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 (≤ 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 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 δ^{15}Nin 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 δ^{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 δ^{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 δ^{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 δ^{15}N values of ~ 0 ‰ (France et al., 1998; Table 1) in contrast to those using sewage N, which become increasingly enriched in δ^{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 δ^{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).

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

$\left[\left(R_{Sample}/R_{Standard}\right)-1\right]*10^3$; 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 ($p \leq 0.015$, 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).

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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References

Abtew, W. , Huebner, R. S., Sunderland, S. 2002. Part I. Hydrological analysis of the 2000-2001 drought in South Florida. Technical Report EMA-405, South Florida Water Management District, West Palm Beach, FL.

Asplia, I., Agemian, H., Chau, A.S.Y., 1976. A semi-automated method for the determination of inorganic, organic, and total phosphate in sediments. Analyst 101, 187-197.

Atkins, R.P., Deeley, D.M., McAlpine, K.W., 1993. Managing the aquatic environment. Fert. Res. 36, 171-175.

Avery, W., 1997. Distribution and abundance of macroalgae and seagrass in Hillsborough Bay, Florida, from 1986 to 1995. In: Treat, S.F. (ed.), Proceedings, Tampa Bay Area Scientific Information Symposium 3. Text, Tampa, FL. 151-165.

Barile, P.J., 2004. Evidence of anthropogenic nitrogen enrichment of the littoral waters of east central Florida. J. Coastal Res. 20(4), 1237-1245.

CEVA, 1993. Marée vertes: Les traitements curatifs. Document du CEVA. CEVA (Centre d'Etude et de Valorisation des Algues), 22610, France.

Costanzo, S.D., O'Donohue, M.J., Dennison, W.C., Loneragan, N.R., Thomas, M., 2001. A new approach for detecting and mapping sewage impacts. Mar. Poll. Bull. 42, 149-156.

Dawes, C.J., 1974. Marine Algae of the West Coast of Florida. University of Miami Press, Miami, FL.

DeBoer, J.A., Guigli, H.J., Isreal, T.L., D'Elia, C.F., 1978. Nutritional studies of two red algae: 1. Growth rate as a function of nitrogen source and concentration. J. Phycol. 14, 266-272.

D'Elia, C.F., Connor, E.E., Kaumeyer, N.L., Keefe, C.W., Wood, K.V., Zimmerman, C.F., 1997. Nutrient Analytical Services: Standard operating procedures. Technical Report Series No. 158-97, Chesapeake Biological Laboratory, Solomons, MD.

Doering, P. H., Chamberlain, R. H., 1999. Water quality and source of freshwater discharge to the Caloosahatchee estuary, Florida. J. American Water Resources Association 35 (4),793-806.

Flannery, M.S., Downing, H.C., Jr., McGarry, G.A., Walters, M.O. 1991. Increased nutrient loading and baseflow supplementation in the Little Manatee watershed. Proc. Tampa Bay Area Scientific Information Symposium 2, 369-396.

France, R., Holmquist, J., Chandler, M., Cattaneo, A., 1998. δ^{15}N evidence for nitrogen fixation Associated with macroalgae from a seagrass-mangrove-coral reef ecosystem. Mar. Ecol. Prog. Ser. 167, 297-299.

Gartner, A., Lavery, P., Smit, A.J., 2002. Use of δ^{15}N signatures of different functional forms of macroalgae and filter feeders to reveal temporal and spatial patterns in sewage dispersal. Mar. Ecol. Prog. Ser. 235, 63-73.

GESAMP, 1990. The state of the marine environment. Joint Group of Experts on the Scientific Aspects of Marine Pollution Rep. Stud. 39. UNEP.

Guist, G.G., Humm, H.J., 1976. Effects of sewage effluents on the growth of *Ulva lactuca*. Florida Sci. 39, 267-271.

Harrison, W.G., Platt, T., Lewis, M.R., 1987. The f-ratio and its relationship to ambient nitrogen concentration in coastal waters. J. Plankton Res. 9, 235-248.

Heaton, T.H.E., 1986. Isotopic studies of nitrogen pollution in the hydrosphere and atmosphere: A review. Chem. Geol. (Isotope Geoscience Section) 59, 87-102.

Hoch, M.P., Cifuentes, L.A., Coffin, R., 1995. Assessing geochemical and biological fate for point source loads of sewage-derived nitrogen and organic carbon in coastal waters of southern Florida. Final Report to the USEPA.

Howarth, R., Anderson, D., Cloern, J., Elfring, C., Hopkinson, C., Lapointe, B., Malone, T., Marcus, N., McGlathery, K., Sharpley A., Walker, D., 2000. Nutrient pollution of coastal rivers, bays, and seas. Issues in Ecology 7, 1-15.

Humm, H. J. 1973. Benthic algae of the eastern Gulf of Mexico. In: Jones, J.I. et al. (eds.), A Summary of Knowledge of the Eastern Gulf of Mexico, 1973. State University System of Florida Institute of Oceanography, St. Petersburg, FL. IIIB: 1-15.

Kaufman, M.I. 1969. Generalized distribution and concentration of orthophosphate in Florida streams. U.S. Geological Survey Map Series 33. The Eastern Gulf of Mexico 1973, The State University System of Florida Institute of Oceanography IIC-46.

Ketchum, B.H., 1967. Phytoplankton nutrients in estuaries. In: Lauf, G.H., (ed.) Estuaries. American Association for the Advancement of Science, Washington, D.C. 329-335.

Ketchum, B.H. and Keen, J. 1947. Unusual phosphorus concentrations in the Florida "Red Tide" sea water. J. Mar. Res. 7(1), 17-21.

Lapointe, B.E., 1981. The effects of light and nitrogen on growth, pigment content, and biochemical composition of *Gracilaria foliifera* var. *angustissima* (Gigartinales, Rhodophyta). J. Phycol. 17, 90-95.

Lapointe, B.E., 1987. Phosphorus and nitrogen-limited photosynthesis and growth of *Gracilaria tikvahiae* (Rhodophyceae) in the Florida Keys: An experimental field study. Mar. Biol. 93, 561-568.

Lapointe, B.E., 1995. A comparison of nutrient-limited productivity in *Sargassum natans* from neritic vs. oceanic waters of the western North Atlantic ocean. Limnol. Oceanogr. 40(3), 625-633.

Lapointe, B.E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnol. Oceanog. 42(5-2), 1119-1131.

Lapointe, B. E., Krupa, S., 1995a. Jupiter Creek septic tank water quality investigation. Final Report to the Loxahatchee River Environmental Control District. Jupiter, FL.

