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Nutrient Inputs from the Watershed and Coastal Eutrophication in the Florida Keys

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Abstract: Widespread use of septic tanks in the Florida Keys increase the nutrient concentrations of limestone groundwaters that discharge into shallow nearshore waters, resulting in coastal eutrophication. This study characterizes watershed nutrient inputs, transformations, and effects along a land-sea gradient stratified into four ecosystems that occur with increasing distance from land: manmade canal systems (receiving waters of nutrient inputs), seagrass meadows, patch reefs, and offshore bank reefs. Soluble reactive phosphorus (SRP), the primary limiting nutrient, was significantly elevated in canal systems compared to the other ecosystems, while dissolved inorganic nitrogen (DIN; NH_4^+ and NO_3^-), a secondary limiting nutrient, was elevated both in canal systems and seagrass meadows. SRP and NH_4^+ concentrations decreased to low concentrations within approximately 1 km and 3 km from land, respectively. DIN and SRP accounted for their greatest contribution (up to 30%) of total N and P pools in canals, compared to dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) that dominated (up to 68%) the total N and P pools at the offshore bank reefs. Particulate N and P fractions were also elevated (up to 48%) in canals and nearshore seagrass meadows, indicating rapid biological uptake of DIN and SRP into organic particles. Chlorophyll *a* and turbidity were also elevated in canal systems and seagrass meadows; chlorophyll *a* was maximal during summer when maximum watershed nutrient input occurs, whereas turbidity was maximal during winter due to seasonally maximum wind conditions and sediment resuspension. DO was negatively correlated with NH_4^+ and SRP; hypoxia (DO < 2.5 mg l^{-1}) frequently occurred in nutrient-enriched canal systems and seagrass meadows, especially during the warm summer months. These findings correlate with recent (<5 years) observations of increasing algal blooms, seagrass epiphytization and die-off, and loss of coral cover on patch and bank reef ecosystems, suggesting that nearshore waters of the Florida Keys have entered a stage of critical eutrophication.

Introduction

Human activities on land inevitably increase nutrient inputs to coastal waters from deforestation, wastewater, fertilizers, and other sources (Peierls et al. 1991; Turner and Rabalais 1991). In the Florida Keys, human activities have almost doubled over the past 20 years, with concomitant increases in energy consumption and nutrient inputs to coastal waters. Approximately 65% of the wastewater in the Keys is disposed of by some 30,000 on-site sewage disposal systems (septic tanks and/or cesspits), a practice that increases nutrient concentrations of limestone groundwaters (Lapointe et al. 1990). Tides and rainfall enhance submarine discharge of enriched groundwaters, enhancing coastal eutrophication (Lapointe et al. 1990; Tomasko and Lapointe 1991). Over the past decade, groundwaters have been recognized as an important pathway for the introduction of nutrients to coastal waters (Johannes 1980), especially those groundwaters subject to human activities and associated nutrient inputs (Capone and Bautista 1985; Simmons et al. 1985; Valiela et al. 1990).

Long-term net flow of nearshore waters from the Gulf of Mexico and Florida Bay toward the Atlantic Ocean and Straits of Florida can transport watershed-derived nutrients from the nearshore waters of the Keys seaward over seagrass meadows

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toward more offshore patch reef and bank reef ecosystems (Lapointe et al. 1992). These tropical seagrass and coral reef ecosystems are adapted to oligotrophic conditions characterized by intense nutrient recycling; excessive nutrient inputs to these systems result in both first-order and second-order ecological changes (Birkeland 1987, 1988), often with undesirable results (Johannes 1975). For example, elevated water-column nutrient concentrations increase phytoplankton standing crops (Laws and Redalje 1979), thereby decreasing available light and increasing sedimentation, major factors causing the decline of hermatypic reef corals (Tomascik and Sander 1985, 1987; Rogers 1990). Nutrient-enhanced productivity of macroalgae (Lapointe and O'Connell 1989) can cause overgrowth and inhibition of reef coral growth and recruitment (Johannes 1975; Birkeland 1977; Smith et al. 1981), leading to loss of coral cover in eutrophic tropical hard-bottom communities. Increased nutrient inputs similarly increase epiphyte loads on seagrasses (Cambridge and McComb 1984; Borum 1985; Silberstein et al. 1986), the major mechanism of seagrass die-off worldwide (Orth and Moore 1984; Silberstein et al. 1986).

While tropical seagrass and coral reef ecosystems can tolerate some level of nutrient enrichment without serious ecological effects, chronic enrichment reduces dissolved oxygen (DO) levels and habitat viability. Reduced DO concentrations and either hypoxia or anoxia occur in eutrophic seagrass meadows, especially during warm or low-light periods, due to decreases in the photosynthesis : respiration ratio (Odum and Wilson 1962; Valiela et al. 1990). Increased nutrient loading from sewage inputs also depress DO levels and induce chemical stress and bacterial contamination on coral reefs (Johannes 1975; Pastorok and Bilyard 1985). Eutrophic marine ecosystems also have increased oxygen demand resulting from the bacterial mineralization of accumulated organic matter (Mee 1988). As DO is of paramount importance to maintaining aerobic metabolism in marine organisms, reduced DO values become critical in determining the quality of tropical habitats and their ability to sustain biologically diverse habitats. Most pollution studies measure DO during daylight hours; however, the minimal daily DO levels occur at night so that daytime measurements lead to misinterpretation of ecosystem status (Johannes 1975). Therefore, we predicted that a significant negative correlation would exist between nutrient enrichment and the minimum daily DO levels in coastal waters of the Florida Keys.

We present here a partial test of the hypothesis that human activities in the Florida Keys result in nutrient enrichment and eutrophication of nearshore waters. To address this hypothesis, our study had the following objectives: to characterize nutrient concentrations and transformations along a nutrient gradient from the watershed-coastal zone interface to more offshore coral reef ecosystems, and to determine relationships between nutrient concentrations, water transparency (turbidity, chlorophyll *a*), and DO along this land-sea gradient. Our nutrient gradient included broad areas of Florida Bay and the Florida Keys and was stratified into four distinct ecosystems—man-made canals, seagrass meadows, patch reefs, and offshore bank reefs—which occur at increasing distances from shore and therefore decreasing nutrient availability from terrestrial inputs.

Materials and Methods

ENVIRONMENTAL SETTING

The Florida Keys, a 160-km archipelago of low-lying carbonate islands stretching from Key Largo to Key West, Florida, are flanked by the Gulf of Mexico and Florida Bay to the north and west and the Straits of Florida and Atlantic Ocean to the south and east; channels between the Keys allow for the net transport of water from the Gulf of Mexico seaward toward the Straits of Florida (Fig. 1; Lapointe et al. 1992).

