Estuarine, Coastal and Shelf Science (1993) **36**, 295–314

Processes Influencing Water Column Nutrient Characteristics and Phosphorus Limitation of Phytoplankton Biomass in Florida Bay, FL, USA: Inferences from Spatial Distributions

James W. Fourqurean[ac], Ronald D. Jones[b] and Joseph C. Zieman[a]

[a]Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903 and [b]Department of Biological Sciences and Drinking Water Research Center, Florida International University, Miami, FL. 33199, U.S.A.

Received 14 February 1992 and in revised form 27 April 1992

Keywords: nutrients; water quality; spatial distribution; chlorophyll distribution; salinity; Florida Keys

The concentrations of nutrients, dissolved and particulate organic matter, salinity and chlorophyll-*a* in the water column were measured over the period of June 1989 to August 1990 at a network of 26 sampling locations across Florida Bay. Florida Bay was hypersaline during this time period, with an average salinity of 41·4. Dissolved organic phosphorus was the dominant form of P in the water column, while soluble reactive P was generally less than 5% of the total P. Organic nitrogen forms dominated the N pool, and NH_4^+ was the dominant form of dissolved inorganic nitrogen. Many of the measured parameters were correlated. Principal Components Analysis extracted three composite variables that described 90·3% of the variation in the original data set. PC_I was highly correlated with total organic N, total N, total organic C and salinity. PC_{II} was correlated with all measures of P and chlorophyll-*a*. PC_{III} was correlated with measures of inorganic N. The spatial distribution of factor scores for these principal components indicate three processes acting independently to control the composition of the water column of Florida Bay: the evaporation-driven concentration of dissolved material in Florida Bay; the delivery of P to Florida Bay through water exchange with the Gulf of Mexico; and the delivery of freshwater with an excess of N with respect to P to Florida Bay. The phytoplankton biomass in the water column of Florida Bay is shown to be P-limited.

Introduction

At the ecosystem level, the role estuaries and lagoons play as sources, sinks or transformers of nutrients has often been inferred from the distribution of various forms of nutrients in the water column in relation to oceanic and upland sources (e.g. Officer, 1979; Biggs & Cronin, 1981; Smith, 1984). In a nutrient-limited embayment, the inverse of this question

[c]Present address: Southeastern Environmental Research Program, Drinking Water Research Center, Florida International University, Miami, FL, 33199, U.S.A.

0272–7714/93/030295 + 20 $08.00/0

becomes important, i.e. ' what are the sources of nutrients necessary to sustain primary production in the system? ' Often this question can also be answered by analysis of the distribution of nutrients within the system.

When sufficient light is present, the availability of nitrogen and/or phosphorus often limits primary production within estuaries and lagoons. The processes that affect the biogeochemistry of nitrogen and phosphorus differ, leading to large variations in the relative abundances of N and P when compared to the open ocean. The nutrient that limits productivity of these systems is a function of the ratio of N to P in the nutrient loading to the system, the loss rate of N and P from the system due to biogeochemical processes such as denitrification, adsorption and sedimentation, and the extent to which nitrogen fixation can make up for nitrogen deficits (see Howarth, 1988 for review). The combination of these factors often leads to N limitation in many coastal marine and estuarine systems (Ryther & Dunstan, 1971; Howarth, 1988), especially in north-temperate areas where river input of nutrients is high and nitrogen fixation is relatively unimportant. While less commonly reported than N limitation, P limitation occurs in some coastal marine ecosystems, especially where the N:P of the nutrient loading is very high (e.g. Harrison *et al.*, 1990) or nitrogen fixation is important (e.g. Smith, 1984). The role of nitrogen fixation in obviating N limitation is enhanced in systems with high water residence time (Smith, 1984) and in clear-water lagoons with high rates of benthic nitrogen fixation (Howarth, 1988). Seasonal shifts in which nutrient limits primary production have been reported for some areas (e.g. McComb *et al.*, 1981; Lyngby, 1990).

Florida Bay is a large shallow lagoon at the southern tip of the Florida peninsula, U.S.A. (*c.* 25°N, 81°W, Figure 1). Florida Bay receives freshwater runoff from the Everglades to the north, and opens to the Gulf of Mexico along its western margin. The main line of the Florida Keys, a Pleistocene reef, separates Florida Bay from the Atlantic Ocean. The sediments of Florida Bay are composed almost entirely of biogenic carbonate mud (Bosence, 1989*a*). Because of the shallow water depths (<3 m), sufficient sediment and clear water (attenuation coefficient usually $<0{\cdot}5\ m^{-1}$, Fourqurean & Zieman, 1991), Florida Bay is carpeted with seagrasses (Zieman *et al.*, 1989). The standing crop and productivity of seagrasses, the dominant producers in Florida Bay, are phosphorus limited (Powell *et al.*, 1989; Fourqurean *et al.*, 1992*a*, *b*), but little work has addressed whether N or P limits phytoplankton biomass or productivity in Florida Bay.

Several potential mechanisms exist for producing P limitation in Florida Bay. In all but the wettest years, Florida Bay is hypersaline, with evaporation exceeding freshwater inputs (Robblee *et al.*, 1989). Hypersaline conditions indicate that water residence time is relatively long in Florida Bay, which may allow for N fixation to make up N deficits (Smith, 1984; Fourqurean *et al.*, 1992*a*). High nitrogen fixation rates are often associated with seagrass beds (see Howarth *et al.*, 1988 for review). The carbonate sediments of Florida Bay may be a sink for P, because geochemical processes, such as P adsorption by carbonates and apatite formation (deKanel & Morse, 1978), may render P unavailable to primary producers (Short, 1987). Also, the ratio of N to P in the freshwaters of the Everglades that flow into Florida Bay is very high, with an N:P of 374:1 in the wet season and 390:1 in the dry season (R.D. Jones, unpubl. data). This excess of P with respect to N is caused by the P-limited nature of the Everglades ecosystem (Scheidt, 1988).

Florida Bay is an area of biogenic sediment accumulation (Bosence, 1989*b*), so weathering of pre-existing substratum is not an important source of nutrients. All of the nutrients needed to support primary production in the system must come from allochthonous sources, either through water-bourne exchange with the Everglades and the Gulf of

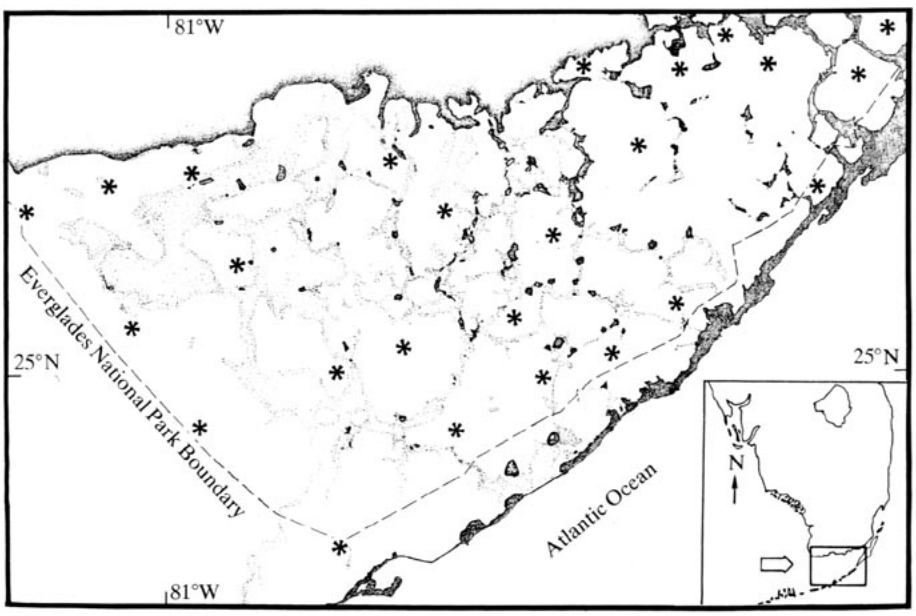

Figure 1. Location map of Florida Bay. Symbols indicate sampling locations. One additional station was located just off the northeast corner of this map in Long Sound. ⊠, shallow carbonate mud banks; [], land masses and mangrove islands.

Mexico, or through the atmosphere-water interface as precipitation, dry deposition or nitrogen fixation.

In this study, we use the regional spatial distribution of nutrients and chlorophyll-*a* to assess the relative importance of freshwater runoff from the Everglades and turbulent mixing with the Gulf of Mexico as sources of nutrients for Florida Bay. We also use the relationships between nutrients and chlorophyll-*a* in the water column to determine if N or P is limiting to phytoplankton biomass in Florida Bay.

