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Drift rhodophyte blooms emerge in Lee County, Florida, USA: Evidence of escalating coastal eutrophication

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Abstract

Macroalgal blooms have increased globally in recent decades as a result of increased nutrient enrichment and eutrophication of coastal waters. In Lee County, Florida, this problem reached a critical stage in 2003/2004 when massive rhodophyte blooms washed ashore, 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 August 2004, prior to hurricane Charley, and again in late October following several months of large freshwater 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 up to 26 km from shore.

Dissolved nutrient concentrations were generally high throughout the study area, with significantly higher concentrations in the Caloosahatchee River. Mean dissolved inorganic nitrogen concentrations in the Caloosahatchee River increased from Ortona Lock (<18 μM) to Franklin Lock (23–28 μM) downstream during both samplings, indicating significant enrichment within the basin. On coastal reefs, mean ammonium concentrations increased six-fold (≤0.20–1.31 μM) and soluble reactive phosphorus increased three-fold (0.30–0.92 μM) from August to October, respectively. Mean reef macroalgae C:N ratios were low and similar in August (13.9) and October (13.5), and C:P and N:P ratios were also low but decreased significantly from August to October (386–242 and 27.4–17.5, respectively). Macroalgal $\delta^{15}N$ values increased from Ortona Lock (+8 to 9‰) to Franklin Lock (+12 to 15‰) during both samplings, were within the sewage nitrogen range, and decreased with increasing distance from shore to ~+3.0‰ at the most offshore reef. Macroalgae (*Gracilaria*, *Hypnea*, *Botryocladia*, *Eucheuma*, *Sargassum*) collected in July 2004 from Lee County beaches had mean $\delta^{15}N$ values >+6.0‰, similar to values for macroalgae on inshore reefs and within the sewage nitrogen range. However, mean $\delta^{15}N$ values of reef macroalgae decreased from August (+5.84‰) to October (+3.89‰) as Caloosahatchee River discharges increased, suggesting relatively larger contributions from nitrogen sources with low $\delta^{15}N$ values (<+3‰), such as rainfall and agricultural fertilizers, in the wet season. Improved management of freshwater releases from Lake Okeechobee, combined with nutrient removal from sewage effluent within the Caloosahatchee River drainage basin, could help mitigate future macroalgal blooms in Lee County's coastal waters.

Keywords: Nitrogen; Phosphorus; Macroalgae; Eutrophication; Southwest Florida

1. Introduction

Point source and non-point source enrichment with nitrogen (N) and phosphorus (P) is now recognized as the most serious pollution problem facing coastal waters worldwide (GESAMP, 1990; Howarth et al.,

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2000; NRC, 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, 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, 2005a,b).

The development of macroalgal blooms is a predictable ecological response to increased nutrient loading in shallow bays, estuaries, and coastal waters (Lapointe et al., 1994; Morand and Briand, 1996; Valiela et al., 1997). Unlike toxic phytoplankton blooms such as red tides, macroalgal blooms lack direct chemical toxicity but typically have a broader range of ecological impacts. Macroalgal blooms can result in the displacement of indigenous species, habitat destruction, oxygen depletion, alteration of biogeochemical cycles, increased grazing, and die-off of seagrasses and coral reefs (Lapointe et al., 1994; McGlathery, 1995; ECOHAB, 1995; Valiela et al., 1997; NRC, 2000; 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). Because the causes and effects of macroalgal blooms are similar in many ways to those associated with toxic phytoplankton species, the scientific community employs the term "harmful algal bloom" (HAB) to describe this diverse array of bloom phenomena (ECOHAB, 1995).

Land-based nutrient discharges to bays and coastal waters along southwest Florida have long been linked to the development of HABs. Sewage-driven eutrophication in Tampa Bay during the 1960s, 1970s, and 1980s led to drift macroalgal blooms that included the rhodophyte *Gracilaria* and the 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 1980s, which included the rhodophytes *Gracilaria*, *Spyridia*, *Hypnea*, and *Agardhiella*, and the chlorophytes *Ulva* and *Caulerpa* (Avery, 1997). Ketchum and Keen (1947) correlated red tide blooms in coastal waters off Sarasota, Florida, with unusually high water column P concentrations and suggested that "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 initiated by the development of a stratified water mass, characterized by a nutrient-rich, reduced salinity, surface layer resulting from freshwater discharges from the combined Charlotte Harbor-Caloosahatchee River drainage basins. Recently, Hu et al. (2006) suggested that the widespread and intense red tide off west-central Florida throughout 2005 resulted from the unusual number of hurricanes in 2004 that caused higher than normal surface runoff and submarine groundwater discharge.