The climate of the Keys is typical of the "wet and dry" tropics, with over 80% of the annual rainfall falling between June and October (100 cm yr^{-1}; MacVicar 1983). Tides in the Keys are semidiurnal on the Atlantic coast and mixed on the Gulf of Mexico coast. Mean sea level varies by 24 cm through the year, with maximum tides occurring between May and October (Marmer 1954).

Human activities have dramatically increased the shoreline development of the Keys upland watershed. During the 1950s and 1960s, extensive canalization by dredge and fill operations were carried out to provide greater water access to residential and commercial properties, and hundreds of km of canals were dredged in the Keys. These canals, as well as contiguous nearshore waters, now represent mixing zones where nutrients derived from human activities (e.g., septic tank leachate; Lapointe et al. 1990) enter nearshore waters. Couplings between nutrient-enriched groundwaters and nearshore waters are maximum during the wet season when submarine groundwater discharge (SGD) is seasonally maximum (Lapointe et al. 1990).

SAMPLING STATIONS

Our study was conducted at 30 stations throughout inner-shelf waters (< 10 m depth) of the Florida Keys and included waters of Looe Key National Marine Sanctuary (L.K.N.M.S.), Key Largo National Marine Sanctuary (K.L.N.M.S.), and Ever-

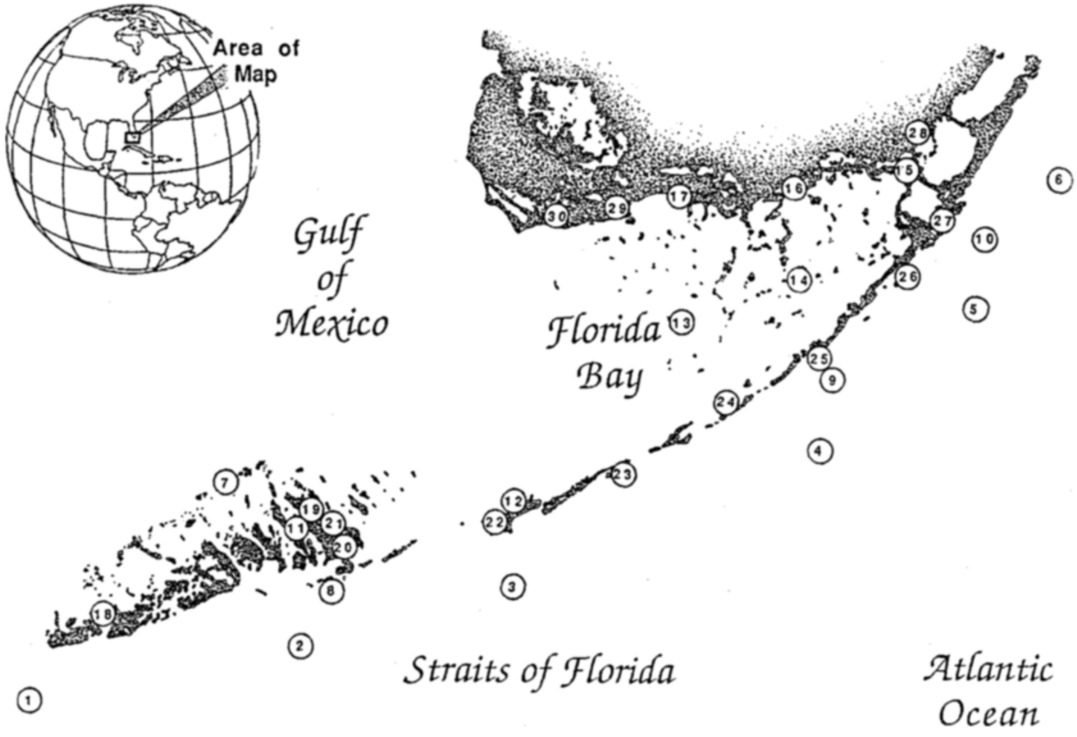

Fig. 1. Map of the Florida Keys showing the location of 30 stations used in this study.

glades National Park (E.N.P.) (Fig. 1; Table 1). The stations were stratified a priori by ecosystem, and included the following: 1. bank reefs (six stations: Sand Key, Looe Key, Sombrero Reef, Alligator Reef, Molasses Reef, and Carysfort Reef), 2. patch reefs (four stations: Munson Island, Sawyer Key, Hens and Chickens, Shark Reef), 3. seagrass meadows (seven stations: Pine Channel, Rachael Key, Rabbit Key, Manatee Keys, Blackwater Sound, Madeira Bay, Garfield Bight), and 4. man-made canal systems (thirteen stations: Boca Chica "sub pens," Port Pine Heights, Doctor's Arm, Mariner's Resort, Boot Key, Duck Key, Port Antigua, Venetian Shores, Ocean Shores, Largo Sound, Glades Canal, Buttonwood Canal, and East Cape Canal). The distance from the most adjacent shoreline was determined (as km) for each station; computed distances from land for bank reefs was > patch reefs > seagrass meadows > canal systems.

SAMPLE COLLECTION AND ANALYSIS

We sampled each of the 30 stations (Table 1) twice, once during peak summer and once during peak winter conditions to characterize the seasonal extremes in measured variables; the samplings occurred between August 9, 1989 and September 19, 1990. Each seasonal sampling was performed within a 1.5-month period to minimize confounding effects of temporal variability in the measured variables.

Temperature, salinity, and DO were measured using a Hydrolab Surveyor II at dawn to determine the minimum daily DO values. Surface and bottom samples were collected to determine an average water-column value as salinity stratification was observed at some of the nearshore canal and seagrass stations. Measurements were made at three surface (0.5 m depth) and three bottom (0.2 m above bottom) locations along a 0.5-km transect perpendicular to the adjacent shoreline, resulting in a total of six independent measurements per station. The depth of the water column varied from 1 m to 10 m among the 30 stations.

Three surface and three bottom water samples were also collected at each station at midday using a 5-l Niskin bottle. The water samples were collected into acid-washed Nalgene bottles, spiked with a biocide ($HgCl_2$, 10 mg l^{-1}) and held on ice until return to the laboratory. Three separate aliquots of the water samples were filtered onto 0.45 μm Gelman GFF filters. One filter was analyzed for chlorophyll *a*, one for particulate phosphorus (PP), and one for particulate nitrogen (PN). Chlorophyll *a* was determined using a Turner Designs Model 10 fluorometer calibrated with known concentrations of reagent-grade chlorophyll. The chlorophyll *a* was extracted from the filters using a modified dimethyl sulfoxide (DMSO)-acetone method (Burnison 1979). PN was determined using a Carlo Erba Elemental Analyzer and PP was determined

TABLE 1. Names, location, temperature, and salinity of the 30 stations in neashore waters of the Florida Keys used for this study.

