

# Nutrient content of seagrasses and epiphytes in the northern Gulf of Mexico: Evidence of phosphorus and nitrogen limitation

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## Abstract

We examined C:N:P ratios of seagrass leaves and epiphytic algae from the eastern shoreline of Grand Bay (Alabama, USA) and the entire shoreline of Big Lagoon (Florida, USA) during the summer of 2001 and March 2003, and used contour plotting of N:P ratios in both locations to examine spatial trends in our data. Results indicated phosphorus limitation for seagrass and epiphytes in each bay. In addition, C:N, C:P, and N:P ratios in both locations showed differences between summer and wintertime values for seagrasses; however, the only epiphytic elemental ratios to differ were C:P and N:P ratios in Grand Bay. Within Grand Bay, phosphorus limitation was stronger in epiphytes than seagrasses, with the largest amount of variation in N:P ratios occurring adjacent to the only developed land on the shoreline. In Big Lagoon, two distinct areas were present in N:P contour plots: the eastern end of the bay that was influenced by water from the Gulf of Mexico and Santa Rosa Sound, and the western end of the bay that was most influenced by Perdido Bay and a developed area along the northern shoreline. Detection of phosphorus limitation within Big Lagoon was not surprising, as both input sources to Big Lagoon are known to be low in phosphorus. However, phosphorus limitation in Grand Bay was unexpected, as both “feeder systems” (Mobile Bay and the Mississippi Sound) have high ambient phosphorus levels. As a result, C:N:P ratios from seagrasses and epiphytes may not accurately reflect ambient nutrient levels in Grand Bay due to decreased availability of some forms of phosphorus or increased competition for the uptake of phosphorus. Overall, our C:N:P analysis suggested that not only was P limitation greater than N limitation in Grand Bay and Big Lagoon, but patterns of nutrient limitation varied both temporally and geographically for inter- and intra-bay comparisons.

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## 1. Introduction

Early detection of eutrophication in marine ecosystems is critical, yet the value of traditional water quality monitoring programs is often questioned (Tomasko et al., 1996). Comparing deviations in the ratios of carbon, nitrogen and phosphorus (C:N:P) retained within plant tissue has been used extensively as an alternative mean of evaluating the nutrient status of coastal waters (Duarte, 1990). In the classic study of marine phytoplankton, Redfield et al. (1963) noted that the ratios of these nutrients tend towards 106:16:1 (i.e. Redfield ratio). In addition, nutrient ratios of epiphytic periphyton have

been documented to be similar to phytoplankton with C:N:P ratios of 119:17:1 (Hillebrand and Sommer, 1999). However, seagrasses and other benthic marine plants possess large quantities of structural carbon, resulting in “seagrass Redfield ratios” tending towards 550:30:1, well above the average phytoplankton ratios (Atkinson and Smith, 1983). Like phytoplankton, seagrasses growing in eutrophic waters have C:N:P ratios that reflect elevated nitrogen and phosphorus levels (Duarte, 1990). Plants residing in nutrient poor waters show significantly higher C:N and/or C:P ratios than those from nutrient rich conditions (Atkinson and Smith, 1983). N:P ratios can also reflect ambient nutrient regimes (Guesewell et al., 2003) and may be more useful than C:N and C:P ratios because they are not reliant on structural carbon, thus reducing inter-plant variability and allowing for a more accurate snapshot of recent water quality. For seagrasses, N:P ratios in excess of 30

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are considered to be evidence of P limitation and ratios less than 25–30 are considered to show N limitation (Duarte, 1990; Fourqurean and Cai, 2001). Continuous monitoring of C:N:P ratios may be advantageous for the early detection of changes in nutrient regimes for environmentally sensitive seagrasses.

In marine ecosystems, nutrients and light are the most common limiting factors that control biomass of primary producers—and these factors are interrelated. Low nutrient, oligotrophic systems tend to have high light availability reaching the benthos, while high nutrient, eutrophic ecosystems have little light reaching the benthos. According to Liebig's law of the minimum, only one factor limits primary producers, and for seagrass beds, the most common factors are light and nutrients. Hence, in low-light environments, one expects to find seagrass and epiphyte C:N:P ratios approaching their respective "Redfield ratios;" and substantial deviation from these "Redfield" values indicates that there is sufficient light to support more biomass and that nutrient supply is the limiting factor (see Fourqurean and Rutten, 2003; Fourqurean et al., 2005).

The current paradigm for nutrient limitation suggests that nitrogen limitation is common in estuarine systems (Howarth and Marino, 1988; Howarth et al., 1988), while phosphorus limitation is more common in freshwater systems (Schelske et al., 1986; Smith et al., 1999). However, this paradigm was derived from research in cool temperate systems (Murrell et al., 2002) and may not be applicable under other conditions (Guildford and Hecky, 2000; Murrell et al., 2002). Recent literature suggests that in some sub-tropical to tropical marine environments P limitation (i.e. Shark Bay, Australia (Atkinson and Smith, 1983) and Florida Bay (Fourqurean et al., 1992)) and iron (Fe) limitation is common (Duarte et al., 1995). However, this limitation can be highly variable, depending on location. For example, inshore seagrass beds along the Atlantic coast of the Florida Keys responded to nitrogen and phosphorus, while offshore seagrasses (~5 km separation) were strongly limited by nitrogen (Ferdie and Fourqurean, 2004). Typically, P limited systems have long water residence times and carbonate sediments (Smith and Atkinson, 1984; Short, 1987); however, in the northern Gulf of Mexico there is evidence of P limitation in seagrasses and phytoplankton in a handful of temperate bays with siliceous sediments and high water turnover (Fourqurean and Cai, 2001; Murrell et al., 2002). In the northeast Gulf of Mexico, nitrogen limitation exists in areas such as Mobile Bay (Bianchi et al., 1999); however, Perdido Bay, Pensacola Bay, and St. Joseph Bay all exhibit signs of sustained or seasonal P limitation or lack of nutrient limitation because of low light availability (Flemer et al., 1998; Fourqurean and Cai, 2001; Murrell et al., 2002). Thus, our objectives were to determine if either N or P limitation was present, and if so, whether this relationship was spatially constant for seagrasses and epiphytic algae of Grand Bay, AL (GB) and Big Lagoon, FL (BL). We report C:N:P values for seagrasses and epiphytes from summer/fall of 2001 and winter of 2003, in addition to spatial trends for intra-bay N:P ratios for both bay systems.