Increases in nutrient loading associated with expanding urbanization of the watershed and with discharges from the Peace and Caloosahatchee rivers may support the macroalgal blooms that emerged in coastal waters of Lee County, Florida in 2003/2004 (Fig. 1). McPherson and Miller (1990) noted that projected increases in nitrogen loading 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 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 in Lee County between Sanibel Island and Bonita Springs in 2003/2004 (Fig. 2A, B and E). The excessive biomass of these rhodophytes caused odor problems and greatly diminished the use of the beaches by tourists. Concerned governments of Lee County and the City of Bonita Springs prompted the present investigation in order to determine if these macroalgal HABs are 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 may 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 dissolved inorganic nitrogen ($DIN = NH_4^+ + NO_3^- + NO_2^-$) and soluble reactive phosphorus (SRP) concentrations in water sampled along inshore to offshore gradients. If nutrient concentrations of lower-salinity inshore waters

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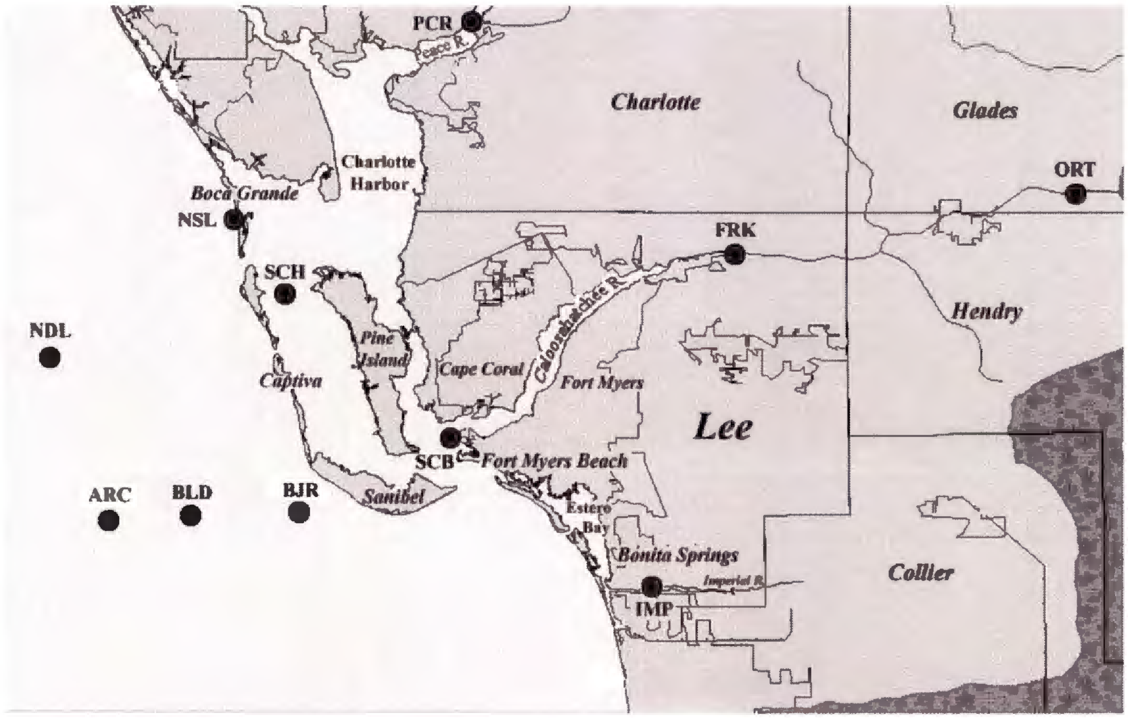

Fig. 1. A map of the Lee County, Florida, USA, area showing station locations for the 2004 study: Ortona Lock (ORT) and Franklin Lock (FRK) on the Caloosahatchee River, Peace River (PCR), Imperial River (IMP), San Carlos Bay (SCB), S. Charlotte Harbor (SCH), 17th Street Reef (NSL), N. Deep Ledge (NDL),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

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 ($\delta^{15}N$; ‰) in macroalgae, which can be used to "fingerprint" the source of N when the various N source $\delta^{15}N$ signatures 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 ^{15}N in aquatic systems can result from N transformations occurring prior to, during, or after 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 southern Florida (Lapointe and Krupa, 1995a,b; Table 1). In contrast, rainfall N, agricultural fertilizer, and peat have $\delta^{15}N$ signatures 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 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 naturally fixed N have low $\delta^{15}N$ values of ~0‰ (France et al., 1998; Table 1), in contrast to those using sewage N, which become more enriched in ^{15}N with increasing sewage N contributions over a $\delta^{15}N$ 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, 2005b) to nearly 40 km

