Intra- and interannual variability in seagrass carbon and nitrogen stable isotopes from south Florida, a preliminary study

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Abstract

$\delta^{13}C$ and $\delta^{15}N$ values were determined for the seagrass *Thalassia testudinum* at four permanent seagrass monitoring stations in south Florida, USA, through a quarterly sampling program over 3-years (1996–1998). All sites are seagrass beds with water depths of less than 6 m. Two sites are located on the Florida Bay side of the Florida Keys, and the other two sites are on the Atlantic side. The data analyzed over the 3 year study period display unique patterns associated with seasonal changes in primary productivity and potentially changes in the N and C pools. The mean carbon and nitrogen isotope values of *T. testudinum* from all four stations vary from -7.2 to $-10.4‰$ and 1.1 to 2.2‰, respectively. However, certain stations displayed anomalously depleted nitrogen isotope values (as low as $-1.2‰$). These values may indicate that biogeochemical processes like N fixation, ammonification and denitrification cause temporal changes in the isotopic composition of the source DIN. Both $\delta^{13}C$ and $\delta^{15}N$ values displayed seasonal enrichment-depletion patterns, with maximum enrichment occurring during the summer to early fall. The intra-annual variations of $\delta^{13}C$ values from the different stations ranged from about 1 to 3.5‰; whereas variations in $\delta^{15}N$ ranged from about 1 to 4.9‰. Certain sites showed a positive relationship between isotope values and productivity. These data indicate $\delta^{13}C$ values display a high degree of seasonal variability as related to changes in productivity. $\delta^{15}N$ values show clear intra-annual variations, but the observed changes do not necessarily follow a distinct seasonal cycle, indicating that changes in DIN will need further investigation.
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1. Introduction

The shallow marine waters surrounding the southern tip of Florida provide an ideal environment for seagrasses, which are the most common benthic community in the region (Fourqurean et al., 2001). In order to better understand the carbon and nitrogen isotopic ratios in seagrass, a times series was constructed from 3 years of quarterly sampling of *Thalassia testudinum* (the dominant species in the study area) at four stations located in southern Florida. All stations are located within the Florida Keys National Marine Sanctuary (FKNMS). Two sites with similar ecological characteristics were selected for study from each side of the Florida Keys (Fig. 1), two on the Florida Bay side and two on the Atlantic Ocean side. These data will help to constrain elements of the carbon and nitrogen cycles affecting this region as recorded by the plants. In this paper we investigate how changes in primary productivity and the seasonal timing of the inter- and intra-annual variations in the carbon and nitrogen ratios of *T. testudinum* are related.

The carbon isotopic changes throughout the Phanerozoic have been well documented in both inorganic

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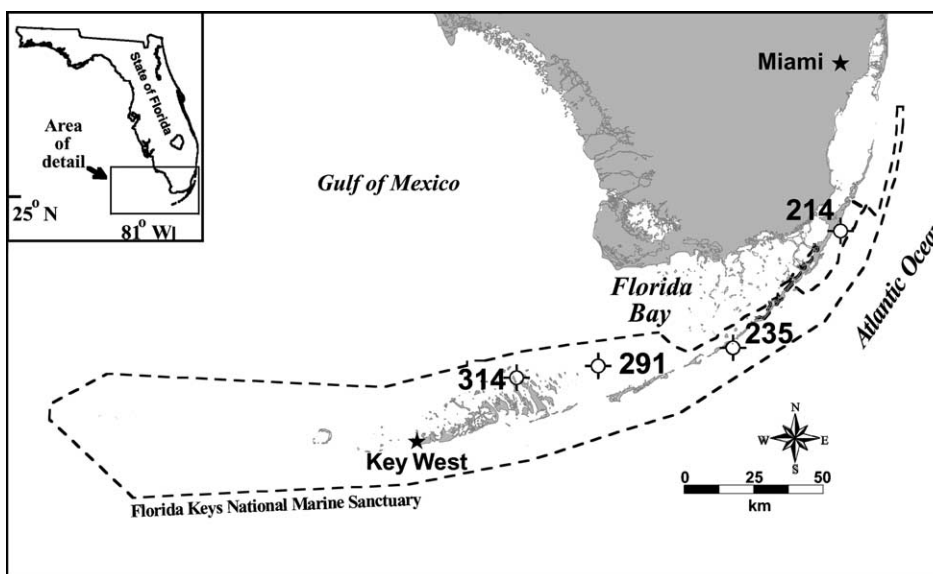*E-mail address:* andersow@fiu.edu (W.T. Anderson).