## 2. Methods

Grand Bay, Alabama (30°23'N, 88°19'W) is west of Mobile Bay, Alabama in the Mississippi Sound (Fig. 1). Excluding minimal local inputs, the primary hydrographic inputs to this system are from the Mississippi Sound and Mobile Bay. Approximately 15% of the mean discharge from Mobile Bay system enters the Mississippi Sound and eventually passes GB (Wallace, 1994; Bianchi et al., 1999). The majority of the bay is shallow (<2 m) with a sand-mud bottom and small amounts of oyster shell. Seagrass beds occur along the edge of the bay in shallow (<1 m) water and are dominated by shoalgrass, *Halodule wrightii* Aschers, and wigeongrass, *Ruppia maritima* Banks ex Koenig. During the spring, wigeongrass dominates while salinities are low; however, as salinities and temperatures increase, wigeongrass dies back and shoalgrass often becomes the most abundant seagrass species (Stutes, 2000; pers. observation). The mean tidal range in GB is 0.4 m with a minimum of 0.03 m and a maximum of 0.8 m (Wallace, 1994).

Big Lagoon, Florida is a small bay on the west side of the Pensacola Bay complex (30°25'N, 87°18'W). This elongated bay connects Perdido Bay, Alabama to Pensacola Bay, Florida (Fig. 1) via the intracoastal waterway. Hydrographic inputs to Big Lagoon are from Pensacola Bay proper to the east and the Perdido Bay to the northwest. It is approximately 11.3 km long and 1.5 km wide, with an average depth of less than 5 m. The tidal range is approximately 0.7 m with a bottom that is composed primarily of sand (Oey, 1995). Big Lagoon is home to extensive beds of shoalgrass and turtlegrass, *Thalassia testudinum*, along both the north and south sides of the bay (FDEP, 2001). Depth limits of seagrasses in Big Lagoon are 2 m and the majority of seagrasses grow in close proximity to the shoreline.

Two 0.01 m<sup>2</sup> quadrats of seagrass were haphazardly collected in June, August, and October from nine or 10 sampling locations along the northern and southern edges of Big Lagoon and between seven and 10 locations along the eastern edge (primarily in the Sandy Bay area) of Grand Bay between during 2001 and in March 2003. Due to inclement weather in Grand Bay, three samples scheduled to be collected in August were collected in September 2001. Samples were transported on ice to the Dauphin Island Sea Lab where they were stored at 0 °C until processing. Samples were prepared by first selecting a minimum of five complete leaves then rinsing and carefully cleaning the blades to remove any sediment and epibionts. Due to senescence of leaves, seagrasses collected in March 2003 were prepared by choosing at least five of the most healthy leaves, and carefully cutting away any dead areas of the seagrass leaf, thus leaving only living tissue for analysis.

The leaves were then carefully scraped clean of epiphytes using a razor blade. The epiphytes were collected into separate containers and both the seagrass and epiphyte samples were dried to a constant weight at 80 °C. Dried plant material was ground and homogenized into a fine powder and C:N ratios were determined using an automated CHN analyzer (Carlo Erba 1500), with a detection limit of 10 ppm for nitrogen (DISL 2000). Phosphorus concentrations were determined by a dry-