Station Number	Name	Location		Ecosystem	Temperature °C		Salinity	
		Latitude	Longitude		Summer	Winter	Summer	Winter
1	Sand Key	25° 13. 28	80° 12. 70	Bank Reef	29.8 ± 0.4	24.7 ± 0.5	36.8 ± 0.1	36.2 ± 0.1
2	Looe Key (L.K.N.M.S.)[a]	24° 32. 80	81° 24. 32	Bank Reef	30.3 ± 0.6	24.9 ± 0.3	36.6 ± 0.1	36.3 ± 0.0
3	Sombrero Reef	24° 46. 16	81° 32. 43	Bank Reef	30.0 ± 0.3	25.1 ± 0.4	36.5 ± 0.0	36.4 ± 0.0
4	Alligator Reef	25° 37. 85	81° 06. 57	Bank Reef	30.7 ± 0.7	24.5 ± 0.5	36.8 ± 0.0	36.5 ± 0.1
5	Molasses Reef (K.L.N.M.S.)[b]	25° 00. 70	80° 26. 72	Bank Reef	29.9 ± 0.3	24.8 ± 0.2	35.6 ± 0.1	36.4 ± 0.0
6	Carysfort Reef (K.L.N.M.S.)	24° 50. 95	80° 37. 22	Bank Reef	30.2 ± 0.4	24.5 ± 0.4	35.4 ± 0.1	36.5 ± 0.0
7	Sawyer Keys	24° 36. 72	81° 22. 43	Patch Reef	30.3 ± 0.4	24.0 ± 0.5	38.7 ± 0.1	37.4 ± 0.1
8	Newfound Harbor Keys	25° 08. 74	80° 17. 68	Patch Reef	30.8 ± 0.6	24.2 ± 0.6	36.5 ± 0.1	37.1 ± 0.1
9	Hens and Chickens	24° 56. 10	80° 56. 20	Patch Reef	30.2 ± 0.3	25.2 ± 0.5	36.6 ± 0.1	36.2 ± 0.1
10	Shark Reef (K.L.N.M.S.)	24° 36. 72	81° 22. 43	Patch Reef	30.6 ± 0.4	24.8 ± 0.7	35.6 ± 0.0	36.4 ± 0.0
11	Pine Channel	25° 13. 90	80° 26. 91	Seagrass	31.7 ± 1.9	22.7 ± 1.6	37.5 ± 0.3	38.0 ± 0.0
12	Rachael Key	25° 04. 25	80° 37. 20	Seagrass	29.5 ± 0.4	25.1 + 0.7	38.7 ± 0.0	38.1 ± 0.1
13	Rabbit Key (E.N.P.)[c]	25° 09. 92	80° 40. 30	Seagrass	29.3 ± 0.6	25.4 ± 1.0	48.5 ± 0.1	46.2 ± 0.3
14	Manatee Keys (E.N.P.)	25° 10. 54	80° 48. 92	Seagrass	30.3 ± 0.9	23.6 ± 1.4	50.8 ± 0.4	48.1 ± 0.3
15	Little Blackwater Sound (E.N.P.)	24° 43. 36	81° 04. 17	Seagrass	31.0 ± 1.3	26.9 ± 1.2	29.9 ± 14	42.4 ± 1.0
16	Madeira Bay (E.N.P.)	24° 58. 70	80° 49. 50	Seagrass	30.4 ± 1.4	23.8 ± 1.2	54.2 ± 0.5	59.8 ± 1.1
17	Garfield Bight (E.N.P.)	24° 41. 51	81° 24. 24	Seagrass	29.7 ± 1.3	27.3 ± 2.3	43.6 ± 10	63.9 ± 4.2
18	Boca Chica Submarine Pens	25° 08. 23	81° 04. 00	Canal	30.0 ± 1.1	23.2 ± 1.0	42.5 ± 1.0	40.0 ± 0.4
19	Port Pine Heights	24° 52. 30	80° 35. 17	Canal	31.5 ± 1.0	23.4 ± 1.1	39.0 ± 0.3	37.8 ± 0.4
20	Mariner's Resort	25° 16. 09	80° 26. 18	Canal	27.2 ± 0.9	22.3 ± 0.9	41.0 ± 1.0	38.8 ± 0.2
21	Doctor's Arm	25° 40. 67	81° 20. 79	Canal	30.2 ± 1.0	23.8 ± 0.9	37.0 ± 0.5	38.1 ± 0.1
22	Boot Key Harbor	25° 08. 50	80° 23. 50	Canal	29.4 ± 1.0	25.5 ± 0.8	37.8 ± 0.6	37.9 ± 0.2
23	Duck Key	25° 05. 96	80° 26. 95	Canal	29.5 ± 0.7	25.5 ± 0.6	36.9 ± 0.3	38.0 ± 0.1
24	Port Antigua	25° 16. 09	80° 26. 18	Canal	30.4 ± 0.8	22.0 ± 1.7	39.7 ± 0.6	40.3 ± 0.3
25	Venetian Shores	24° 47. 00	80° 35. 50	Canal	30.5 ± 0.7	25.0 ± 0.6	40.9 ± 1.3	37.8 ± 0.2
26	Ocean Shores	24° 41. 56	81° 20. 63	Canal	29.9 ± 1.2	24.0 ± 0.6	37.5 ± 0.4	32.6 ± 11
27	Largo Sound	24° 35. 32	81° 42. 02	Canal	31.8 ± 0.3	26.1 ± 0.7	46.8 ± 0.4	39.2 ± 0.7
28	Glades Canal (C-111)	24° 51. 49	80° 33. 58	Canal	31.1 ± 0.8	24.0 ± 1.2	33.0 ± 6.7	42.2 ± 0.3
29	Buttonwood Canal (E.N.P.)	24° 41. 82	81° 05. 36	Canal	29.8 ± 1.0	25.4 ± 0.7	35.4 ± 2.5	38.0 ± 3.6
30	East Cape Canal (E.N.P.)	24° 35. 32	81° 42. 02	Canal	29.0 ± 1.3	25.8 ± 0.6	35.9 ± 1.0	37.8 ± 0.4

[a] Looe Key National Marine Sanctuary (L.K.N.M.S.).
[b] Key Largo National Marine Sanctuary (K.L.N.M.S.).
[c] Everglades National Park (E.N.P.).

using persulfate digestion followed by analysis of soluble reactive phosphorus (SRP; Murphy and Riley 1962).