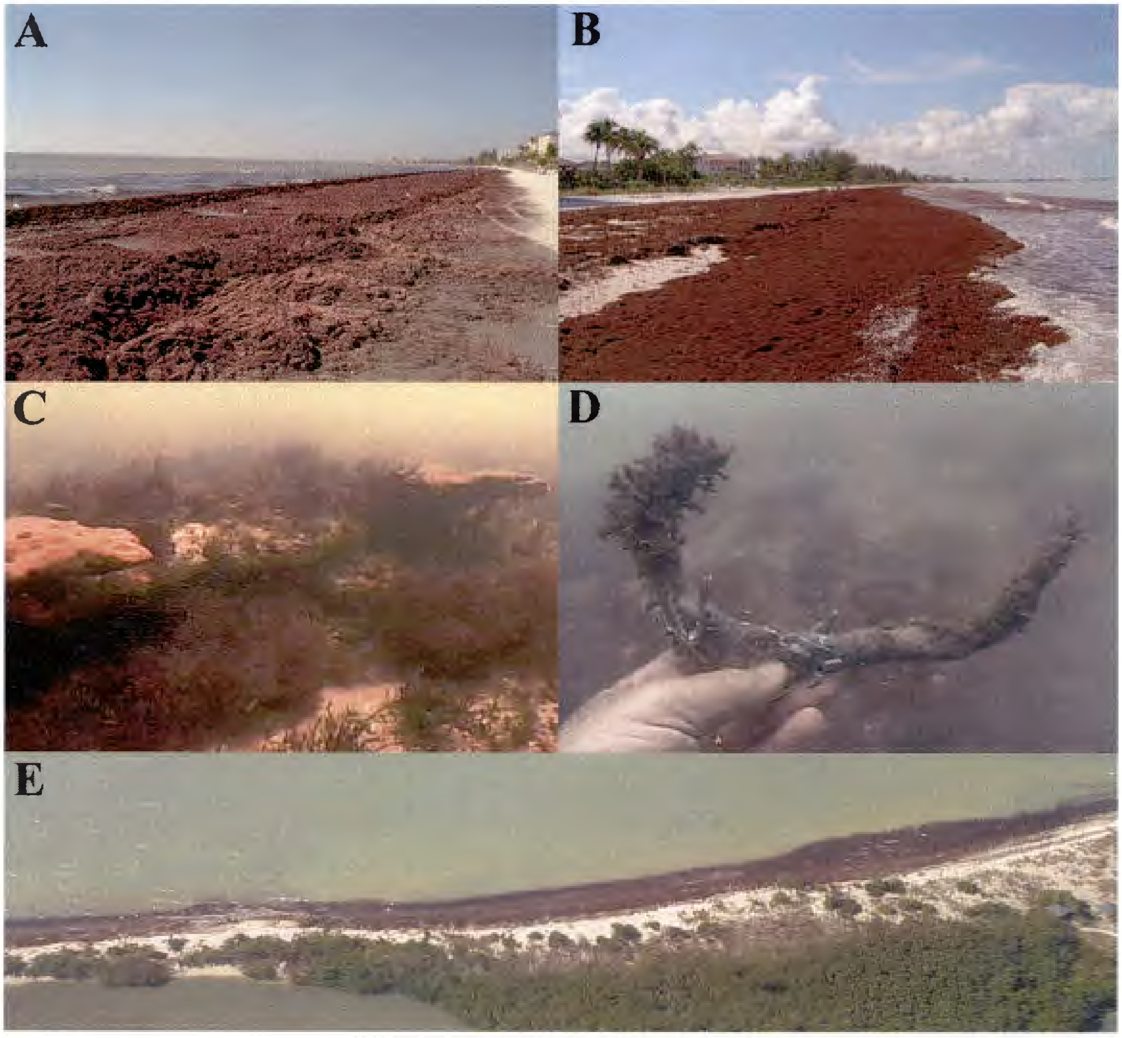

Fig. 2. Red drift macroalgae in coastal waters of Lee County, Florida, USA: (A) rhodophytes, Bonita Springs Beach, January 2004; (B) rhodophytes, Bonita Springs Beach, July 2004; (C) rhodophytes, 17th Street Reef, August 2004; (D) rhodophytes attached to the tube of the suspension feeding polychaete *Chaetopterus variopedatus*, Bonita Springs Beach, August 2005; (E) drift rhodophytes in shallow water along beaches in southern Lee County.

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 sewage N loading was relatively constant compared to the large, non-point source, agricultural N loads transported into coastal waters during wet years when large freshwater releases from the Everglades occurred (Lapointe et al., 2004). We initiated our Lee County study in early August 2004, prior to landfall of three hurricanes that impacted Florida during 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, DBHYDRO rainfall data), we had an opportunity to test this hypothesis when re-sampling in late October 2004.

2. Materials and methods

2.1. Sample collection and analysis

Samples of the water column and attached macroalgae and/or seagrasses were collected 8–10 August (dry season) and 28–29 October (wet season), 2004, along an inshore to offshore gradient extending from the Caloosahatchee River into Lee County coastal waters

Table 1
$\delta^{15}N$ values of various natural and anthropogenic nitrogen sources

Source and 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	Lapointe and Krupa (1995a)
Tequesta Monitor Well #6	+4.6	Lapointe and Krupa (1995b)
Tequesta Monitor Well #10	+11.8	Lapointe and Krupa (1995b)
Upwelled nitrate		
North Atlantic Ocean	+4.8	Sigman et al. (2000)
Inorganic fertilizer	0 to +3.0	Owens (1987)
Peat	0 to +3.0	Heaton (1986)
Atmospheric ammonia	−3.13	Paerl and Fogel (1994)
Atmospheric nitrate	+1.0	Paerl and Fogel (1994)

(Fig. 1). Nine fixed stations were sampled in both August and October, including 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); 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 the station farthest 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

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

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

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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, University of Maryland System, Solomons, MD (NASL). A Technicon Auto-Analyzer II was used for nitrate (NO_3^-) and soluble reactive phosphate (SRP) determination, and a Technicon TRAACS 800 was used for ammonium (NH_4^+) and nitrite (NO_2^-) analyses. Detection limits were 0.21 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). The *f*-ratio [NO_3^-/($NO_3^- + NH_4^+$)] was used 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 0.03 μM for TDP (D'Elia et al., 1997). Dissolved organic nitrogen (DON = TDN − DIN) and dissolved organic phosphorus (DOP = TDP − SRP) concentrations were determined by calculation.