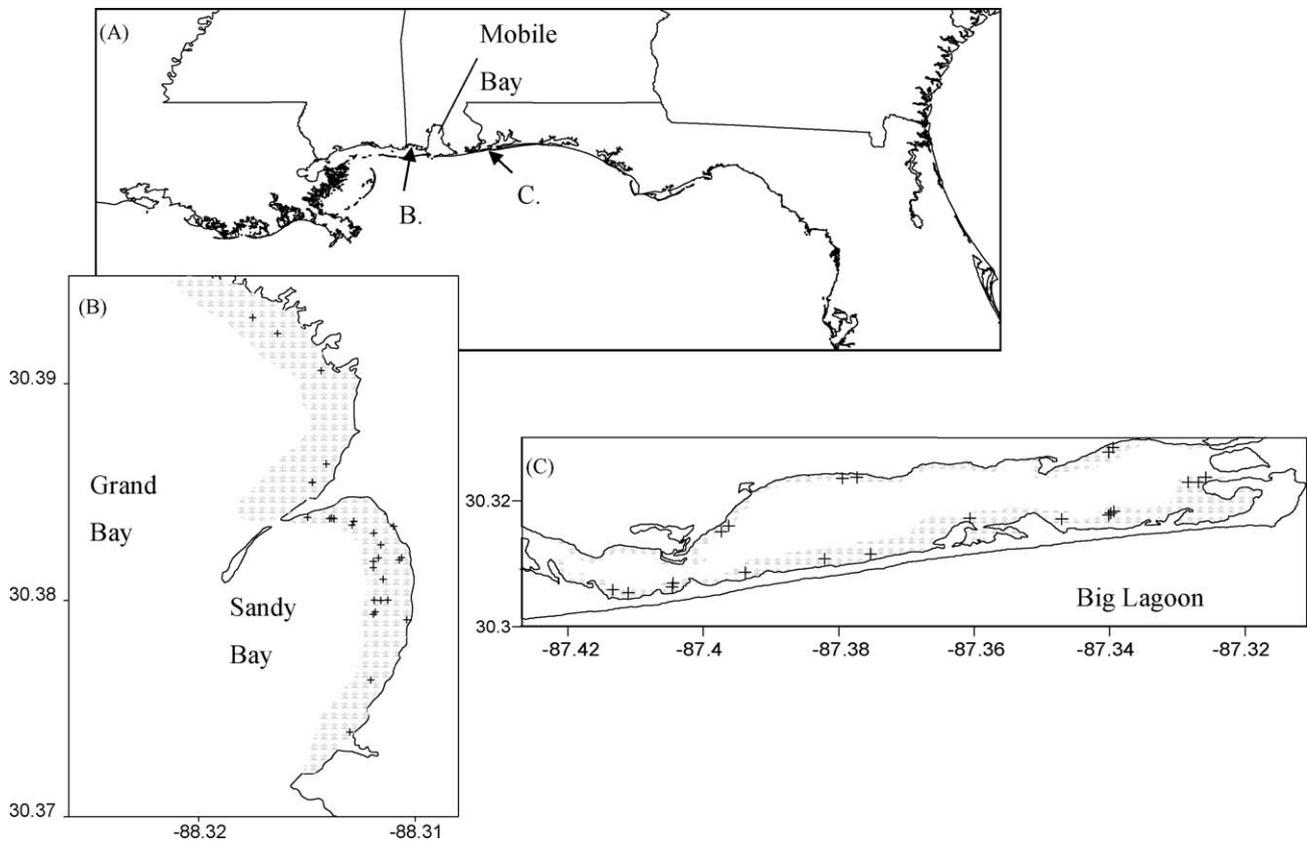


Fig. 1. Map of study sites located in the northern Gulf of Mexico. Shaded areas represent where seagrasses are common and crossmarks indicate locations where seagrasses were collected for C:N:P analysis.

oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean et al., 1992). All ratios were calculated on a mole:mole basis.

Summer 2001 and winter 2003 C:N, C:P, and N:P ratios for seagrasses and epiphytes were compared using a one-way ANOVA. When these data could not be transformed to meet the test assumptions, a Kruskal–Wallis ANOVA on ranks was utilized. Summertime comparisons of elemental ratios of seagrasses and epiphytes for both bays were compared at each sample date using a one-way ANOVA with date as the independent variable. Any significant differences were examined using a Tukey's post-hoc test. When the data did not fit the assumptions of ANOVA, a  $\log_{10}(X)$  transformation was utilized. Summer and winter spatial patterns of N:P ratios were examined using contour plots and the trends were plotted using geostatistical gridding software (Surfer 8.02<sup>TM</sup> surface mapping system).

### 3. Results

#### 3.1. Summer versus winter

For both locations, there was a significant decline in C:N (GB— $F_{1,59} = 15.97$ ,  $p < 0.001$ ; BL— $H = 41.41$ ,  $p < 0.001$ ), C:P (GB— $F_{1,58} = 106.43$ ,  $p < 0.001$ ; BL— $F_{1,67} = 124.84$ ,  $p < 0.001$ ), and N:P (GB— $F_{1,58} = 23.00$ ,  $p < 0.001$ ; BL— $F_{1,67} = 27.70$ ,  $p < 0.001$ ) ratios between summer and winter periods. In GB, C:N ratios declined by 10%, C:P ratios declined

42%, and N:P ratios declined 30% (Fig. 2). Big Lagoon C:N, C:P, and N:P ratios declined 30%, 52%, and 35%, respectively (Fig. 3).

Epiphytic C:N, C:P, and N:P ratio in GB and BL experienced much less variation than seagrasses between the summer and winter. Significant differences between seasons were only detected in Grand Bay C:P ( $F_{1,53} = 12.08$ ,  $p = 0.001$ ) and N:P ( $F_{1,53} = 8.64$ ,  $p = 0.005$ ) ratios. In GB, mean C:N ratios declined minimally between summer and winter, but the decline in C:P and N:P ratios was more substantial (Fig. 2). For BL, mean epiphytic C:N, and N:P ratios remained moderately unchanged and C:P increased during this period (Fig. 3).