Aliquots of spiked, filtered water samples (six per station for each nutrient species) were frozen until analysis for dissolved nutrients. Total dissolved N (TDN), dissolved inorganic nitrogen (DIN=NH_4^+ + NO_3^- + NO_2^-), and total dissolved P (TDP) were determined on a Technicon Autoanalyzer II according to standard Technicon Industrial methodology (Technicon 1973). Analysis of TDN (D'Elia et al. 1977) and TDP (Menzel and Corwin 1965) utilized persulfate digestion techniques. Concentrations of NO_2^- are typically low or undetectable in surface waters of the Keys (Lapointe et al. 1990); accordingly, concentrations of NO_3^- plus NO_2^- are referred to as NO_3^-. Dissolved organic nitrogen (DON) was estimated as TDN minus DIN. SRP is generally low or undetectable in surface waters of the Keys (e.g., 20–50 nM); therefore, we determined SRP concentrations by the Murphy and Riley (1962) method using a Bausch and Lomb spectrophotometer fitted with a 10-cm cell for maximum sensitivity. Dissolved organic phosphorus (DOP) was estimated as TDP minus SRP. We used one unfiltered aliquot from each sample to determine turbidity on a Hach Model 2100A Turbidimeter using Formazin standards (United States Environmental Protection Agency 1983).

Results

DISSOLVED AND PARTICULATE NUTRIENTS

Two-way ANOVA indicated that NH_4^+ concentrations were significantly elevated (>1 μM) in the water column of canal systems and seagrass meadows compared to patch and bank reef stations (<0.3 μM; Fig 2; Table 2). NO_3^- concentrations were also elevated in canal systems and seagrass meadows (>0.8 μM) compared to lower concentrations (<0.4 μM) at patch and bank reef stations (Fig. 3). Thus, NH_4^+ and NO_3^- concentrations decreased with increasing distance from land and were generally <1.0 μM further than 3 km from land (Figs. 4 and 5). PN was also elevated in canal systems and sea-

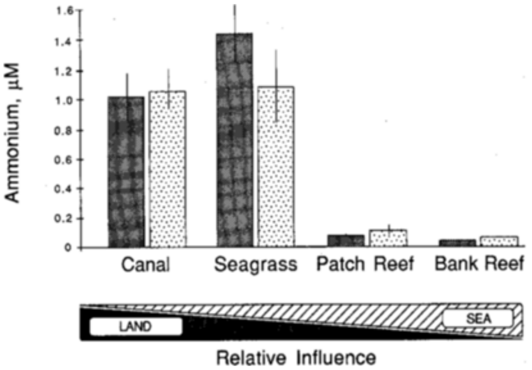

Fig. 2. Concentrations of water column ammonium in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

grass meadows relative to more offshore patch and bank reef stations (Fig. 6).

The percentage of total N available as DIN, relative to DON and PN, was highest in canal and seagrass systems and lowest on patch and bank reefs (Table 3). An average of 18% of the total N occurred as DIN in canal and seagrass systems, compared to 31% as PN and 50% as DON (Table 3). This contrasts with patch and bank reef stations, where an average of 8% of the total N was present as DIN, 25% as PN, and 68% as DON (Table 3).

SRP and PP concentrations were significantly higher in nearshore canal systems compared to the seagrass, patch reef, and bank reef stations (Table 2). SRP concentrations were significantly elevated in canals (>0.3 µM; Fig. 7), with the highest SRP concentrations occurring at the Buttonwood Canal at Flamingo, which averaged 1.43 µM during the summer sampling. SRP and DOP concentrations both decreased with increasing distance from land and were generally <0.3 µM and <0.7 µM beyond 1 km from land, respectively (Figs. 8 and 9). Particulate P concentrations were also elevated in canal systems relative to the other ecosystems (Fig. 10); the highest concentrations occurred at the Buttonwood Canal at Flamingo.

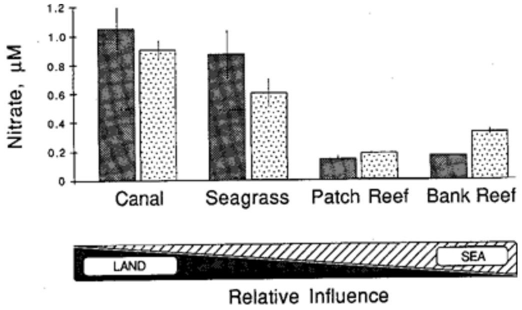

Fig. 3. Concentrations of water column nitrate in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

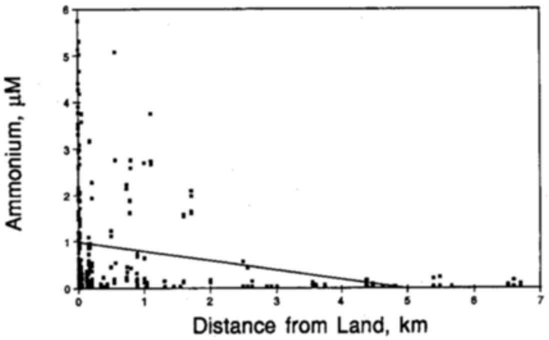

Fig. 4. Concentrations of water column ammonium in nearshore waters of the Florida Keys versus distance from land.

The percentage of total P available as SRP, relative to DOP and PP, was highest in the canal systems and lowest on the bank reefs. An average of 30% of the total P was present as highly available SRP in canal systems, compared to 22% for DOP and 48% for PP (Table 3). This contrasts with the bank reefs where an average of 14% of total P occurred as SRP, 30% as PP, and 63% as DOP (Table 3).

The DIN:SRP ratios were significantly elevated in nearshore canal and seagrass systems (>15:1) compared to lower values (<7:1) at the patch and bank reef ecosystems (Table 2; Fig. 11).

CHLOROPHYLL *A* AND TURBIDITY

Two-way ANOVA indicated that chlorophyll *a* was significantly elevated in nearshore canal and seagrass ecosystems with higher values in summer compared to winter (Table 2). The lowest values occurred at the bank reef stations (<0.3 µg l^{-1}) and the highest values in canals (e.g., >1.0 µg l^{-1}) and

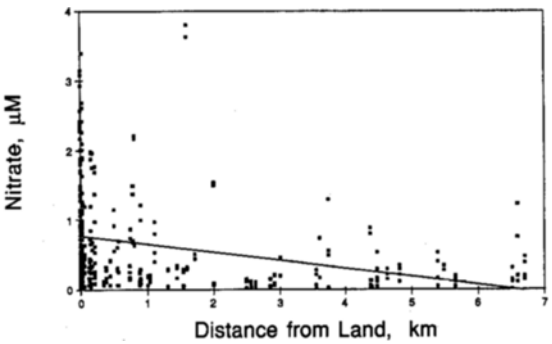

Fig. 5. Concentrations of water column nitrate in nearshore waters of the Florida Keys versus distance from land.