Samples of macroalgae or seagrass 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, Belton-Johnson 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 five to eight different plants per species) of macroalgae were sorted, cleaned of visible epiphytes and sediments, identified (Dawes, 1974; Littler and Littler, 2000), and rinsed briefly (3–5 s) 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 an IBM compatible Labtronics Inc. DP500 software data collection system (D'Elia et al., 1997). All tissue 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 $[(R_{Sample}/R_{Standard}) - 1] \times 10^3$, where $R = {}^{15}N/{}^{14}N$.

2.2. Statistical analyses

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 versus October) included all sites sampled. In order to assess water column characteristics 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 natural and artificial reefs in Lee County coastal waters (Table 2). In both August and October, *B. occidentalis* was collected from all five reef sites. Other rhodophytes collected from reefs included *A. subulata*, *E. isiforme* var. *denudatum*, *G. cervicornis*, *G. tikvahiae*, *H. musciformis*, and *Rhodymenia divaricata*.

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

Overall, ammonium 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 October values were > 0.55 μM at all sites (Fig. 3). At the five coastal reef sites, mean ammonium 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).

Nitrate 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 minimum 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 nitrate 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),

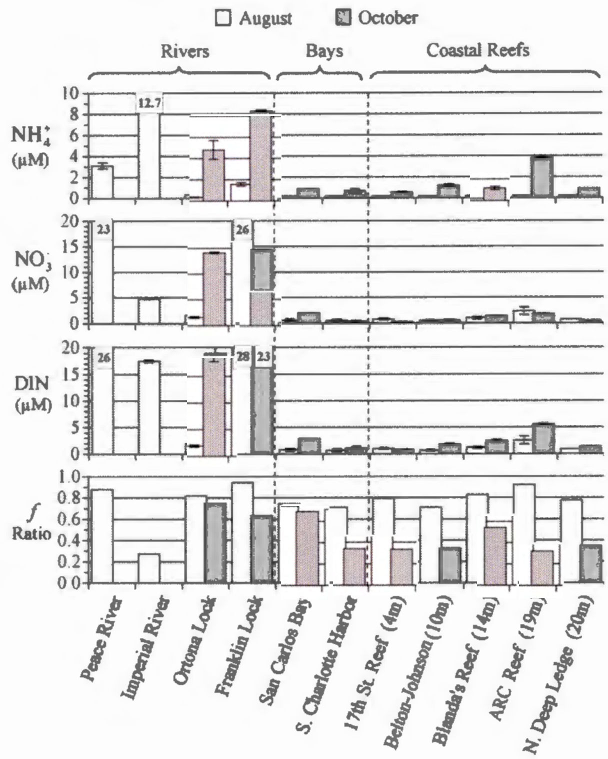

Fig. 3. Mean concentrations (μM, ±1 S.D., $n = 2$) of water column dissolved inorganic nitrogen (DIN), ammonium (NH_4^+), nitrate (NO_3^-) and *f*-ratios (NO_3^-:DIN) in August and October 2004 at sampling stations in Lee County, Florida, USA.

Table 3
Water column nutrient concentrations at study sites in Lee County, Florida, USA in August and October 2004

	n	Ammonium (μM)	Nitrate + nitrite (μM)	DIN (μM)	*f*-Ratio (NO_3^{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

Values represent means ± 1 S.D.

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 concentration occurred in the Peace River (16.80 μM), which was significantly ($p < 0.001$, THSD) higher than all other sites, and the minimum concentration (0.14 μM) occurred at San Carlos Bay (Fig. 4). In October, the maximum SRP concentration (3.74 μM) occurred at S. Charlotte Harbor downstream of the Peace River (which was not sampled) and the minimum (0.19 μM) occurred at N. Deep Ledge farthest from shore (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).