Methods

Shallow mud banks divide Florida Bay into relatively discrete basins. In order to cover all of Florida Bay, we chose 26 sample sites, generally near the centers of these basins, quasi-evenly spaced across the bay (Figure 1). There were eight sampling periods between the summer of 1989 and the summer of 1990. For each sampling period, two days were required to adequately cover the entire bay; the dates of the sampling periods were June 27 & 28, July 25 & 26, August 22 & 23, November 8 & 9, and December 7 & 8, 1989, and April 10 & 11, July 1 & 2 and August 20 & 21, 1990.

Dissolved oxygen was measured 10 cm below the surface using an oxygen electrode (Orbisphere model 2607). pH was determined immediately at each site on four successive aliquots of water using a standard, temperature corrected combination pH electrode. Salinity was determined with a refractometer with a resolution of 1 ppt.

At each station, duplicate samples for dissolved inorganic nutrient analysis were collected from 10 cm below the surface using acid washed and sample rinsed 60 mL

syringes. Multiple syringe volumes contributed to each sample. Samples were filtered through pre-ashed and pre-weighed 25 mm diameter GF/F filters into acid washed and sample rinsed 60 mL HDPE bottles. These bottles were capped, immediately placed on ice in the dark, and transported back to the lab for analysis. The volume of sample passed through each filter was recorded, and each filter was placed in a separate container and frozen for later analysis.

Unfiltered water samples for determination of total C, N and P and dissolved organics were collected in duplicate 60 mL acid-washed and sample rinsed HDPE bottles. Bottles were filled 10 cm below the surface. Care was taken to exclude all air bubbles from the sample bottles by capping them underwater. They were then placed in the dark on ice and transported back to the lab. All filtered and unfiltered water samples were stored in the dark at 3° C until analysis.

For a subset of the sampling periods (December 1989; April, July and August 1990), chlorophyll-*a* (chl-*a*) concentration was determined. At each site, 60 mL samples were collected about 10 cm below the surface and filtered through 13 mm GF/F glass fibre filters. These filters were placed in 2·0 mL spectrophotometric grade acetone in capped vials, and stored on ice in the dark for transportation back to the laboratory.

The filtered samples were analysed for soluble reactive phosphate (SRP), nitrate (NO_3^-), nitrite (NO_2^-) and ammonium (NH_4^+). These inorganic nutrients were determined on a four channel autoanalyser (Alpkem model RFA 300). Accuracy of inorganic nutrient determinations were repeatedly checked against standard benchtop wet chemistry (Parsons *et al.*, 1984) and a new fluorescence method for NH_4^+ analysis (Jones, 1991). All analyses of dissolved inorganic nutrients were completed within 48 h after collection.

The filters collected in the field were ashed for 4 h at 500 °C, and the volatile fraction of the residue on the filters was defined as particulate organic matter (POM; APHA, 1980). Particulate phosphorus (PP) was determined from the filters by the ashing and acid hydrolysis technique of Solórzano and Sharp (1980).

Unfiltered samples were used for the determination of total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP). TOC was measured by acidifying to pH < 2, purging the sample with CO_2-free air, and analysing for total carbon using a hot platinum catalyst direct injection analyser (Shimadzu model TOC-5000). Total nitrogen (TN) was measured using an Antec 7000N total nitrogen analyser. TP was determined using a dry ashing and acid hydrolysis technique (Solórzano & Sharp, 1980). Chl-*a* content of the acetone extracts was determined fluorometrically (Strickland & Parsons, 1972).

Some parameters were not measured directly, but were calculated by difference. Dissolved inorganic nitrogen (DIN) was calculated as the sum of $NO_3^- + NO_2^- + NH_4^+$. Total organic nitrogen (TON) was defined as TN-DIN. Dissolved organic phosphorus (DOP) was defined as TP-(PP + SRP). All of the ratios of C:N:P calculated and cited in this paper are on a mole:mole basis.

For preliminary description of the data, the mean, standard error of the mean (SE), minimum and maximum of all observations of all variables at each station and time were calculated. For investigation of changes in water quality variables with time, the mean values for each variable were calculated for each separate cruise.

Because further analysis of seasonal trends in the data was beyond the scope of our data, for additional statistical analyses one time-averaged mean value for each measured water quality parameter was calculated for each station. A correlation matrix was generated for these time-averaged values, and two-tailed probabilities for significance were computed.

TABLE 1. Summary statistics for all observations, including all stations and all water quality survey cruises. BD = Below Detection

Variable	Mean	SE	Minimum	Maximum	*n*
Temperature (°C)	27·8	0·2	19·0	32·2	213
Salinity (ppt)	41·40	0·4	18·0	59·0	213
Dissolved O_2 (ppm)	7·32	0·09	3·08	10.83	183
pH	8·14	0·02	7·59	8·74	176
NO_3^- (μM)	0·59	0·06	BD	6·13	187
NO_2^- (μM)	0·13	0·01	BD	0·94	213
NH_4^+ (μM)	1·89	0·15	0·02	11·03	213
DIN (μM)	2·68	0·21	0·06	14·37	187
TON (μM)	43·3	1·7	0·7	122·8	185
TN (μM)	45·6	1·6	7·0	123.2	211
SRP (μM)	0·03	<0·01	BD	0·33	185
PP (μM)	0·18	0·02	0·04	3·48	213
DOP (μM)	0·37	0·02	0·04	2·03	208
TP (μM)	0·58	0·03	0·13	4·09	208
Chl-*a* (μg/L)	1·05	0·07	0·34	4·86	98
TOC (μM)	623·1	24·4	104·0	1763·0	207
Susp. organics (mg AFDW/L)	12·34	0·55	3·50	91·50	211

In order to assess the underlying patterns in the distribution of the measured parameters in Florida Bay, Principal Components Analysis (PCA) was used to extract composite variables (principal components) from the original set of time-averaged variables. Because the goal of this analysis was to describe underlying spatial pattern, variables for which the daily variation at one station was greater than the spatial variation across Florida Bay (temperature, pH and dissolved oxygen) were eliminated from the PCA. The PCA solution was rotated (using VARIMAX rotation) in order to facilitate the interpretation of the principal components. At each station, the factor scores for each prinicpal component variable were calculated.

Results

During the period of these surveys, Florida Bay was warm and hypersaline, with an average temperature of $27{\cdot}8 \pm 0{\cdot}2$ °C (± 1 SE) and an average salinity of $41{\cdot}4 \pm 0{\cdot}4$ ppt (Table 1). Dissolved oxygen was in general quite high, with an average value of $7{\cdot}32 \pm 0{\cdot}09$ ppm, and pH averaged $8{\cdot}14 \pm 0{\cdot}02$. Dissolved inorganic nutrient concentrations (NO_3^-, NO_2^-, NH_4^+) were low in general, and represented a minor fraction of the total nutrient pool when compared to organic and particulate forms of N and P. The average of the measured molar DIN:SRP ratios was 152 ± 18 and TN:TP averaged 101 ± 5. TOC concentration averaged $623{\cdot}1 \pm 24{\cdot}4$ μM and the average TOC:TN ratio was 16 ± 2. The average POM concentration was $12{\cdot}34 \pm 0{\cdot}55$ mg AFDW L^{-1}.

Means of all stations for each sampling cruise

Both temperature and salinity exhibited the expected seasonal variation (Figure 2). Baywide average temperature maxima were recorded in both August 1989 and August

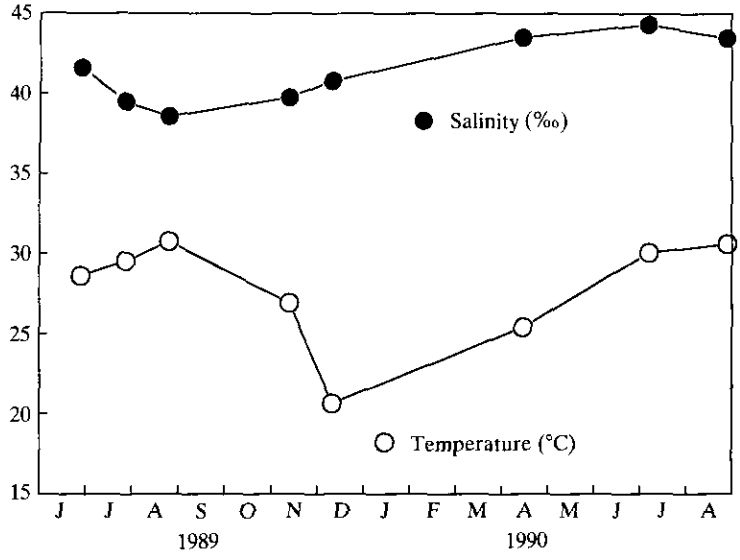

Figure 2. Average temperature and salinity across all sample sites for each sampling date.