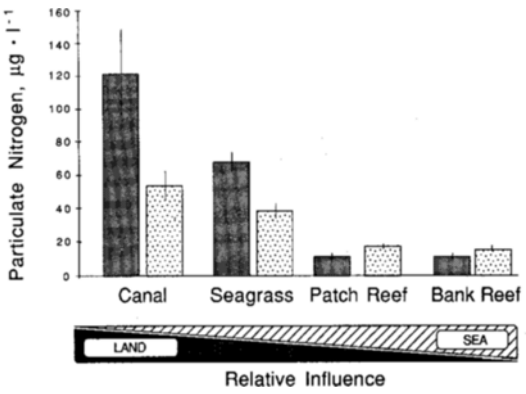

Fig. 6. Concentrations of water column particulate nitrogen in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

seagrass meadows of Florida Bay (e.g., Garfield Bight, Buttonwood Canal; Fig. 12). Higher values occurred during summer (up to 23.4 $\mu g\ l^{-1}$) compared to winter (up to 4.5 $\mu g\ l^{-1}$; Fig. 12).

In contrast to chlorophyll *a*, turbidity was significantly higher in winter rather than summer (Table 2; Fig. 13). The highest turbidity values were in canal and seagrass systems during winter (values up to 71.2 NTU), with significantly lower values in summer (values up to 5.7 NTU; Fig 13). The bank reef stations had the lowest values, generally <0.5 NTU (Fig. 13).

Over the study as a whole, chlorophyll *a* correlated significantly ($p < 0.001$) and positively with NH_4^+ ($r = 0.38$), SRP ($r = 0.42$), TDN ($r = 0.39$), TDP ($r = 0.41$), PN ($r = 0.37$), and PP ($r = 0.59$). Turbidity significantly correlated with PN ($r = 0.62$) and PP ($r = 0.69$).

Dissolved Oxygen

Two-way ANOVA indicated that DO values were significantly lower in canal and seagrass systems during both seasons and that DO values were lower during summer compared to winter (Table 2; Fig. 14). The lower DO concentrations in nearshore waters are obvious when DO is plotted versus distance from land (Fig. 15). While dawn DO averaged between 5.0 mg l^{-1} and 6.5 mg l^{-1} at the bank reef stations, lower and often hypoxic (<2.5 mg l^{-1}) values occurred in canal and seagrass systems during summer. Severe hypoxia (<1 mg l^{-1} DO) was observed during summer at several Florida Bay stations—for example, Rabbit Key and Garfield Bight—and several canal stations. Ten out of the 30 stations had average dawn DO concentrations less than 4.0 mg l^{-1} during summer.

Dawn DO correlated significantly ($p < 0.0001$) and negatively with NH_4^+ ($r = -0.47$; Fig. 16), NO_3^- ($r = -0.26$), SRP ($r = -0.40$), TDN ($r = -0.52$), TDP ($r = -0.41$), chlorophyll *a* ($r = -0.25$), PN ($r = -0.24$), and PP ($r = -0.43$).

TABLE 2. Summary of two-way analysis of variance for measured variables as partitioned for main effects of station, season, and their interaction.

Variable	Source of Variation	Percent of Total Variation Accounted For	F-Ratio	Prob >F
Ammonium	Between stations	16.1	23.29	0.000
	Between seasons	0.1	0.28	0.592
	Interaction	0.5	0.77	0.509
Soluble reactive phosphate	Between stations	4.7	6.00	0.001
	Between seasons	0.0	0.02	0.894
	Interaction	0.0	0.06	0.982
Nitrate plus nitrite	Between stations	40.8	21.11	0.000
	Between seasons	0.8	1.28	0.086
	Interaction	2.2	1.15	0.338
DIN:SRP	Between stations	14.0	16.60	0.000
	Between seasons	1.7	6.09	0.014
	Interaction	1.8	2.14	0.094
Total dissolved nitrogen	Between stations	21.7	36.52	0.000
	Between seasons	4.2	20.99	0.000
	Interaction	2.0	3.24	0.022
Total dissolved phosphorus	Between stations	2.1	2.63	0.050
	Between seasons	0.1	0.49	0.482
	Interaction	1.2	1.45	0.228
Particulate nitrogen	Between stations	5.7	7.30	0.000
	Between seasons	1.6	6.22	0.013
	Interaction	1.3	1.66	0.175
Particulate phosphorus	Between stations	10.0	13.23	0.000
	Between seasons	3.0	10.41	0.001
	Interaction	2.0	2.56	0.054
Chlorophyll *a*	Between stations	5.8	8.00	0.000
	Between seasons	3.2	13.23	0.000
	Interaction	6.1	8.32	0.000
Turbidity	Between stations	4.3	5.98	0.001
	Between seasons	4.7	19.20	0.000
	Interaction	2.3	3.09	0.027
Dawn oxygen	Between stations	22.9	42.10	0.000
	Between seasons	10.0	55.12	0.000
	Interaction	0.7	1.34	0.264

TABLE 3. Relative contribution (%) of dissolved inorganic (DIN, SRP), dissolved organic (DON, DOP), and particulate (PN, PP) fractions to the total nitrogen and phosphorus pools at canal, seagrass, patch reef, and bank reef ecosystems.

Location	Season	Nitrogen			Phosphorus		
		DIN	DON	PN	SRP	DOP	PP
Canal	Summer	17.3	58.2	24.5	24.6	27.3	48.1
	Winter	19.1	42.7	38.2	34.6	17.3	48.1
Seagrass	Summer	12.4	66.3	21.3	20.6	26.1	53.3
	Winter	24.2	36.7	39.1	23.6	31.8	44.6
Patch Reef	Summer	7.2	66.3	26.5	22.4	44.0	33.6
	Winter	6.0	70.5	23.5	14.8	54.0	31.2
Bank Reef	Summer	12.7	60.0	27.3	18.2	49.3	32.5
	Winter	5.6	73.2	21.2	10.9	62.7	26.4

