

Limnol. Oceanogr., 37(1), 1992, 162-171
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Phosphorus limitation of primary production in Florida Bay: Evidence from C:N:P ratios of the dominant seagrass *Thalassia testudinum*

Abstract—Florida Bay is a shallow, seagrass-dominated embayment on the southern tip of Florida. Variation of C, N, and P content of leaves of *Thalassia testudinum* was measured on two spatial scales: locally (10–100 m) in relation to a point source of nutrients associated with a bird colony in eastern Florida Bay and regionally (10–100 km) across all of the bay. Locally, the P content of leaves decreased from a high of 0.16% P (wt/wt) 30 m from the nutrient source to a low of 0.08% 120 m from the source; the C and N content (34.9 and 2.1%) was independent of distance from the nutrient source. Due to variations in P content, C:P and N:P, but not C:N, varied locally. Regionally, P content varied greatly, from 0.05 to 0.20%; C (29.4–39.5%) and N (1.7–2.7%) showed considerably less variation. Variation in C:P and N:P across the bay encompassed a range nearly as great as reported for all seagrasses around the world combined; C:N showed little variation. Local variation around the nutrient point source indicated that C:P and N:P were indicators of P availability, and trend analysis of the regional spatial variation in C:P and N:P showed that P availability was greatest in northwest, and least in eastern, Florida Bay. This pattern mirrored abundance of seagrasses and productivity in the bay. *T. testudinum* from the bay appears to be P limited and N saturated, even in the sparsest seagrass communities.

The dominant primary producer in Florida Bay is the seagrass *Thalassia testudi-*

Acknowledgments

We thank K. Halama, M. McManus, S. Pultz, and A. H. Powell for assistance with field collections and D. Yozzo, R. Cutter, and D. Osgood for help with laboratory analysis. S. L. Williams, R. M. Chambers, D. L. Childers, and two anonymous reviewers made comments on earlier drafts of this paper that strengthened the finished work. Salinity data in Fig. 2 were collected in conjunction with J. Bugden and R. Jones of Florida International University. The National Audubon Society research office in Tavernier, Florida, provided laboratory space and logistical support. M. Robblee of Everglades National Park research center supplied boats, laboratory space, and discussion.

Financial support was provided by a John D. and Catherine T. MacArthur Foundation grant to the National Audubon Society and a National Park Service Cooperative Agreement (contract CA-5280-0-9009) with J.C.Z. at the University of Virginia.

Over a range of two orders of magnitude in standing crop, areal leaf productivity of *T. testudinum* shows a consistent and linear relationship to leaf standing crop ($r^2 = 0.92$, Zieman et al. 1989). This relationship holds over a wide range of sediment properties and water depths. Because of this pattern, any factor controlling the standing crop of *T. testudinum* in the bay will also control the primary production of this dominant autotroph.

Florida Bay is a roughly triangular embayment on the southern tip of the Florida peninsula (~25°N, 81°W; Fig. 1). It is bounded on the north by the mainland of Florida and on the south and east by the emergent Pleistocene reef ridge of the main Florida Keys. Its western margin is open to the Gulf of Mexico, and it receives freshwater runoff from the Everglades that lie directly to the north. In all but the wettest years, it is a negative estuary, with hypersalinity caused by evaporation exceeding freshwater inputs (Fig. 2).

The entire bottom of this shallow (<3 m) bay is dominated by seagrasses, but there is a strong gradient in the development of the seagrass community from the enclosed northeastern sections of the bay to the open western sections (Zieman et al. 1989). The communities of northeast Florida Bay are generally dominated by sparse *T. testudinum*, with somewhat denser cover on localized areas of increased sediment accumulation. Seagrass cover increases dramatically toward the west, where dense stands of *T. testudinum* are often intermixed with the seagrasses *Halodule wrightii* and *Syringodium filiforme*. The sparse *T. testudinum* communities of northeast Florida Bay are nutrient limited (Powell et al. 1989, 1991). Upon fertilization with bird excrement, seagrass density increases and *H. wrightii* replaces *T. testudinum* as the dominant species. Seagrass beds from many