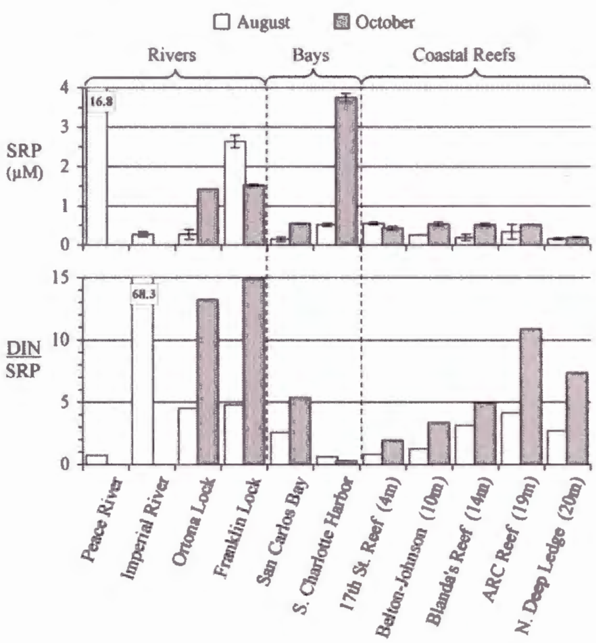

Fig. 4. Mean water column SRP concentrations (μM, ±1 S.D., $n = 2$) and DIN:SRP ratios in August and October 2004 at sampling stations in Lee County, Florida, USA.

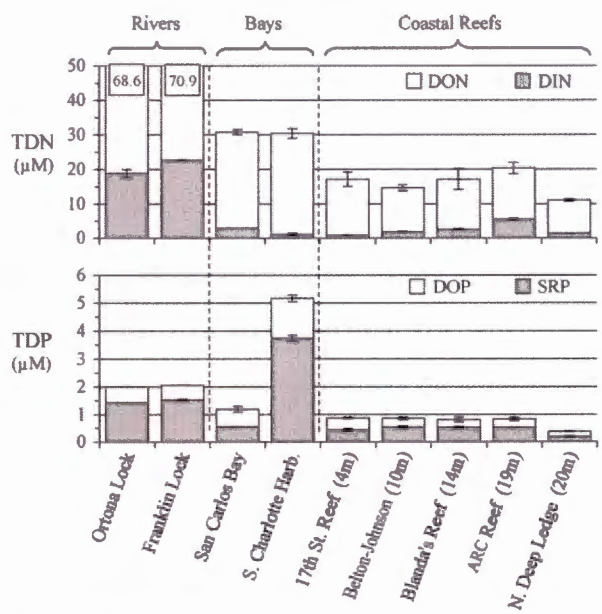

Fig. 5. Mean water column TDN and TDP concentrations (μM, ±1 S.D., $n = 2$), with relative contributions of organic and inorganic forms, in October 2004 at sampling stations in Lee County, Florida, USA.

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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 significantly ($p < 0.001$, THSD) higher concentrations in the rivers (70.92 μM maximum at Franklin Lock) than at other sites. Lower DON concentrations 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 found in S. Charlotte Harbor (1.42 μM), which 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 higher salinity (36.0‰) bottom layer (12–19 m depth).

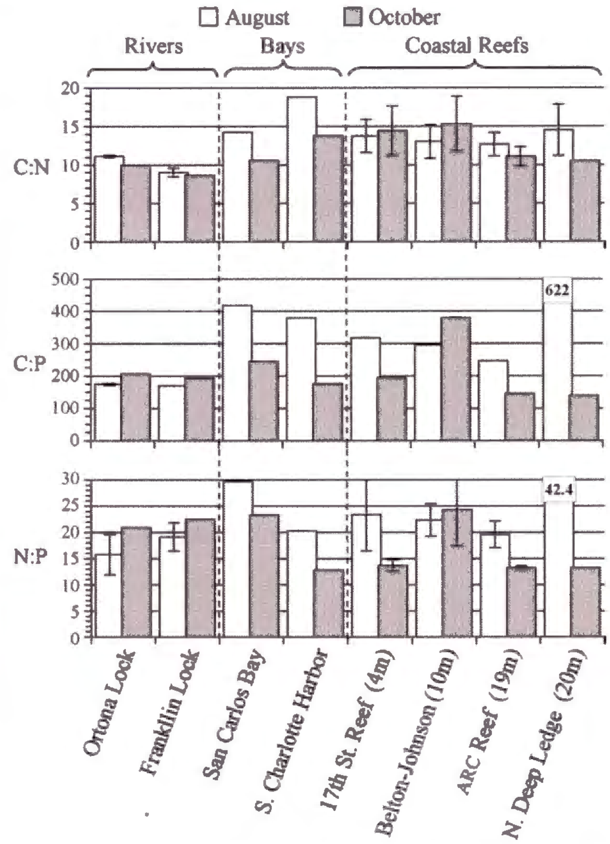

Fig. 6. Mean tissue C:N, C:P, and N:P molar ratios (±1 S.D., n = 1–8) in macroalgae collected in August and October 2004 at sampling stations in Lee County, Florida, USA.

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

Table 4
Tissue C:N, C:P, and N:P molar ratios and $\delta^{15}N$ in macroalgae from coastal study sites in Lee County, Florida, USA in August and October 2004

	C:N ratio	C:P ratio	N:P ratio	$\delta^{15}N$ (‰)
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 ($n = 13$)

Values represent means ± 1 S.D.