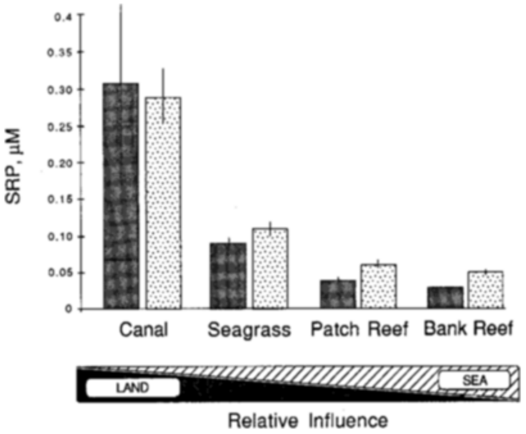

Fig. 7. Concentrations of water-column soluble reactive phosphorus (SRP) in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

Discussion

Our results are consistent with previous studies demonstrating anthropogenic nutrient inputs into nearshore waters and do not falsify the hypothesis that human activities enhance coastal eutrophication in the Florida Keys. The large-scale dynamics of these nutrient inputs to the shallow, nearshore waters of the Florida Keys are clear from our study. Human activities on land enrich groundwaters with NH_4^+ and SRP (Lapointe et al. 1990), contributing to elevated concentrations of these nutrients in nearshore canal and seagrass meadows. This enrichment causes phytoplankton blooms and increased concentrations of PN, PP, chlorophyll *a*, and turbidity. Extensive populations of nutrient-limited phytoplankton, tropical macroalgae, and seagrasses (Lapointe 1987, 1989; Powell et al. 1989) provide an efficient biological sink for such nutrient inputs, a process enhanced by favorable year-round light and temperature. The kinetics of dissolved nutrient cycling by marine microbes and plants is very rapid (e.g., seconds-minutes; Pomeroy 1960; Suttle and Harrison 1988) and dissolved organic pools (DON, DOP), which are important to biological cycling (Jackson and Williams 1985), come to dominate the total nutrient pools with increasing distance from land. Because DIN is less limiting to primary production compared to SRP in nearshore waters of the Keys (Lapointe 1987, 1989), NH_4^+ and NO_3^- remain elevated in the water column at a greater distance from land compared to SRP. Our findings corroborate those of Smith et al. (1981) that measurement of the limiting nutrient, in our case SRP, may be a poor indicator of eutrophication. Measurements of TDN, TDP, PN, PP, and chlorophyll *a* will better reflect long-term trends in nutrient enrichment.

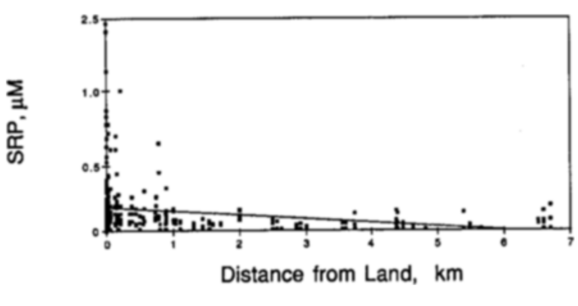

Fig. 8. Concentrations of water-column soluble reactive phosphorus (SRP) in nearshore waters of the Florida Keys versus distance from land.

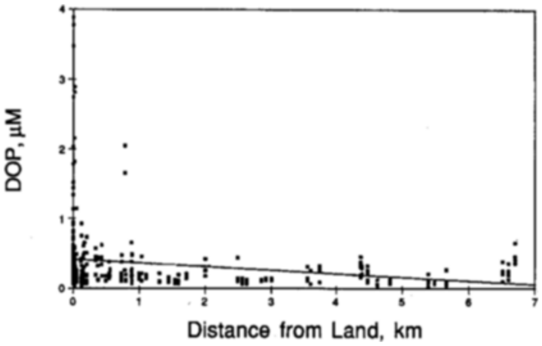

Fig. 9. Concentrations of water-column dissolved organic phosphorus (DOP) in nearshore waters of the Florida Keys versus distance from land.

Nutrient-enhanced productivity of marine plants in the Keys resulting from anthropogenic nutrient inputs leads to increased production of "new" organic matter. The distinction between "new" and

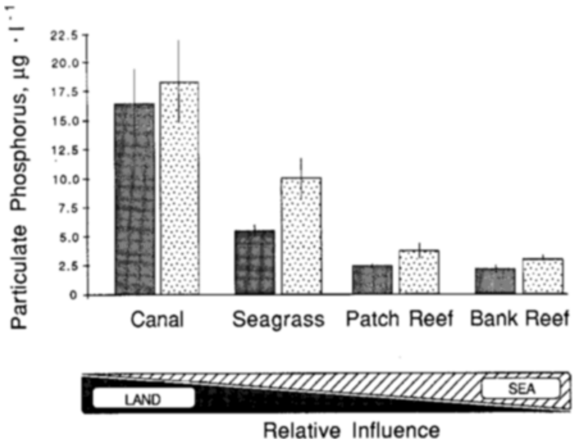

Fig. 10. Concentrations of water-column particulate phosphorus in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

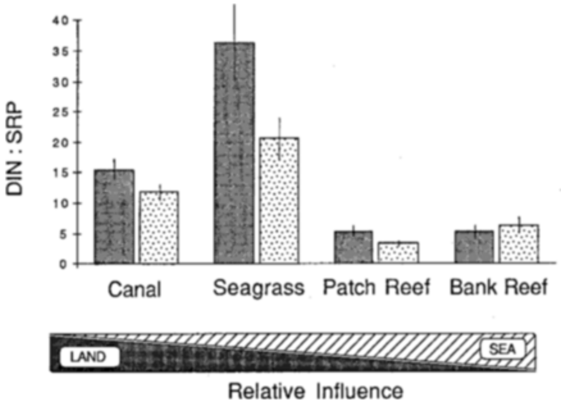

Fig. 11. Ratio of water-column dissolved inorganic nitrogen: Soluble reactive phosphorus (DIN:SRP) in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

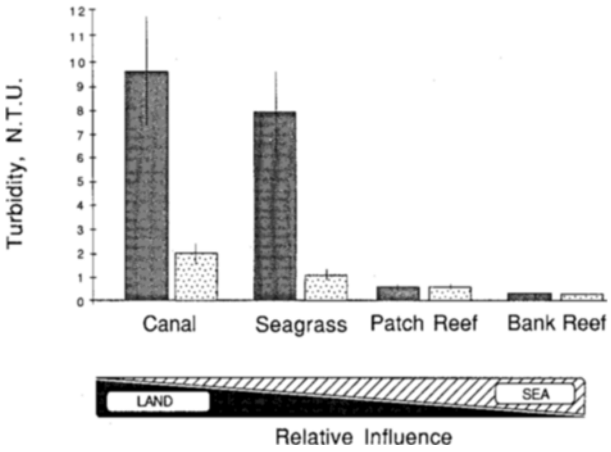

Fig. 13. Water column turbidity in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

"regenerated" forms of nutrients supporting primary production in coastal and oceanic waters was emphasized by Dugdale and Goering (1967). In their sense, NH$_4^+$ represented regenerated sources of autochthonous N resulting from remineralization within the benthos or the water column whereas NO$_3^-$ represented new allochthonous N sources such as upwelling. In applying this concept to the Keys, NH$_4^+$, the major form of N in sewage which is introduced to nearshore waters by submarine groundwater discharge (Lapointe et al. 1990), would clearly represent a new N source in this system. In addition, SRP enrichment of groundwaters and nearshore waters by human activities represents new sources of P that would enhance coastal eutrophic processes in the Keys.