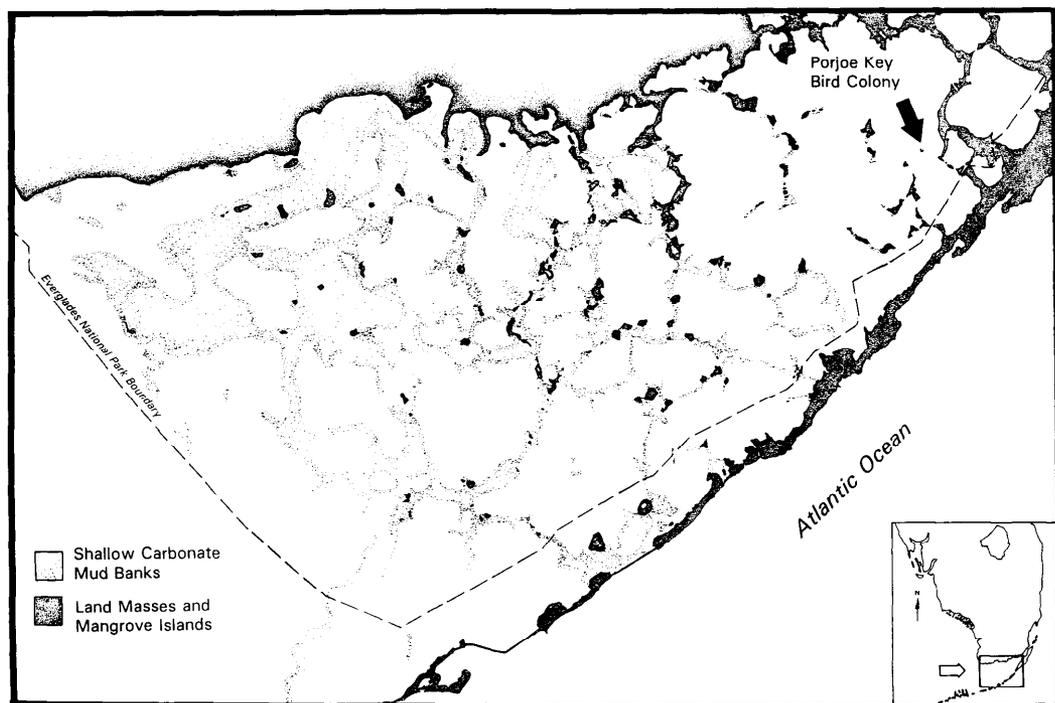


Fig. 1. Map of Florida Bay. Position of the Porjoe Key bird colony is indicated.

other locations have also been shown to be nutrient limited (e.g. Orth 1977; Short et al. 1990).

Elemental composition of plant biomass has been used to assess the nutrient status of plant's environment. The composition of marine phytoplankton tends toward the Redfield ratio (Redfield 1958) of 106 mol C : 16 mol N : 1 mol P, and deviations from this ratio have been used to infer nutrient limitation in phytoplankton. The nutrient content of plant tissue has been shown to be an indicator of the nutrient availability for macrophytes as well as phytoplankton (Gerloff and Kromholz 1966), but the well-known Redfield ratio cannot be used for seagrasses due to the increased complexity and structural carbohydrate composition of benthic plants over phytoplankton (Atkinson and Smith 1983). Atkinson and Smith (1983) suggested a macrophyte analog for the phytoplankton Redfield ratio of 550 mol C : 30 mol N : 1 mol P and noted a difference in C : N : P ratios between macrophyte species from areas of high nutrients and those from low-nutrient environments. Species

from low-nutrient environments have substantially higher proportions of C to N and P than those from more nutrient-rich areas.

In addition to these interspecies differences, nutrient availability affects elemental composition of tissues of single macrophyte species. *Zostera marina* grown in a highly organic mud has a lower C : N ratio than *Z. marina* grown in a low-organic, and presumably lower nutrient, sandy substratum (Short 1987). C : N : P ratios of the macroalgae change upon experimental P enrichment, and seasonal shifts in C : N : P of macroalgae have been used to infer seasonality in nutrient limitation (e.g. Lapointe 1987).

In northeast Florida Bay, additions of bird feces to seagrass beds increases the N and P contents of leaf tissue of *H. wrightii* and the P content of *T. testudinum* leaves (Powell et al. 1989). In the Bahamas, addition of either N or P changes the N : P ratio of *S. filiforme*, with N addition raising the N : P and P addition lowering the N : P (Short et al. 1990).

Large bird colonies occupy a few of the mangrove islands in northeast Florida Bay.

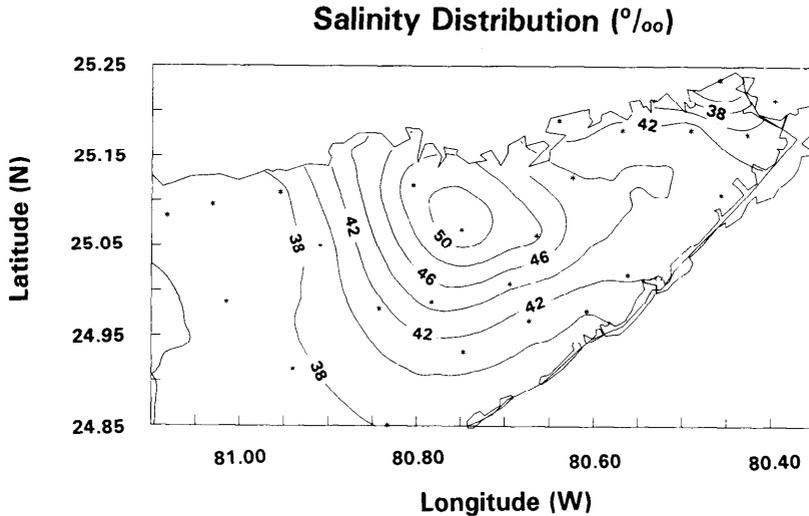


Fig. 2. Map of salinity isopleths in Florida Bay. Data represent averages from eight cruises conducted between June 1989 and July 1990.