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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

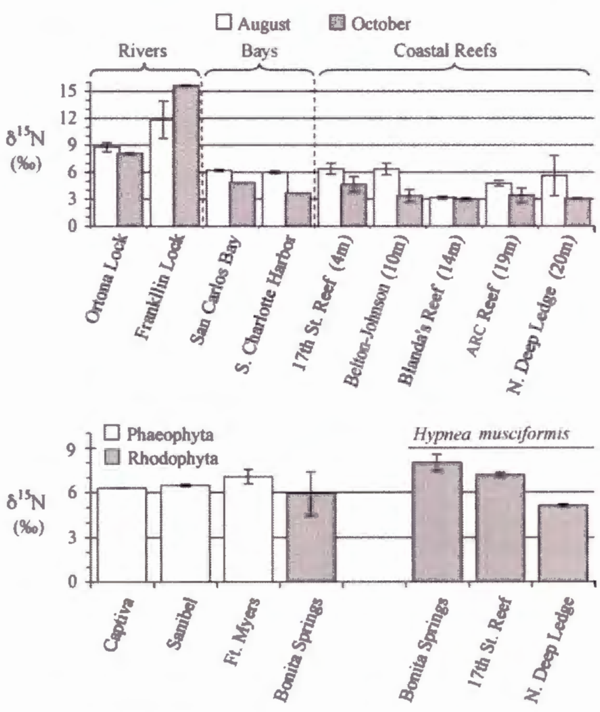

Fig. 7. (A) Mean tissue $\delta^{15}N$ (‰, ±1 S.D., $n = 2$–8) of macroalgae collected in August and October 2004 at sampling stations in Lee County, Florida, USA, and (B) from Bonita Springs Beach in July and August 2004, including a comparison among beach and reef samples of the rhodophyte *Hypnea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

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 ^{15}N-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. 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., 2005a,b), and the Florida Keys (Lapointe et al., 1994, 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. 2E). Our results documented significant N and P enrichment extending at least 26 km from shore in fall of 2004, supporting previous suggestions that river discharges can cause widespread enrichment of coastal waters off southwest Florida (Slobodkin, 1953; Yang et al., 1999; Hu et al., 2006; Brand and Compton, 2007). Considering that these macroalgal HAB phenomena are symptomatic of cultural eutrophication in shallow, coastal waters of south Florida (Humm, 1973; Lapointe et al., 1994), 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 bloom that washed ashore on Bonita Springs Beach in July 2004, prior to hurricane Charley, was dominated by the genera *Gracilaria*, *Hypnea*, and *Agardhiella*. Humm (1973) noted that rhodophytes dominated (51%) the benthic macroalgal communities in the eastern Gulf of Mexico, compared to chlorophytes (31%) and phaeophytes (18%). We found diverse attached rhodophyte communities to be common on natural and artificial reefs throughout the study area prior to hurricane Charley, indicating that source populations for these drift blooms were 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 unsuitable for 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-rich conditions, some of these rhodophytes are capable of very rapid growth and bloom formation. For example, *G. 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 $m^{-2}\,s^{-1}$, 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 $m^{-2}\,s^{-1}$) 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 (low C:N ratios) compared to macroalgae on reefs in 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 *G. tikvahiae*. For example, growth rates as high as 0.37 doublings day^{-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 day^{-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

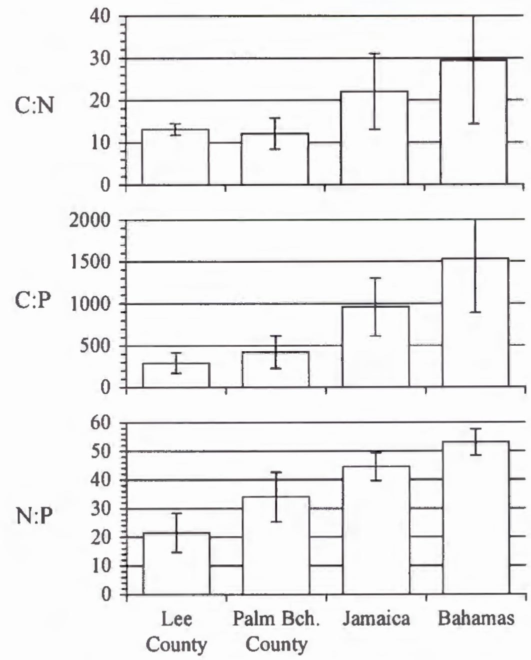

Fig. 8. A comparison of mean tissue C:N, C:P, and N:P molar ratios (±1 S.D., n = 3–6) in macroalgae from Lee County, Florida, USA (this study), with macroalgae from southeastern Florida (Lapointe et al., 2005a), Jamaica, and the Bahamas (Lapointe et al., 1992).

associated with sewage, urban stormwater runoff, and discharges from the Caloosahatchee and Peace rivers.

The low C:P and N:P ratios of rhodophytes in Lee County 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), overall, they were generally low, averaging 314 and 22.5, respectively, and decreased significantly as runoff increased following hurricanes Charley, Frances, and Jeanne. 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 (892–2816) and N:P (73–250) ratios developed in Pine Channel (Lapointe, 1987). Low SRP concentrations (<0.1 μM) in the Florida Keys obviously preclude *G. tikvahiae* from forming blooms there, 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).