Fig. 1. Location map indicating the locations of the stations within the boundaries of the Florida Keys National Marine Sanctuary (FKNMS).

(shells and tests of organisms, and preserved carbonates) and organic matter (OM) preserved in sedimentary sequences (Hayes et al., 1999; McKenzie, 1985; Veizer et al., 1999). Times series analyses of the isotopic composition of sediment trap material in lakes have shown seasonal cycles of isotopic enrichment due to changes in productivity (Lee et al., 1987; Teranes and Bernasconi, 2000; Teranes et al., 1999). The deployment of sediment traps in near shore environments is not practical due to the shallow water nature of the FKNMS, where water depths are typically less than 10 m. Since seagrasses continually "sample" their environment via CO_2 fixation and growth, repeated sampling of seagrass may help to create a stable isotope time series for the area and provide an isotope record of changes in ecosystem productivity.

Seagrasses form an important part of shallow water benthic environments in many coastal zones. Yet, these communities are susceptible to a variety of anthropogenic disturbances, especially changes in water quality caused by an increase in the nutrient flux to the near shore environment (Short and Wyllie-Echeverria, 1996). Isotopic composition of seagrasses may prove to be a valuable tracer of anthropogenic nutrient inputs to the coastal zone (e.g. McClelland and Valiela, 1998). The data analyzed over the 3-year study period show cyclic trends associated with seasonal change in primary productivity and potentially changes in the nitrogen and carbon source pools. Additionally, the analysis of our time series indicates that food web studies need to take into account spatial and temporal changes in the stable isotopic composition of primary producers when interpreting food web structure from isotopic data.

2. C and N isotopic variability in seagrass

Seagrasses have proven to be very good indicators of their local environments due to their long life, organic turnover rate, and sessile nature (Fourqurean et al., 1997). Therefore as these plants grow, the carbon and nitrogen isotopes incorporated into their biomass can be used to construct a biogeochemical time series, when sampled throughout the year at pre-selected sites. This sampling approach and the resultant time series will allow for an improved understanding of temporal changes in C and N sources and other environmental conditions affecting these plants' physiology. The sources of C and N for seagrass growth vary in both space and time, and the isotopic information within the plants' leaves can indicate the mechanisms responsible for these variations (Fourqurean et al., 1997; Lin et al., 1991; McClelland and Valiela, 1998; Zieman et al., 1984). For example, variability in light intensity can cause a change in the carbon isotopic ratio within a plant due to changes in productivity. Enhanced productivity can result in a decrease in plant isotopic discrimination, resulting in a relative isotopic enrichment. Grice et al.'s (1996) experimental work demonstrated that carbon isotopes are enriched in plants from high light, high productivity environments. Spatial and temporal variability in productivity and the isotopic composition of seawater DIC lead to high variability in carbon isotopic composition of seagrass as a function of species and location. The review by Hemminga and Mateo (1996), based on literature for 31 seagrass species, indicates that $\delta^{13}C$ values range between −24 and −3‰, with an unimodal distribution. The highest frequency

observed in their frequency study was between -11 and $-10‰$.

Carbon isotope ratios in plants are regulated by photosynthetic fixation of CO_2, which is transferred through stomatal openings or diffuses through the cellular membranes. The isotopic signature of most terrestrial plants typically falls within two groups, largely determined by photosynthetic pathway (C_3 or C_4). In C_3 plants this fixation and transfer results in the isotopic fractionation of carbon which is predominately controlled by two factors: (1) the CO_2 concentration inside and outside of the leaf or cell; and (2) the biologic fractionation factor due to the isotopic discrimination of ribulose-1,5-bisphosphate carboxylase enzyme (rubisco) (Farquhar et al., 1989; Francey and Farquhar, 1982). Terrestrial C_4 plants have $\delta^{13}C$ values between -16 and $9‰$ (Schleser, 1995); C_3 plants have a comparatively larger isotopic discrimination, and their values range between -35 and $20‰$, with a mean around $-27‰$ (Boutton, 1991; Schidlowski et al., 1983; Smith and Epstein, 1971). The isotopic composition of seagrasses would seem to indicate membership in the C_4 group, but they are C_3 plants (Hemminga and Mateo, 1996). There are several reasons for enriched $\delta^{13}C$ values in seagrasses, which include carbon limitation in the boundary layer near the plant, resulting in a decrease in ^{13}C discrimination or through the use of HCO_3^- as a carbon source. It is unclear if *Thalassia* spp. can utilize HCO_3^- (Hemminga and Mateo, 1996); certain studies show that some species use only CO_2 (Adel, 1984; Benedict et al., 1980), other work indicates that HCO_3^- is being utilized (Durako and Hall, 1993). Other marine primary producers such as some diatoms have the ability to utilize HCO_3^- as a carbon source, and therefore have more enriched $\delta^{13}C$ values than the typical C_3 plant (Laws et al., 1995). Additionally, temperature changes can also affect the amount of CO_2 dissolved in water, resulting in a positive correlation between temperature and marine plants' $\delta^{13}C$ values (Francois et al., 1993; Kennedy and Robertson, 1995; Rau et al., 1991).

