Chinese Journal of Oceanology and Limnology
Vol. 29 No. 4, P. 775-789, 2011
DOI: 10.1007/s00343-011-0506-8

Sewage pollution in Negril, Jamaica: effects on nutrition and ecology of coral reef macroalgae

B. E. LAPOINTE[1, *], K. THACKER[2], C. HANSON[2], L. GETTEN[2]
[1] *Harbor Branch Oceanographic Institute at Florida Atlantic University, 5600 US 1 North, Ft. Pierce, FL 34946, USA*
[2] *Negril Coral Reef Preservation Society, P. O. Box 2563, Negril, Jamaica, West Indies*

Received Mar. 8, 2011; revision accepted Mar. 29, 2011

Abstract Coral reefs in the Negril Marine Park (NMP), Jamaica, have been increasingly impacted by nutrient pollution and macroalgal blooms following decades of intensive development as a major tourist destination. A baseline survey of DIN and SRP concentrations, C:N:P and stable nitrogen isotope ratios ($\delta^{15}N$) of abundant reef macroalgae on shallow and deep reefs of the NMP in 1998 showed strong P-limitation and evidence of increasing sewage pollution. In 1999, a sewage collection and treatment project began diverting wastewater from the resort and urban areas to a pond system that discharged partially-treated effluent into the South Negril River (SNR). These sewage discharges significantly increased concentrations of NH_4^+ and SRP (N:P ~13) in the SNR, which flows into Long Bay and around Negril's "West End". Concentrations of SRP, the primary limiting nutrient, were higher on shallow reefs of the West End in 2001 compared to 1998. Stable nitrogen isotope ratios ($\delta^{15}N$) of abundant reef macroalgae on both shallow and deep reefs of the West End in 2002 were significantly higher than baseline values in 1998, indicating an escalating impact of sewage nitrogen pollution over this timeframe. The increased nutrient concentrations and $\delta^{15}N$ enrichment of reef macroalgae correlated with blooms of the chlorophyte *Chaetomorpha linum* in shallow waters of Long Bay and *Codium isthmocladum* and *Caulerpa cupressoides* on deep reefs of the West End. Sewage treatment systems adjacent to coral reefs must include nutrient removal to ensure that DIN and SRP concentrations, after dilution, are below the low thresholds noted for these oligotrophic ecosystems.

Keyword: macroalgae; sewage; carbon; nitrogen; phosphorus; stable nitrogen isotopes; eutrophication

1 INTRODUCTION

Nutrient pollution from land-based sources is a primary threat to the marine environment of the Caribbean and impediment to sustainable use of its coastal resources (MEA, 2005; UNEP, 2006). Sewage is a major and increasing source of nitrogen (N) and phosphorus (P) pollution and contributes to eutrophication and public health threats along many Caribbean coastlines (Windom, 1992). One common symptom of sewage-driven eutrophication on coral reefs is the development of benthic macroalgal blooms (Barnes, 1973; Johannes, 1975; Smith et al., 1981; Lapointe, 1997; Lapointe et al., 2005a, b). Hermatypic (reef-forming) corals have adapted physiological mechanisms of nutrient recycling that allows these symbiotic calcifying organisms to flourish in clean, clear water with very low concentrations of dissolved inorganic nitrogen ($DIN=NH_4^++NO_3^-+NO_2^-$) and soluble reactive phosphorus (SRP; Muscatine and Porter, 1977; McConnaughey et al., 2000). Accordingly, low level increases in concentrations of DIN or SRP from sewage discharges can stress coral reefs and lead to alternative stable states dominated by fleshy, non-calcifying macroalgae (Smith et al., 1981; Lapointe, 1997; Lapointe et al., 2005a, b).

The natural beauty of Negril and surrounding areas on the northwest coast of Jamaica, which included clear waters, fringing coral reefs (Goreau, 1959), and a 10-km long, fine-grained carbonate

* Corresponding author: blapoin1@hboi.fau.edu

sand beach in Long Bay, was discovered by tourists in the mid-1970's. Since then the area has undergone rapid growth and tourism development and today ranks as the third largest tourist destination in Jamaica. Macroalgal blooms in Negril's coastal waters were first noted in 1991 when conspicuous blooms of the filamentous green macroalga *Chaetomorpha linum* smothered coral reefs and seagrass communities in Long Bay (Goreau, 1992; Lapointe and Thacker, 2002). Water quality monitoring of Negril's wetlands and coastal waters provided the first evidence that this phenomenon resulted from rapidly increasing nutrient pollution from sewage (Wade, 1992). In response to the sewage problem, the European Union (EU) provided funds for the National Water Commission (NWC) to engage DHV Burrow Crocker to design a sewage collection and treatment system for the Negril area, especially the large tourist resorts along Long Bay (Jelier and Roberts, 1992). A review panel including Jamaican and internationally-renown scientists raised concern that the design features of the proposed pond treatment system (STP, Fig.1) would not provide adequate nutrient removal and predicted that the effluent discharged from the ponds would contaminate the South Negril River (SNR) and downstream coral reefs along the West End and beaches in Long Bay (Goreau, 1992). Tissue analysis of the phaeophytes *Sargassum polyceratium* and *Turbinaria turbinata* for carbon:nitrogen:phosphorus (C:N:P) ratios indicated that nutrient loading from the SNR was an important source of phosphorus supporting macroalgal growth on shallow reefs around Negril's West End (Lapointe, 1992).

The European Union funded a water quality monitoring program for the Negril Marine Park (NMP) that was officially established in 1998. The monitoring program, which was conducted by the Negril Coral Reef Preservation Society's (NCRPS) "Reef Rangers", included seasonal (winter, summer) water quality monitoring for DIN and SRP concentrations and C:N:P contents of reef macroalgae, which accounted for 57% to 67% biotic cover at twelve reef stations (six shallow, six deep) in the NMP (Fig.1) in 1998. These biochemical measurements provide a quantitative index to gauge the type (N vs. P) and degree of nutrient-limitation of reef macroalgae (Lapointe et al., 2005a). We also analyzed the reef macroalgae for stable nitrogen isotopes ($\delta^{15}N$) to discriminate among various natural and anthropogenic N sources supporting the blooms.

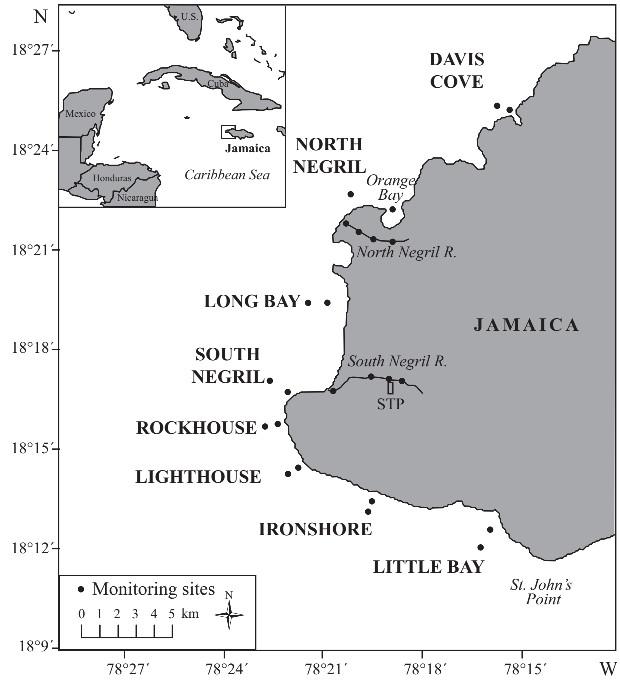

Fig.1 Reef sampling stations in the Negril Marine Park (MNP), Negril, Jamaica

A recent review by Risk et al. (2009) concluded that the measurement of stable nitrogen isotopes in macroalgae provides a cost-effective and objective means of quantifying spatial and temporal variability in sewage stress on coral reefs, which is an increasing problem both in the Caribbean region and globally (MEA, 2005; UNEP, 2006). The monitoring program also included monthly sampling for DIN and SRP concentrations at four stations along the SNR and North Negril River (NNR) beginning in January 1998, prior to the municipal sewage discharges from the ponds discharging into the SNR that began in summer of 1999.

We hypothesized that the increasing municipal sewage discharges would result in escalating DIN and SRP concentrations in the SNR and that the spatial pattern of DIN and SRP enrichment in the SNR would reflect increased enrichment from the sewage pond discharges. Additionally, we hypothesized that macroalgal blooms on coral reefs around the West End would be increasingly affected by sewage discharges from the SNR after summer 1999, which would be reflected by elevated SRP concentrations on shallow reefs at the West End—nutrients potentially limiting the growth of the reef macroalgae. Lastly, we hypothesized that macroalgae on the West End reefs would show $\delta^{15}N$ enrichment above the baseline 1998 values.