Lapointe, B. E., Krupa, S., 1995b. Tequesta Peninsula septic tank/water quality investigation. Final Report to the Loxahatchee River Environmental Control District. Jupiter, FL.

Lapointe, B.E., Thacker, K., 2002. Community-based water quality and coral reef monitoring in the Negril Marine Park, Jamaica: Land-based nutrient inputs and their ecological consequences. In: Porter, J.W., Porter, K.G. [Eds.], The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC Press, Boca Raton, FL. pp. 939-963

Lapointe, B.E., Ryther, J.H., 1979. The effects of nitrogen and seawater flow rate on the growth and biochemical composition of *Gracilaria foliifera* var. *angustissima* in mass outdoor cultures. Bot. Mar. XXII, 529-537.

Lapointe, B.E., Barile, P.J., Matzie, W.R., 2004. Anthropogenic nutrient enrichment of seagrass and coral reef communities in the Lower Florida Keys: Discrimination of local versus regional nitrogen sources. J. Exp. Mar. Biol. Ecol. 308(1), 23-58.

Lapointe, B.E., Littler, D.S., Littler, M.M., 1992. Nutrient availability to marine macroalgae in siliciclastic versus carbonate-rich coastal waters. Estuaries 15(1), 75-82.

Lapointe, B.E., Tenore, K.R., Dawes, C.J., 1984. Interactions between light and temperature on

the physiological ecology of *Gracilaria tikvahiae* (Gigartinales: Rhodophyta): I. Growth, photosynthesis and respiration. Mar. Biol. 80, 161-170.

Lapointe, B.E., Tomasko, D.A., Matzie, W.R., 1994. Eutrophication and trophic state classification of seagrass communities in the Florida Keys. Bull. Mar. Sci. 54, 696-717.

Lapointe, B. E.,Barile, P. J., Littler, M. M., Littler, D. S., Gasque, C., 2005a. Macroalgal blooms on southeast Florida coral reefs: I. Nutrient stoichiometry of the invasive green alga *Codium isthmocladum* in the wider Caribbean indicates nutrient enrichment. Harmful Algae 4, 1092-1105.

Lapointe, B.E., Barile, P.J., Littler, M.M., Littler, D.S., 2005b. Macroalgal blooms on southeast Florida coral reefs: II. Cross-shelf discrimination of nitrogen sources indicates widespread assimilation of sewage nitrogen. Harmful Algae, 4, 1106-1122.

LaRock, P., Bittaker, H.L., 1973. Chemical data of the estuarine and nearshore environments in the Eastern Gulf of Mexico. The State University System of Florida Institute of Oceanography IIC-8.

Lindau, C.W., Delaune, R.D., Patrick, W.H. Jr., Lambremont, E.N., 1989. Assessment of stable isotopes in fingerprinting surface water inorganic nitrogen sources. Water Air Soil Poll. 48, 489-496.

Littler, D.S., Littler, M.M., 2000. Caribbean Reef Plants. Offshore Graphics, Washington, D. C.

Lovejoy, S.B., Dunkelberg, B., Lee, J.G. 1990. Sources and quantities of nutrients entering the Gulf of Mexico. The environmental status of Gulf of Mexico. Gulf of Mexico Program 41-43.

McCarthy, J. J., Taylor, W. R., Taft, J. L. 1975. The dynamics of nitrogen and phosphorus cycling in the open waters of Chesapeake Bay. In: Church, T. M. (editor), Marine Chemistry of the Coastal Environment, 664-681. ACS Symposium Series, # 18.

McClelland, J.W., Valiela, I., 1998. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Mar. Ecol. Prog. Ser. 168, 259-271.

McGlathery, K. J., 1995. Nutrient and grazing influences on a subtropical seagrass community. Mar. Ecol. Prog. Ser. 122, 239 – 252.

McPherson, B. F.,Miller, R.L. 1990. Nutrient distribution and variability in the Charlotte Harbor estuarine system, Florida. Water Research Bull. 26:67-81.

Miller, R.L., Kraemer, T.F., McPherson, B.F., 1990. Radium and radon in Charlotte Harbor estuary, Florida. Estuar. Coast. Shelf S. 31, 439-457.

Morand, P., Briand, X., 1996. Excessive growth of macroalgae: A symptom of environmental disturbance. Bot. Mar. 39, 491-516.

National Research Council, 2000. Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution. Ocean Studies Board, Water Science and Technology Board.

Odum, H.T., 1953. Dissolved phosphorus in Florida waters. Florida Geological Survey Report of Investigation 9 (Pt. 1), 1-40.

Owens, N. P. J., 1987. Natural variations in ^{15}N in the marine environment. Adv. Mar. Biol. 24, 389-451.

Paerl, H. W., Fogel, M. L., 1994. Isotopic characterization of atmospheric nitrogen inputs as sources of enhanced primary production in coastal Atlantic Ocean waters. Mar. Biol. 119(4), 635-645.

Pew Oceans Commission, 2003. America's Living Oceans: Charting a Course for Sea Change. A Report to the Nation. May 2003. Pew Oceans Commission, Arlington, VA.

Rothschild, W. 2005. Red tide kills 79 manatees off southwest Florida in 2005. Sarasota Herald Tribune, December 10.

Rogers, D. K. 1991. Pollution is behind invasion of seaweed. St. Petersburg Times, St. Petersburg, FL. August 14.

Sammarco, P.W., Risk, M.J., Schwarcz, H.P., Heikoop, J.M., 1999. Cross-continental shelf trends in coral δ^{15}N on the Great Barrier Reef: Further consideration of the reef nutrient paradox. Mar. Ecol. Prog. Ser. 180, 131-138.

Savage, C., Elmgren, R., 2004. Macroalgal δ^{15}N values trace decrease in sewage influence. Ecol. Appl. 14(2), 517-526

Sfriso, A., Pavoni, B., Marcomini, A., Orio, A.A., 1992. Macroalgae, nutrient cycles, and pollutants in the Lagoon of Venice. Estuaries 15, 517-528.

Sigman, D.M., Altabet, M.A., McCorkle, D.C., Francois, R., Fisher, G., 2000. The δ^{15}N of nitrate in the southern ocean: Nitrogen cycling and circulation in the ocean interior. J. Geophys. Res. C 105, 19599-19614.

Slobodkin, L. B. 1953. A possible initial condition for red tides on the west coast of Florida. J. Mar. Res. 12 (1),148-155.