Nitrogen values of seagrasses are related to source and potentially physiological processes. In general, biotic processes can cause large variations in local dissolved inorganic nitrogen (DIN) pools. For example, denitrification results in the loss of isotopically light ^{14}N, which enriches the remaining DIN pool with ^{15}N. Both nitrification and denitrification in marine settings have large discriminatory effects ranging from 10 to 40‰ (Cline and Kaplan, 1975; Mariotti et al., 1984). The loss of ^{14}N from the dissolved inorganic nitrogen (DIN) pool in an estuary can lead to a relative enrichment in ^{15}N of DIN. In contrast plants with nitrogen fixing capabilities have $\delta^{15}N$ values ranging between -2 and $2‰$, which is near the isotopic composition of the atmosphere, 0‰ (Peterson and Fry, 1987). McClelland and Valiela (1998) demonstrated that $\delta^{15}N$ values from seagrass in estuaries near Waquoit Bay, Massachusetts, were correlated with nitrogen derived from local wastewater within the watersheds. There are other natural processes that can alter the $\delta^{15}N$ values as well. In Tomales Bay, California, isotopic analysis of *Zostera marina* displayed unusually enriched values $>11‰$, with values increasing along a transect from the mouth of the bay towards the head of the bay. However, this trend was related to both nutrient limitation and progressive denitrification of the N supplied from an oceanic source, not anthropogenic N from pollution (Fourqurean et al., 1997). Nutrient limitation will play a role in the nitrogen isotopic composition of seagrasses. Such effects have been well documented in the open ocean settings, where $\delta^{15}N$ values of POM is linearly related to the degree of ocean surface water nitrate utilization (Altabet and Francois, 1993). In general, plants discriminate against heavier isotopes, preferentially incorporating the lighter ^{14}N, thus marine plants typically have lower $\delta^{15}N$ values than the source nitrate utilized by the plant.

3. Methods

Samples were collected from four permanent monitoring stations located in the Florida Keys National Marine Sanctuary (FKNMS), which has an area of approximately 9000 km^2 (Fig. 1). All four sites were seagrass beds in less than 6 m of water. The two Florida Bay-side sites were dense *Syringodium filiforme*-dominated beds with significant biomass of the target species, *T. testudinum*. The two Reef-side sites on the Atlantic side of the Keys were *T. testudinum*-dominated seagrass beds. Muddy carbonate sediments underlied the seagrass at all sites. Sites were sampled seasonally using SCUBA every 3 months from January 1996 through August of 1998. For each collection, five arbitrary, intact shoots were collected from a 10 m diameter area. All green leaves were cut from the shoots and used in sample processing. The collected *T. testudinum* leaves were gently scraped clean of epiphytes, dried to a constant weight ($<70°$ C) then and homogenized using a mortar and pestle.