2 MATERIAL AND METHOD

2.1 Sampling and analysis of dissolved inorganic nutrients

To establish a nutrient baseline for the Negril Marine Park, replicate (n=4) water samples from shallow (2–4 m) and deep (9–18 m) reefs were sampled at six locations (Davis Cove, North Negril, Long Bay, South Negril, Ironshore, and Little Bay; Fig.1) during winter (January–February) and summer (July–August) of 1998. SCUBA divers collected the water samples into clean, 0.5-L Nalgene bottles that were placed on ice in a dark cooler and transported to the NCRPS lab where they were immediately filtered (0.45 μm GF/F filter) and frozen until analysis. These low-level marine samples were analyzed within 28 d for ammonium (NH_4^+), nitrate plus nitrite (NO_3^-+NO_2^-), and SRP (PO_4^{3-}) at the Harbor Branch Environmental Laboratory (HBEL) in Ft. Pierce, FL. The samples were analyzed on a Bran and Luebbe TRAACS 2000 Analytical Console (nitrate plus nitrite) or an Alpkem nutrient autoanalyzer (ammonium, nitrite, SRP). Detection limits were 0.08 μmol/L for ammonium, 0.05 μmol/L for nitrate plus nitrite, 0.003 μmol/L for nitrite, and 0.001 μmol/L for SRP. The methods for collection, handling, and processing of the water samples for low level nutrient analysis followed a strict quality assurance/quality control protocol developed by the HBEL to prevent problems associated with sample contamination and excessive holding times and to provide accurate and reliable data (Gunsalus, 1997).

To assess the effects of the sewage pond discharges on the SNR, replicate (n=2) river samples were collected monthly at four monitoring stations on both the SNR and North Negril River (NNR; Fig.1) between 1998 and 2002. The SNR stations included those used for the NCRPS watershed monitoring program: Upstream Effluent (0.25 km above the point of sewage discharge from the sewage ponds), Effluent Discharge (at the point of discharge from the ponds), Downstream Effluent (~0.75 km below the discharge), and the "Bridge" where the SNR discharges into Long Bay and reefs of the West End. A similar spatial sampling network of four stations was established on the NNR (Fig.1) as reference sites for the SNR monitoring program. The surface water grab samples were collected into clean, 0.5-L Nalgene bottles that were placed on ice in a dark cooler and transported to the NCRPS lab where they were immediately filtered (0.45 μm GF/F filter) and frozen until analysis. These samples were analyzed within 28 d for NH_4^+, NO_3^-+NO_2^-, and PO_4^{3-} on a Hach DR-2000 spectrophotometer calibrated using standard curves per manufacturer's methods. The SNR and NNR samples had relatively low salinities (<10) and high DIN and SRP concentrations and were accordingly analyzed by standard EPA methods (EPA 350.1, EPA 353.2, and EPA 365.1).

Nutrient sampling was performed on June 29, 2001, at four shallow reef stations around the West End that were hypothetically impacted by the increasing wastewater discharges from the SNR. Water samples were collected from shallow reefs at South Negril, Rockhouse, Lighthouse, and Ironshore (Fig.1). Two of these stations (South Negril, Ironshore) were used in the baseline 1998 NMP water quality monitoring program and provided comparative data. Replicate (n=4) near-bottom (0.5 m above the reef surface) water samples were collected from the shallow reef stations into clean, 0.5-L Nalgene bottles and placed on ice in coolers for transport back to the NCRPS lab. In the lab, the samples were filtered through 0.45 μm GF/F filters and frozen until analysis for low-level DIN and SRP concentrations at HBEL in Ft. Pierce, FL, following the same methods described above.

2.2 Sampling and analysis of reef macroalgae for C:N:P and $\delta^{15}N$

During the 1998 baseline survey, abundant reef macroalgae from six shallow (2–4 m depth) and six deep (9–18 m) reefs in the NMP were sampled in winter and summer and analyzed for C:N:P and $\delta^{15}N$ analysis. Samples of macroalgae were collected by SCUBA divers from the twelve reef sites into plastic Ziploc® bags and held in a cooler during transport back to the NCRPS lab. The samples were sorted to species, cleaned of calcium carbonate sediments and epiphytes, briefly (3–5 s) rinsed in deionized water, dried in a laboratory oven (65°C) to constant weight, and powdered with a mortar and pestle. At least two species of macroalgae were sampled from each of the twelve reef sites, which typically included the phaeophytes *Sargassum polyceratium*, *S. hystrix*, *Lobophora variegata*, and the chlorophytes *Chaetomorpha* spp., *Codium* spp., and *Cladophora fuliginosa.* Each macroalgal sample represented a composite of at least five individual thalli to ensure a high degree of representativeness. Comparative sampling of reef macroalgae for $\delta^{15}N$ values following the 1999 sewage diversion was performed at four shallow reefs (2–4 m; South Negril, Rockhouse, Lighthouse, and Ironshore) and four deep reefs (9–18 m South Negril, Rockhouse, Lighthouse, Ironshore) around the West End on May 1, 2002.

Powdered macroalgae were analyzed for C:N:P contents at Nutrient Analytical Services, Chesapeake Biological Laboratory, University of Maryland System, Solomons, MD. Tissue C and N were measured on an Exeter Analytical, Inc. (EAI) CE-440 Elemental Analyzer, whereas 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). Replicate (n=2) samples of dried macroalgae were analyzed for total N and ^{15}N atom % by Isotope Analytical Services, Inc. (Los Alamos, New Mexico) with a Carlo-Erba N/A 1500 elemental analyzer using Dumas combustion; the purified nitrogen gas was measured by a VG Isomass mass spectrometer. The standard used for stable nitrogen isotope analysis was N_2 in air. The δ^{15}N values, were calculated as:

$$[(R_{\text{sample}}/R_{\text{standard}})-1]\times 10^3, \text{ with } R = {}^{15}\text{N}/{}^{14}\text{N}$$

2.2.1 Statistical analysis

We used two-way ANOVA to analyze the baseline DIN and SRP concentration data for the NMP reefs in 1998; t-tests were used for comparison of selected data from the West End in 1998 (South Negril, Ironshore) with more recent data collected there in 2001. Two-way ANOVA was also used to analyze C: N:P contents of macroalgae collected from shallow and deep reefs within NMP in 1998; t-tests were used to compare δ^{15}N values of macroalgae from shallow and deep reefs in 1998 and with selected data from the West End in 1998 (South Negril, Ironshore) with more recent data collected in 2002.

3 RESULT

3.1 Dissolved inorganic nutrients

DIN concentrations were significantly (F=4.89, P=0.038, n=49) higher on shallow compared to deep reefs in 1998, with an annual mean of 1.15 μmol/L on shallow reefs and 0.78 μmol/L on deep reefs (Table 1) DIN concentrations did not vary significantly between dry (winter) and wet (summer) seasons; DIN averaged 1.12 μmol/L in winter and 1.19 μmol/L in summer on shallow reefs, and 0.74 μmol/L and 0.82 μmol/L on deep reefs, respectively (Table 1) NH_4^+, rather than NO_3^-, was the dominant form of DIN on both shallow and deeps reefs.

In contrast to DIN, SRP concentrations varied significantly between the dry (winter) and wet (summer) seasons of 1998. SRP averaged 0.017 μmol/L on both shallow and deep reefs in the winter, and increased significantly (F=17.89, P=0.000 4, n=49) to 0.047 μmol/L on shallow reefs and 0.040 μmol/L on deep reefs in summer, respectively. Because of the seasonal differences in SRP concentrations, the DIN: SRP ratio decreased from 58.7 and 49.3 on shallow and deep reefs in winter to 38.5 and 33.4 during summer, respectively (Table 1).

NH_4^+ concentrations increased at all four stations in the SNR between 1998 and 2002 following the sewage pond discharges that began in summer of 1999 (Fig.2). NH_4^+ concentrations increased year-by-year after 1999 at all stations, with maximum values of 382 μmol/L at Upstream Effluent, 937 μmol/L at Effluent Discharge, 411 μmol/L at Downstream Effluent, and 98.5 μmol/L at the Bridge (Fig.2). Over the five-year period of study, average NH_4^+ concentrations were 30.9 μmol/L at Upstream Effluent, 111 μmol/L at Effluent Discharge, 57.3 μmol/L at Downstream Effluent, and 23.9 μmol/L at the Bridge.

Similar increases in SRP concentrations were observed in the SNR following the sewage pond discharges in 1999 (Fig.3). SRP concentrations increased after 1999 at all stations, with maximum values of 47.6 μmol/L at Upstream Effluent, 54.2 μmol/L at Effluent Discharge, 68.4 μmol/L at Downstream Effluent, and 13.6 μmol/L at the Bridge (Fig.3). Over the five-year period of study, average SRP concentrations were 4.24 μmol/L at Upstream Effluent, 15.5 μmol/L at Effluent Discharge, 8.14 μmol/L at Downstream Effluent, and 3.42 μmol/L at the Bridge.