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The phaeophyte *S. fluitans* also washed ashore on Lee County beaches in the summer 2004. Populations of pelagic *Sargassum* (*S. natans*, *S. fluitans*) have been present for centuries and are 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 C:N, C:P, and N:P ratios decrease while productivity and growth rate increase. For example, C:N, C:P, and N:P ratios of *S. natans* in the Sargasso Sea decreased significantly from mean values of 49.4, 877, and 18.1–27.9, 347, and 10.2, respectively, 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, Florida, a massive influx of *Sargassum* in 1990 caused a blockage in the cooling system intakes, 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 ammonium ($\leq$0.20 μM versus 1.31 μM) and a three-fold increase in SRP (0.30 μM versus 0.92 μM) as far as ~26 km from shore.

The increased importance of ammonium relative to nitrate 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) season samplings. Although the *f*-ratio was historically used by oceanographers to gauge the relative importance of upwelled nitrate to phytoplankton growth (McCarthy et al., 1975; 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 ammonium. Nitrate concentrations in Lee County's coastal waters were statistically similar (~0.9 μM) in August and October, compared to the six-fold increase (0.20 μM versus 1.31 μM) in ammonium concentrations that resulted in the decreased *f*-ratio. This ammonium 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 ammonium 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 ammonium enrichment of N-limited coastal waters following the onset of the wet season in Lee County.

Although considerable nutrient loadings from Caloosahatchee River discharges are linked to water releases from Lake Okeechobee, comparisons of macroalgal $\delta^{15}N$ values along the Caloosahatchee River provide evidence of significant N enrichment from within the basin itself. Algal tissue $\delta^{15}N$ values increased westward (downstream) from Ortona Lock (+8 to 9‰) to Franklin Lock (+16‰) along the Caloosahatchee River. This $\delta^{15}N$ increase correlated with increasing 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 versus 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, ~76 million l day^{-1} (MLD) of sewage effluent receiving advanced wastewater treatment (AWT; DIN and SRP concentrations of ~214 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 δ^{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, 2005b). The δ^{15}N values of macroalgae decreased with increasing distance from shore, but remained at or above +3‰ at N. Deep Ledge, 26 km offshore. Although these high δ^{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 may be of similar magnitude (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. Significant N enrichment of the water column to at least 26 km from shore could support growth not only of macroalgae, but of phytoplankton as well. Blooms of the red tide dinoflagellate, *K. brevis*, develop along this coastline at similar distances from shore (Tester and Steidinger, 1997).

While the present study's scope is insufficient to resolve the relative importance of specific sewage N sources, multiple sources on the southwest Florida watershed may contribute. Historically, the Caloosahatchee River and Lake Okeechobee were not directly connected, but canal projects connecting them were undertaken in the 1880s in order to control lake levels. This resulted in "new" nutrient sources to the Caloosahatchee River from the Lake Okeechobee watershed that receives natural drainage from the Kissimmee River basin to the north, and "back-pumped" drainage from the Everglades Agricultural Area to the south and the St. Lucie basin to the east (Steinman et al., 2002). Consequently, runoff from dairy and cattle farms in the Kissimmee basin, domestic treated sewage discharged into surface waters or re-used in agricultural areas, and septic tank leachate in the expanded watershed may all contribute to the sewage δ^{15}N signature we observed at Ortona and Franklin locks on the Caloosahatchee River.

Significant reductions in reef macroalgae δ^{15}N values from August (+5.84‰) to October (+3.89‰) may reflect an increased contribution from rainfall and agricultural N sources, following high Lake Okeechobee discharges after the 2004 hurricanes (Fig. 9). The δ^{15}N values of N in rainfall, organic peat, and fertilizers used on sugarcane and citrus farms in south Florida have δ^{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

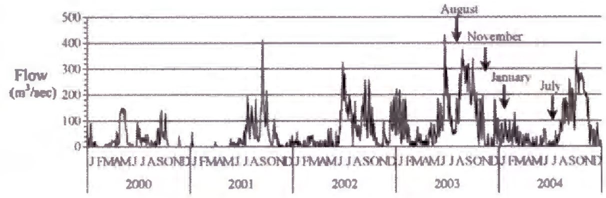

Fig. 9. Daily mean flow rates ($m^3 s^{-1}$) at Franklin Lock on the Caloosahatchee River, Florida, USA from 2000–2004. Arrows indicate drift rhodophyte bloom events on Lee County beaches.