All isotopic analyses were measured at the SERC Stable Isotope Laboratory using standard elemental analyzer isotope ratio mass spectrometer (EA-IRMS) procedures. The EA is used to combust organic material forming N_2 and CO_2, which were measured on a Finnigan MAT Delta C IRMS in a continuous flow mode. The samples' isotopic ratios (R) are reported in the standard delta notation (‰): δ (‰) $= [(R_{sample}/R_{standard})-1] \times 1000$. These results are presented with respect to the international standards of atmospheric nitrogen (AIR, N_2) and Vienna Pee Dee belemnite (V-PDB) for carbon. Analytical reproducibility of this study based on sample replicates is better than $\pm 0.2‰$ for $\delta^{15}N$ and $\pm 0.08‰$ for $\delta^{13}C$.
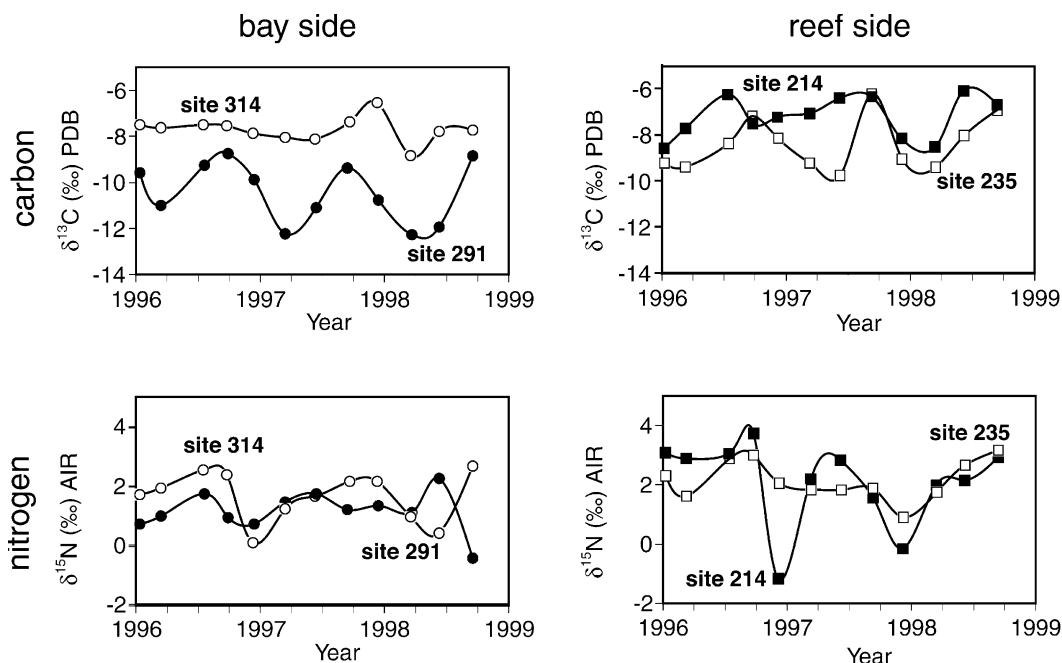
Fig. 2. Time series plots of all quarterly collected isotopic data from *Thalassia testudinum*, from 1996 to 1998. Data are from four stations in the FKNMS located on both sides of the Florida Keys.

All samples were also analyzed for total C, N and phosphorus content following the methods described in Fourqurean and Zieman (2002). The aerial primary productivity [g (dry weight)/m²/day] and specific productivity (new leaf material [mg]/total leaf material [g]/day) was also determined for the seagrass bed at each site (Fourqurean et al., 2001).

We used standard regression techniques to test for significant relationships between isotope ratios and biological and environmental factors thought to influence the isotopic composition of the seagrasses. In most cases a linear model was applied, but we also used an interative process to determine the best fit of a sine function to the time series:

$$R = \text{mean} + A \times \text{sine}(\text{DOY} + \Phi) \qquad (1)$$

where R is the estimated value of the time series, mean is the mean of the time series, A is the amplitude of the sine function, and Φ is a phase angle that adjusts the timing of the sine function. We used this additional approach to test whether or not the trends we observed in the time series were related to seasonal changes in productivity, as idealized as a sinusoidal pattern, with enhanced productivity during spring and summer followed by a decrease in productivity in fall and winter. This model has been shown to describe the intra-annual pattern in the growth and abundance of seagrasses in south Florida (Fourqurean et al., 2001).

4. Results

Distinct differences in both carbon and nitrogen isotope values of *T. testudinum* were found in the total 48 samples measured from all four sites over the 3-year study period (Fig. 2). The mean carbon isotope values for all sites varied between −10.41 and −7.20‰ (Table 1). The range from within each study site fell between 2 and 5‰. Station 214, on the Atlantic side of the Keys, had the most enriched mean value, with the absolute maximum value of −6.1‰. The site with the second most enriched value (−6.3‰) was the other Atlantic side site, station 235, although its mean value was almost 1‰ lower than station 214. The most depleted value of the data set came from site 291 on the Bay side of the Keys (−12.3‰). There were no apparent first-order trends over the 3 years. Yet, there were several distinct second-order carbon isotopic enrichment–depletion cycles, which varied in magnitude from about

Table 1
Complied ¹³C (‰) *Thalassia testudinum* values from all stations

Station	n	Mean	S.E.	Min	Max	Range
214	12	−7.20	0.27	−8.6	−6.1	2.5
235	12	−8.44	0.33	−9.8	−6.3	3.5
291	12	−10.41	0.38	−12.3	−8.7	3.5
314	12	−7.70	0.16	−8.8	−6.5	2.3

1 to about 3‰. The timing of these second-order enrichment–depletion trends varied from site to site. Station 291 displayed a strong seasonal cycle in its carbon isotope values, with maximum values occurring in late summer to early fall and minimum values occurring in winter (Fig. 2). In contrast, site 314 did not display a consistent enrichment–depletion pattern through the entire study period. However, there was a 2‰ enrichment–depletion pattern in the last year, 1998–1999, at this site. The Atlantic side sites also displayed similar second-order enrichment–depletion patterns, but with different timing. In the first year site 214 and 235 had opposite trends. Where the maximum $\delta^{13}C$ of site 235 occurred in the fall of 1996, this coincided with the minimal value at site 214 for the same year. From the summer of 1997 until the end of the study period, both sites' time series showed a similar pattern, with yearly maximum values occurring during the summer, and minimum values occurring in fall and winter.