#### 3.2. Summertime comparisons

In GB, mean  $\pm$  S.E. C:N ratios for seagrasses varied significantly among months ( $F_{2,38} = 3.408$ ,  $p = 0.044$ ) and ranged between  $14.6 \pm 1.2$  and  $17.4 \pm 0.6$  (Fig. 2). August and October were significantly different from each other (Tukey,  $p = 0.041$ ); however, neither were significantly different from June. Values declined between June and August, but increased in excess of June values during October. Although not significant, C:P ratios declined steadily from  $614.2 \pm 30.7$  in June to  $556.7 \pm 16.0$  in October. N:P ratios varied significantly ( $F_{2,37} = 6.089$ ,  $p = 0.005$ ) and ranged between  $45.2 \pm 4.63$  in August to  $31.5 \pm 1.1$  in October. Post-hoc comparison suggested that August and October were significantly different from each other (Tukey,  $p = 0.004$ ). For BL, there were no

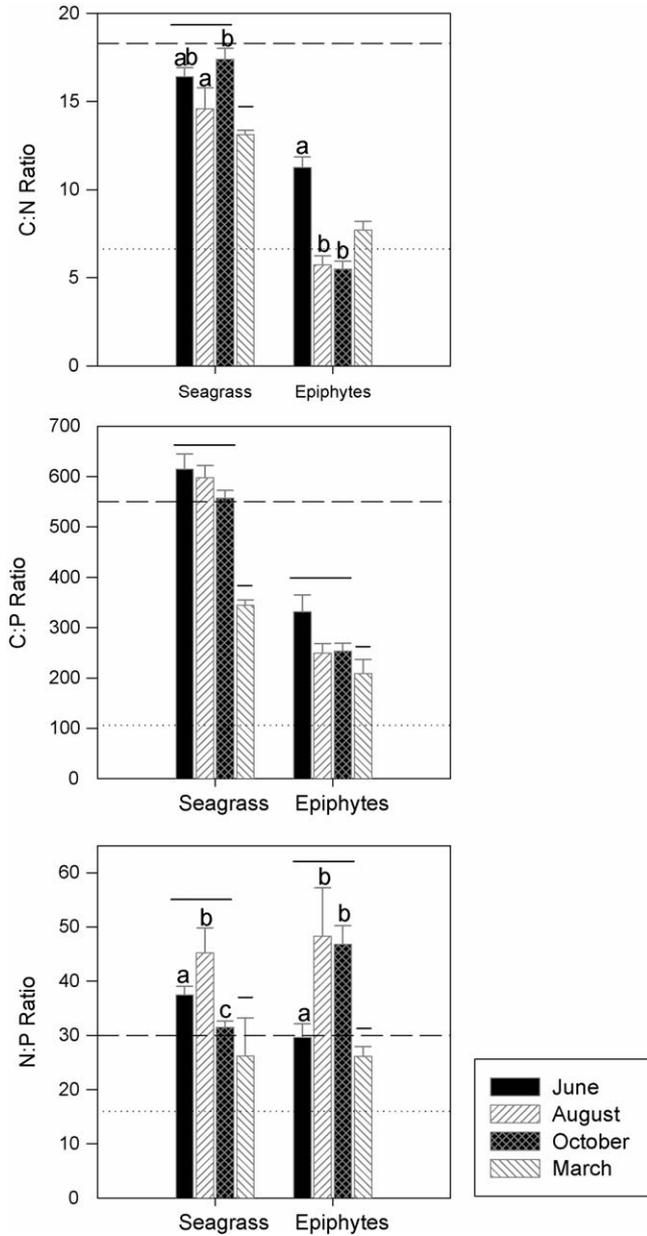


Fig. 2. Mean  $\pm$  S.E. of elemental ratios for *Halodule wrightii* and epiphytes in Grand Bay, AL. Horizontal bars represent significant seasonal comparisons and letters represent significant summertime bi-monthly post-hoc comparisons. The dashed line designates the seagrass Redfield ratio and the dotted line represents the Redfield ratio for phytoplankton.