Steidinger, K.A., Vargo, G.A., Tester, P.A., Tomas, C.R. 1998. Bloom dynamics and physiology of *Gymnodinium breve* with emphasis on the Gulf of Mexico. In: Anderson, D.A., Cembella, A.D., Hallegraeff, G.M., (eds.), Physiological Ecology of Harmful Algal Blooms. Springer-Verlag, New York, NY. pp. 133-154.

Steinman, A.D., Havens, K.E., Carrick, H.J., VanZee, R., 2002. The past, present, and future hydrology and ecology of Lake Okeechobee and its watersheds. In: Porter, J.W. and K.G. Porter, The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC Press, Boca Raton, FL. pp. 19-37.

Tang, X. K., Yuan, D. X., and Lin, S. B. 2003. Depression and effect of red tide on water quality index by *Gracilaria tenuistipitata*. Mar. Env. Sci. 22(2), 24-27.

Task Group Report, 1967. Sources of nitrogen and phosphorus in water supplies. J. AWWA 59, 344-366.

Tester, P. A. and Steidinger, K. A. 1997. *Gymnodinium breve* red tide blooms:Initiation, transport, and consequences of surface circulation. Limnol. Oceanogr. 42(5, part 2),1039-1051.

Thompson, M. L., Schaffner, L. C., 2001. Population biology and secondary production of the suspension feeding polychaete *Chaetopterus* cf. *variopedatus*: Implications for benthic-pelagic coupling in lower Chesapeake Bay. Limnol. Oceanogr. 46(8):1899-1907.

Umezawa, Y., Miyajima T., Yamamuro M., Kayanne H., Koike, I., 2002. Fine-scale mapping of land-derived nitrogen in coral reefs by δ^{15}N in macroalgae. Limnol. Oceanogr. 47(5), 1405-1416.

U.S. Commission on Ocean Policy, 2004. An Ocean Blueprint for the 21st Century. Final Report of the U.S. Commission on Ocean Policy. Washington, D.C.

Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42, 1105-1118.

Virnstein, R.W., Carbonara, P.A., 1985. Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River lagoon, Florida. Aquat. Bot. 23, 67-82.

Wayland, M., Hobson, K.A., 2001. Stable carbon, nitrogen, and sulfur isotope ratios in riparian food webs on rivers receiving sewage and pulp-mill effluents. Canad. J. Zool., 79, 5-15.

Wilson, W. B., Ray, S. 1958. Nutrition of red tide organisms. U. S. Fish. Wild. Serv. Gulf Fish Invest. Ann. Rep., pp. 62-65.

Yang, H., Weisberg, R. H., Niiler, P. P., Sturges, W., and W. Johnson. 1999. Lagrangian circulation and forbidden zone on the west Florida shelf. Cont. Shelf. Res. 19, 1221-1245.

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.).

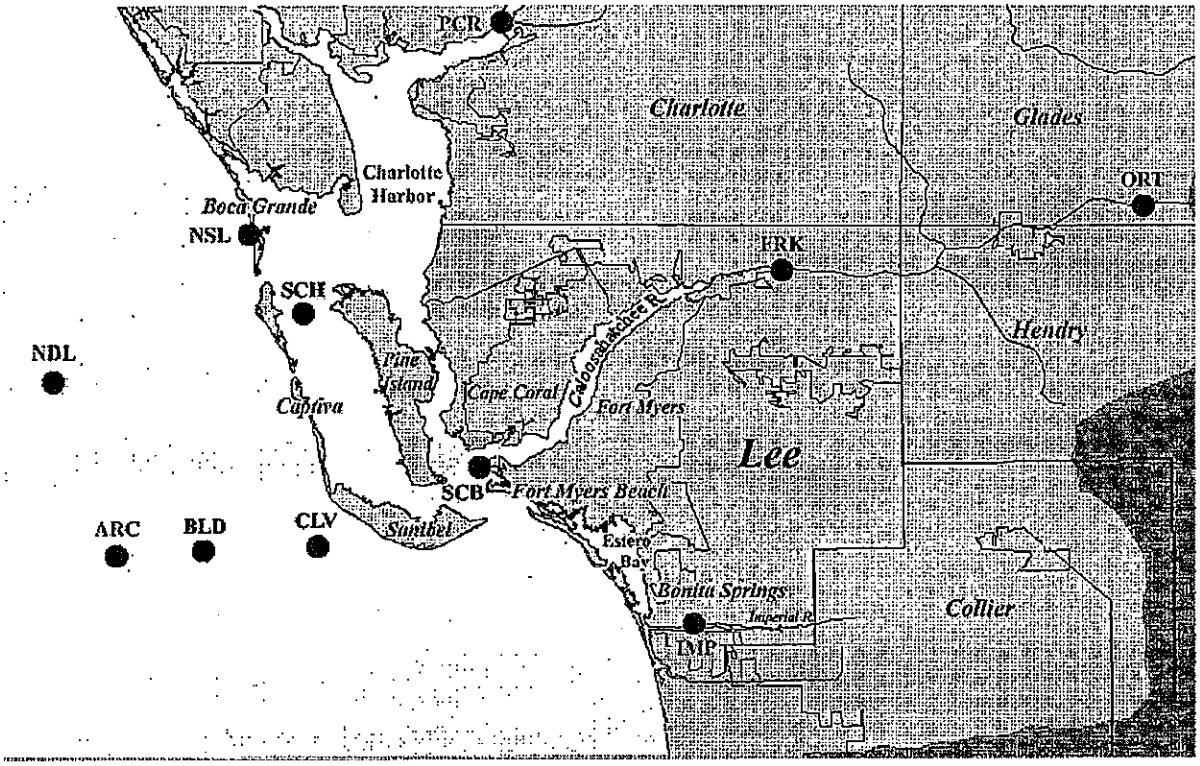
PCR
Charlotte
Glades
Charlotte Harbor
Boca Grande
NSL
ORT
FRK
SCH
Hendry
NDL
Pine Island
Cape Coral
Caloosahatchee R.
Fort Myers
Captiva
Lee
SCB
Fort Myers Beach
ARC
BLD
CLV
Sanibel
Estero Bay
Bonita Springs
Imperial R.
Collier
IMP