Associated with these colony islands are extensive areas of increased seagrass density that extend 100–200 m from the colony islands. These dense seagrass beds, found in an otherwise sparsely vegetated and nutrient-limited area, are caused by large nutrient inputs from bird feces deposited on the islands (Powell et al. 1991). These bird colonies are analogous to point sources of nutrient supply in an otherwise nutrient-limited, oligotrophic area.

In this study, we propose that the nutrient content of leaves of the dominant seagrass in the bay, *T. testudinum*, can be used as an indicator of the relative availability of N and P in the Florida Bay system. To investigate the validity of elemental composition as indicators of nutrient status over the regional scale, we examine the local variation in nutrient content of *T. testudinum* leaves in relation to a point source of nutrients associated with a bird colony. Further, we hypothesize that the regional gradient in seagrass density, and therefore primary production, across the bay is caused by nutrient availability. The variation in nutrient availability should manifest itself as decreasing N and P content from the dense seagrass beds of western Florida Bay to the sparse beds of the northeastern portions of the bay.

To determine variation in the nutrient content of *T. testudinum* leaves near the localized nutrient inputs associated with bird

colonies, we collected samples along three separate transects perpendicular to the shoreline of Porjoe Key, a small island (~1 ha) with a large bird colony consisting of ~640 pairs of birds (Powell et al. 1991) in northeast Florida Bay (Fig. 1). Samples were taken at distances of 30, 60, 90, and 120 m from the shore.

Fifty sites, located arbitrarily across the bay, were sampled to assess the regional variation in nutrient content of *T. testudinum* leaves. These samples were collected in various environments and water depths. Core tubes (15-cm diam) were used to collect three replicate subsamples from each sampling location during summer 1987, 1988, and 1989. Green leaf tissue was separated from nonphotosynthetic biomass in the core. Leaves were gently scraped and washed in flowing tapwater to remove adhering epibionts and sediments. These washed samples were lyophilized to a constant weight and homogenized by milling to a fine powder. Standing crop was determined as the dry weight of the green leaves per square meter.

C and N contents were determined for duplicate subsamples of each sample by oxidation in a Carlo Erba model 1500 CHN analyzer. P content was measured with a modification of the method presented by Solórzano and Sharp (1980) for particulate total P determination. Duplicate subsam-

Table 1. Variation in nutrient concentration (as % of dry wt) of *Thalassia testudinum* leaf tissue as a function of distance from the bird colony island, Porjoe Key, and the results of one-way ANOVA for each element.

| Distance from island (m) | %C | %N | %P |
|--------------------------|------------|-----------|-------------|
| 30 | 34.76±0.06 | 2.10±0.18 | 0.161±0.002 |
| 60 | 34.82±1.72 | 2.12±0.06 | 0.120±0.015 |
| 90 | 34.86±0.86 | 2.10±0.14 | 0.097±0.010 |
| 120 | 35.08±0.02 | 2.14±0.01 | 0.078±0.001 |
| ANOVA results | | | |
| <i>F</i> -ratio | 0.04 | 0.04 | 30.88 |
| <i>P</i> | 0.98 | 0.99 | 0.003 |

ples of each sample were weighed (5–20 mg) into tared, glass scintillation vials; 0.5 ml of 0.17 M Na₂SO₄ and 2.0 ml of 0.017 M MgSO₄ were added to each vial, and the vials were dried in an oven at 90°C. Standards were treated identically. Dry vials containing samples and standards then were ashed at 500°C for 3 h. After cooling, 5.0 ml of 0.2 N HCl was added to each vial, the vials were capped and then placed in an oven at 80°C for 30 min. Each vial was diluted with 10.0 ml of deionized water, shaken, and allowed to stand overnight to allow the ash to settle. Phosphate concentration of the solution in the vials was determined colorimetrically. We found this method to yield 95–103% of the reported P content of NBS standard orchard leaves.

Variation in nutrient content of *T. testudinum* leaves around the bird colony island was examined with ANOVA examining the effect of distance from the islands on the percent C, N, and P (wt/wt) of the leaf tissue. For the samples collected from across the bay, the relationships between the C:N, C:P, and N:P of seagrass leaves and seagrass standing crop were examined with linear regression.