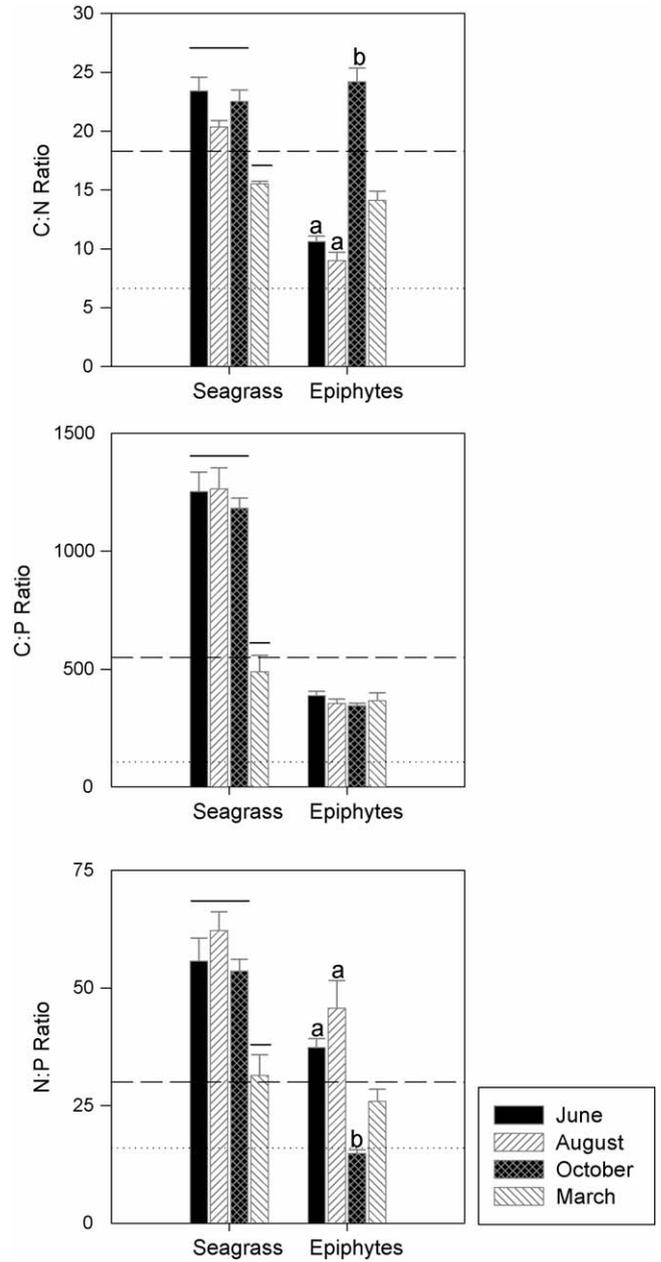


Fig. 3. Mean  $\pm$  S.E. of elemental ratios for *Thalassia testudinum* and epiphytes in Big Lagoon, FL. Horizontal bars represent significant seasonal comparisons and letters represent significant summertime bi-monthly post-hoc comparisons. The dashed line designates the seagrass Redfield ratio and the dotted line represents the Redfield ratio for phytoplankton.

significant differences among months for any elemental ratios (Fig. 3). Mean C:N ratios ranged between  $23.4 \pm 1.2$  in June and  $20.3 \pm 0.5$  in August, but rose again in October to  $22.5 \pm 1.0$ . C:P values ranged between  $1264.7 \pm 89.5$  and  $1183.0 \pm 42.3$  with the August measurement being greater than June and October. Finally, mean N:P values ranged between  $53.56 \pm 2.5$  and  $62.2 \pm 4.0$  with values that increased in August and declined in October (Fig. 3).

Bi-monthly C:N and N:P measurements for epiphytes varied significantly among months ( $F_{2,37} = 32.701$ ,  $p < 0.001$  and  $F_{2,34} = 5.764$ ,  $p = 0.007$ , respectively); however, the monthly differences were dissimilar between bays (Figs. 2 and 3). In

GB, mean elemental ratios in June were significantly greater for C:N (Tukey,  $p < 0.001$  for both months) and smaller for N:P (Tukey,  $p = 0.020$  for August and  $p = 0.023$  for October) than in August and October. C:N values ranged between  $5.5 \pm 0.4$  and  $11.3 \pm 0.6$  and N:P values ranged between  $29.6 \pm 2.5$  and  $48.3 \pm 8.9$ . For BL, mean elemental ratios in June and August were significantly smaller in October for C:N ratios ( $F_{2,47} = 58.126$ ,  $p < 0.001$ ; Tukey,  $p < 0.001$  for both months) and larger for N:P ratios ( $F_{2,47} = 62.23$ ,  $p < 0.001$ ; Tukey,  $p < 0.001$  for both months). C:N ratios ranged from  $8.9 \pm 0.7$  to  $24.2 \pm 1.2$  and N:P ratios ranged in value from  $14.8 \pm 0.8$  to  $45.7 \pm 5.9$ . Mean C:P values ranged between  $249.1 \pm 19.4$  and

$331.1 \pm 34.0$  in GB, with a decline between June and August (Fig. 2). In BL, C:P values had a modest bi-monthly decline with values ranging between  $388.7 \pm 17.8$  in June to  $345.2 \pm 11.2$  in October (Fig. 3).

3.3. N:P contour plots

Contour plotting of N:P ratios of seagrass in GB indicated that N:P ratios were in excess of 30 during summer and ranged between 25 and 30 in winter. This suggests that seagrasses in GB were P limited during the summer but not during the winter (Fig. 4). For summer N:P ratios, P limitation was stronger in the

southern part of GB (and more specifically Sandy Bay) than in the northern part of the bay. During March, N:P values were lower than in the summer, indicating a decrease in the severity of P limitation. Regardless of month, the largest amount of variation in GB occurred in the northeast corner of Sandy Bay, near the only developed land in the eastern part of the bay. The areas adjacent to the development showed N:P ratios that approach or were less than the seagrass Redfield ratio, but the amount of P limitation quickly increased away from this area (Fig. 4A).

Contour plotting of seagrass N:P values in BL indicated two distinct areas of influence (Fig. 5A). In both areas, N:P ratios