Fig. 1

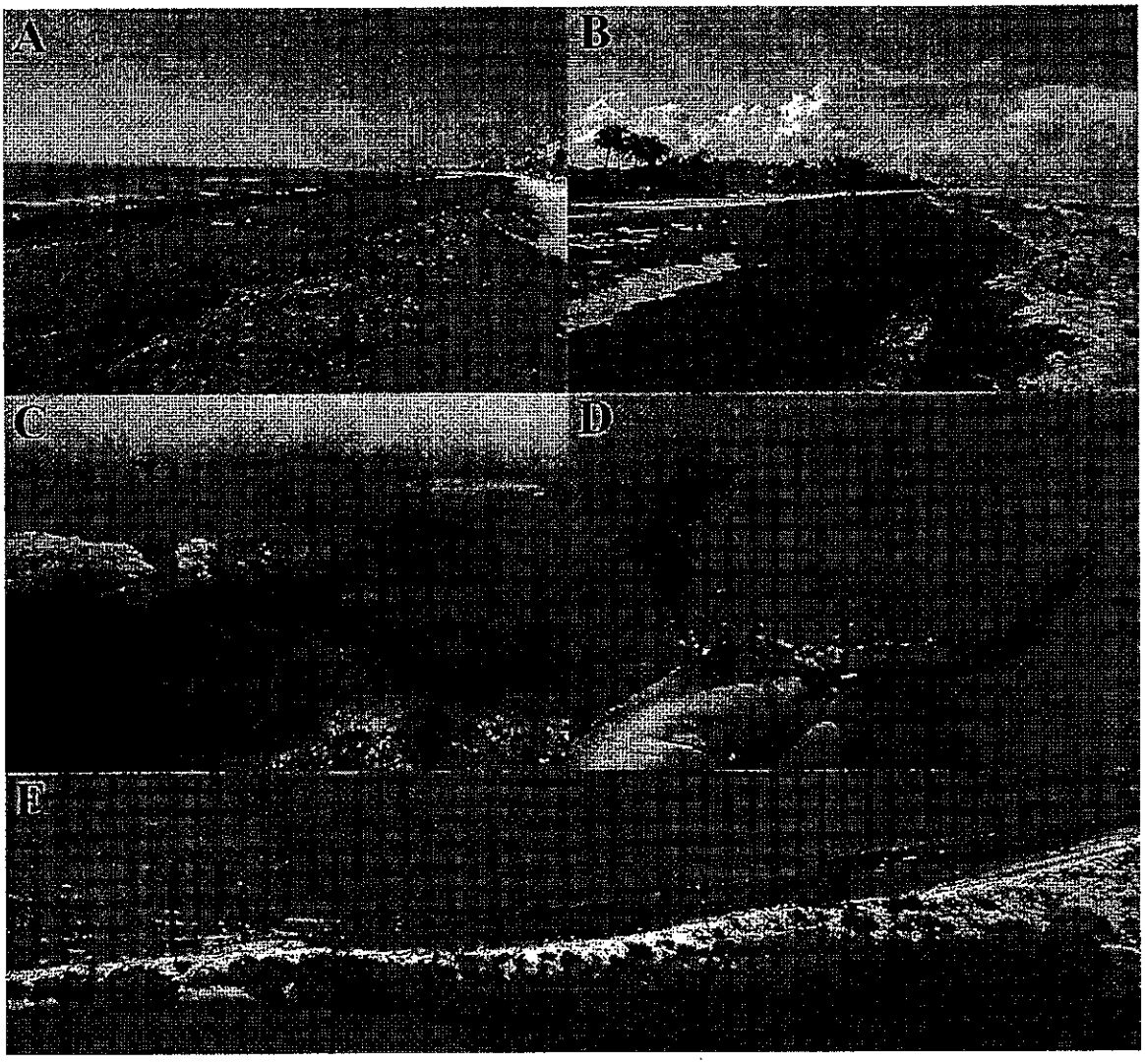

Fig. 2

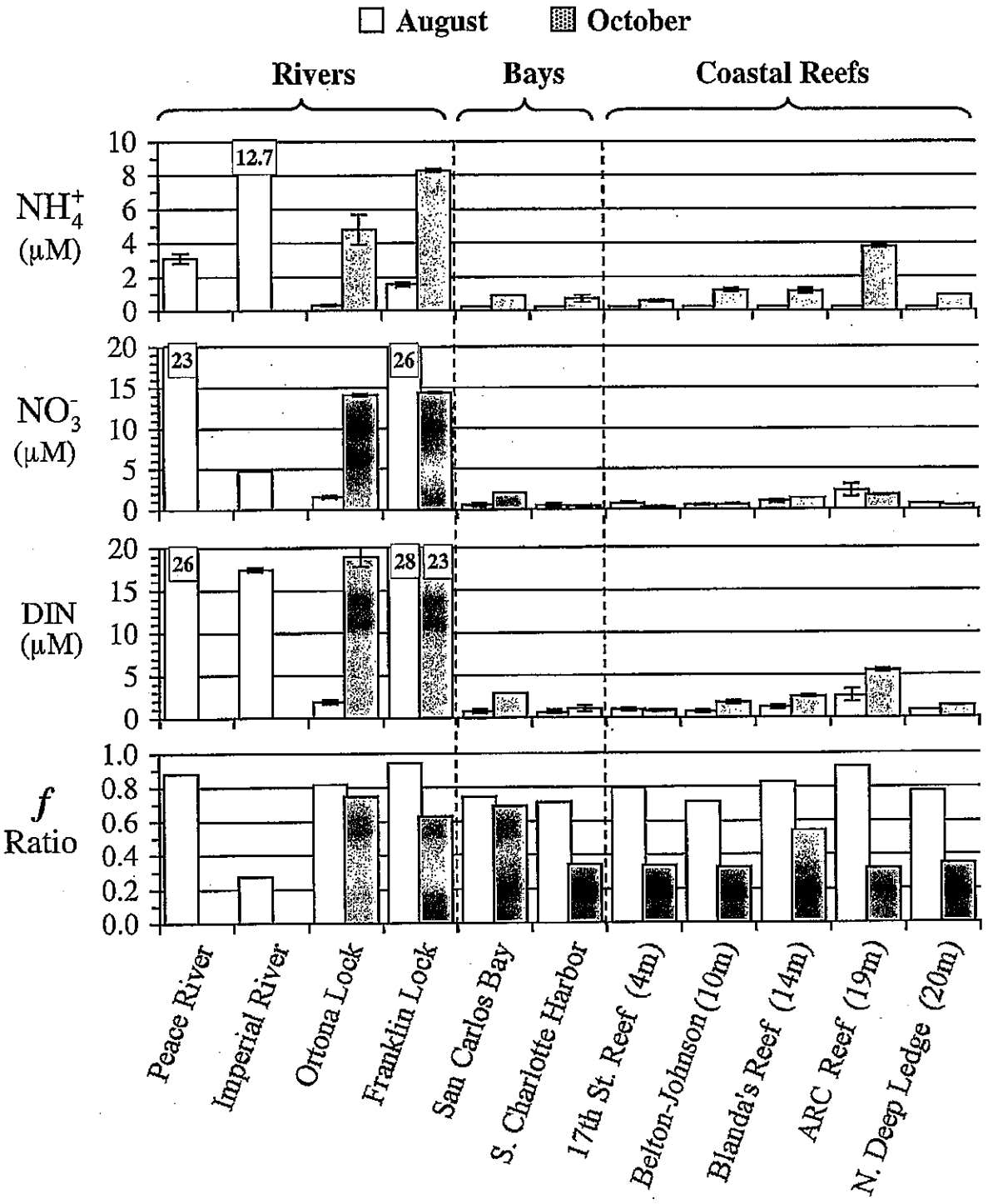
August
October
Rivers
Bays
Coastal Reefs
NH_4^+ (μM)
NO_3^- (μM)
DIN (μM)
f Ratio
12.7
23
26
26
28
23
Peace River
Imperial River
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harbor
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)