1990 (30·8 °C and 30·6 °C, respectively). The minimum average temperature, 20·7 °C, was measured on the December, 1989 survey. Falling salinity was recorded during the summer rainy season of 1989; the minimum baywide average salinity (38·6 ppt) was recorded on the August, 1989 survey. Salinity then rose during the autumn, winter and spring, reaching a maximum of 44·3 ppt on the July, 1990 survey, before falling to 43·8 ppt on the August, 1990 survey.

The relative dominance of the forms of P and inorganic N were the same throughout the period of these surveys (Figure 3). DOP was the most dominant form of P in the water column, comprising over 50% of the TP on each sampling date. PP made up the second most abundant fraction of the total P. SRP made up the smallest fraction, and was generally less than 5% of total P. NH_4^+ was the dominant form of inorganic N. NO_3^- concentrations were $\frac{1}{4}$ to $\frac{1}{2}$ of the NH_4^+ concentration, and NO_2^- made up a small, but measurable, fraction of the DIN pool on each sampling date. Average TOC varied from 500–880 μM, and TON from 38–57 μM during the sampling period (Figure 3). It was beyond the scope of the data set to analyse these baywide averages at each sampling time for seasonal trends.

Means of all cruises at each sampling station

At all stations across Florida Bay, salinity was greater than normal seawater (Figure 4). Salinity was around 37 ppt along the western edge of Florida Bay, and increased towards the centre of the bay, where a salinity maximum of over 50 ppt was found. Salinity was also low (35 ppt) in the extreme northeast portion of the bay as a result of freshwater runoff from the Everglades, and increased towards the south and west.

SRP was low across the entire bay, but tended to be somewhat higher in the central part of the bay (Figure 5). DOP was highest (0·6 μM) in the northwest, and decreased to the southeast, producing isopleths that ran in a SW-NE direction (Figure 5). A large area of low (<0·3 μM) DOP occurred parallel to the main line of the Florida Keys. The pattern in the distribution of PP was slightly more complex, but followed the same general pattern as DOP, with a high of 0·7 μM in the northwest and a low of <0·1 μM in a zone

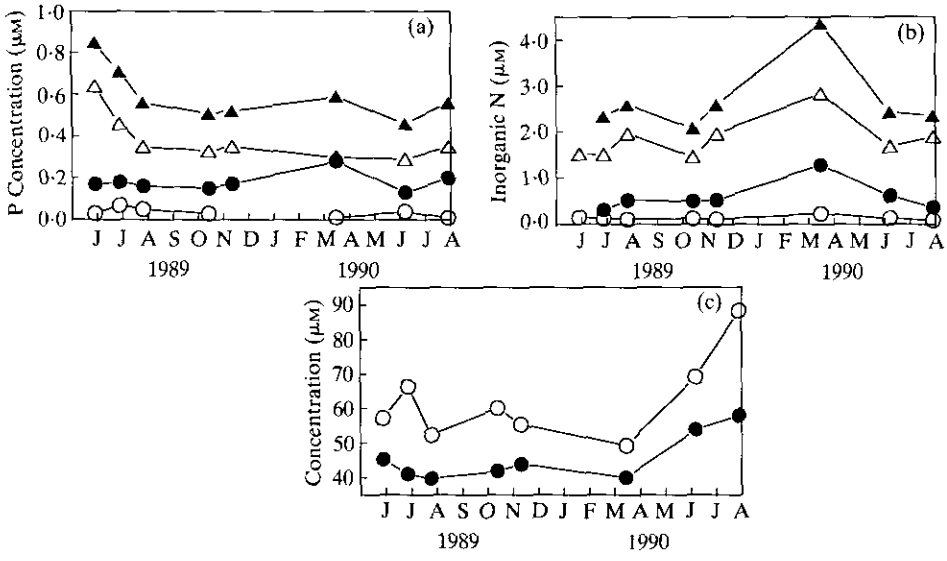

Figure 3. Average concentrations of forms of (a) phosphorus, ▲, total P; △ DOP; ●, PP; ○, SRP; (b) dissolved inorganic nitrogen ▲, DIN; △, NH_4^+; ●, NO_3; ○, NO_2; and (c) total organic carbon and nitrogen ○, TOC ($^* 10^{-1}$); ●, TON; across all sample sites for each sampling date.

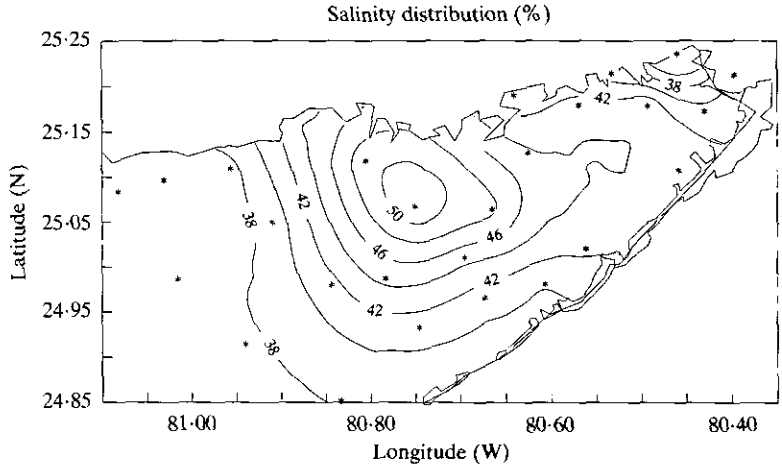

Figure 4. Average salinity at each station across all sampling dates for Florida Bay (June 1989–August 1990). Asterisks indicate sample collection sites.

paralleling the Florida Keys (Figure 5). DOP and TOP were the dominant forms of P in the water column, therefore the pattern in the distribution of TP mirrored their distributions. High TP of $>1{\cdot}4$ μM was found in the northwest, and TP minima of $<0{\cdot}4$ μM were found in the broad swath along the Florida Keys (Figure 5).

In contrast to the distribution of P across Florida Bay, the maximum DIN concentrations (>7 μM) were found in the extreme northeastern part of the bay (Figure 6). DIN

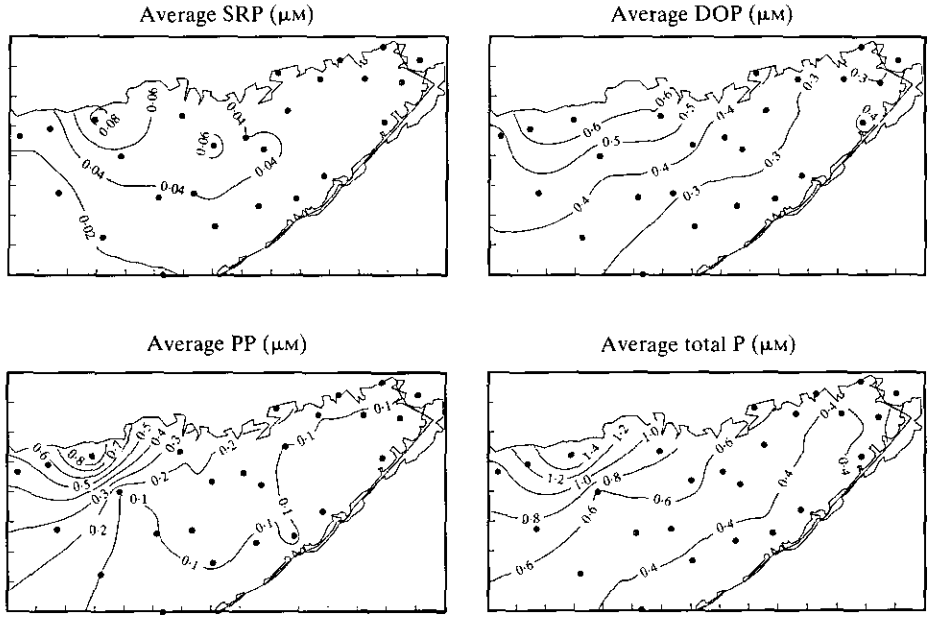

Figure 5. Average concentrations of forms of phosphorus at each station across all sampling dates for Florida Bay (June 1989–August 1990). Dots indicate sample collection sites.