Evaluations of the spatial trends in the plant elemental composition across the bay were made with trend surface analysis (Legendre and Fortin 1989). C:P, C:N, and N:P molar ratios were computed for each sample, and these values were plotted against geographic position. Polynomial equations of the *X* (–1 × long) and *Y* (lat) spatial coordinates were fitted to each data set (C:P, C:N, and N:P) with least-squares regression. The appropriate degree of the trend surface for each data set was determined with stepwise regression, with each step being an increase in the degree of the trend

surface. Only steps that significantly increased the *r*², as measured by a statistically significant (*P* = 0.05) increase in *F*, were allowed.

There was no systematic variation in C or N content of *T. testudinum* leaves as a function of distance from the local nutrient source of the bird colony island, but there were significant differences in P content (ANOVA, *F* = 30.88, *P* = 0.003, Table 1). Leaves of plants from 30 m had twice as much P (as % of dry wt) as those from 120 m. Due to the lack of differences in C or N content, there were no significant differences in C:N as a function of distance from the nutrient source (Fig. 3). There were large differences in C:P and N:P, with low values close to the island that increased with distance from it (Fig. 3); these strong gradients were caused by differences in P content and constant C and N content.

The concentration of P in *T. testudinum* leaf tissue varied widely in the samples collected from across the bay, while the concentration of C and N showed considerably less variation (Table 2). There was about a fourfold difference between the minimum and maximum obtained for %P (0.05–0.20%), but %C varied from 29.4 to 39.5% and %N varied from 1.71 to 2.67%. The mean C, N, and P concentrations (±1 SD) were 34.6±2.0%, 2.20±0.23%, and 0.095±0.039%.

Due to relatively constant concentrations of C and N in the leaf tissue, coupled with a large range of P concentrations, C:P and N:P ratios varied fourfold, but C:N ranged from only 15.7 to 22.8 (Table 2). The mean C:P, C:N, and N:P ratios (±1 SD) were 1,070±340, 18.5±1.9, and 58.6±19.3.

There were strong relationships between P content of leaves and seagrass standing

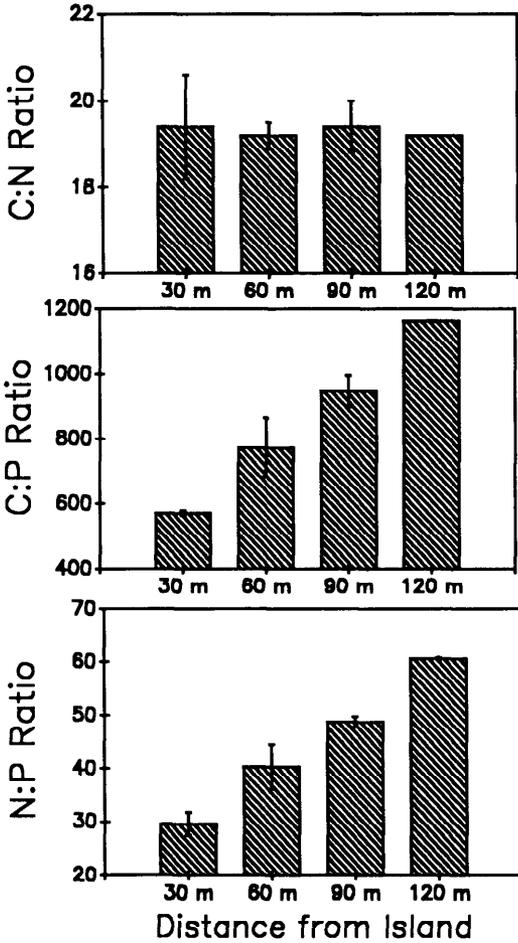


Fig. 3. C : N : P ratios as a function of distance from the Porjoe Key bird colony island. Error bars indicate ± 1 SE, $n = 3$.

crop, but standing crop was independent of N content. At high P content (low C : P), standing crop was high, and at low P content (high C : P), standing crop was low (Fig. 4). This relationship explained about a third of the variation in the data ($r^2 = 0.37$) and was statistically highly significant ($F = 27.3$, $P < 0.001$). A similar result was obtained with N : P as a predictor of standing crop ($r^2 = 0.31$, $F = 20.8$, $P < 0.001$). N content of seagrass leaves, as measured by C : N, showed no relationship to seagrass standing crop ($r^2 < 0.01$, $F = 0.01$, $P = 0.91$).