In contrast to the SNR, overall lower values and no significant temporal change in NH_4^+ and SRP concentrations occurred in the NNR during the period of study. Maximum NH_4^+ concentrations were 7.14 μmol/L at Extreme Top, 10.36 μmol/L at Top, 13.93 μmol/L at Midpoint, and 12.5 μmol/L at the Bridge, respectively (Fig.4). Average NH_4^+ concentrations over the five-year study were 2.12 μmol/L at Extreme Top, 2.17 μmol/L at Top, 3.51 μmol/L at Midpoint, and 2.50 μmol/L at Bridge. Maximum SRP concentrations were 2.74 μmol/L at Extreme Top, 3.22 μmol/L at Top, 2.74 μmol/L at Midpoint, and 3.71 μmol/L at the Bridge,

Table 1 Mean concentrations (μmol/L) of dissolved ammonium, nitrate plus nitrite, dissolved inorganic nitrogen (DIN= ammonium+nitrate+nitrite), soluble reactive phosphorus (SRP), and the DIN:SRP ratio in 1998

Season	Depth	Site	Ammonium	Nitrate+Nitrite	DIN	SRP	DIN:SRP
Winter	Shallow	Davis Cove	1.71±1.78	0.50±0.17	2.21±1.85	0.023±0.008	92.2
		North Negril	0.71±0.87	0.49±0.12	0.93±0.72	0.024±0.013	47.8
		Long Bay	0.63±0.10	0.35±0.21	0.72±0.50	0.02±0.009	45.1
		South Negril	0.70±0.12	0.82±0.08	1.34±0.32	0.028±0.008	41.5
		Ironshore	0.22±0.08	0.20±0.05	0.31±0.17	0.010±0.003	21.7
		Little Bay	0.70±0.37	0.37±0.09	1.07±0.29	0.019±0.005	49.7
		Mean±1SD	0.93±1.08	0.44±0.22	1.12±1.08	0.017±0.010	58.7
	Deep	Davis Cove	0.50±0.39	0.56±0.17	0.87±0.52	0.038±0.025	24.1
		North Negril	0.50±0.29	0.58±0.47	0.96±0.73	0.018±0.007	57.1
		Long Bay	0.42±0.26	0.30±0.12	0.48±0.23	0.018±0.011	31.9
		South Negril	0.65±0.08	0.40±0.23	1.04±0.25	0.030±0.0	29.9
		Ironshore	0.45±0.13	0.21±0.06	0.43±0.21	0.010±0.003	43.0
		Little Bay	0.74±0.45	0.14±0.01	0.88±0.45	0.008±0.0	110
		Mean±1SD	0.54±0.30	0.39±0.28	0.74±0.49	0.017±0.016	49.3
Summer	Shallow	Davis Cove	1.59±1.81	0.42±0.14	1.81±1.84	0.034±0.026	50.3
		North Negril	0.67±0.54	0.29±0.11	0.96±0.64	0.062±0.035	19.8
		Long Bay	0.72±0.41	0.35±0.09	1.07±0.36	0.045±0.041	53.2
		South Negril	0.61±0.41	0.34±0.13	0.95±0.52	0.065±0.025	14.5
		Ironshore	0.73±0.56	0.59±0.14	1.32±0.66	0.033±0.014	57.9
		Little Bay	0.56±0.17	0.48±0.14	1.04±0.23	0.042±0.025	36.4
		Mean±1SD	0.80±0.83	0.41±0.16	1.19±0.89	0.047±0.029	38.5
	Deep	Davis Cove	0.49±0.30	0.35±0.11	0.78±0.39	0.042±0.028	31.1
		North Negril	0.21±0.05	0.48±0.29	0.70±0.34	0.013±0.002	65.0
		Long Bay	0.44±0.28	0.49±0.33	0.93±0.37	0.066±0.043	25.5
		South Negril	0.50±0.16	0.30±0.05	0.80±0.18	0.026±0.015	40.9
		Ironshore	0.31±0.04	0.30±0.04	0.61±0.06	0.043±0.025	18.9
		Little Bay	0.64±0.08	0.36±0.11	1.00±0.18	0.049±0.019	25.2
		Mean±1SD	0.44±0.24	0.39±0.21	0.82±0.32	0.040±0.027	33.4

Values represent means (±1SD) with n=8 for nutrients at each station and n=48 for pooled means

respectively (Fig.5). Average SRP concentrations over the five-year study were 0.75 μmol/L at Extreme Top, 0.61 μmol/L at Top, 0.68 μmol/L at Midpoint, and 0.59 μmol/L at Bridge.

Sampling SRP concentrations on shallow reefs of the West End in June 2001, following the sewage discharges into the SNR, indicated significantly higher concentrations than observed on these reefs in 1998. The SRP concentrations on shallow reefs at South Negril in 2001 averaged 0.150 μmol/L and ranged from 0.098 to 0.201 μmol/L. This is significantly (t-test, P<0.000 1) greater than the SRP concentrations measured at this site in 1998 when the SRP concentrations averaged 0.065 μmol/L and ranged from 0.041 to 0.111 μmol/L (Fig.6). Conversely, no significant differences occurred in SRP concentrations at Ironshore between 1998 and 2001, when the averages were 0.042 μmol/L (range: 0.011 to 0.054 μmol/L) and 0.103 μmol/L (range: 0.026 to 0.212 μmol/L), respectively (Fig.6).

3.2 C:N:P and δ^{15}N analysis of reef macroalgae

Tissue C:N:P contents of macroalgae at the shallow and deep reef sites in 1998 showed significant spatial patterns. Overall, levels of tissue %C in macroalgae did not vary significantly between shallow and deep reefs or winter and summer, with means ranging

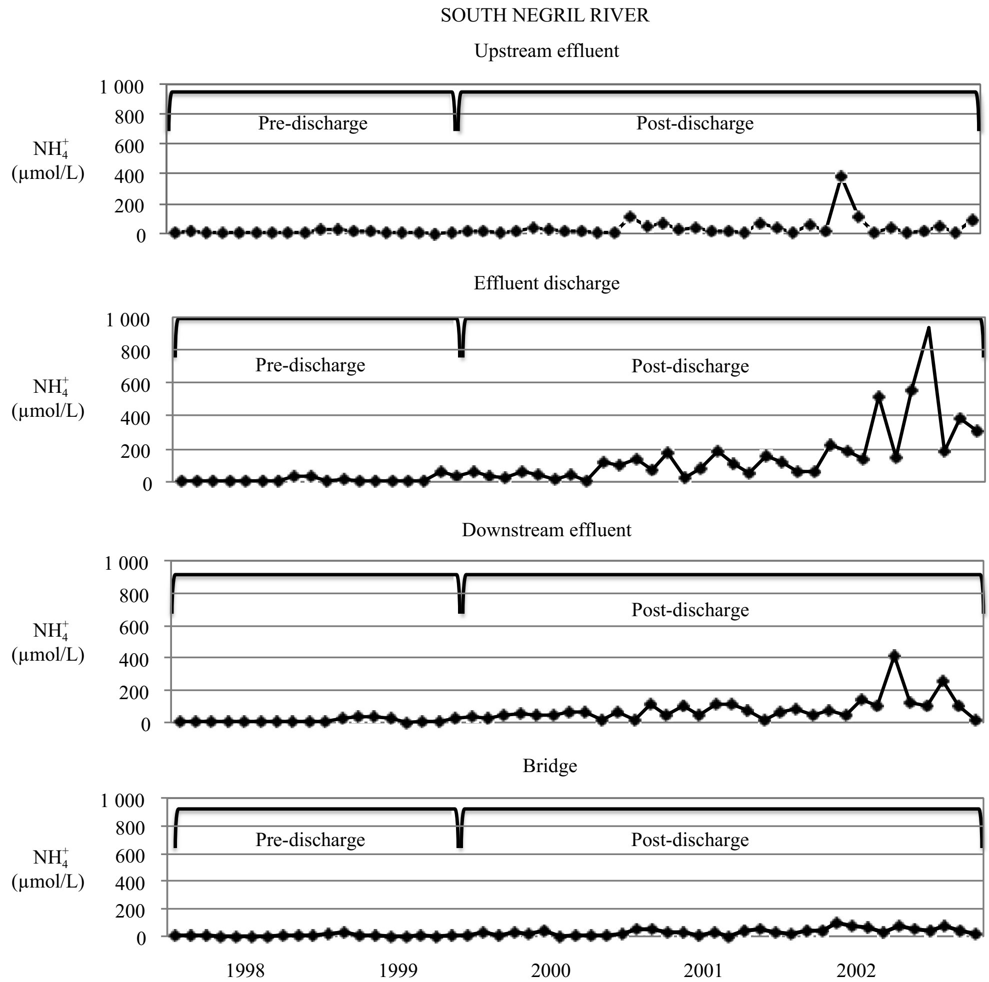

Fig.2 Ammonium (NH_4^+) concentrations at the four South Negril River monitoring stations between 1998 and 2002

from 24.6% to 26.3%C (Tables 2 and 3). Tissue %N did not vary significantly between seasons, although levels were significantly (F=15.48, P=0.000 2) higher on shallow (1.66%N) compared to deep (1.02%N) reefs in summer but not winter (1.27%N vs. 1.05%N, respectively; Tables 2 and 3). In contrast to %N, %P of macroalgae did not vary with depth in either season (means ranged from 0.06% to 0.04% dry weight; Tables 2 and 3). The generally higher %N on shallow compared to deep reefs were reflected in lower mean C:N and C:P ratios on shallow compared to deep reefs in both winter (23.2 vs. 29.7; 1 476 vs. 1 694) and summer (21.2 vs. 29.9; 1 364 vs. 1 670). The N:P ratio of macroalgal tissue was consistently >50, and mean values decreased from shallow to deep reefs both in both winter (64.2 vs. 59.4) and summer (65.4 vs. 54.0).