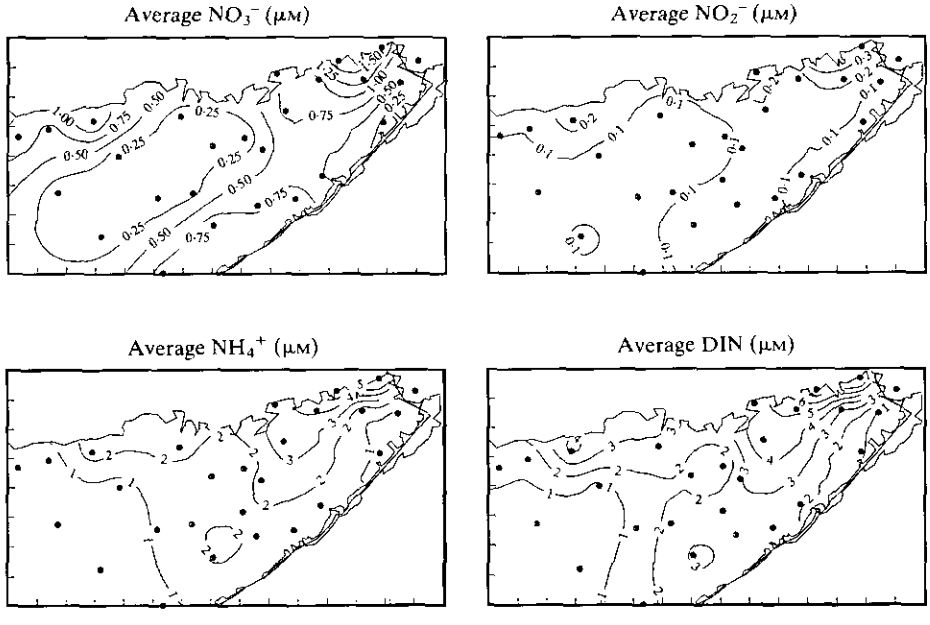

Figure 6. Average concentrations of forms of dissolved inorganic nitrogen at each station across all sampling dates for Florida Bay (June 1989–August 1990). Dots indicate sample collection sites.

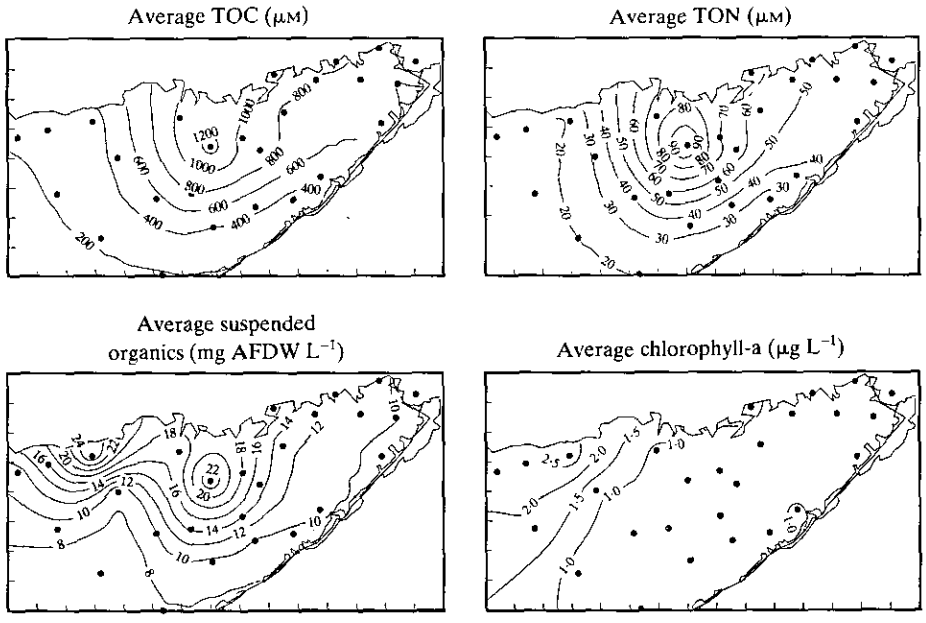

Figure 7. Average concentrations of total organic carbon, total organic nitrogen, suspended organic material and chl-*a* at each station across all sampling dates for Florida Bay (June 1989–August 1990). Dots indicate sample collection sites.

concentrations decreased towards the south and west, with values $<1\ \mu M$ along the western mouth of Florida Bay. In general, the DIN pattern was driven by concentrations of NH_4^+, which had a maximum of $>6\ \mu M$ in the northeast and a minimum of $<1\ \mu M$ along the western end of the Bay (Figure 6). The same pattern was apparent for NO_2^-, with a high of $>0{\cdot}3\ \mu M$ in the northeast and low of $<0{\cdot}1$ in the west (Figure 6). The pattern in NO_3^- was slightly more complicated, with lows of $<0{\cdot}25\ \mu M$ in western and central Florida Bay, and higher values to the north, south and east (Figure 6).

Both TOC and TON were highest in central Florida Bay, and decreased towards the east, west and south (Figure 7). There were two areas of high POM concentrations. One was centred on the area of high salinity, TOC and TON in the centre of Florida Bay, and the other was in the northwestern part of the bay (Figure 7). The pattern of chl-*a* distribution across the bay (Figure 7) was similar to the distribution of TP (Figure 5), with maximum values $>2\ \mu g\ L^{-1}$ in the northwest and low values $<1\ \mu g\ L^{-1}$ in most of Florida Bay.

The ratio of TN to TP in the water column of northwest Florida Bay was only slightly above the 16:1 of the Redfield ratio, but over most of the bay the N:P ratio was much higher (Figure 8). The maximum N:P ratios, over 140:1, were found in the centre of the bay. In the northeast section of Florida Bay, where freshwater runoff ameliorated the buildup of salinity due to evaporation (Figure 4), N:P was 100:1 to 120:1, slightly lower than the maximum.

Examination of the correlation matrix indicates there were some strong correlations between variables (Table 2). Of the 91 possible pairwise comparisons, there were 23 significant ($P \leqslant 0{\cdot}01$) correlation coefficients. These significant correlations fell into three main groups. All of the measures of dissolved inorganic N concentration (NO_3^-, NO_2^-,

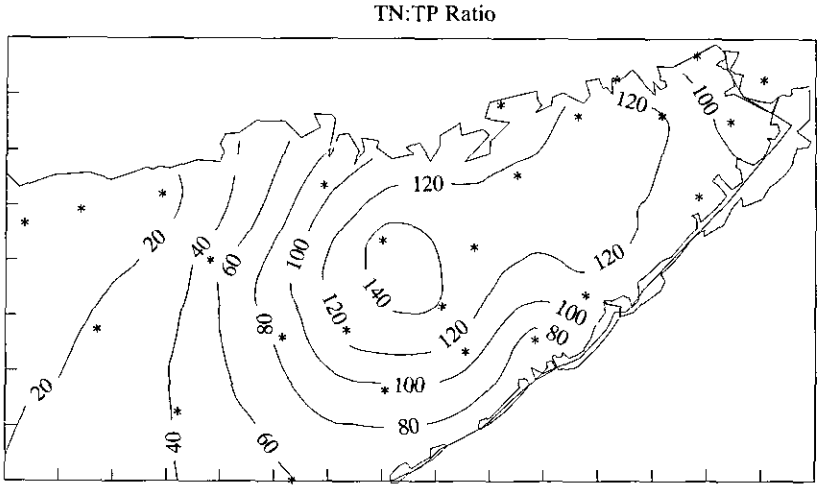

Figure 8. Average ratio of total nitrogen to total phosphorus in the water column at each station across all sampling dates in Florida Bay (June 1989–August 1990). Asterisks indicate sample collection sites.

NH_4^+ and DIN) were correlated with one another, but with nothing else. The second group of correlated variables consisted of salinity, TON, TN, and TOC. POM was also correlated with measures of TN and TON. The complex forms of P (TP, PP and DOP), as well as chl-*a*, made up the third group of inter-correlated variables.

Mean chl-*a* concentrations at each station was statistically dependent on the mean TP concentration (Figure 9). A linear relationship (chl-$a = 1{\cdot}53(\text{TP}) + 0{\cdot}17$) described 77% of the variation in the data, and was significant at $P < 0{\cdot}001$. The slope of this line was significantly different from 0 ($t = 8{\cdot}9$, $P < 0{\cdot}001$), but the intercept was not ($t = 1{\cdot}5$, $P = 0{\cdot}16$). There were no significant correlations between any measured form of N and chl-*a* (Table 2).