Fig. 3

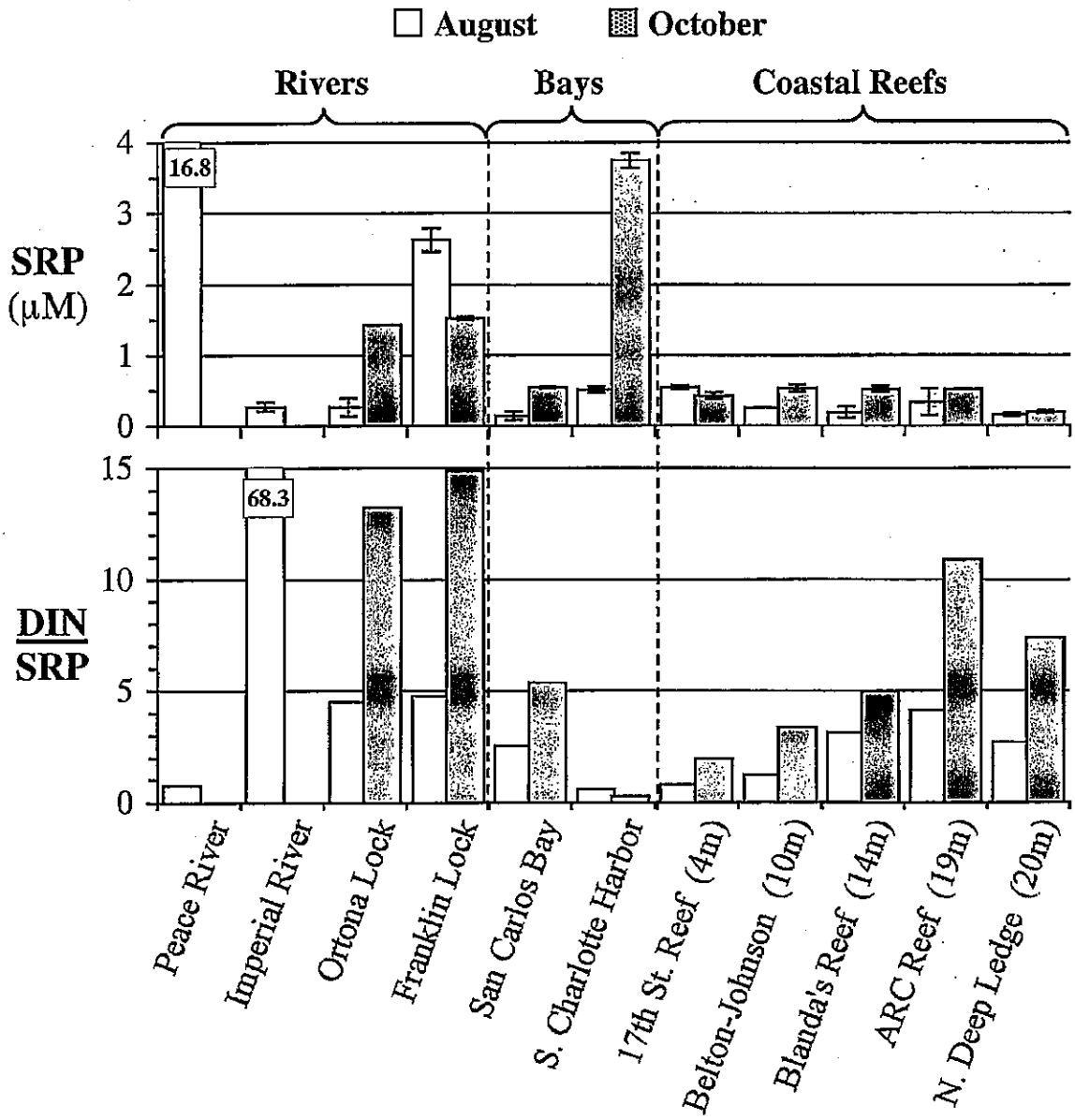
August
October
Rivers
Bays
Coastal Reefs
SRP
(μM)
16.8
68.3
DIN
SRP
Peace River
Imperial River
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harbor
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)