The $\delta^{15}N$ values of macroalgae sampled from the shallow and deep reef sites in 1998 varied spatially but not seasonally (Tables 2 and 3). The mean $\delta^{15}N$ value of macroalgae on the six shallow reefs in winter 1998 was +3.26, a value significantly (t-test, P=0.044) higher than the mean value of +1.90 for macroalgae on the deep reefs (Table 2). During summer, the mean $\delta^{15}N$ value of macroalgae on the six shallow reefs was +4.04, a value significantly (t-test, P=0.043) higher than the mean value of +1.65 for macroalgae on the deep reefs (Table 3). The highest values (+6.49 to +9.85) occurred on the shallow reefs at South Negril and Little Bay, respectively, which are adjacent to urban areas or bay waters impacted by sewage pollution (Tables 2 and 3).

The macroalgae sampled at the West End shallow reef sites (South Negril, Rockhouse, Lighthouse, Ironshore) in 2002 following sewage diversion were taxonomically similar to those sampled in 1998 (Tables 2 and 3). The mean $\delta^{15}N$ value of

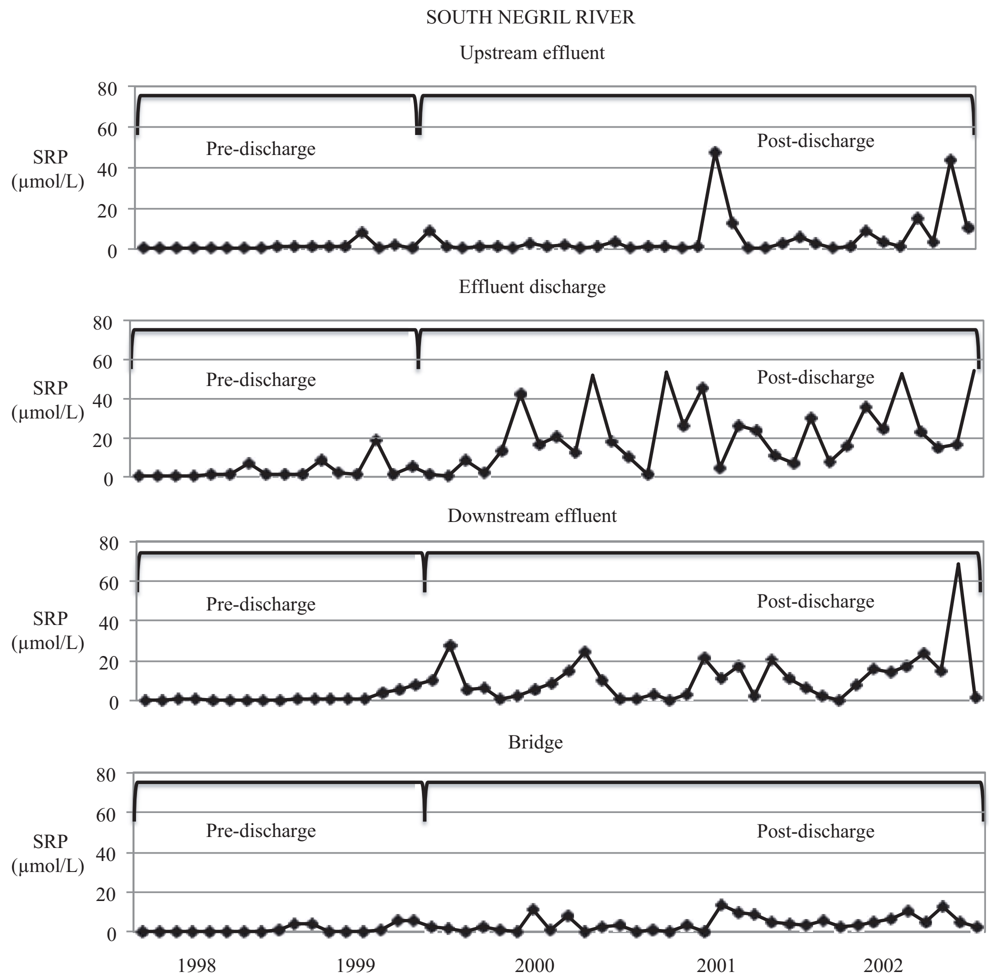

Fig.3 Soluble reactive phosphorus (SRP) concentrations at the four South Negril River monitoring stations between 1998 and 2002

macroalgae on the South Negril shallow reef in 2002 was +8.59±1.24 (ranging from +7.67 to +11.07), a value significantly (*t*-test, $P<0.000\,1$) higher than the mean of +4.71±1.10 (ranged from +2.06 to +5.81) for macroalgae at this reef in 1998 (Fig.7). The mean $\delta^{15}N$ value for macroalgae on the shallow reefs at Rockhouse was +5.3±0.89 (ranging from +4.3 to +7.59) and at Lighthouse was +4.7±0.99 (ranging from +3.64 to +6.03; Fig.7). The mean $\delta^{15}N$ value of macroalgae at the most downstream shallow reef at Ironshore in 2002 was +5.11±1.65 (ranging from +3.15 to +7.18), a value similar (*t*-test, $P=0.25$, not significant) to the mean of +4.01 (ranging from +3.31 to +5.06) for macroalgae at this reef in 1998 (Fig.7).

Considerable $\delta^{15}N$ enrichment occurred in macroalgae on the deep reefs of the West End between 1998 and 2002. Unlike the shallow reefs that had taxonomically similar macroalgae in 1998 and 2002, the deep reefs supported conspicuous blooms of the chlorophytes *Codium isthmocladum* and *Caulerpa cupressoides* in 2002. Neither of these species had been observed in abundance on the deep reefs of the West End in previous SCUBA surveys (Goreau, 1992) nor were they collected in 1998 from the deep reef at Ironshore (Tables 2 and 3). The overall mean $\delta^{15}N$ value of macroalgae on the deep reef at South Negril was +5.08±1.53 (ranged from +2.49 to +7.23) in 2002, a value significantly (*t*-test, $P<0.000\,1$) higher than the mean of +1.71 (ranged from +0.91 to +3.50) for macroalgae at this reef in 1998 (Fig.8). The mean $\delta^{15}N$ value for macroalgae on the deep reefs at Rockhouse was +6.24 (ranging from +4.55 to +7.84) and at Lighthouse was +4.34 (ranging from +3.26 to +5.62). The mean $\delta^{15}N$ of macroalgae on the deep reef at Ironshore in 2002 was +5.72 (ranging from +4.85 to +6.99), a value significantly (*t*-test, $P<0.000\,1$)

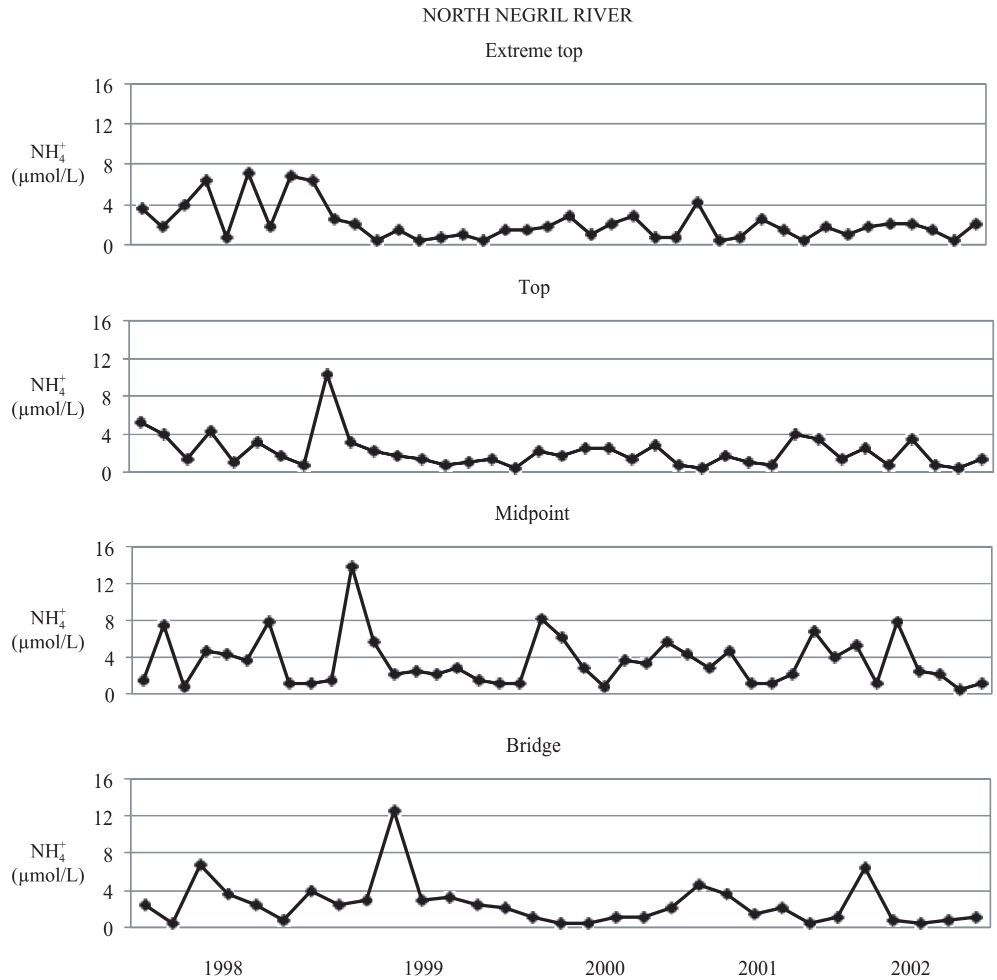

Fig.4 Ammonium (NH_4^+) concentrations at the four North Negril River monitoring stations between 1998 and 2002