PCA identified three composite variables, or principal components (hereafter called PC_I, PC_{II} and PC_{III}) that passed rule N for significance at $P \leqslant 0{\cdot}05$ (Overland & Preisendorfer, 1982), indicating that there were three separate modes of variation within the data (Table 3). These three principal components accounted for 90·3% of the total variance of the original variables (33·5%, 31·8% and 24·9% for PC_I, PC_{II} and PC_{III}, respectively). Factor loadings (Table 3) are the correlations between the original variables and the principal components. PC_I had high positive factor loadings for the variables TON, TN, TOC and salinity, and moderate positive factor loadings for POM and SRP. PC_{II} had high positive factor loadings for the variables TP, PP, DOP, chl-*a* and POM, and a moderate positive loading for SRP. PC_{III} had high factor loadings for all of the inorganic N variables (DIN, NO_2^-, NH_4^+ and NO_3^-). Note that each of these principal components corresponds to one of the groups of inter-correlated variables in the correlation matrix (Table 2).

The spatial distribution of the factor scores on PC_I for each sample site are plotted in Figure 10(a). High positive scores on PC_I were correlated with high salinity, TOC, TN and TON, and were found in the centre of the bay. The western fringe of Florida Bay was characterized by high negative scores on PC_I, indicating areas of relatively low salinity, TOC, TON and TN.

The northwest portion of Florida Bay was characterized by high positive scores on PC_{II} [Figure 10(b)], denoting high TP, PP, DOP, SRP, chl-*a* and POM. A broad swath of

TABLE 2. Correlation matrix of averages across time of each parameter at each station. Two-tailed significance tests, * = $P<0.01$, ** = $P<0.001$

	SAL	NO_3^-	NO_2^-	NH_4^+	DIN	TON	TN	SRP	PP	DOP	TP	CHL	DOC
SAL	1·00												
NO_3	−0·39	1·00											
NO_2	−0·35	0·85**	1·00										
NH_4^+	−0·10	0·66**	0·83**	1·00									
DIN	−0·18	0·79**	0·89**	0·98**	1·00								
TON	0·81**	−0·20	0·01	0·31	0·20	1·00							
TN	0·77**	−0·12	0·11	0·41	0·31	0·99**	1·00						
SRP	0·46	−0·04	0·01	0·05	0·05	0·41	0·41	1·00					
PP	−0·27	0·28	0·19	−0·03	0·06	−0·28	−0·25	0·44	1·00				
DOP	−0·12	−0·01	0·05	−0·00	0·02	−0·03	0·00	0·43	0·82**	1·00			
TP	−0·19	0·17	0·14	−0·01	0·05	−0·16	−0·13	0·49	0·97**	0·93**	1·00		
CHL	−0·35	0·17	0·01	−0·24	−0·14	−0·45	−0·44	0·27	0·92**	0·73**	0·88**	1·00	
DOC	0·69**	−0·07	0·19	0·45	0·35	0·96**	0·98**	0·35	−0·26	−0·02	−0·15	−0·45	1·00
AFDW	0·41	0·08	0·11	0·13	0·13	0·51*	0·51*	0·73**	0·65**	0·60	0·68**	0·46	0·46

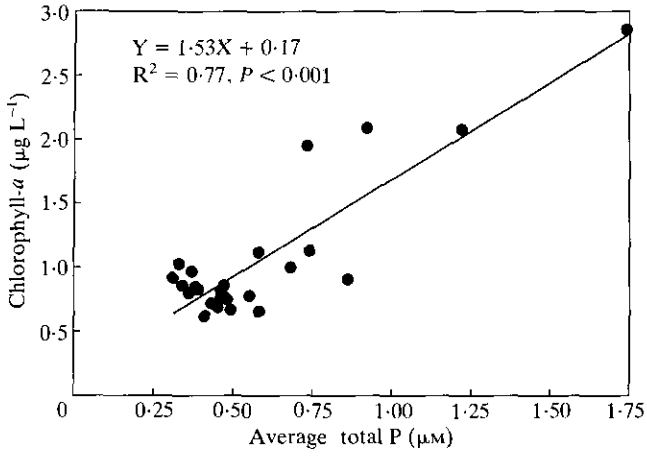

Figure 9. Relationship between the average TP and chl-*a* concentrations. Each point represents the average measures at one station for all sampling dates.

TABLE 3. Results of Prinicipal Components Analysis. Factor loadings (correlations between the raw variables and the principal components) for the first three principal components after rotation (VARIMAX rotation). For clarity, loadings with a magnitude ≥0·5 are shown in boldface type

	Principal Component		
Variable	PC_I	PC_{II}	PC_{III}
TON	**0·98**	−0·08	0·05
TN	**0·98**	−0·06	0·15
DOC	**0·94**	−0·10	0·22
Salinity	**0·86**	−0·08	−0·33
TP	−0·09	**0·98**	0·07
PP	−0·21	**0·96**	0·11
DOP	0·02	**0·89**	0·00
Chl-*a*	−0·39	**0·88**	−0·06
Suspended Organics	**0·57**	**0·76**	0·07
SRP	**0·53**	**0·60**	−0·04
DIN	0·16	−0·01	**0·97**
NO_2	−0·03	0·08	**0·96**
NH_4^+	0·26	−0·07	**0·93**
NO_3^-	−0·23	0·12	**0·87**
% Total Variation	33·5	31·8	24·9

negative scores on PC_{II} parallelled the main line of the Florida Keys. This area had relatively low concentrations of all forms of P in the water column, as well as low chl-*a* and suspended organic material.

PC_{III} was highly, positively correlated with concentrations of all measured forms of dissolved inorganic N (NO_3^-, NO_2^-, NH_4^+ and DIN). High scores on PC_{III} were found in

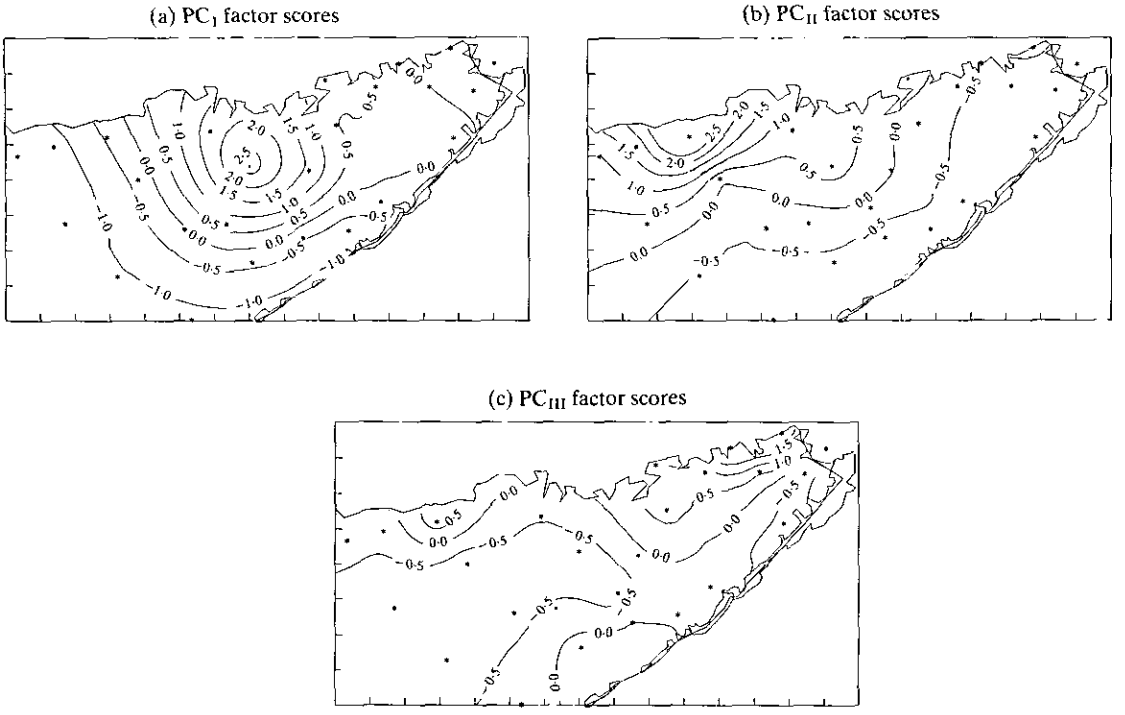

Figure 10. Factor scores for principal component I–III. (a) PC_I is positively correlated with total organic nitrogen, total nitrogen, dissolved organic carbon and salinity; (b) PC_{II} is positively correlated with concentrations of all forms of phosphorus, chl-*a* and suspended organic material; (c) PC_{III} is positively correlated with all of the forms of dissolved inorganic nitrogen (see Table 5·3 for factor loadings).

the northeast corner of Florida Bay [Figure 10(c)]. An extensive region of negative scores was found to extend from the western boundary of Florida Bay in towards the central bay, indicating low concentrations of dissolved inorganic N in these areas.

