted businesses.	1
Gentrification and island "big house" construction and teardowns.	1
Business visibility.	1
Licensing –	
No licensing required for resort properties that lack on-site management.	2
Lack of enforcement of occupational licenses.	1
Unlicensed contractors.	1
Provide clear descriptions or definitions of different types of licensed contractors and their responsibilities.	1
Code Enforcement –	
No heavy handed or <u>volunteer</u> code enforcement.	2
More education on codes and regulations.	2
Approved plans are not followed and enforced. Review and revise regulations to address this issue.	1
Media –	
Negative publicity regarding environmental conditions, traffic and hurricane recovery.	8

Economy and Work Force –	
Cost of tolls and transponders.	**12**
Attracting and retaining work force challenging due to tolls, traffic, gas prices, housing costs and competitive off-island commercial growth.	**12**
Closure of South Seas and occupancy of resort properties.	**4**
Cost of doing business, return on investment and seasonal business planning more difficult.	**3**
Rising costs to lease commercial space.	**3**
Property taxes and insurance, including health insurance.	**2**
Concerned with formula retail impacts.	**2**
Impact of Summerlin Road and South Lee County growth.	**2**
Local residents have difficulty affording rising prices of goods and services on island.	**1**
Diversity of Island community declining.	**1**
City Policies and Services –	
Attitude and responsiveness of City employees - Must be more proactive and supportive. Adopt a "can-do" and cooperative attitude.	**3**
Timely response to correspondence.	**2**
Commerce needs to be a priority of City Council.	**1**
City should contract with and utilize on-island businesses.	**1**
Stay the course with City and Chamber of Commerce partnership	**1**
Infrastructure –	
Cell phone and Wi-Fi coverage and reception for guests and business.	**3**

City of Sanibel

Locally Owned Business Initiatives

BUSINESS ROUNDTABLES - June 23, 24, and 26, 2006

Composite Report from Discussion Groups

Question: **2. What specific steps can the City take to assist locally owned businesses?** **Recommendations:**	**No. of Discussion Groups that Reported an Issue (1-15)**
Media –	
City to put out positive messages to the media, including negative messages regarding hurricanes.	**1**
Help with business information: distribute facts vs. fiction.	**1**
Transportation –	
Encourage reasonable and frequent public transportation and a potential circulator both on and off-island.	**4**
Provide coupon book/reduced tolls for visitors staying on island or temporary transponder/debit card.	**2**
Improve traffic control, particularly at Jerry's.	**2**
Construct parking garage. Provide public parking.	**2**
Remove delineators.	**2**
Reduce cost of beach parking. "Beach Free' parking days.	**1**
Toll program for workers.	**1**

Create awareness that bridge toll is one way.	**1**
Bike paths must be improved – safety and function.	**1**
Provide frontage road connecting commercial centers along Periwinkle.	**1**
Consider roundabouts	**1**
Traffic management to be improved: • Two lanes of traffic at peak hours. One way system.	**1**
Place bike path behind businesses along Periwinkle.	**1**
Develop overall plan for traffic management.	**1**
Promote (City) alternative means of travel.	**1**
Communication and Participation -	
Improve public relations to counter negative publicity.	**3**
Establish small business committee or advisory board with City Council liaison.	**3**
Coordinate communication and partnership efforts between Visitors and Convention Bureau, Chamber of Commerce and City Hall.	**2**
Improve communication with residents and visitors.	**1**
Hold more informal meetings.	**1**
Expand web site.	**1**
Develop overall communication strategy.	**1**
List on-island businesses and services as part of City's web page.	**1**
Improve inter-business referral system.	**1**
Small business networking groups.	**1**
City to hire person for public relations to promote Island and counter negative press.	**1**
Regulations and Fees -	
Improve and streamline permitting in terms of time and expense.	**6**

Reduce parking limitations, vegetation landscape buffers and signage requirements.	4
Increase value (cost) for activities exempt from obtaining a building permit	4
Lower sign permit fees.	3
Minimize permit fees and fines.	3
Allow for improvements and Code flexibility to update non-conforming and outdated resort properties.	2
Provide more flexible signage regulations.	2
Allow office sharing.	2
Have greater flexibility to change signs.	2
Maintain affordable short-term vacation rental stock.	1
Amend City regulations impacting businesses and in turn impacting guests.	1
Review City regulations to enable closer storage of beach equipment.	1
Better customer service and clarity in explaining regulations.	1
Amend the LDC Sec. 126.632 Findings to reflect long-term loss of resort housing.	1
Permit outdoor dining. Establish outdoor dining in resort housing district.	1
Fast track permits for smaller jobs.	
Remove 28-day rental period in non-resort housing area. Allow weekly rental.	
Create a Task Force for: • Signage • Lighting	1
More flexibility with outdoor display of merchandises for businesses.	1
Allow tethered balloons and banners for business advertising.	1
Environment -	
Clean the beaches. Identify and secure funding.	4
Joint City Council/State action on water quality.	2

Redevelopment, Planning and Design -	
"Facelift" and improve appearance of Periwinkle.	4
Move ahead with sensitive redevelopment. No more large formula stores.	2
Keep part of old bridge for fishing pier and for Historical Monument.	1
Upgrade properties to be more up-to-date and competitive.	1
Allow commercial floor areas to be maintained as part of redevelopment.	1
Provide regulations and tax incentives for redevelopment.	1
Promote mixed use. Provide incentives to encourage employee housing above existing business sites.	1
Consumer wants shopping environment that is attractive, pretty, island feeling!	1
Need to provide an environment that does not look like Walmart – unique shopping experience.	1
Provide GUIDELINES to address Island character! • Why allow buildings out of scale.	1
City should plan for commercial districts to make sense.	1
Update regulations, but retain flavor of island.	1
Encourage quality in everything including public facilities.	1
Encourage business to improve the physical appearance of the Island buildings and landscaping.	1
Reduce sign cluster along roadways and excess duplication of City and other informational signs.	1
Development of a Town Center for potential outdoor events and activities.	1
Define businesses preferred colors paint chart.	1
Licensing -	
More special events are needed.	2
Change occupational license requirement to be less <u>expensive</u> and <u>easier</u> on business.	2
Increase number of special events permits per location/business.	2