Three-dimensional scatterplots of the elemental ratios of *T. testudinum* leaves vs. geographic sampling location indicated

Table 2. Summary of the results of elemental analysis of *Thalassia testudinum* leaf tissue from 50 sites across Florida Bay. Percentages calculated on a wet element/dry wt basis; ratios calculated on a mol/mol basis.

| | %C | %N | %P | C : P | C : N | N : P |
|--------|------|------|-------|-------|-------|-------|
| Mean | 34.6 | 2.20 | 0.095 | 1,070 | 18.5 | 58.6 |
| SD | 2.0 | 0.23 | 0.039 | 340 | 1.9 | 19.3 |
| SE | 0.3 | 0.03 | 0.005 | 48 | 0.3 | 2.7 |
| Median | 34.3 | 2.24 | 0.074 | 1,138 | 17.9 | 62.4 |
| Min | 29.4 | 1.71 | 0.053 | 448 | 15.7 | 20.3 |
| Max | 39.5 | 2.67 | 0.201 | 1,721 | 22.8 | 89.4 |

some obvious spatial patterns (Fig. 5). C : P and N : P ratios were lower in the western parts of the bay and larger in the north and east, indicating that leaves in the western sections contained more P, relative to C and N, than leaves from the northern and eastern sections. Any spatial pattern in the C : N data was less clear. Note that the range of values for C : N was much smaller than for C : P or N : P (Fig. 5).

Trend surface analysis indicated that there were highly significant spatial trends in elemental ratios. First-degree trend surfaces explained ~60% of the variation in the C : P and N : P data (Table 3, Fig. 6). These first-degree surfaces produced isopleths that ran from southwest to northeast, with minima in the northwest and maxima in the east. The spatial relationship in the C : N data was more complex: a second-degree trend surface explained 47% of the variation in C : N. This second-degree surface had a minimum in central Florida Bay behind the main line of the Florida Keys, with C : N values increasing in all directions within the bay from that minimum.

Bird colonies are large point sources of nutrients in the Florida Bay system. Single birds can deposit as much as 4 g (dry wt) d^{-1} of nutrient-rich feces (Powell et al. 1989), and colonies typically contain as many as 1,000 pairs of birds (Powell et al. 1991). Bird feces contains high concentrations of both P and N (3.6% P and 19.3% N by wt, N : P = 11.8, Powell et al. 1989). The amount of P in *T. testudinum* leaves collected from around Porjoe Key bird colony showed a strong gradient with distance from the source of nutrients, but the concentration of N in

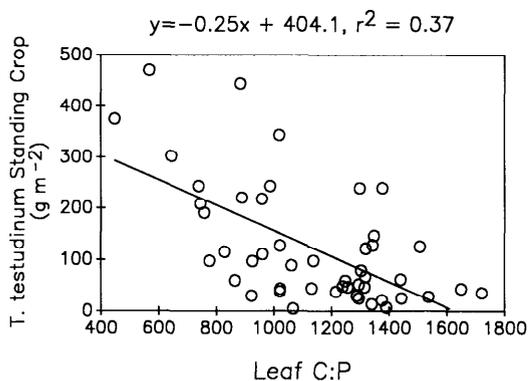


Fig. 4. The relationship between leaf C:P and standing crop of *Thalassia testudinum*. The linear relationship was statistically significant.

the leaves did not change (Table 1, Fig. 3), indicating that *T. testudinum* around the bird colonies incorporated more P, but not more N, into leaf tissue in response to increased nutrient availability. Thus, P content of leaves is a good indicator of the availability of P in this environment. The lack of a response to increased N availability indicates that *T. testudinum* is N saturated, even as far as 120 m from the source of nutrients in a very oligotrophic area. This result agrees with earlier results (Powell et al. 1989) indicating that *T. testudinum* beds are P limited in northeast Florida Bay.

Atkinson and Smith (1983) documented variation in the elemental ratios of seagrass leaf tissue on a global scale and noted that plants collected from high-nutrient environments had lower C:N and C:P ratios than plants collected from low-nutrient environments. Since that publication, more work has been done on elemental ratios of seagrasses (Table 4). These studies indicate that there is a wide range in the concentrations of C, N, and P in seagrasses. Although this global variation seems large, the variation in C:P and N:P for Florida Bay *T. testudinum* leaves (Table 2) is almost as great as all of the documented variation for 19 other seagrass species from around the world combined (Table 4). The mean and the median of the Florida Bay *T. testudinum* C:P are greater than all but one reported C:P value in the literature, and the mean and median of the N:P are both greater than