Discussion

The spatial patterns in the nutrient and chl-*a* data indicated there were three independent processes acting to determine the characteristics of the water column of Florida Bay. Each of these processes affected a different suite of measured variables. These three processes may be interpreted as: 1. The decomposition of organic matter and the evaporation-driven concentration of material in the centre of Florida Bay [represented by PC_I, Figure 10(a)]; 2. The delivery of P to Florida Bay via water exchange with the near-shore waters of the Gulf of Mexico, especially in northwest Florida Bay [represented by PC_{II}, Figure 10(b)]; and 3. The delivery of excess N with respect to P via freshwater runoff from the Everglades, especially in northeast Florida Bay [represented by PC_{III}, Figure 10(c)].

This work also provided three complementary lines of evidence for P limitation of phytoplankton biomass in Florida Bay: 1. Very low, largely immeasurable concentrations of SRP in the water column, while substantial concentrations of dissolved inorganic N, chiefly NH_4^+, were present (Figures 5 and 6); 2. The ratio of N to P in the water column of Florida Bay are much higher than the 16:1 of the Redfield ratio (Table 1, Figure 8); and 3.

The concentrations of chl-*a* in the water column were strongly, positively correlated to the concentration of measures of complex forms of P (dissolved organic P, particulate P and total P), but were not significantly related to any measure of either inorganic or organic N (Table 2, Figure 9).

Processes affecting water column characteristics

An often-used proxy for the relative importance of freshwater and oceanic sources to the water composition at a given position in an estuary is the concentration of materials with respect to salinity or chlorinity (Officer, 1979; Smith, 1984). Deviations from the concentrations of nutrients predicted by the conservative mixing of the two end-member waters required to produce the observed salinity are interpreted as indicators of the system acting as a source or sink (see Biggs & Cronin, 1981 for review). This technique works well for a system that can be approximated with a one-dimensional model, such as a river-dominated estuary or a lagoon in a desert with no appreciable riverine inputs. Unfortunately, a simple one-dimensional model does not adequately represent water flow within Florida Bay, because freshwater enters the bay along the entire northern margin of this triangular bay, seawater floods the bay along its entire western boundary, and variation in the precipitation-evaporation budget is unknown. Owing to these factors, salinity does not indicate the relative importance of freshwater runoff and ocean water to the chemical composition of the water at a particular location. Therefore, in order to evaluate the relative importance of nutrient sources to Florida Bay, we must analyse the two-dimensional distributions of material across the bay.

There were many pronounced spatial gradients in the 14 measured parameters (Figures 5–7). Principal components analysis provided a means of simplifying the interpretation of these gradients by identifying the underlying similarities in the individual patterns, thereby reducing the number of patterns to be analysed. The three component variables identified in the PCA explained more than 90% of the variance in the original data set (Table 3). Taken separately, each PC represents a different factor affecting the concentration of nutrients and chl-*a* in Florida Bay.

As evidenced by the hypersaline conditions (Figure 4), evaporation exceeded runoff and precipitation for Florida Bay, therefore there must have been a net advection of water into Florida Bay from the Gulf of Mexico to replace water lost due to evaporation. PC_1 was strongly correlated with salinity, TOC, TON and TN, and represented the effects of concentration of salt due to evaporation, and decomposition of organic matter. Maximum values for factor scores of PC_1, indicating the maximum concentration of materials due to evaporation, were found in the centre of Florida Bay [Figure 10(a)].

The concentrations of TOC and TON found in central Florida Bay were too high to be a product of evaporation-driven concentration alone. TOC and TON were more concentrated than Gulf of Mexico water by a factor of 6 (Figure 7), while salinity, a conservative tracer, was only 1·3 times as concentrated (Figure 4). The TOC and TON unaccounted for by simple concentration may be a result of the recent mass mortality and subsequent decomposition of over 4000 ha. of seagrass beds which was centred in central Florida Bay (Robblee *et al.*, 1991). The N:P of seagrass leaves from central Florida Bay is around 50:1 (Fourqurean *et al.*, 1992*a*), but TN:TP ratios of 100:1 to 140:1 occurred where PC_1 was high (Figures 8 and 10). If the source for the dissolved organic matter in central Florida Bay were decomposing seagrasses, an N:P ratio greater than 50:1 suggests either rapid uptake of the P from decomposing seagrass leaves, or substantial fixation of new N.

PC_{II} may be interpreted as an indicator of P availability, because all of the forms of complex P, as well as chl-*a*, were strongly correlated with PC_{II}, [Figure 10(b)]. SRP, however, was not as strongly correlated with PC_{II}, indicating that measures of SRP in the water column were of limited value when assessing the relative availability of P across Florida Bay.

The gradient in P availability across Florida Bay, as represented by PC_{II} [Figure 10(b)], suggested that P enters the system in northwest corner of Florida Bay from the near-shore waters of the Gulf of Mexico. Water advected into Florida Bay to balance the water lost from the bay due to evaporation brings P into Florida Bay, and the P is rapidly removed from the water column. The strong gradient in the TN to TP ratio in Florida Bay (Figure 8) is evidence of the rapid uptake of P, with respect to N, in Florida Bay. P taken out of the water column ends up in the sediments and seagrass biomass. The signal of P availability in the seagrass beds of Florida Bay (Fourqurean *et al.*, 1992*a*) mirrors the pattern in P availability in the water column suggested by PC_{II} [Figure 10(b)]. The closure of the PC_{II} isopleths against the shoreline in northwestern Florida Bay is a consequence of a turbidity maximum caused by recurrent sediment resuspension in a major tidal channel, and is not indicative of a major terrestrial source of P in the vicinity.

We can identify two factors that cause the majority of the P to enter Florida Bay near the northern end of its mouth instead of along the entire western margin of the bay: the difference in the source of the water just outside Florida Bay and the relative magnitude of turbulent mixing in the north and south. The water offshore of the northern end of the mouth of Florida Bay is very different in character from the water offshore of the southern end. The presence of distinct epibenthic fish (Sogard *et al.*, 1989) and decapod crustacean (Holmquist *et al.*, 1989*a*) faunas on the mudbanks from the northern and southern end of the mouth suggest a difference in the water masses just offshore of Florida Bay. At the northern end, the water is turbid and appears to be influenced by runoff from the Florida peninsula, while at the southern end, the water is much clearer and is influenced by the Gulf Stream and Atlantic Ocean. Concentrations of POM found in the water support this observation (Figure 7). Some of the rivers along the west coast of Florida have high natural and anthropogenic loads of P (Fraser & Wilcox, 1981), and may influence the water that gets advected into Florida Bay at the northern end of the mouth. At the southern end, however, the water is influenced by the oligotrophic Gulf Stream, which has very low concentrations of P.

Not only is the source of water different from the north to the south along the mouth of Florida Bay, but there is a gradient in tidal energy and therefore a gradient in the magnitude of the turbulent mixing of water between the Gulf of Mexico and Florida Bay. In a hypersaline estuary such as Florida Bay, turbulent mixing dominates the exchange of materials with the ocean. Near the northern end of the mouth, tidal range is almost 4 times as great as at the southern end (Holmquist *et al.*, 1989*b*), leading to greater mixing of Florida Bay and ocean waters in the north.

Freshwater input into Florida Bay ameliorated the concentration of salts due to evaporation in the northeast corner of the bay (Figure 4). The area of reduced salinities (below 44 ppt) in northeast Florida Bay was coincident with high factor scores on PC_{III} [Figure 10(c)]. The magnitude of PC_{III} was positively correlated with concentrations of dissolved inorganic N in the water column. There are two possible explanations of the high DIN values in northeast Florida Bay: 1. High loading rates of N with respect to P in freshwater runoff from the Everglades; and 2. the lack of utilization of inorganic N due to severe P limitation in northeast Florida Bay. Whatever the reason, it was clear that freshwater

runoff into northeast Florida Bay from the Everglades was not a major source of P, relative to N, for Florida Bay.

The concentrations of NH_4^+ in northeast Florida Bay were relatively high, with averages of over 4 μM over the course of this study (Figure 6), and a maximum value of 11·03 μM (Table 1). While these values seem very high compared to most tropical waters, they are typical of measurements from Florida Bay (Everglades National Park and South Florida Water Management District, unpubl. data). We have also checked the accuracy of our NH_4^+ determinations using standard benchtop wet chemistry (Parsons *et al.*, 1984) and a new fluorescence method (Jones, 1991); both of these methods corroborate the values reported in this paper.