The higher SRP concentrations in canal systems compared to other ecosystems suggests human activities are a significant source of land-based P input. Watershed inputs of new P—the primary limiting nutrient to growth of fleshy tropical macroalgae (Lapointe 1987; Lapointe et al. 1992) and seagrasses (Short et al. 1990) in shallow carbonate-rich waters—would have a greater stimulatory effect than N on primary production and enhancement of eutrophication in nearshore Keys waters. No other major source of new P input exists in these waters; the significantly elevated SRP con-

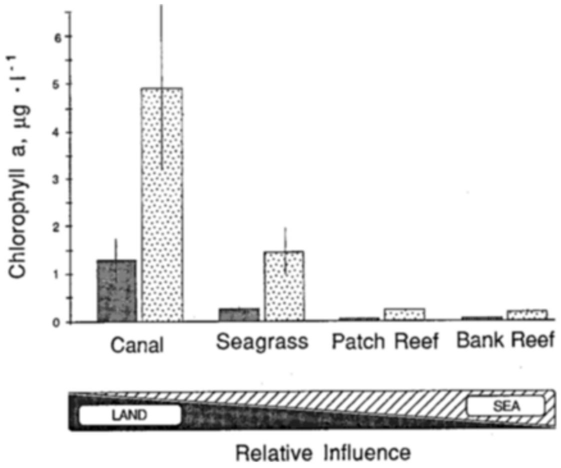

Fig. 12. Concentrations of water-column chlorophyll *a* in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

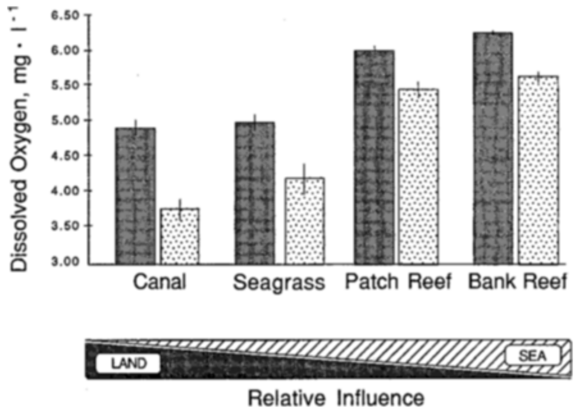

Fig. 14. Concentrations of water-column dissolved oxygen at dawn in canal (n = 78), seagrass (n = 42), patch reef (n = 24), and bank reef (n = 36) ecosystems of the Florida Keys during summer (light shading) and winter (dark shading). Values represent means ± 1 standard error.

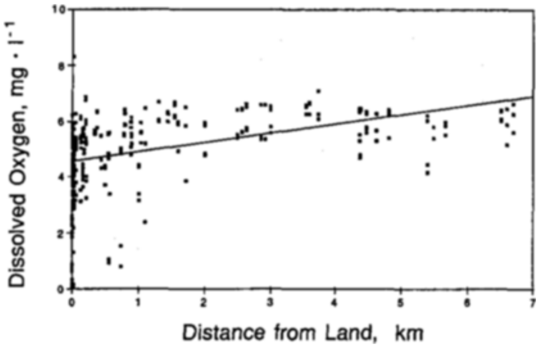

Fig. 15. Concentrations of water column dissolved oxygen at dawn in nearshore waters of the Florida Keys versus distance from land.

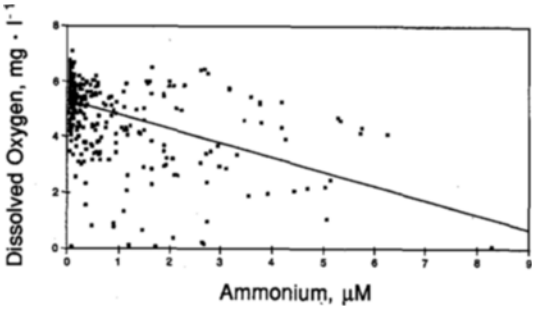

Fig. 16. Negative correlation ($p < 0.001$, $r = -0.47$) of water-column dissolved oxygen at dawn and ammonium in nearshore waters of the Florida Keys.

centrations in canal systems agrees with previous observations of elevated P-loading from sewage-enriched groundwaters (Lapointe et al. 1990). That concentrations of SRP decrease faster with increasing distance from land than either NH_4^+ or NO_3^- indicates more rapid biological uptake of this primary limiting nutrient. Elevated DOP concentrations (~0.20 μM) extended further from land than SRP, suggesting that this P pool could provide dissolved P to more offshore patch and bank reef communities through biological cycling (e.g., alkaline phosphatase hydrolosis; Lapointe 1989; Jackson and Williams 1985). The highest SRP and DOP concentrations of all bank reef stations occurred at Sand Key offshore Key West, the bank reef closest to concentrated human activities (including a 7 MGD coastal sewage outfall). Black-band disease (*Phormidium corallyticum*) has proliferated on hermatypic corals at Sand Key during the past 5 years (personal observation), possibly due to P-enrichment that triggers bacterial infections on corals (Walker and Ormond 1982).

In contrast to SRP, concentrations of NH_4^+ and NO_3^- were similar among the canal and seagrass ecosystems compared to lower concentrations in the patch and bank reef ecosystems. While the elevated NH_4^+ in canal and nearshore seagrass systems is consistent with previous studies of sewage inputs via groundwater discharge (Lapointe et al. 1990), biological cycling and storage may further contribute to the elevated NH_4^+ in seagrass meadows. For example, the elevated water-column NH_4^+ may arise, in part, from a "leaky" N storage capacity in seagrass meadows undergoing long-term nutrient enrichment. NH_4^+, the dominant N species in tropical seagrass pore waters (Short 1987), could begin to diffuse into the water column as pore water NH_4^+ concentrations become elevated during eutrophication, stimulating phytoplankton blooms. SRP concentrations would remain relatively low, as we observed, because of primary P-limitation in these waters (Lapointe 1987) and adsorption of SRP onto carbonate surfaces (DeKanel and Morse 1978). Additionally, seagrasses and macroalgae that dominate primary production in these waters have high N-fixation rates (see Capone 1988 for review), also contributing to excess N. SRP exported from canal systems would also enhance N-fixation rates in nearshore waters—a process that is itself P-limited (Redfield 1958; Doremus 1982). Thus, enhanced N-fixation in nearshore seagrass meadows resulting from land-based human P inputs should be viewed as a polluting process (Horne 1977).