higher than the mean of +2.04 (ranging from +1.00 to +3.15) for macroalgae at this reef in 1998 (Fig.8).

4 DISCUSSION

4.1 Phosphorus-limitation in the Negril Marine Park

The results of this study provide the first case study of the temporal dynamics of escalating sewage pollution on a Caribbean coral reef. Although problems caused by sewage pollution of coral reefs have been documented for decades, much of the early research was conducted in Kaneohe Bay, Hawaii. Johannes (1975) noted that the first documented impacts of sewage pollution occurred on lagoon slopes in the middle and northern areas of Kaneohe Bay, where nutrient enrichment from a sewage outfall caused blooms of the “green bubble alga” *Dictyosphaeria cavernosa*. Extensive blooms of this chlorophyte overgrew and killed corals, contributed to hypoxia and anoxia, and led to a reduction of fish populations (Maragos, 1972; Johannes, 1975).

In Negril, macroalgal blooms began to overgrow corals reefs in the early 1990’s, following years of increasing tourism and urbanization on the watershed of these biologically diverse and economically important ecosystems. Surveys in 1998 showed that reefs in NMP were dominated by frondose macroalgae, which accounted for 57%–67% biotic cover (Lapointe and Thacker, 2002). Biologically diverse, coral dominated reefs are adapted to low concentrations of water column nutrients (Muscatine and Porter, 1977), and nutrient enrichment generally results in an alternative state dominated by either macroalgae (>2 cm) or algal turf (<2 cm) communities. The 1998 water column nutrient data showed that DIN already exceeded N thresholds (0.5–1 μmol/L) for benthic algal blooms on coral reefs, whereas

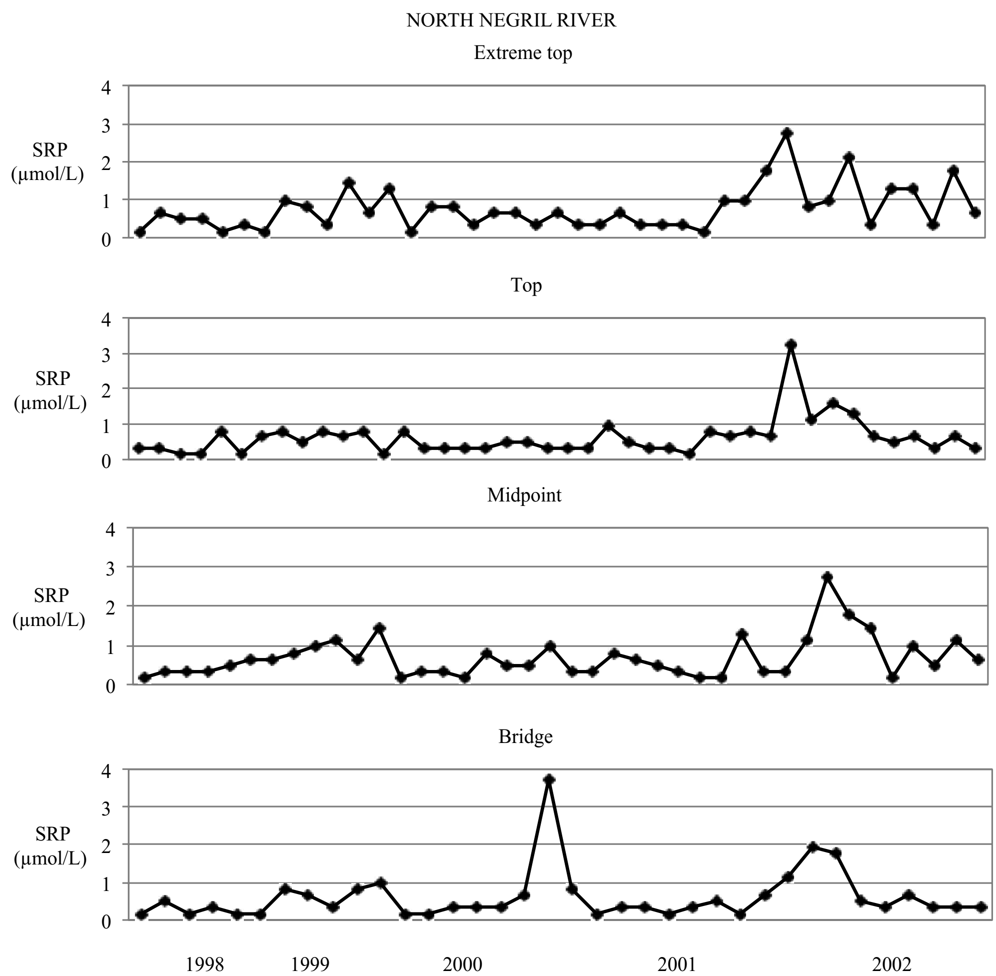

Fig.5 Soluble reactive phosphorus (SRP) concentrations at the four North Negril River monitoring stations between 1998 and 2002

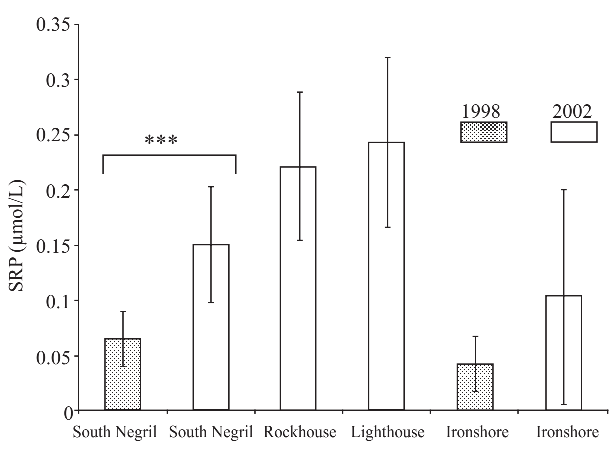

Fig.6 Average (±S.D.) soluble reactive phosphorus (SRP) concentrations on shallow reefs along the West End in 1998 and 2001

Asterisks (***) indicate significant ($P<0.000\ 1$) statistical differences

SRP concentrations (<0.045 μmol/L) were below the 0.1 μmol/L threshold (Lapointe, 1997). The resulting DIN:SRP ratios, ranging from 33 to 59, suggested P-limitation (Lapointe et al., 1992). Similarly high DIN:SRP ratios were observed at Discovery Bay, Jamaica, where values ranging from 33:1 to 103:1 (Lapointe, 1997) resulted from submarine groundwater discharges enriched in NO_3^- relative to SRP (D'Elia et al., 1981). In the NMP, DIN was dominated by NH_4^+, rather than NO_3^-, and water column SRP concentrations increased during the 1998 summer wet season, underscoring concerns about sewage and/or agricultural runoff (Lapointe and Thacker, 2002; NRC, 2000).