Fig. 4

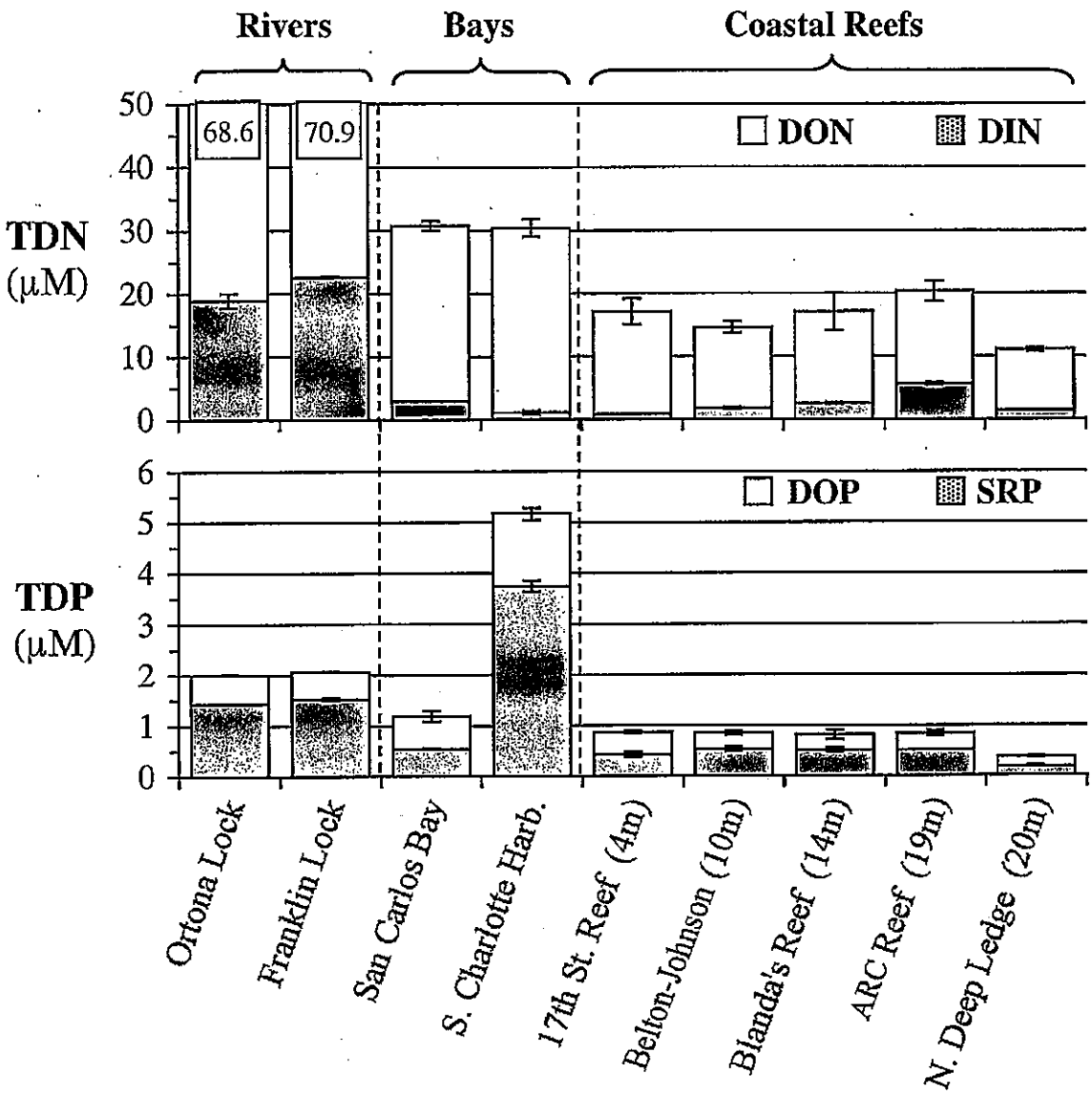
Rivers
Bays
Coastal Reefs
TDN
(μM)
50
40
30
20
10
0
68.6
70.9
DON
DIN
TDP
(μM)
6
5
4
3
2
1
0
DOP
SRP
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harb.
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)

Fig. 5

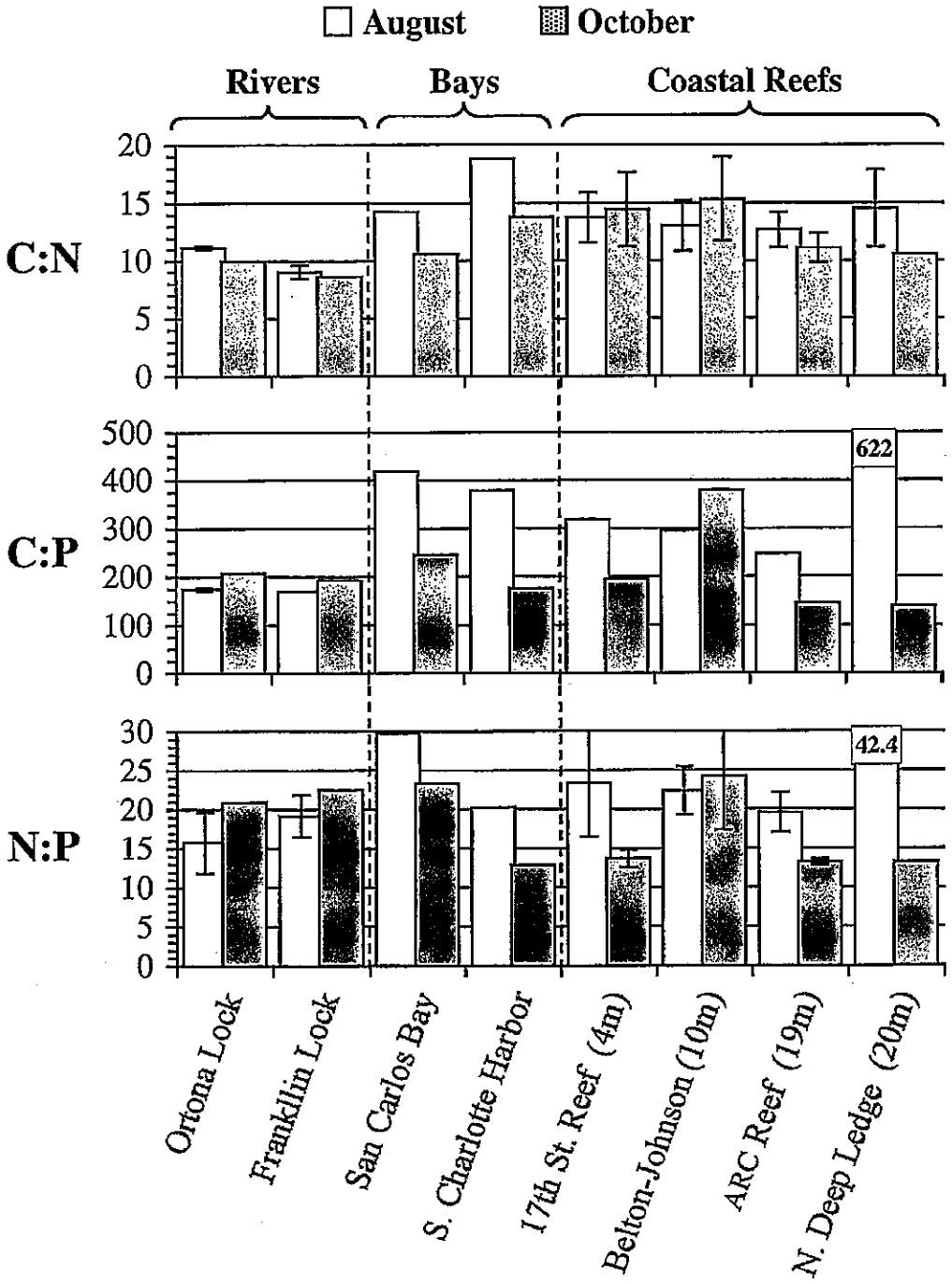
August
October
Rivers
Bays
Coastal Reefs
C:N
C:P
N:P
622
42.4
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harbor
17th St. Reef (4m)
Belton-Johnson (10m)
ARC Reef (19m)
N. Deep Ledge (20m)