The major form of DIN in the runoff of the Everglades is NH_4^+, while the major form of DIN in most freshwaters is NO_3^-. This is most likely due to an NH_4^+ source in the highly reducing sediments of the mangrove fringe of the Everglades (R.D. Jones, unpubl. data), and the suppression of nitrification. The Everglades are typified by high light levels reaching the sediment surface and high CO concentrations (R.D. Jones, unpubl. data); both of these conditions can suppress nitrification (Vanzella *et al.*, 1989).

Hypersalinity to the degree measured in this study is a common occurrence in Florida Bay at the present time; in central Florida Bay, periods of salinity greater than 50 ppt have occurred at least once a decade since the 1950's (M.B. Robblee, unpubl. data). However, hypersalinity of this magnitude may be at least partially due to man's modifications of the watershed for Florida Bay. Using evidence from fluorescent banding of a coral in southwest Florida Bay, Smith *et al.* (1989) estimated up to a 59% reduction of freshwater inflow to the bay as a result of upstream diversion of freshwater, beginning in about 1912. It is possible that before man so severely changed the hydrology of this area that freshwater flow from the Everglades may have played a more important role in delivering nutrients to northeast Florida Bay. The high ratio of N to P in the freshwater of the Everglades (> 350: 1, R.D. Jones, unpubl. data), however, suggests that even at increased flows the loading of P into northeast Florida Bay would be unimportant compared to P brought into Florida Bay from the Gulf of Mexico.

Evidence for P limitation of phytoplankton biomass

Ryther and Dunstan (1971) interpreted the observation that dissolved inorganic N concentrations are often undetectable when there are still measurable concentrations of dissolved inorganic P to be an indicator of general N limitation in the coastal marine environment. The opposite occurred in Florida Bay, with SRP concentrations very close to detection limits (Figure 5) and appreciable concentrations of DIN (Figure 6), suggesting P limitation of the water column in Florida Bay. However, standing stocks of nutrients are imperfect predictors of nutrient availability, because rapid regeneration may keep nutrient availability high, even though standing stocks are low (Howarth, 1988). Also, there are many phytoplankton species and communities capable of utilizing nutrients at concentrations far below detectable limits (Hecky & Kilham, 1988).

Phytoplankton require N and P in a ratio approximating the Redfield ratio of 16:1 (Redfield, 1958), and deviations of the ratio of dissolved inorganic N to dissolved inorganic P from 16:1 have often been used as an indicator of nutrient limitation (e.g. Boynton *et al.*, 1982). The DIN:SRP ratio in Florida Bay averaged 152:1, far above the Redfield ratio of 16:1, indicating potential P limitation. Because of the arguments against using inorganic nutrient concentrations as indicators of availability presented above, the interpretation of the ratio of two such measures can be questioned. Using the ratio of TN

to TP may avoid some of the problems associated with the DIN:SRP ratio. In a system with rapid recycling of nutrients, the concentrations of TN and TP measure the maximum possible relative availability of N and P. At the western edge of Florida Bay, where the bay opens to the Gulf of Mexico, TN:TP was near the Redfield ratio (Figure 8). In the centre of the bay, however, extreme deviations from 16:1 were found, with a baywide average of 101:1. This indicates a severe shortage of P with respect to N in the water column for most of Florida Bay.

The abundance of phytoplankton, as measured by chl-*a* concentration, was a function of the concentration of TP in Florida Bay (Figure 9). This finding was similar to Schindler's (1977) for whole-lake experiments: mean annual chlorophyll concentration of experimental lakes was a function of the mean annual TP concentration, regardless of the ratio of N:P in the loadings to the lake. The lack of a significant relationship between Florida Bay chl-*a* concentration and any measure of N concentration (Table 2) strengthens the contention that P availability limits phytoplankton biomass in Florida Bay.

These three lines of evidence all suggest that phytoplankton biomass in Florida Bay is limited by P availability, and that N is found in excess of phytoplankton needs. Other nearby embayments are not P limited, however, and have chlorophyll concentrations much higher than found in Florida Bay. In Tampa Bay (ca. 28°N, 82·5°W), chlorophyll concentrations ranged between 5–80 $\mu g\ L^{-1}$, and are considered light limited (Johansson *et al.*, 1982). In Charlotte Harbor (ca. 27°N, 82°W), a wide range of chlorophyll concentrations has been found, from 0·1–199 $\mu g\ L^{-1}$ (Fraser & Wilcox, 1981; McPherson *et al.*, 1990). In contrast to the apparent P limitation of Florida Bay, Charlotte Harbor is N limited. Because of very high concentrations of dissolved inorganic P in the freshwater inflow (up to 100 μM), the N:P ratio of the loadings to Charlotte Harbor is less than 1, consequently the DIN:SRP ratios in Charlotte Harbor are always less than 4, and usually less than 1 (Fraser & Wilcox, 1981; McPherson *et al.*, 1990).

Mechanisms contributing to P limitation of Florida Bay

As reviewed by Howarth (1988), the factors that control whether N or P will limit primary production in a coastal marine system are the ratio of N:P in the loadings to the system, the different biogeochemical processes acting on N and P in the system, and the potential for N fixation to supply N to the system. Each of these factors potentially is important in producing P limitation in Florida Bay.

The two sources of water-borne nutrient loadings into Florida Bay are freshwater runoff from the Everglades and exchange of water with the Gulf of Mexico. The N:P ratio in the freshwater loading is very high ($>350{:}1$, R.D. Jones, unpubl. data), while the N:P ratio of the loading from the Gulf of Mexico is close to the Redfield ratio ($<20{:}1$, Figure 8). The supply of excess N with respect to P in the runoff from the Everglades is an important factor responsible for P limitation of the Florida Bay system.

The steep gradient in the TN:TP from western Florida Bay to the centre of the bay, where the TN:TP was greater than 140:1 (Figure 8), indicated a rapid removal of P from the water advected into Florida Bay from the Gulf of Mexico. Because there are no significant water to atmosphere fluxes of P, the P withdrawn from water column must be ending up in the benthos. There are three main mechanisms for transfer of P from the water column to the benthos: 1. Sorption of P onto particles; 2. The settling of particulate forms of P; and 3. Active uptake of complex forms of dissolved P, especially by microorganisms. Once in the benthos, P seems to be tightly held and recycled, where it supports the significant, P limited primary production of the seagrasses that carpet Florida Bay.

We have not measured the magnitude of N fixation for Florida Bay, but in other tropical and subtropical lagoons N fixation has been shown to be very important. Using ecosystem nutrient budgets, Smith (1984) has calculated that N fixation is responsible for 56–97% of net N inputs to Shark Bay, Australia; Christmas Island Lagoon; and Canton Atoll. In a recent review, Howarth (1988) concluded that benthic N fixation may be the mechanism by which tropical, oligotrophic lagoons tend to be more P-limited than north-temperate lagoons. Seagrass beds can have very high rates of N fixation associated with them (Howarth *et al.*, 1988), but N fixation estimates have not been made for Florida Bay.

Seagrasses dominate the primary production of Florida Bay, with baywide average production rates of new seagrass leaves of about 0·4 gC $m^{-2}day^{-1}$ (Zieman *et al.*, 1989). Seagrasses are rooted on the bottom, and they require sufficient light penetration of the water column in order to survive. In many instances around the world, eutrophication of the water column has led to the extirpation of seagrass beds because reduction of light reaching seagrass leaves leads to reduced seagrass photosynthesis (e.g. Orth & Moore, 1983; Cambridge & McComb, 1984). Because of this, seagrasses are dominant primary producers only in areas where primary production in the water column is nutrient limited.

Due to the link between eutrophication of the water column and loss of seagrass cover from many areas around the world, it has been suggested that anthropogenic nutrients flowing into Florida Bay from agricultural and municipal areas in the watershed may be a factor in the recent dieoff of seagrasses in Florida Bay (e.g. Lapointe, 1989). While small scale loss of seagrass beds (within ca. 10–50 m of shore) has undoubtedly occurred adjacent to heavily developed residential canal systems (personal observations and B.E. Lapointe, pers. comm.), the nutrient measurements made in this study do not indicate any baywide eutrophication. In fact, our evidence suggests that the main source of P for the Florida Bay system is water exchange with the Gulf of Mexico, and that relatively little P enters Florida Bay via runoff from the Everglades. At the present time, there is no evidence that anthropogenic nutrients, especially P, are entering Florida Bay from the agricultural and municipal areas to the north of the bay. It is important to note, however, that the seagrass-dominated condition of Florida Bay is a direct result of the nutrient-limited nature of the water column. Anthropogenic inputs of large amounts of P to this system have the potential of releasing the nutrient limitation of the water column. In spite of the nutrient-limited nature of Florida Bay, inputs of large amounts of anthropogenic nutrients would not increase the seagrass productivity of this natural, seagrass-dominated system. The results of this in Florida Bay would surely be the same as elsewhere in the world: the loss of seagrass cover due to competition with phytoplankton and epiphytic algae for light.