The baseline C:N:P ratios of reef macroalgae in 1998 provided the best evidence of P-limitation on coral reefs of the NMP prior to the sewage diversion in 1999. The generally lower C:N ratios on shallow

Table 2 Percent carbon (C), nitrogen (N), phosphorus (P) and molar C:N, C:P and N:P ratios, and δ^{15}N in frondose macroalgae at six shallow and six deep stations in the Negril Marine Park, winter 1998

Location	Depth	Species	%C	%N	%P	C:N	C:P	N:P	δ^{15}N
Davis Cove	Shallow	*Codium intertextum*	16.9	1.21	0.05	16.2	867	53.8	3.08
Davis Cove	Shallow	*Sargassum polyceratium*	29.2	1.07	0.03	31.7	2 496	79.3	3.26
Davis Cove	Shallow	*Cladophora fuliginosa*	20.5	1.06	0.04	22.5	1 314	58.9	3.04
North Negril	Shallow	*Lobophora variegata*	35.9	1.6	0.06	26.1	1 534	59.3	1.9
North Negril	Shallow	*Sargassum polyceratium*	28.1	1.09	0.05	30	1 441	48.4	0.25
North Negril	Shallow	*Chaetomorpha linum*	21.2	1.87	0.06	13.2	906	69.3	2.84
North Negril	Shallow	*Sargassum hystrix*	29.6	1.17	0.04	29.4	1 897	65	2.69
Long Bay	Shallow	*Sargassum polyceratium*	27.9	1.02	0.04	31.8	1 788	56.7	2.3
Long Bay	Shallow	*Cladophora fuliginosa*	23.4	1.11	0.03	24.5	2 000	82.2	0.37
Long Bay	Shallow	*Sargassum hystrix*	28.8	1.14	0.05	29.4	1 477	50.7	2.47
South Negril	Shallow	*Codium isthmocladum*	12.2	1.05	0.03	13.5	1 043	77.8	5.99
South Negril	Shallow	*Cladophora fuliginosa*	19.1	1.38	0.05	16.1	979	61.3	4.58
South Negril	Shallow	*Chaetomorpha linum*	23.8	1.8	0.06	15.4	1 017	66.7	4.21
South Negril	Shallow	*Sargassum polyceratium*	27.8	1.26	0.04	25.7	1 782	70	5.29
South Negril	Shallow	*Sargassum hystrix*	–	–	–	–	–	–	6.49
Ironshore	Shallow	*Sargassum polyceratium*	–	–	–	–	–	–	4.32
Ironshore	Shallow	*Lobophora variegata*	–	–	–	–	–	–	3.64
Little Bay	Shallow	*Sargassum polyceratium*	–	–	–	–	–	–	2.69
Little Bay	Shallow	*Lobophora variegata*	–	–	–	–	–	–	3.63
Little Bay	Shallow	*Codium isthmocladum*	–	–	–	–	–	–	2.99
Little Bay	Shallow	*Sargassum hystrix*	–	–	–	–	–	–	2.62
Little Bay	Shallow	*Dictyota divaricata*	–	–	–	–	–	–	3.01
		Mean±1 SD	24.6±6.2	1.27±0.28	0.05±0.01	23.2±7.0	1467±485	64.2±10.6	3.26±1.52
Davis Cove	Deep	*Cladophora fuliginosa*	21.4	1.15	0.03	21.6	1 829	85.2	2.56
Davis Cove	Deep	*Codium isthmocladum*	14	0.84	0.04	19.4	897	46.7	0.96
Davis Cove	Deep	*Sargassum hystrix*	28.7	0.94	0.05	35.5	1 472	41.8	2.15
North Negril	Deep	*Lobophora variegata*	36.3	1.05	0.04	40.2	2 327	58.3	1.6
North Negril	Deep	*Sargassum hystrix*	29.2	0.81	0.03	41.9	2 496	60	-0.73
Long Bay	Deep	*Sargassum hystrix*	30.3	0.89	0.04	39.6	1 942	49.4	3.06
Long Bay	Deep	*Sargassum polyceratium*	30.1	1.08	0.05	32.4	1 544	48	1.99
South Negril	Deep	*Cladophora fuliginosa*	24.3	1.3	0.03	21.7	2 077	96.3	0.88
South Negril	Deep	*Sargassum hystrix*	28.9	0.98	0.05	34.3	1 482	43.6	2.84
South Negril	Deep	*Codium isthmocladum*	15.9	0.98	0.04	18.9	1 019	54.4	2.84
Ironshore	Deep	*Sargassum polyceratium*	28	1.28	0.05	25.4	1 436	56.9	2.99
Ironshore	Deep	*Sargassum hystrix*	28.2	1.29	0.04	25.4	1 808	71.7	1.08
Little Bay	Deep	*Lobophora variegata*	–	–	–	–	–	–	1.86
Little Bay	Deep	*Sargassum hystrix*	–	–	–	–	–	–	2.52
		Mean±1 SD	26.3±6.4	1.05±0.17	0.04±0.01	29.7±8.6	1694±482	59.4±17.0	1.90±1.07

(21.2–23.2) compared to deep (29.7–29.9) reefs reflected enrichment from land-based N sources, a spatial pattern also evident in lower C:P ratios on shallow (1 364–1 476)compared to deep (1 670–1 694) reefs. The N:P ratios of reef macroalgae were consistently >50 in both wet and dry seasons, demonstrating strong year-round P-limitation (Atkinson and Smith, 1983; Lapointe et al., 1992). Similarly strong P-limitation was also noted for reef macroalgae at Discovery Bay, where N:P ratios of

Table 3 Percent carbon (C), nitrogen (N), phosphorus (P) and molar C:N, C:P and N:P ratios, and δ15N in frondose macroalgae at six shallow and six deep stations in the Negril Marine Park, summer 1998

Location	Depth	Species	%C	%N	%P	C:N	C:P	N:P	$\delta^{15}N$
Davis Cove	Shallow	*Sargassum hystrix*	31.00	0.76	0.02	47.4	3 597	76.4	1.63
Davis Cove	Shallow	*Cladophora fuliginosa*	23.10	1.12	0.04	24.0	1 597	67.1	2.21
North Negril	Shallow	*Lyngbya* sp.	28.80	2.59	0.08	12.9	884	68.9	2.56
North Negril	Shallow	*Chaetomorpha linum*	24.40	2.14	0.07	13.3	911	69.2	1.4
North Negril	Shallow	*Acanthophora spicifera*	24.90	2.06	0.07	14.1	852	61.1	1.77
North Negril	Shallow	*Sargassum polyceratium*	31.00	1.09	0.04	33.1	2 043	62.3	2.55
South Negril	Shallow	*Bryothamnion triquetrum*	20.70	1.36	0.04	17.7	1 317	75.0	2.53
South Negril	Shallow	*Acanthophora spicifera*	23.30	1.54	0.04	17.6	1 450	83.1	4.48
South Negril	Shallow	*Spyridia hypnoides*	24.80	1.84	0.07	15.7	948	60.9	4.82
South Negril	Shallow	*Chaetomorpha gracilis*	23.30	1.52	0.05	17.8	1 171	66.2	5.8
South Negril	Shallow	*Sargassum polyceratium*	29.90	1.50	0.06	23.2	1 384	60.2	5.1
South Negril	Shallow	*Cladophora fuliginosa*	27.30	2.88	0.08	11.0	873	79.8	5.01
South Negril	Shallow	*Chaetomorpha linum*	27.10	2.78	0.09	11.3	758	67.4	4.52
Ironshore	Shallow	*Codium isthmocladum*	17.40	1.18	0.05	17.1	943	55.4	3.43
Ironshore	Shallow	*Sargassum polyceratium*	28.80	1.08	0.04	31.0	1 918	62.3	3.84
Little Bay	Shallow	*Chaetomorpha gracilis*	27.70	2.29	0.10	14.1	710	50.8	9.85
Little Bay	Shallow	*Sargassum polyceratium*	28.40	0.81	0.04	40.8	1 979	48.9	3.26
Little Bay	Shallow	*Codium isthmocladum*	21.20	1.26	0.04	19.6	1 216	62.6	8.00
		Mean±1 SD	25.7±3.8	1.66±0.66	0.06±0.02	21.2±10.4	1364±700	65.4±9.2	4.04±2.2
Davis Cove	Deep	*Cladophora fuliginosa*	23.60	1.08	0.03	25.4	1 984	78.7	0.85
Davis Cove	Deep	*Sargassum hystrix*	31.70	0.71	0.02	51.9	3 613	70.1	2.52
Davis Cove	Deep	*Codium isthmocladum*	15.60	0.80	0.04	22.7	1 005	44.7	1.9
North Negril	Deep	*Sargassum hystrix*	36.50	1.18	0.03	36.0	2 952	82.7	2.64
North Negril	Deep	*Cladophora fuliginosa*	27.90	1.50	0.04	21.6	1 675	78.1	1.29
South Negril	Deep	*Codium isthmocladum*	16.30	1.02	0.05	18.6	761	41.3	0.15
South Negril	Deep	*Sargassum polyceratium*	31.40	0.99	0.05	36.9	1 472	40.2	1.38
South Negril	Deep	*Cladophora fuliginosa*	23.90	1.16	0.04	24.0	1 608	67.7	1.7
South Negril	Deep	*Lobophora variegata*	36.00	1.08	0.04	38.8	2 079	54.1	1.48
Ironshore	Deep	*Codium repens*	15.70	1.18	0.05	15.5	805	52.4	2.4
Ironshore	Deep	*Sargassum hystrix*	28.50	0.89	0.04	37.2	1 791	48.5	1.67
Little Bay	Deep	*Lobophora variegata*	23.70	1.06	0.05	26.0	1 182	45.8	2.56
Little Bay	Deep	*Codium isthmocladum*	15.70	0.76	0.03	24.0	1 195	50.1	1.86
Little Bay	Deep	*Sargassum polyceratium*	29.30	0.84	0.04	40.6	1 982	49.3	1.56
		Mean±1 SD	25.4±7.4	1.02±0.21	0.04±0.01	29.9±10.3	1670±882	54.0±20.4	1.65±0.68

abundant reef macroalgae averaged 45:1 during the summer wet season (Lapointe, 1997). Recently, Greenaway and Gordon-Smith (2006) questioned the persistent P-limitation of reef macroalgae based on seawater DIN:SRP ratios, arguing that Discovery Bay becomes P-limited only following heavy rainfall. Dodds (2003) noted the problems of misusing DIN: SRP ratios to infer trophic status, especially under oligotrophic conditions, which often leads to erroneous conclusions. Consistently high N:P ratios in reef macroalgae clearly indicated sustained P-limitation in the NMP in 1998, despite significant seasonal variability in rainfall (Lapointe and Thacker, 2002). Broad geographic surveys of C:N:P ratios in reef macroalgae from South Florida, Bahamas, and Caribbean region showed persistently high C:P and N:P ratios of reef macroalgae in these carbonate-rich environments (Lapointe et al., 2005a), supporting earlier conclusions of sustained P-limitation on fringing reefs of the north coast of Jamaica (Lapointe