Fig. 6

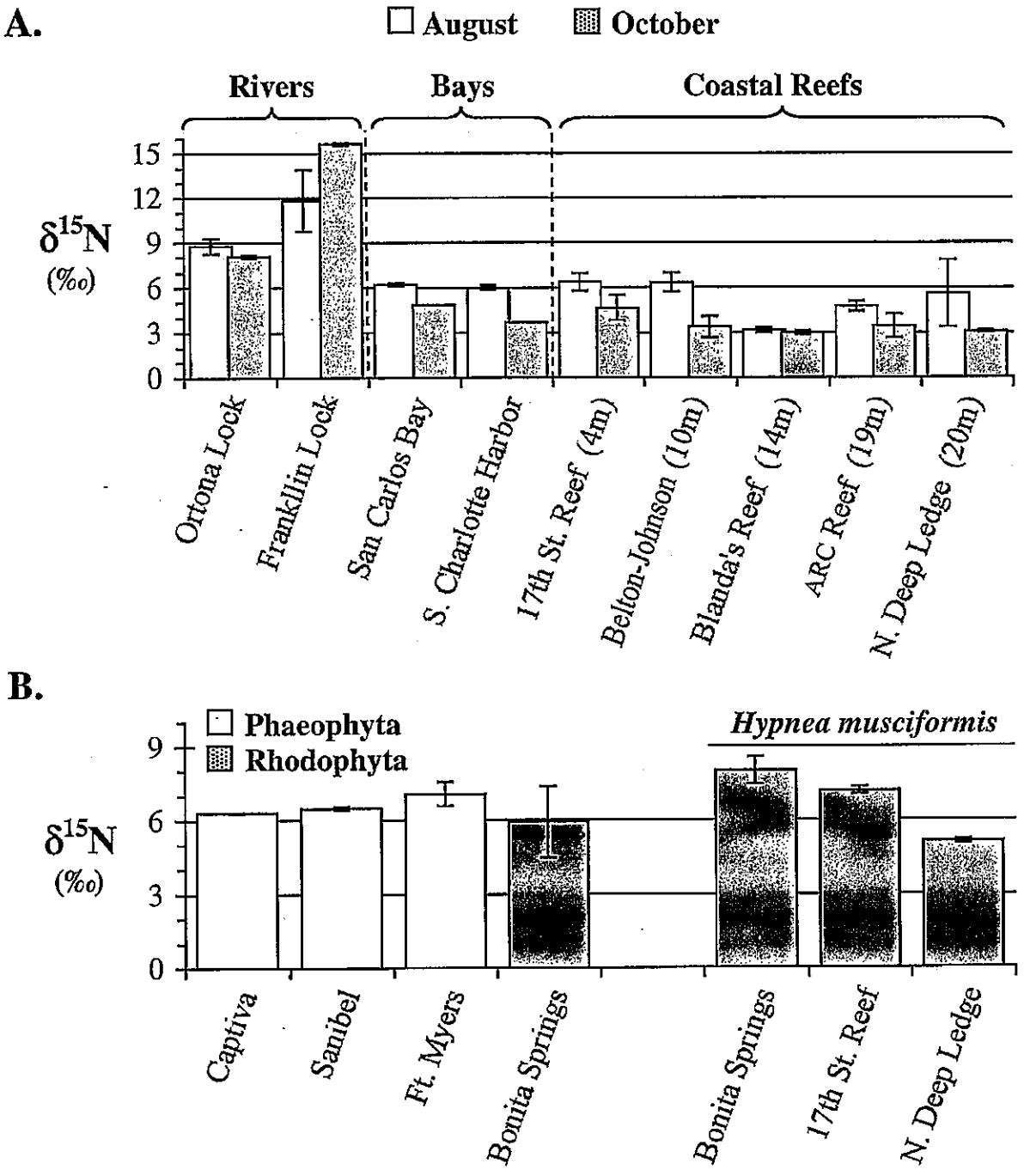
A.
August
October
Rivers
Bays
Coastal Reefs
δ15N
(‰)
15
12
9
6
3
0
Ortona Lock
Franklin Lock
San Carlos Bay
S. Charlotte Harbor
17th St. Reef (4m)
Belton-Johnson (10m)
Blanda's Reef (14m)
ARC Reef (19m)
N. Deep Ledge (20m)
B.
Phaeophyta
Rhodophyta
Hypnea musciformis
δ15N
(‰)
9
6
3
0
Captiva
Sanibel
Ft.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