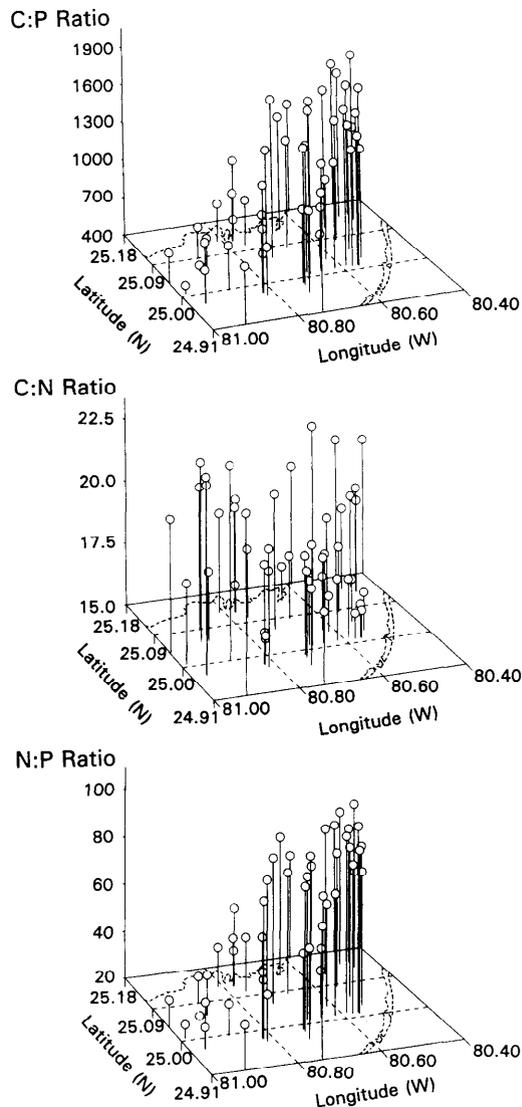


Fig. 5. Three-dimensional scatterplots of C:P, C:N, and N:P data. Note that the scales of the Z-axes vary.

the previously reported maximum N:P. There is very little variation in the C:N of Florida Bay *T. testudinum* leaves compared to the literature, and all of the values were lower than the literature mean and median C:N of 25. These results indicate that, when compared to seagrasses from around the world, *T. testudinum* leaves from Florida Bay have much lower P content and higher N content than average. These deviations suggest P limitation of seagrasses in the bay.

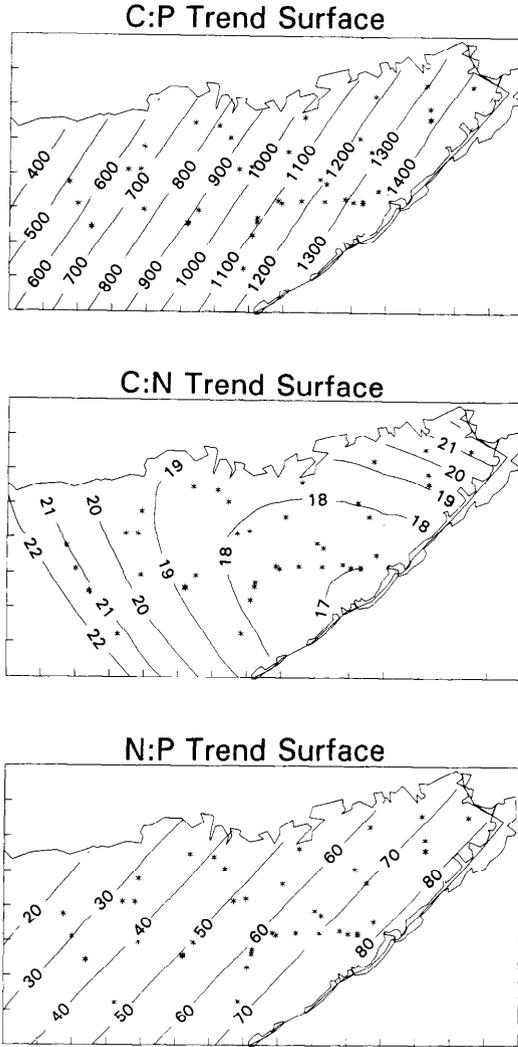


Fig. 6. Plots of the isopleths of the trend surfaces of C:P, C:N, and N:P given in Table 3. Asterisks indicate sampling locations.

Across the bay, the standing crop of *T. testudinum* was positively correlated with the amount of P in the leaf tissue (Fig. 4). These data suggest that P availability, as measured by P content of the leaves, influ-

ences primary production, because standing crop serves as a proxy for leaf production in the bay (Zieman et al. 1989). Conversely, the data suggest that N availability is not a factor controlling seagrass standing crop or leaf production in the bay. The variation in the *T. testudinum* standing crop not explained by variation in the P content of the leaves (Fig. 4) was probably due to the large range in other environmental variables across the bay. Light limitation of seagrasses may play a large role in controlling seagrass standing crop, especially in areas of high turbidity or very dense seagrass beds. Environmental stability and sediment characteristics, such as texture and depth, may also contribute to variation in the standing crop.