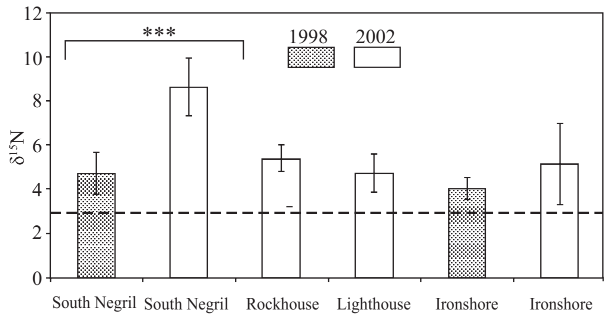

Fig.7 Average δ^{15}N of macroalgae on shallow reefs along the West End in 1998 and 2002

Asterisks (***) indicate significant (P<0.000 1) statistical differences

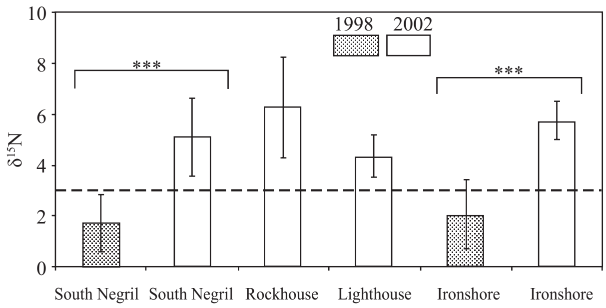

Fig.8 Average δ^{15}N of macroalgae on deep reefs along the West End in 1998 and 2002

Asterisks (***) indicate significant (P<0.000 1) statistical difference

et al., 1992). Although the DIN:SRP ratios closely matched the algal C:N:P ratios during winter in our Negril study, we concur with Dodds (2003) and suggest that algal tissue C:N:P ratios are the best overall indicator to trophic status because they integrate variable concentrations of water column N and P over time.

4.2 Nutrient enrichment of the South Negril River and downstream coral reefs

Five years of monitoring the SNR and NNR rivers documented the significant increases in NH_4^+ and SRP concentrations in the SNR following the sewage discharges since 1999. Such an enrichment phenomenon did not occur in the NNR and the spatial sampling along the SNR clearly indicated the sewage pond outfall as the point source of enrichment. The diversion of sewage from the tourist hotels and residences along the beaches and coastline, combined with inadequate treatment within the ponds, led to NH_4^+ and SRP concentrations up to 937 and 54 μmol/L, respectively, in the SNR at the effluent discharge outfall. These elevated concentrations resulted in low NH_4^+:SRP ratios of 13:1, which are typical of secondarily treated sewage effluent and represented a major source of nutrient enrichment, especially P, to the SNR. That the NH_4^+ and SRP concentrations at the downstream Bridge station averaged 23.9 and 3.42 μmol/L, respectively, with a similarly low NH_4^+:SRP ratio of 13:1, indicates little removal of the sewage-derived NH_4^+ and SRP via nitrification/denitrification or biological uptake in the highly colored waters of the SNR.

Accordingly, tidal discharges from the SNR were an increasing source of nutrient enrichment to coastal waters of Long Bay and reefs at the West End between 1999 and 2002. This was especially evident for SRP, which showed an approximate three-fold increase at South Negril and a two-fold increase at Ironshore between our 1998 and 2001 samplings. All the SRP concentrations averaged >0.1 μmol/L at the West End reef stations in 2001, and the DIN:SRP ratio decreased from 1998 values, indicating escalating P-rich sewage pollution. Considering the high level of P-limitation that occurred in the NMP in the 1998 survey, the increasing P-enrichment explains the three-fold increase in macroalgal biomass that occurred at the South Negril shallow reef following sewage diversion and contamination of the SNR with NH_4^+ and SRP (Lapointe and Thacker, 2002). In 1998, the siphonaceous *Codium isthmocladum* and *Codium repens* were present, but not abundant, at the shallow and deep reefs at South Negril and Ironshore. Surveys by the NCRPS Reef Rangers indicated that following the sewage diversion after 1999, expansive blooms of *C. isthmocladum* occurred on the deep reefs of the West End. This chlorophyte also formed massive blooms on deep coral reefs in southeast Florida over the past two decades in areas impacted by sewage outfalls (Lapointe, 1997); tissue C:N:P analysis suggested that P-enrichment from sewage and other sources was a primary factor supporting these harmful algal blooms (Lapointe et al., 2005a, b). Another chlorophyte, the rhizomatous *Caulerpa cupressoides*, rarely seen along the deep reefs of South Negril and Ironshore in 1998 also developed blooms along these deep reef sites by the 2001 sampling. On shallow reefs in Long Bay, "green tides" comprised of *Chaetomorpha linum* expanded in areas most directly influenced by the increasing sewage pollution and discharges of the SNR. All these chlorophytes -*Codium* spp., *Caulerpa* spp., and *Chaetomorpha* spp. — are well known "nutrient indicator species" as they typically form blooms around sources of P enrichment in tropical waters, such as guano-rich seabird rookeries (Lapointe et al., 2005a; Urnezis, 1995).

4.3 Sewage pollution causes $\delta^{15}N$ enrichment of reef macroalgae

The spatial and temporal patterns of ^{15}N enrichment of macroalgae from the twelve reef sites during 1998 revealed the influence of the SNR as a source of sewage pollution to the NMP. The highest $\delta^{15}N$ values (+4.5–9.9) of macroalgae in the winter and summer sampling were on the shallow reefs at South Negril and Little Bay, supporting previous observations on the importance of human sewage in supplying nutrients to reefs along this coastline (Lapointe, 1992). During both seasons, the lowest $\delta^{15}N$ values (<+2.0) were on the deep reefs, especially at the North Negril deep reef that was the deepest of all twelve stations. These low $\delta^{15}N$ values are in the range reported for natural nitrogen fixation (~ 0; France et al., 1998), but could also reflect fertilizer N that ranges from -2 to +2 (Risk et al., 2009). Similar high values were reported for corals in Kingston Harbor (Mendes et al., 1997), where $\delta^{15}N$ values of *Montastrea faveolata* along a sewage pollution gradient were enriched >+5 at Harbour Shoal and Drunkenmans Cay, which are influenced by Kingston's wastewater discharges; lower values of <+2 occurred in coral tissue from an unpolluted reference site at Middle Cay on Pedro Bank. The elevated $\delta^{15}N$ values of macroalgae on shallow reefs around the urban areas in Negril are consistent with sewage N pollution and are similar to values of seagrasses and macroalgae reported by Costanzo et al. (2001) from Moreton Bay, Australia, where $\delta^{15}N$ values ranged from +9 in close proximity to sewage outfalls to levels of +3 in more distant areas experiencing lower levels of sewage N. Similar values and patterns of $\delta^{15}N$ enrichment in macroalgae have been reported for a wide variety of coral reefs worldwide, generally showing patterns of highest values and enrichment in close proximity to sewage inputs and decreasing values with increasing distance away from the sewage source (Risk et al., 2009).

The significant $\delta^{15}N$ enrichment of macroalgae on shallow and deep reefs at South Negril and Ironshore between 1998 and 2002 supports the hypothesis of increasing sewage pollution at the West End following the sewage diversion to the SNR. The shallow reef at South Negril was the station most directly impacted by sewage pollution from the SNR, and macroalgae $\delta^{15}N$ values increased to >+8, levels similar to those of macroalgae experiencing direct exposure to sewage pollution (Lapointe et al., 2005b; Risk et al., 2009). The significant increases in $\delta^{15}N$ of macroalgae to values >+4 on deep reefs between South Negril and Ironshore suggest that reefs along this entire coastline were impacted by increasing sewage pollution between 1998 and 2002.