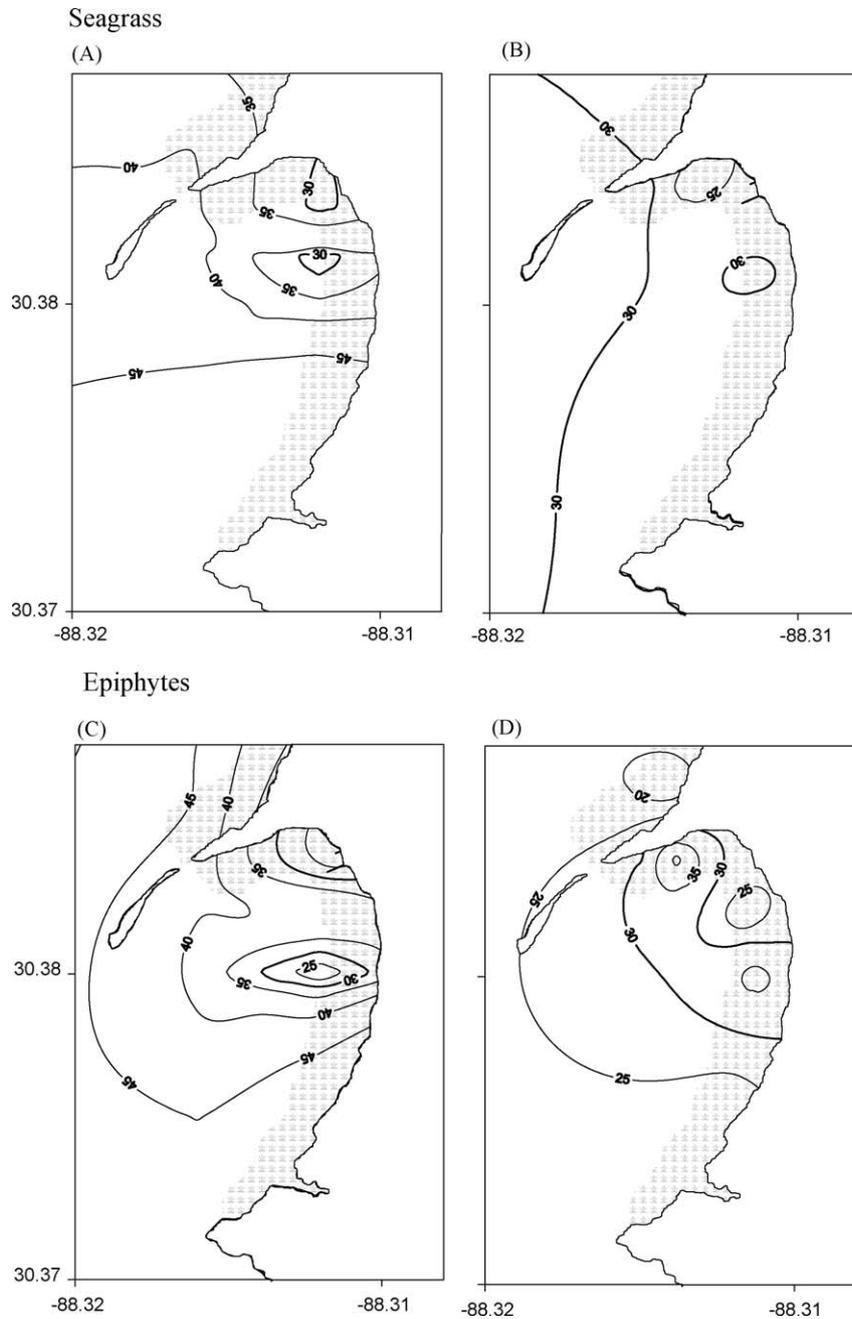


Fig. 4. Contour plots of *Halodule wrightii* N:P ratios in Grand Bay, AL during each sample period. The X axis represents the longitude and the Y axis represents latitude. The contour interval is 2 for seagrasses and 1 for epiphytes. Interpretation of these data should be restricted to locations that contain seagrasses (see shaded areas in Fig. 1).

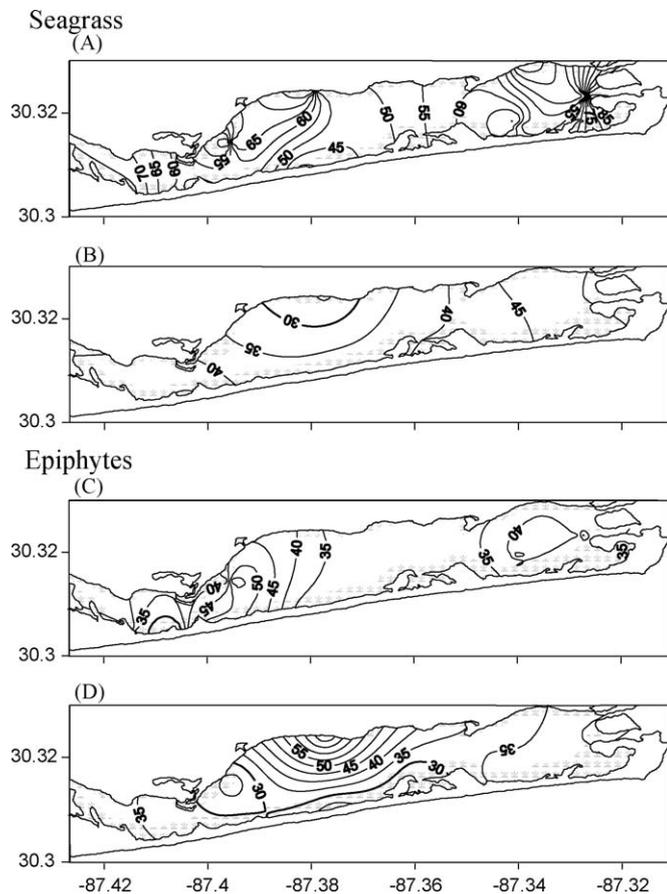


Fig. 5. Contour plots of *Thalassia testudinum* N:P ratios in Big Lagoon, FL during each sample period. The X axis represents the longitude and the Y axis represents latitude. For seagrasses and epiphytes, the contour interval is 2. Interpretation of these data should be restricted to locations that contain seagrasses (see shaded areas in Fig. 1).

indicated that the entire bay system was P limited during summer 2001 and March 2003, but west of  $\sim 87.35^\circ\text{W}$  longitude, N:P ratios were the highest near the extreme western end of the bay, near the Perdido Bay input, and the northern shoreline. During March, N:P ratios were elevated along the southern shoreline of the bay compared to the northern shoreline. For the remaining part of the bay (east of  $\sim 87.35^\circ\text{W}$  longitude), N:P ratios during each period increased west to east towards the mouth of BL.