There is an ongoing controversy over what nutrient ultimately limits primary production in the marine environment, with N and P implicated most often. Redfield (1958) suggested that P availability must ultimately limit primary production, because microorganisms are capable of fixing atmospheric N. In other words, if there is P available, there is a mechanism to make N available. This view is generally held by marine geochemists, who generally deal with large temporal and spatial scales. Marine biologists work on smaller time and space scales, however. They point to work with experimental cultures of phytoplankton that suggests N is most often limiting to population growth rates (e.g. Goldman et al. 1979). Ryther and Dunstan (1971) concluded that N is generally limiting to primary production in coastal waters, because N fixation is not effective in supplying N on small time and space scales, although it may be important in the geochemical balance of C:N:P.

Limnologists have shown that P is limiting in lakes. Lakes tend to be more closed

Table 3. Results of the least-squares regression fitting of trend surfaces describing spatial variation in elemental composition (Z) of *Thalassia testudinum* leaves from Florida Bay. X = -1 (long), Y = lat.

| Elemental ratio | Trend surface equation | R ² | F-ratio | P |
|-----------------|-------------------------------------------------------------|----------------|---------|---------|
| C:P | $Z = 1.84E5 + 1,870X - 1,260Y$ | 0.59 | 33.9 | <0.0001 |
| C:N | $Z = 7.31E4 + 2,320X + 1,630Y + 21.5X^2 + 41.6Y^2 + 45.9XY$ | 0.47 | 7.9 | <0.0001 |
| N:P | $Z = 1.18E4 + 113X - 107Y$ | 0.63 | 40.4 | <0.0001 |

Table 4. Elemental composition (atomic ratios) of seagrass leaf material from field studies examining both N and P.

| Species | Location | C:P | C:N | N:P | Reference |
|---------------------------------|---------------|-------|-----|-----|-------------------------|
| <i>Amphibolis griffithii</i> | W. Australia | 535 | 27 | 20 | Atkinson and Smith 1983 |
| <i>Amphibolis antarctica</i> | W. Australia | 343 | 24 | 14 | Walker and McComb 1988 |
| <i>Cymodocea nodosa</i> | Corsica | 408 | 27 | 15 | Atkinson and Smith 1983 |
| <i>Cymodocea serrulata</i> | N. Queensland | | | 19 | Birch 1975 |
| <i>C. serrulata</i> | N. Queensland | 638 | 35 | 18 | Atkinson and Smith 1983 |
| <i>Enhalus acoroides</i> | N. Queensland | | | 16 | Birch 1975 |
| <i>E. acoroides</i> | N. Queensland | 444 | 25 | 18 | Atkinson and Smith 1983 |
| <i>E. acoroides</i> | Palau | 1,000 | 21 | 48 | Atkinson and Smith 1983 |
| <i>Halodule univervis</i> | N. Queensland | | | 13 | Birch 1975 |
| <i>H. univervis</i> | N. Queensland | 623 | 35 | 18 | Atkinson and Smith 1983 |
| <i>Halodule wrightii</i> | Florida Bay | | | 58 | Powell et al. 1989 |
| <i>H. wrightii</i> | Texas | | | 18 | Pulich 1989 |
| <i>Phyllospadix scouleri</i> | California | 509 | 21 | 24 | Atkinson and Smith 1983 |
| <i>Posidonia australis</i> | W. Australia | 197 | 33 | 6 | Walker and McComb 1988 |
| <i>Posidonia oceanica</i> | Corsica | 956 | 25 | 39 | Atkinson and Smith 1983 |
| <i>Posidonia ostenfeldia</i> | W. Australia | 1,070 | 37 | 29 | Atkinson and Smith 1983 |
| <i>Posidonia sinuosa</i> | W. Australia | 512 | 32 | 16 | Atkinson and Smith 1983 |
| <i>Ruppia maritima</i> | Virginia | 457 | 16 | 29 | Atkinson and Smith 1983 |
| <i>R. maritima</i> | Texas | | | 18 | Pulich 1989 |
| <i>Syringodium isoetifolium</i> | N. Queensland | | | 13 | Birch 1975 |
| <i>Syringodium filiforme</i> | Bahamas | 1,390 | 30 | 47 | Short et al. 1985 |
| <i>Thalassia hemprichii</i> | N. Queensland | 599 | 22 | 27 | Atkinson and Smith 1983 |
| <i>Thalassia testudinum</i> | Barbados | | | 32 | Patriquin 1972 |
| <i>T. testudinum</i> | Florida Bay | | | 44 | Powell et al. 1989 |
| <i>Zostera capricorni</i> | N. Queensland | | | 17 | Birch 1975 |
| <i>Z. capricorni</i> | N. Queensland | 302 | 34 | 9 | Atkinson and Smith 1983 |
| <i>Zostera marina</i> | California | 274 | 7 | 38 | Atkinson and Smith 1983 |
| <i>Z. marina</i> | Virginia | 584 | 14 | 41 | Atkinson and Smith 1983 |
| <i>Z. marina</i> | Rhode Island | 481 | 18 | 27 | Atkinson and Smith 1983 |
| Mean | | 596 | 25 | 25 | |
| Median | | 509 | 25 | 19 | |
| Min | | 197 | 7 | 6 | |
| Max | | 1,390 | 37 | 58 | |
| No. of values | | 19 | 19 | 29 | |
| No. of species | | 16 | 16 | 19 | |