5 CONCLUSION

Globally, escalating nutrient pollution and eutrophication have led to an increase in the frequency and intensity of harmful algal blooms (HABs; Glibert et al., 2005). One mechanism causing HAB outbreaks is increasing nutrient concentrations and alteration of N:P ratios from increasing sewage pollution (Windom, 1992). For example, during the 1980's in Tolo Harbor, Hong Kong, increased human activities and sewage inputs decreased the N:P ratio by 50%, which correlated with a ten-fold increase in red tide (dinoflagellate) outbreaks (Lam and Ho, 1989). Similarly, in our study, increased SRP concentrations and decreased N:P ratios resulting from increasing sewage pollution in Negril triggered macroalgal blooms in P-limited coral reef communities, resulting in taxonomic shifts towards the chlorophyte genera *Codium*, *Caulerpa*, and *Chaetomorpha*. Although previous reviews of macroalgal blooms on Jamaican coral reefs have suggested that these phenomena resulted only from overfishing and reduced herbivory (Hughes, 1994; Jackson et al., 2001), such interpretations have ignored a considerable body of evidence supporting the importance of bottom-up controls. Previous studies in Negril concluded nutrient pollution was not a factor in the development of macroalgal blooms (Hughes, 1994), but those studies included no measurements of nutrients or other environmental variables that could provide a proxy of nutrient pollution. Nutrient pollution derived from sewage is a well-recognized threat to oligotrophic coral reef ecosystems (Windom, 1992; MEA, 2005; UNEP, 2006). Accordingly, sewage treatment systems adjacent to coral reefs must include nutrient removal to ensure that DIN and SRP concentrations, after dilution, are below the low thresholds noted for these oligotrophic ecosystems (Bell, 1992). We stress that it will be necessary to continue monitoring the rivers and coastal waters of the NMP to understand the long-term consequences of sewage pollution and altered biogeochemistry originating from the watershed (Vitousek et al., 1997; Likens, 2001). We hope that this study illustrates how informed, community-based, long-term research enhances the success of understanding large and complex environmental problems.

6 ACKNOWLEDGEMENT

The authors gratefully acknowledge the generous support of Hedonism II, Sandals, and Beaches by providing accommodation during this research. Dr. Peter Bell and staff of the Harbor Branch Environmental Laboratory provided assistance with water sampling and nutrient analysis. We are especially grateful to Laura Herren and Elsa Hemmings for data management and statistical analysis. This research was supported by grants from the European Union and the Friends of Jamaica to the Negril Coral Reef Preservation Society. This is contribution No. 1830 from the Harbor Branch Oceanographic Institute at Florida Atlantic University, Ft. Pierce, FL, USA. We dedicate this paper to the memory of Katy Thacker (1952–2004). Katy, founder of the Negril Coral Reef Preservation Society, lost her battle with cancer on Earth Day, April 22, 2004. She devoted the best years of her life to protect Negril's coral reefs, and also educated locals and tourists about the need to preserve these biologically diverse ecosystems. This study would not have been possible without her creative and persistent efforts to establish the first "Ridge to Reef" water quality monitoring program for the Negril Marine Park and its watersheds.

References

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.

Atkinson M, Smith S V. 1983. C:N:P ratios of benthic marine plants. *Limnol. Oceanogr*., **28**(3): 568-774.

Barnes E. 1973. Sewage pollution from tourist hotels in Jamaica. *Mar. Poll. Bull*., **4**(7): 102.

Bell P R F. 1992. Eutrophication and coral reefs: Some examples in the Great Barrier Reef lagoon. *Water Research*, **26**: 553-568.

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.

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.

D'Elia C F, Webb K L, Porter J W. 1981. Nitrate-rich groundwater inputs to Discovery Bay, Jamaica: A significant source of N to local reefs? *Bull. Mar. Sci*., **31**: 903-912

Dodds W K. 2003. Misuse of dissolved inorganic N and soluble reactive P concentrations to indicate nutrient status of surface waters. *J. N. Am. Benthological Soc*., **22**(2): 171-181.

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

Glibert P, Seitzinger S, Heil C, Burkholder J M, Parrow M W, Codispoti L A, Kelly V. 2005. The role of eutrophication in the global proliferation of harmful algal blooms. *Oceanography*, **18**(2): 198-209.

Goreau T F. 1959. The ecology of Jamaican coral reefs. 1. Species composition and zonation. *Ecology*, **40**: 67-90.

Goreau T J. 1992. Negril: environmental threats and recommended actions. *In*: Thacker K ed. Protecting Jamaica's Coral Reef Ecosystems: Water Quality Issues. Final Report. p.9.

Greenaway A M, Gordon-Smith D A. 2006. The effects of rainfall on the distribution of inorganic nitrogen and phosphorus in Discovery Bay, Jamaica. *Limnol. Oceanogr*., **51**(5): 2 206-2 220.

Gunsalus N M. 1997. High frequency monitoring of wastewater nutrient discharges and their ecological effects in the Florida Keys National Marine Sanctuary: Appendix I, Quality Assurance Summary, Nutrient Analysis. Final Report to the Water Quality Protection Program, United States Environmental Protection Agency, Marathon, Florida. 28p.

Hughes T P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science*, **265**: 1 547-1 551.

Jackson J B C, Kirby M X, Berger W H, Bjorndal K A, Botsford L W, Bourque B J, Bradbury R H, Cooke R, Erlandson J, Estes J A, Hughes T P, Kidwwell S, Lange C B, Lenihan H S, Pandolfi J M, Peterson C H, Steneck R S, Tegner M J, Warner R R. 2001. Historical over-fishing and the recent collapse of coastal ecosystems. *Science*, **293**: 629-638.

Jelier C A, Roberts S. 1992. Negril sewerage and sewerage treatment. *In*: Thacker K ed. Protecting Jamaica's Coral Reef Ecosystems: Water Quality Issues. Final Report. p.131.

Johannes R E. 1975. Pollution and degradation of coral reef communities. *In*: Wood E J F, Johannes R E eds. Tropical Marine Pollution. Elsevier Scientific Publishing Company, Oxford, UK. p.13-51.

Lam C W Y, Ho K C. 1989. Red tides in Tolo Harbor, Hong Kong. *In*: Okaichi T, Anderson D M, and Nemoto T eds. Red Tides: Biology, Environmental Science, and Toxicology. Elsevier Scientific Publishing Company, New York, USA. p.49-52.

Lapointe B E, Barile P J, Littler M M, Littler D S, Bedford B J, 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**: 1 092-1 105.

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**: 1 106-1 122.

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, Porter K eds. The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC Press, Boca Raton, FL, USA. p.939-963.

Lapointe B E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnol. Oceanogr*., **42**: 1 119-1 131.

Lapointe B E. 1992. Nutrient thresholds for macroalgal overgrowth and eutrophication of coral reef ecosystems. *In*: Thacker K ed. Protecting Jamaica's Coral Reef Ecosystems: Water Quality Issues. Final Report. p.131.

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

Likens G. 2001. Biogeochemistry, the watershed approach: some uses and limitations. *Mar. Fresh. Res*., **52**: 5.

Maragos J E. 1972. A Study of the Ecology of Hawaiian Reef Corals. Thesis. University of Hawaii, Honolulu, Hawaii.

MEA (Millennium Ecosystem Assessment). 2005. Ecosystems and Human Well-Being: Biodiversity Synthesis. World Resources Institute, Washington, D.C., USA.

Mendes J M, Risk M J, Schwarsz H P, Woodley J D. 1997. Stable isotopes of nitrogen as measures of marine pollution: a preliminary assay of coral tissue from Jamaica. *Proc. Int. Coral Reef Symp*., **2**: 1 869-1 872.

McConnaughey T A, Adey W H, Small A M. 2000. Community and environmental influences on reef coral calcification. *Limnol. Oceanogr*., **45**(7): 1 667-1 671.

Muscatine L, Porter J. 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *BioScience*, **27**: 454-460.

NRC (National Research Council). 2000. Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution. Ocean Studies Board, Water Science and Technology Board, National Academy Press, Washington, D.C., USA.

Risk M, Lapointe B E, Sherwood O A, Bedford B J. 2009. The use of $\delta^{15}N$ in assessing sewage stress on coral reefs. *Mar. Poll. Bull*., **58**: 793-802.

Smith S V, Kimmerer W J, Laws E A, Brocknand R E, Walsh T W. 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pac. Sci*., **35**(4): 279-402.

UNEP (United Nations Environmental Programme). 2006. Marine and coastal ecosystems and human well-being: A synthesis report based on the findings of the Millennium Ecosystem Assessment.

Urnezis C M. 1995. Alkaline phosphatase activity and phosphorus limitation in marine macroalgae from the Florida Keys and the Bahamas. Master's thesis. Nova Southeastern University, Ft. Lauderdale, FL, USA. 113p.

Vitousek P M, Aber J D, Howarth R W, Likens G E, Matson P A, Schindler D W, Schlesinger W H, Tilman D. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. Appl*., **7**: 737-750.

Wade B. 1992. Nutrient levels in Negril wetland and coastal waters. *In*: Thacker K ed. Protecting Jamaica's Coral Reef Ecosystems: Water Quality Issues. Final Report. p.91-104.

Windom H. 1992. Contamination of the marine environment from land-based sources. *Mar. Poll. Bull*., **35**: 32-36.