For epiphytes, contour plots in GB showed a general increase in P limitation in a pattern similar to seagrasses during the summer 2001, with the degree of P limitation being less near the northeast shoreline of Sandy Bay (Fig. 4C). For March 2003, N:P values all indicated a decrease in the degree of P limitation in GB. There were four areas where ratios were unique (Fig. 4D). Like seagrasses, the largest variation in N:P ratios occurred in close proximity to the only developed land on the eastern side of Grand Bay.

In BL, contour plots of epiphytic N:P ratios indicated that, like seagrasses, the bay had two distinct areas. During the summer 2001, the western bay (west of  $\sim 87.35^\circ\text{W}$  longitude), summertime N:P values were the most pronounced in the central part of the western bay and declined in both directions

away from this area (Fig. 5C). In March, N:P ratios were higher along the northern shoreline compared to the southern shoreline and the degree of P limitation was most pronounced in the central region of the bay. In eastern part of BL (east of  $\sim 87.35^\circ\text{W}$  longitude), N:P ratios declined near the mouth of the bay during the summer 2001 and increased slightly towards the mouth during March 2003 (Fig. 5B and C).

#### 4. Discussion

In both Grand Bay and Big Lagoon there was evidence that phosphorus was the primary limiting nutrient for both seagrass leaves and epiphytic algae. During the summer, seagrass C:P and N:P ratios were in excess of the seagrass Redfield ratio while epiphyte ratios were greater than the Redfield ratio (and often the seagrass Redfield ratio). Evidence of P limitation does not, however, mean that nitrogen levels had no influence on C:N ratios. *Thalassia testudinum* C:N values were greater than the seagrass Redfield ratio in BL and *Halodule wrightii* C:N values were less than the seagrass Redfield ratio in GB, but it is important to note that there may be inherent nutrient content differences among seagrass species. In addition, between summer and winter, C:N decreased for seagrasses and remained the same for epiphytes. Winter decreases in seagrass C:N and N:P ratios often occur as plant growth decreases as a function of decreases in light availability and low temperatures (Fourqurean et al., 1997; Armitage et al., 2005).

P limitation in BL for epiphytes and seagrasses was not unexpected, as Murrell et al. (2002) and Flemer et al. (1998) each have reported that P limitation in phytoplankton was not uncommon in the two “feeder” systems (Perdido Bay, AL and Pensacola Bay, FL) of BL, and has been suggested for seagrasses and phytoplankton in other eastern Gulf of Mexico embayments (Myers and Iverson, 1981; Fourqurean et al., 1992; Flemer et al., 1998; Fourqurean and Cai, 2001; Fourqurean and Zieman, 2002; Murrell et al., 2002). BL is considered an oligotrophic bay where responses to nutrient loading in seagrasses and epiphytic algae are often strong (Wear et al., 1999; FDEP, 2001). Monitoring of the Escambia River, the main freshwater source for the Pensacola Bay complex, from 1973 to 1994 indicated that total N: total P ratio averaged  $40 \pm 26$  (mean  $\pm$  S.D.,  $n = 147$ ) (Alexander et al., 1996), suggesting that P delivery is low and P limitation is favored (Murrell et al., 2002). In addition, P limitation in seagrasses may have been exacerbated by an increase in epiphytic load between 2000 and 2001 (FDEP, 2001).

In Grand Bay, apparent P limitation in seagrasses and epiphytes was surprising. The Mississippi Sound is the primary hydrological input to Grand Bay, although  $\sim 15\%$  of the outflow from Mobile Bay enters the east end of Mississippi Sound near GB. Mobile Bay is the sixth largest watershed in the USA and is subject to extensive anthropogenic nutrient loading from the Alabama River. Dissolved inorganic total N:P loading ratios in Mobile Bay and Mississippi Sound have been estimated at  $\sim 20:1$ ,  $16:1$  (Turner and Rabalais, 1999) and dissolved inorganic total N:P ratios in Grand Bay have been estimated at  $7.8:1$  (Johnson and Heck, 2003). These N:P ratios suggest

that nitrogen should limit seagrass growth in GB, but this prediction is contradicted by our N:P data for seagrasses and epiphytes. Unlike other P limited estuaries, Grand Bay experiences substantial water turnover, high ambient nutrient levels, and possesses siliceous sediments. In low turnover, hypersaline bays, for example, Shark Bay (Australia), Spencer Gulf (Australia) and Florida Bay (USA), biochemical fluxes of N allow for adequate N recycling, enabling P limitation (Smith, 1984; Smith and Atkinson, 1984; Smith and Veeh, 1989; Fourqurean et al., 1992). Tropical and sub-tropical seagrass beds can be P limited due to the complication of inorganic P binding to biogenic sediments (Short, 1987; Powell et al., 1989), and seagrass systems in the northern Gulf of Mexico may be P limited simply due to the decreased freshwater delivery of phosphorus to these bays (i.e. Perdido Bay, Big Lagoon, Pensacola Bay, and possibly St. Joseph Bay) (Myers and Iverson, 1981; Flemer et al., 1998; Fourqurean and Cai, 2001; Murrell et al., 2002).