Fig. 7

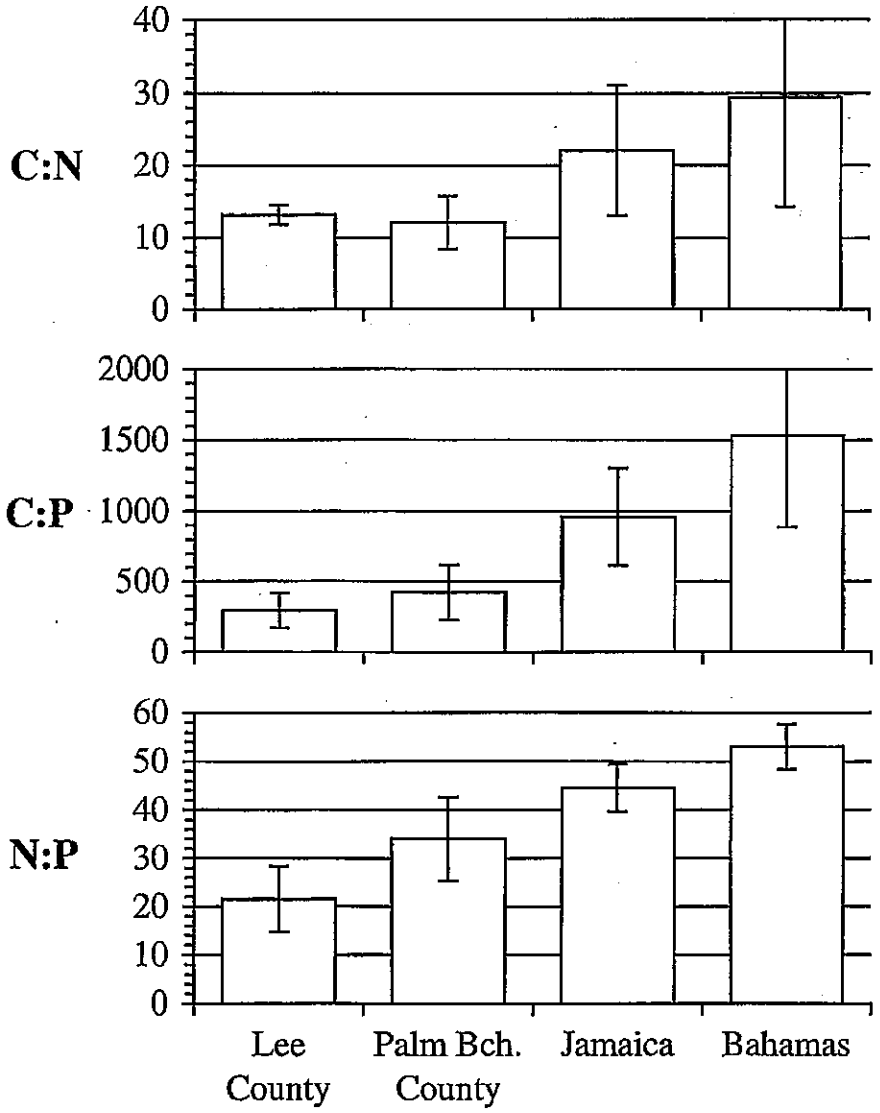
C:N
40
30
20
10
0
C:P
2000
1500
1000
500
0
N:P
60
50
40
30
20
10
0
Lee County
Palm Bch. County
Jamaica
Bahamas

Fig. 8

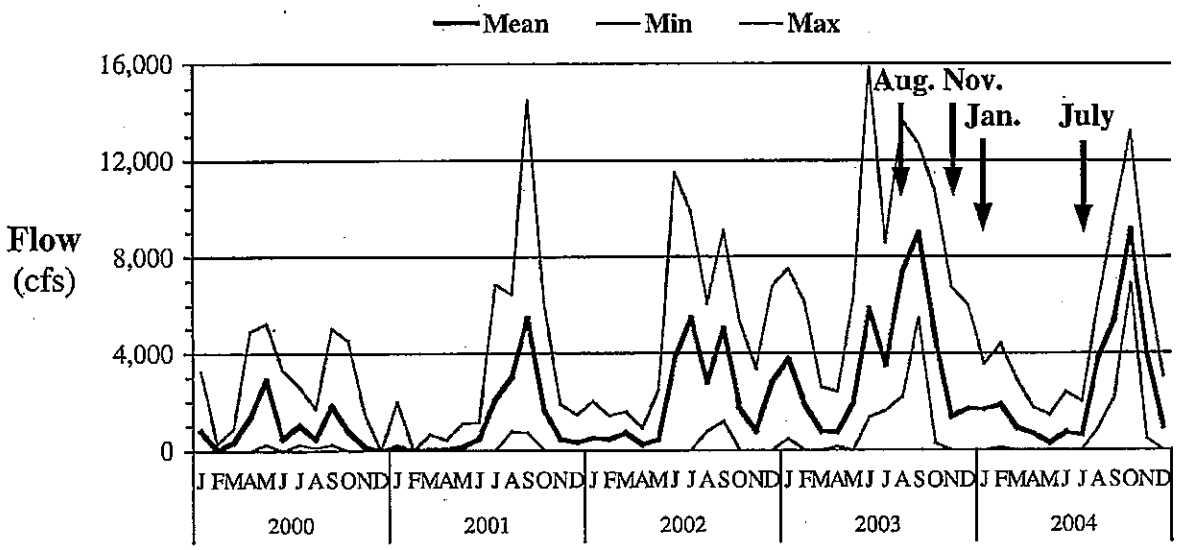
Mean
Min
Max
16,000
12,000
8,000
4,000
0
Flow
(cfs)
Aug.
Nov.
Jan.
July
J FMAMJ JASOND
2000
2001
2002
2003
2004

Fig. 9

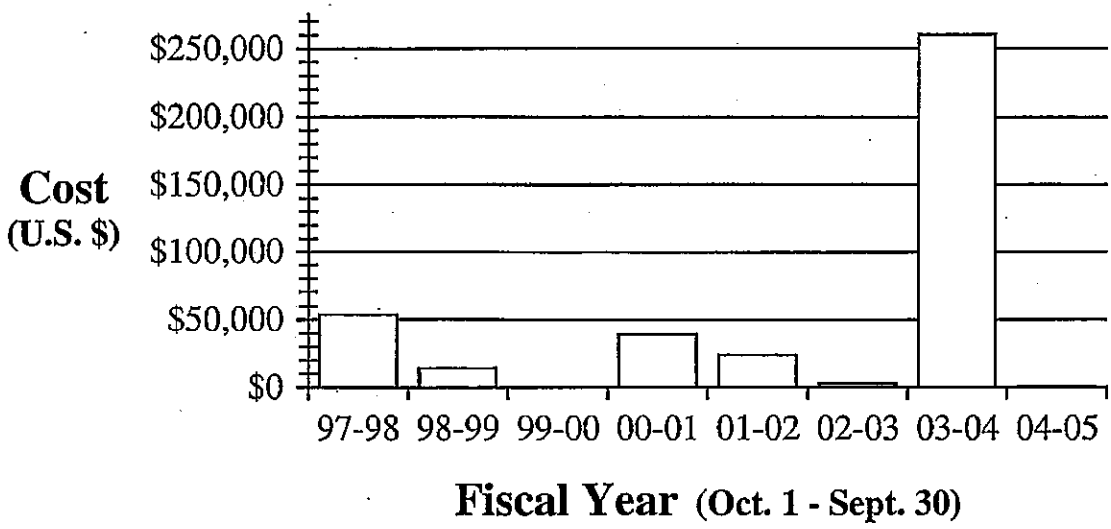
$250,000
$200,000
$150,000
$100,000
$50,000
$0
Cost
(U.S. $)
97-98
98-99
99-00
00-01
01-02
02-03
03-04
04-05
Fiscal Year (Oct. 1 - Sept. 30)

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*									

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)