DON, which dominated the TDN pool in October at Franklin Lock) contributions from these sources, which would lower the δ^{15}N signature of macroalgae in downstream coastal waters. In the Lower Florida Keys, elevated macroalgal δ^{15}N values reflect sewage N sources from local sources in the Keys during drought periods when little agricultural runoff of DON from the Everglades occurs. In wet years, however, increased stormwater runoff from agricultural areas lowers the δ^{15}N values of macroalgae to those similar to source signatures of fertilizer 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; Turner et al., 2006). SRP concentrations in rivers along the southwest coast of Florida are substantially higher than in most other North American rivers (Lovejoy et al., 1990; Flannery et al., 1991) and correlate with the natural phosphatic rock abundance in this region (Kaufman, 1969). The greatest contribution of SRP to these waters has been, however, 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 Bittaker, 1973). Runoff from the Peace River following Hurricane Charley would have contributed to observed increases in mean SRP concentrations in coastal waters, from 0.30 μM in early August to 0.92 μM in October. These represent very high SRP concentrations (dominating the TDP pool) as only ∼0.1 μM is required to satisfy growth requirements of macroalgae (Lapointe, 1997) and the red tide dinoflagellate, *K. brevis* (Wilson and Ray, 1958).

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

The development of macroalgal blooms in coastal waters of Lee County and their 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 discharge into the estuary. Although the initial beach accumulation of red drift macroalgae in August 2003 followed major discharges (>340 $m^3 s^{-1}$) 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 freshwater and to increased chlorophyll *a* that develops downstream (Doering and Chamberlain, 1999). Considering the importance of light to the growth of these rhodophytes, development of benthic macroalgal HABs may be favored during periods of low-to-moderate Caloosahatchee River flows, which occurred during and after the 2000/2001 South Florida drought (Abtew et al., 2002; Fig. 9). 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., 2005b). Periods of 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 rhodophyte blooms that occurred in 2003 and early 2004 did not re-emerge in 2005 with the increased nutrient loading that followed the 2004 hurricanes (Fig. 9). However, a severe *K. brevis* bloom developed off southwest Florida throughout 2005, which led to a widespread hypoxic zone and mortalities of benthic communities, fishes, sea turtles, birds, and manatees (Hu et al., 2006; 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 rhodophyte bloom development. The inshore bays (Estero Bay, San Carlos Bay) and shallow coastal waters of 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, our surveys indicated extensive populations of *G. tikvahiae*, *A. 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 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. 2A, B, and E), where odor and aesthetic problems diminish their use by residents and tourists alike.

Excessive macroalgal biomass can have major impacts on coastal economies through loss of tourism and increased beach cleanup costs. 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 problems associated with blooms of the rhodophyte *Hypnea musciformis* (Cesar et al., 2002; http://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, costs of beach seaweed removal programs were historically nominal but increased dramatically to $260,503 in fiscal year 2003/2004 with the onset of the rhodophyte blooms (U.S.; Lee County Visitor and Convention Bureau; Fig. 10). Following the termination of these blooms by hurricane Charley in 2005, beach cleanup costs decreased (Fig. 10).

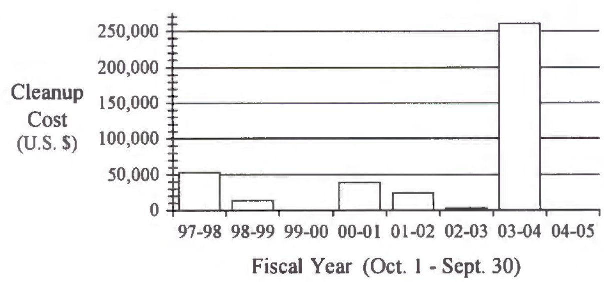

Fig. 10. Beach cleanup costs in Lee County, Florida, USA, during the period 1997–2005 ($ U.S.).

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Because physical harvesting of macroalgae is costly and often insufficient to control macroalgal blooms, water quality restoration is usually necessary (Morand and Briand, 1996). The emergence of rhodophyte blooms in Lee County indicates that nutrient loading to these inshore waters is increasing. Brand and Compton (2007) analyzed the historical abundance of *K. brevis* along the southwest Florida coast and reported a 13–18-fold increase between the period 1954–1963 and 1994–2002, concluding this was a response to increased nutrient availability. Accordingly, nutrient reduction strategies will be required to moderate algal blooms in the future. In 1979, following macroalgal blooms and considerable seagrass loss in Hillsboro Bay, Florida, the local sewage treatment plant initiated wastewater N removal and by 1994 macroalgal cover decreased by >90% while seagrass cover increased from 0.2 ha in 1986 to over 28 ha in 1995 (Avery, 1997). In the Venice Lagoon, Italy massive blooms of *Ulva* and *Gracilaria* that developed in the 1970s and 1980s have greatly diminished in recent years following the enactment of Italian laws restricting the use of phosphate detergents (Acri et al., 2005). The unusually high biomass of *Ulva* in the Venice Lagoon in the 1980s played a primary role in nutrient storage and cycling, thereby regulating development of phytoplankton blooms (Sfriso et al., 1992). In Lee County, extensive blooms of rhodophytes could play a similar role in regulating nutrient cycles and phytoplankton blooms, including *K. brevis*. Data generated from past and present water quality monitoring programs should be used to model the effects of various nutrient sources, including discharges from the Peace and Caloosahatchee rivers, on the development of these HABs. Such a water quality model could help guide nutrient reduction strategies while improving our understanding of how biological, chemical, and physical factors interact to generate macroalgal and phytoplankton HABs.

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