P limitation along the eastern shore of Grand Bay may be due to the inability of seagrasses and epiphytes to utilize P in the form it is delivered, or possibly by interference with the uptake of P by arsenate. P delivery from Mobile Bay to Mississippi Sound is high, between 12 and 20:1 N:P ratio (Rabalais et al., 1996; Pennock et al., 1999); however, dissolved phosphate levels are actually very low ( $<0.3 \mu\text{M}$ ) (Pennock et al., 1999). It is estimated that three quarters of the total P delivered is tied up as particulate phosphorus (Pennock et al., 1999) and must be “freed” prior to being utilized. Because GB does not have a freshwater source of P, the labile P arriving from Mobile Bay and the Mississippi Sound may be used up by phytoplankton prior to reaching GB. As a result, epiphytes and seagrass must compete with marine phytoplankton (mean chlorophyll levels of  $2\text{--}7 \mu\text{g l}^{-1}$  (Pennock, 1995)) for the remaining nutrient resources. Without an allochthonous input of P, nutrient stocks may be dependent on remineralization of organic matter within the sediments (Caraco et al., 1990).

The presence of arsenate, a common form of arsenic in coastal waters (As(V)), may also interfere with the uptake of phosphorus by seagrasses and epiphytes. It has been demonstrated that arsenate can be mistaken for phosphorus by the phosphate transport system of plants (Dixon, 1997), uncoupling phosphorylation and inhibiting phosphate uptake (Fourqurean and Cai, 2001). In addition, high phosphate levels can also inhibit arsenate uptake, resulting in an inverse relationship between phosphorus availability and arsenate content of marine seagrasses. This inverse relationship is present in the eastern Gulf of Mexico; however, there was a direct relationship between arsenic and P concentrations in Florida Bay (Fourqurean and Cai, 2001). Although we did not test for arsenate levels in the seagrass of GB, it is estimated that arsenic levels in Mobile Bay are extremely elevated (EPA, 1997) and may be influential on the phosphorus uptake of plants.

Because epiphytes lack rhizome nutrient stores and the ability to access porewater, it has been suggested that epiphytes may play a critical role in the detection of eutrophication by reacting to ambient water quality faster than seagrasses (Fourqurean et al., 1992; Lin et al., 1996; Stapel and

Hemminga, 1997; Wear et al., 1999; Marba et al., 2002). Seagrasses have the ability to resorb to the rhizome and roots approximately 20% of the N and P stored within the leaves prior to senescence (Stapel and Hemminga, 1997; Hemminga et al., 1999), but without a root system, epiphytes lack this ability. As a result, changes in seagrass elemental ratios represent changes in nutrient allocation and relative nutrient availability, while changes in epiphyte elemental ratios should only represent changes in relative nutrient availability.

In previous studies conducted in the laboratory or in mesocosms, epiphytes responded quickly to nutrient inputs (Tomasko and Lapointe, 1991; Williams and Ruckelshaus, 1993). However, for similar experiments conducted in situ, the responses were muted due to the impact of epiphytic grazers (Lin et al., 1996; Heck et al., 2000). In our study, epiphytes did respond to short-term water quality changes. For example, the decrease in the N:P ratio at BL during October (Fig. 3) was not indicative of a decline in P levels but rather a decline in N levels brought on by a period of decreased rainfall ( $\sim 14.75$  cm deficit) prior to the October sampling date (NOAA/NWS, 2005). Between August and October, P in the water column increased from  $0.11 \mu\text{M}$  in August to  $0.55 \mu\text{M}$  in September then declined again to  $0.35 \mu\text{M}$  during October while nitrogen levels remained between  $1.16$  and  $1.93 \mu\text{M}$  (Johnson and Heck, 2003). The drop in epiphyte N:P ratio was accompanied by an increase in epiphyte C:N but no changes in epiphyte C:P levels. On a longer time scale, variation in epiphyte elemental ratios between the summer 2001 and winter 2003 may not only reflect changes in water quality, but may also reflect a change in epiphyte species composition.

By contrasting the spatial aspects elemental ratios of seagrasses and epiphytes, we may gain insight into the relative contribution of other nutrient sources. For example, in GB the high degree of variation in N:P ratios in the Sandy Bay area may indicate an anthropogenic source of nutrients to the plants in that part of the shoreline. The area immediately surrounding GB is a low lying swamp land with a shallow water table (pers. observ.). Sandy Bay is also the location of the only housing development on this part of GB and residents are dependent on septic systems that may provide additional nutrients to seagrasses and epiphytes. The influence of septic systems located near coastal seagrass meadows has been well documented and has been linked to variations in nutrient loads available to seagrasses (Lapointe and Clark, 1991; Short et al., 1996; Tomasko et al., 2001). In BL, the apparent separation of the bay into two distinct areas may indicate two possible nutrient sources for the bay. In the western part, Perdido Bay and housing development along the northern edge of the bay may be responsible for nutrient input (i.e. runoff and lawn fertilizer), but for the eastern part of the bay, there is minimal development, thus N:P ratios may be responding to the inflow of water from Santa Rosa Sound during each tidal cycle. Use of spatially derived data sets and contour mapping of seagrass has had limited use as it relates to seagrass and nutrients. Previous authors have used these techniques to map changes in nutrient ratios over large areas (i.e. Florida Keys) (Fourqurean and Cai, 2001; Fourqurean and Zieman, 2002), however, we have

demonstrated that this technique may be useful to identify point and non-point sources of nutrient inflow to seagrass meadows at a much smaller scale.

In conclusion, our data suggest that GB and BL are dynamic systems whose seagrasses and epiphytes predominantly experience P limitation with a high degree of spatial variation. For BL, this was not unexpected, but in GB this was surprising. Despite long term data on P levels in the water column that suggest N limitation should be occurring, elemental ratios of seagrasses and epiphytes each indicated P limitation. This study demonstrates the variability of C:N:P ratios and patterns of nutrient limitation, suggesting that more can be learned about the interaction between nutrients and plants and how these are ultimately transcribed into elemental ratios.

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