Submarine discharge of nutrient-enriched groundwaters with high N:P ratios may exacerbate the intense P-limitation in nearshore waters of the Keys. Watershed N:P inputs that exceed the Redfield ratio lead to P-limitation, whereas lower watershed N:P values result in N-limitation (Howarth 1988). The N:P ratios of sewage-enriched groundwaters are >100:1 in the Keys (Lapointe et al. 1990) due to selective adsorption of SRP onto calcium carbonate surfaces (DeKanel and Morse 1978). The elevated DIN:SRP ratios we observed in nearshore canal and seagrass systems relative to offshore patch and bank reefs suggest that the high N:P ratio of land-based nutrient inputs contributes to a significant cross-shelf trend in N:P availability and possibly nutrient regulation of primary production. While nearshore canal systems and seagrass meadows tend to have elevated N:P ratios (>15) and are primarily P-limited (Lapointe 1987, 1989), more offshore patch and bank reefs have lower N:P ratios (6:1), suggesting a more N-limited oceanic influence (Redfield 1958).

Significant seasonal differences were apparent in turbidity and chlorophyll *a*—two variables that are important determinants of water clarity. Seasonal factors accounted for most of the variability in turbidity, due to increased wind stress during winter northeasters that resuspend bottom sediments; this increased turbidity during winter is reflected in higher water column PN and PP concentrations. Such short-term wind mixing, coupled with long-term net tidal flow seaward in our study area (Lapointe et al. 1992), are major mechanisms that transport nutrients to more offshore waters. In contrast, chlorophyll *a* concentrations were higher during summer, especially in canal systems and seagrass meadows of Florida Bay. Because nutrient loading determines the upper limit of phytoplankton standing crop (Laws and Redalje 1979) and because of greater watershed nutrient loading during the summer wet season in the Keys (Lapointe et al. 1990), increased nutrient (primarily P) input during the summer increases the phytoplankton standing crop. Marsh (1977) similarly found that human activities increased terrestrial runoff of P that stimulated phytoplankton blooms in coastal waters of Guam during the rainy season. Thus, water clarity in the Keys is regulated by short-term meteorological events that increase turbidity and particulate nutrients, primarily in winter, and by increased nutrient loading during the rainy season that increases phytoplankton standing crops. While short-term increases in chlorophyll *a* following rainfall are obvious, many long-time residents have also noticed a long-term (decadal) trend in the "greening" of nearshore waters. This suggests that phytoplankton standing crops may have increased historically, possibly in response to watershed nutrient inputs.

The significant negative correlation between DO and ammonium (as well as other nutrient variables) underscores the importance of nutrient enrichment to hypoxia in these waters. Nutrient inputs to nearshore waters increase standing crops of phytoplankton, seagrasses, and macroalgae, all of which lead to increased light-limitation of benthic photosynthesis by shading and selective light absorption; increased community respiration also consumes oxygen (Valiela et al. 1990). Additional oxygen demand results from the mineralization of new organic matter resulting from nutrient inputs. Mee (1988) suggested that "critical eutrophication" be defined as a state when "the net flux of limiting nutrients incorporated into plant biomass is such that the rate of production of new organic matter exceeds the net rate of oxygen supply needed to oxidize it." Tropical marine organisms live closer, on the average, to their lower DO limit compared to biota in temperate waters (Johannes 1975); thus, even slight depression of DO associated with eutrophication and hypoxia in the Keys could have important effects on the diversity and productivity of coastal food webs.

Nutrient concentrations and hypoxia were of similar magnitude between canal systems known to be impacted by septic tanks in the Keys and extensive seagrass meadows in western Florida Bay. The highest SRP, PP, and TDN concentrations of our study occurred in and around upper western Florida Bay, an area recently afflicted by a large-scale die-off of the turtle grass *Thalassia testudinum* (Robblee et al. 1991). Because of riverine drainage and extensive canalization in south Florida, the watershed for this area includes much of the southwest Florida mainland, including the Everglades. Human activities in this watershed over the past century have included urbanization, drainage of wetlands, and agriculture. Such activities are well known to increase nutrient loading to coastal ecosystems (Peierls et al. 1991; Turner and Rabalais 1991) at levels that can even exceed those of fertilized agroecosystems (Nixon et al. 1986). Agriculture combined with water management practices in south Florida, have greatly increased nutrient loading (especially P) that threatens water quality relationships throughout the entire Everglades wetland system (Belanger et al. 1989) and possibly downstream coastal receiving waters. The large scale of such mainland watershed nutrient inputs to coastal waters, combined with net flow of alongshore currents of southwest Florida toward Florida Bay and the Florida Keys (Lapointe et al. 1992), suggests that these nutrient inputs may contribute to the elevated nutrient concentrations and hypoxia we observed in western Florida Bay and, possibly, more downstream waters of the Florida Keys.

In summary, human activities in the Florida Keys are significantly contributing to increased N and P inputs to nearshore waters, enhancing coastal eutrophication. The coral reef and seagrass ecosystems that inhabit nearshore waters of our study area are adapted to oligotrophic and mesotrophic conditions, respectively, (Birkeland 1987) such that nutrient enrichment above some unknown threshold will initiate ecosystem change. Studies (Tomasko and Lapointe 1991) have already documented elevated epiphyte loads, reduced blade turnover rates, and reduced productivity of the turtle grass *Thalassia testudinum* in nutrient-enriched waters adjacent to populated islands in the Keys. Coral reef ecosystems of the Keys are near the northern end of their latitudinal range, which itself may be controlled by elevated nutrient availability (Johannes et al. 1983). Thus, significant enrichment of patch and bank reef ecosystems with DON, DOP, PN, and PP resulting from chronic nearshore eutrophication could lead to increased algal cover at the expense of coral (Littler and Littler 1985). These mechanisms may already be afflicting coral reef ecosystems of the Keys, and may explain the apparent ecological dysfunction and changes in coral communities that have occurred on reefs of the Florida Keys over the past decades (Dustan and Halas 1987).

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