systems than the coastal ocean or estuaries and therefore have relatively long residence times of water. Schindler (1981) suggested that short residence times of water in coastal areas would flush the products of N fixation and remineralization out of the area, allowing for N limitation. Conversely, Smith (1984, p. 1159) concluded that "if hydrographic fluxes are small, then biochemical fluxes of nitrogen are likely to obviate nitrogen limitation while phosphorus is exhausted." High-salinity embayments, or inverse estuaries, have long water residence times because water exchange is dominated by mixing instead of stream flow. Shark Bay (Smith and Atkinson 1984) and Spencer Gulf (Smith and Veeh 1989), two inverse estuaries in Australia, have been shown to

be P limited. Both are dominated by seagrasses and have very low nutrient concentrations in the water column.

In Shark Bay, the C:P ratio of benthic macrophyte biomass increases greatly from the outer, oceanic mouth of the bay through the interior metahaline and hypersaline regions as a result of decreased P availability from the open ocean to the interior of the bay (Atkinson 1987). Similarly, the pattern of C:P and N:P ratios of leaf tissue from *T. testudinum* across Florida Bay (Fig. 6) suggests that P availability decreases greatly from a maximum in the more oceanic northwest to a minimum in the enclosed east. In contrast, the C:N ratio pattern (Fig. 6) shows that relative N availability is greatest in the center of the bay.

From the salinity isopleths (Fig. 2), it can be seen that some freshwater enters the eastern half of the bay, ameliorating the increase in salinity caused by evaporation. Because of tidal exchange with the Gulf of Mexico and the evaporation-driven advection of water into the bay, the water residence time roughly correlates with the distance into the bay from the western edge. The maximum N availability in the center of the bay, as indicated by C:N ratios (Fig. 6), may be a consequence of interacting factors. The relatively long water residence times of the central bay compared to the western bay would allow the slow accumulation of N via N fixation. Increased development of the sediments in the central portion of the bay, compared to the eastern bay, may promote N fixation and facilitate retention of fixed N in the system.

The pattern of maximal P availability in the northwest and minimal P availability in the east (Fig. 6) suggests that the source of P for Florida Bay lies toward the west of the bay. We hypothesize the source of P for the bay is dissolved and suspended P in water brought in from the Gulf of Mexico by tidal mixing and net advection caused by evaporation across the bay. The pattern in nutrient availability would be sharpened by removal of P by the seagrass communities near the source. Further, the pattern in P availability suggests that little, if any, P is brought into the bay via freshwater runoff from the Everglades.

Florida Bay is similar to Shark Bay and Spencer Gulf in three respects: all have dominant seagrass communities, all are inverse estuaries for extended periods, and all are P limited. The long residence time of water in Florida Bay indicated by its hypersaline nature is a potential cause of P limitation of primary production in the bay. Another potential contributing factor to P limitation is the composition of sediments in the bay. Generally, seagrass leaves are bathed in low-nutrient waters, while their belowground roots and rhizomes occur in the enriched medium of pore water (see Short 1987). Seagrasses growing in terrigenous sediments seem to have ample P for growth, but lack N. However, there is evidence that P is limiting to seagrass growth

in biogenic carbonate sediments (Short et al. 1985; Powell et al. 1989). The biogenic carbonate sediment in Florida Bay has the ability to bind inorganic phosphate, potentially rendering it unavailable to primary producers (Short 1987).

Due to the oligotrophic nature of the water generally overlying seagrasses, the primary nutrient source for seagrass growth is the interstitial water of the sediments in which they are rooted (Short 1987). The concentration of nutrients in pore water is a function of not only the present rate of nutrient supply to the sediments, but also long-term diagenesis. Therefore, in a coastal sedimentary environment, nutrient concentration in the sediment is a long-term integrator of nutrient availability. The nutrient concentrations of seagrass tissue therefore provide a tool for examining nutrient availability over much longer time scales than could be determined by typical field research. Whatever the ultimate reason for P limitation of Florida Bay, this study indicates that the spatial pattern in nutrient content of seagrass tissues may be used to infer ecosystem-scale phenomena.

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Submitted: 6 February 1991

Accepted: 8 August 1991

Revised: 9 September 1991