Reduce duplicate occupational licenses.	1
Follow State mandates for effective insurance as part of licensing.	1
Flexibility in number of special events.	1
Educate homeowners regarding contractor licensing.	
Uniform landscape contractor licensing.	
Need to insure licensing is uniformly administered and that license regulations are enforced.	1
Utilize e-mail for more city communication – especially those with occupational licenses.	1
Stop discouraging special events (in season).	1
Code Enforcement -	
Police resort rental properties.	1
Provide a warning first rather than a notice of violation.	1
Protect homeowners from unlicensed contractors.	1
More enforcement of illegal rentals.	1
Market -	
Promote more quality and off-season special events.	2
Improve occupancy rates.	2
Come up with creative promotions.	1
Define who we are: ecotourism, resort, residential?	1
Examine changing demographics of area.	1
Recognize change in the market (younger).	1
Decide who should be responsible for defining who we are?	1
Economy and Work Force -	
Some way to handle tolls for employees with emphasis on Island employees not just City employees also private sector.	3
More affordable housing for local business work force.	2

Help control rent rates.	1
Lower Chamber of Commerce dues; change fee structure; more responsive to small businesses.	1
Create insurance network for small businesses.	1
Develop a Buy-Local campaign.	1
City Policies and Services -	
User friendly front desk and planner accessible to answer questions in Planning Department. Planning Department needs to be more responsive.	4
Establish a mediator or liaison to address business concerns.	2
Improve administrative system to respond to correspondence.	2
Acknowledge all groups that support Community.	1
Provide welcome and orientation package/program to newly licensed island businesses.	1
Promote specialty shops vs. off-island formula retail.	1
Respond to all telephone calls within 24 hours.	1
City Council Agendas and Meetings should be more predictable and timely.	1
Unified spirit of cooperation through City departments to support business.	1
Recognize and acknowledge local businesses.	1
Help businesses: "stay out of business' business".	1
Help small business be part of community (identify).	1
Reduce excessive police presence that creates a negative impression to the public.	1
City to promote and use Island businesses as first choice for goods and services.	1
Culture of City government should be to enable rather than just say No.	1

Infrastructure -	
Allow cell towers. Improve cell phone coverage.	**3**
On-site drainage improvement/requirements needed.	**1**
Develop Wi-Fi on island.	**1**
Provide better lighting for nighttime activities.	**1**

City of Sanibel

Locally Owned Business Initiative

BUSINESS ROUNDTABLES - June 23, 24, and 26, 2006

Composite Report from Discussion Groups

Question: **3. How can communication be improved between local businesses, residents and the City?**	**No. of Discussion Groups that Reported a Communication Improvement (1 – 15)**
Meet again next year to see how we have done. Hold more Round Tables and Town Meetings.	**9**
Form small business committee, issues task force or advisory council with City Council liaison.	**5**
Coordinate communication between residents and businesses.	**5**
Improve City's web site through: • Practicality • Functionality • Access to current information, licenses, hurricane passes, etc. • Update information regularly	**3**
Provide quarterly updates via public meetings and targeted newsletters.	**3**
Submit weekly Friday facts as e-mail BLOG.	**3**
City Council meetings should be more accessible and timely for businesses and provide designated times fro businesses to express their views.	**3**
Establish island Wi-Fi.	**2**
Inform local business of potential projects upcoming within the calendar year that local business could bid on.	**2**
City should communicate with property owners and citizens regarding need to check contractors for insurance and licenses.	**2**

E-networking – increase opportunities and reinforce e-mail groups.	**2**
Help improve communication between small and larger businesses by: • Round table meetings between these groups • Facilitate Chamber efforts • Increase cooperation and sharing of business resources	**1**
Sanibel Vision Statement – is everyone on the same page?	**1**
Take specific actions after round table discussion.	**1**
Produce posters rather than only brochures that communicate message on environmental protection.	**1**
City procedures/answers should be consistent.	**1**
Provide for affordable web services so small businesses can be marketed.	**1**
Improve cooperation between different segments of business community.	**1**
Provide contractors lists on City web site.	**1**
Bring together different areas of neighborhoods at meetings like this forum.	**1**
Promote island facilities.	**1**
Increase public relations to counter bad headlines.	**1**
More on web site such as homeowner education about contractors.	**1**
City information column in newspaper each week – what City is working on.	**1**
City public relations/ombudsman person to be hired.	**1**
Communicate how we want development or improvements to the City to look like?	**1**
Need to improve appointment scheduling and access to City employees.	**1**
Communicate on issues like the City has been doing with hurricanes.	**1**
Meet with non-resident owners.	**1**
Different marketing is needed for "high end" vs. "low end" markets.	**1**
Bulletin boards need to be more visible.	**1**
Need to be more proactive with state and regional agencies with what is going on here especially after storm recovery.	**1**

Are businesses being included in community, i.e., regarding H_2O quality?	1
Advance water release warnings to the public.	1
Work with the county to establish a toll reduction day and off-season program.	1
Form small business networking groups.	1
Businesses promotion on city web site.	1
What are businesses doing today to communicate and support one another? • Businesses need to come together • Businesses need to support business •	1
Distill existing and future research to community and businesses. • Provide (Did you know) reports, etc. •	1
Provide public notices of special events to community.	1