Acknowledgements

We thank J. Bugden, R. Chambers, D. Childers, K. Halama, P. Lorenzo, M. McManus, and S. Pultz for help in collecting and analysing samples. R. Price, S. Smith and an anonymous reviewer commented on earlier versions of this paper. B. Hayden provided statistical consultation. Logistical support was provided by M. Robblee of South Florida Research Center in Everglades National Park and G. Powell at the National Audubon Society. Funding for this project was supplied through cooperative agreement no. CA-5280-0-9009 between USNPS and UVA, and cooperative agreement no. CA-5280-0-9010 between USNPS and FIU.

References

APHA 1980 Standard methods for the examination of water and wastewater, 15th edition. American Public Health Association. Washington, DC. 1134 pp.

Biggs, R. B. & Cronin, L. E. 1981 Special characteristics of estuaries. pp. 3–24. In *Estuaries and nutrients* (Nelson, B. J. & Cronin, L. E., eds). Humana, Clifton, New Jersey, 643 pp.

Bosence, D. 1989*a* Surface sublittoral sediments of Florida Bay. *Bulletin of Marine Sciences* **44,** 434–453.

Bosence, D. 1989*b* Biogenic carbonate production in Florida Bay. *Bulletin of Marine Sciences* **44,** 419–433.

Boynton, W. R., Kemp, W. M. & Keefe, C. W 1982 A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production. In *Estuarine comparisons* (Kennedy, V. S., ed.). Academic Press, New York, pp. 93–109.

Cambridge, M. L. & McComb, A. J. 1984 The loss of seagrasses in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany* **20,** 229–243.

DeKanel, J. & Morse, J. W. 1978 The chemistry of orthophosphate uptake from seawater on to calcite and aragonite. *Geochimica Cosmochica Acta* **42,** 1335–1340.

Fourqurean, J. W., Zieman, J. C. & Powell, G. V. N. 1992*a* Phosphorus limitation of primary production in Florida Bay: evidence from the C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography* **37,** 162–171.

Fourqurean, J. W., Zieman, J. C., Powell, G. V. N. 1992*b* Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology* **114,** 57–65.

Fraser, T. H. & Wilcox, W. H. 1981 Enrichment of a subtropical estuary with nitrogen, phosphorus and silica. pp. 481–498. In *Estuaries and nutrients* (Nelson, B. J. & Cronin, L. E., eds). Humana, Clifton, New Jersey, 643 pp.

Harrison, P. J., Hu, M. H., Yang, Y. P. & Lu, X. 1990 Phosphate limitation in estuarine and coastal waters of China. *Journal ofExperimental Marine Biology Ecology* **140,** 79–87.

Hecky, R. E. & Kilham, P. 1988 Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnology and Oceanography* **33** (4 part 2), 796–822.

Holmquist, J. G., Powell, G. V. N. & Sogard, S. M. 1989*a* Decapod and stomatopod communities of seagrass-covered mud banks in Florida Bay: Inter- and intra-bank heterogeneity with special reference to isolated subenvironments. *Bulletin of Marine Sciences* **44,** 251–262.

Holmquist, J. G., Powell, G. V. N. & Sogard, S. M. (1989*b* Sediment, water level and water temperature characteristics of Florida Bay's grass-covered mud banks. *Bulletin of Marine Sciences* **44,** 348–364.

Howarth, R. W. 1988 Nutrient limitation of net primary production in marine ecosystems. *Annual Review of Ecology* **19,** 89–110.

Howarth, R. W., Marino, R., Lane, J. & Cole, J. J. 1988 Nitrogen fixation in freshwater, estuarine and marine ecosystems. 1. Rates and importance. *Limnology Oceanography* **33** (4 part 2), 669–687.

Johansson, J. O. R., Steidinger, K. A. & Carpenter, D. C. 1982 Primary production in Tampa Bay, Florida: a review. pp. 279–297. In *Proceedings of the Tampa Bay area scientific information symposium* (Treat, S. A., Simon, J. L., Lewis, R. R., Whitman, R. L., eds), Bellwether Press, pp. 279–297.

Jones, R. D. 1991 An improved fluorescence method for the determination of nonamolar concentrations of ammonium in natural waters. *Limnology Oceanography* **36,** 814–819.

Lapointe, B. E. 1989 Macroalgal production and nutrient relations in oligotrophic areas of Florida Bay. *Bulletin of Marine Sciences* **44,** 213–323.

Lyngby, J. E. 1990 Monitoring the nutrient availability and limitation using the marine macroalgae *Ceramium rubrum* (Huds.) C.Ag. *Aquatic Botany* **38,** 153–161.

McComb, A. J., Atkins, R. P., Birch, P. B., Gordon, D. M. & Lukatelich, R. J. 1981 Eutrophication of the Peel-Harvey estuarine system, Western Australia. pp. 323–342. In *Estuaries and nutrients* (Nelson, B. J. & Cronin, L. E., eds), Humana, Clifton, New Jersey, 643 pp.

McPherson, B. F., Montgomery, R. T. & Emmons, E. E. 1990 Phytoplankton productivity and biomass in the Charlotte Harbor estuarine system, Florida. *Water Resources Bulletin* **26,** 787–800.

Officer, C. B. 1979 Discussion of the behaviour of nonconservative dissolved constituents in estuaries. *Estuarine Coastal Marine Science* **9,** 91–94.

Orth, R. J. & Moore, K. J. 1983 Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* **222,** 51–53.

Overland, J. E. & Preisendorfer, R. W. 1982 A significance test for principle components applied to a cyclone climatology. *Monthly Weather Review* **110,** 1–4.

Parsons, T. R., Maita, Y. & Lalli, C. M. 1984 A manual of chemical and biological methods for seawater analysis. Pergammon Press, New York, 173 pp.

Powell, G. V. N., Kenworthy, W. J. & Fourqurean, J. W. 1989 Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bulletin of Marine Sciences* **44,** 324–340.

Redfield, A. C. 1958 The biological control of chemical factors in the environment. *American Sciences* **46,** 561–600.

Robblee, M. B., Barber, T. R., Carlson, P. R., Durako, M. J., Fourqurean, J. W., Muehlstein, L. K., Porter, D., Yarbro, L. A., Zieman, R. T. & Zieman, J. C. 1991 Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress* **71,** 297–299.

Robblee, M. B., Tilmant, J. T. & Emerson, J. 1989 Quantitative observations on salinity. *Bulletin of Marine Sciences* **44,** 523.

Ryther, J. H., Dunstan, W. M. 1971 Nitrogen, phosphorus and eutrophication in the coastal marine environment. *Science* **171,** 1008–1013.

Scheidt, D. J. 1988 Nutrient enrichment in the Everglades. *National Wetlands Newsletter (May–June)*, 5–70.

Schindler, D. W. 1977 The evolution of phosphorus limitation in lakes. *Science* **195,** 260–262.

Short, F. T. 1987 Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquatic Botany* **27,** 41–57.

Smith, S. V. 1984 Phosphorus vs. nitrogen limitation in the marine environment. *Limnology Oceanography* **29,** 1149–1160.

Smith, T. J. III., Hudson, J. H., Robblee, M. B., Powell, G. V. N. & Isdale, P. J. 1989 Freshwater flow from the Everglades to Florida Bay: A historical reconstruction based on fluorescent banding in the coral *Solenastrea bournoni*. *Bulletin of Marine Sciences* **44,** 274–282.

Sogard, S. M., Powell, G. V. N. & Holmquist, J. G. 1989 Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida Bay mudbanks. *Bulletin of Marine Sciences* **44,** 179–199.

Solórzano, L. & Sharp, J. H. 1980 Determination of total dissolved phosphorus and particulate phosphorus in natural waters. *Limnology Oceanography* **25,** 754–758.

Strickland, J. D. H. & Parsons, T. R. 1972 A practical handbook of seawater analysis. *Bulletin Fishery Research Board Canada* **167,** 1–311.

Vanzella, A., Guerrero, M. A. & Jones, R. D. 1989 Effect of CO and light on ammonium and nitrite oxidation by chemolithotrophic bacteria. *Marine Ecology Progress Series* **57,** 69–76.

Zieman, J. C., Fourqurean, J. W. & Iverson, R. L. 1989 Distribution, abundance and productivity of seagrasses and macralgae in Florida Bay. *Bulletin of Marine Sciences* **44,** 292–311.