The nitrogen isotopic data from our study sites also indicated seasonality, but the specific patterns were not identical to those observed in the carbon isotopic data. Mean values for all stations varied from 1.14 to 2.15‰ (Table 2). All sites show distinct enrichment-depletion patterns in $\delta^{15}N$ values, with minimum values occurring during the late fall to early winter (Fig. 1). The most negative $\delta^{15}N$ value (−1.2‰) occurred at station 214 during the fall of 1996, while the most enriched value of 3.7‰ from all the sites occurred at the same station during the late summer of the same year. Station 214 had the highest range in $\delta^{15}N$ values (4.9‰), whereas the other site on the reef side of the Keys had the lowest range (2.3‰). Just as with the carbon data, the nitrogen data did not display any appreciable first-order trends, but second-order trends were present. Most of these second-order enrichment-depletion cycles observed in the data had a magnitude of less than 3‰. However, station 214 had the largest change of 4.9‰ (the actual range for this site) from later summer to fall of 1996 (Fig. 2). In general each station has an enrichment trend of about 2‰ from the winter to the summer, followed by a similar depletion trend into late fall.

$\delta^{13}C$ values from all stations were positively correlated with the previously reported C:P ratios of the seagrass leaves (Fig. 3 A). As the P concentration decreases relative to C, the $\delta^{13}C$ values showed an enrichment

trend. For example, the sample with the highest C:P ratio (1883) also had one of the most enriched $\delta^{13}C$ values of −6.32‰. When C:P ratios were below 1200, the range of the isotopic values from the stations is the highest, ranging between −12.5 and −6.5‰. Conversely, there was no significant correlation of $\delta^{15}N$ values with C:N ratio (Fig. 3B). However, low C:N ratios between 12 to 22 had a wide range of $\delta^{15}N$ values (−1.2 to 3.2‰). The general trend showed that as nitrogen becomes more limiting, the range in the $\delta^{15}N$ values decreases. The range in $\delta^{15}N$ values between C:N ratios of 24 to 26 is less than half of the 12 to 22 example above (Fig. 3B).

All stations' $\delta^{13}C$ and $\delta^{15}N$ values were also compared with two different measures of productivity, aerial productivity and specific productivity. These two different means of measuring productivity have different advantages. The measurement of specific productivity provides an indicator of physiological state as evidenced by the rate of growth of individual plants. The aerial measurement is an indication of the production of new organic matter in the ecosystem and is a function of the specific growth rate and the plants density. This point is important as seagrass abundance can be spatially het-
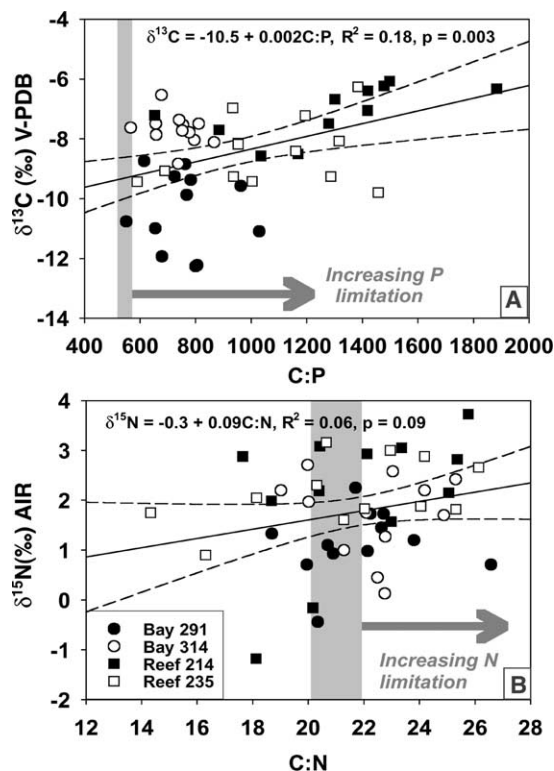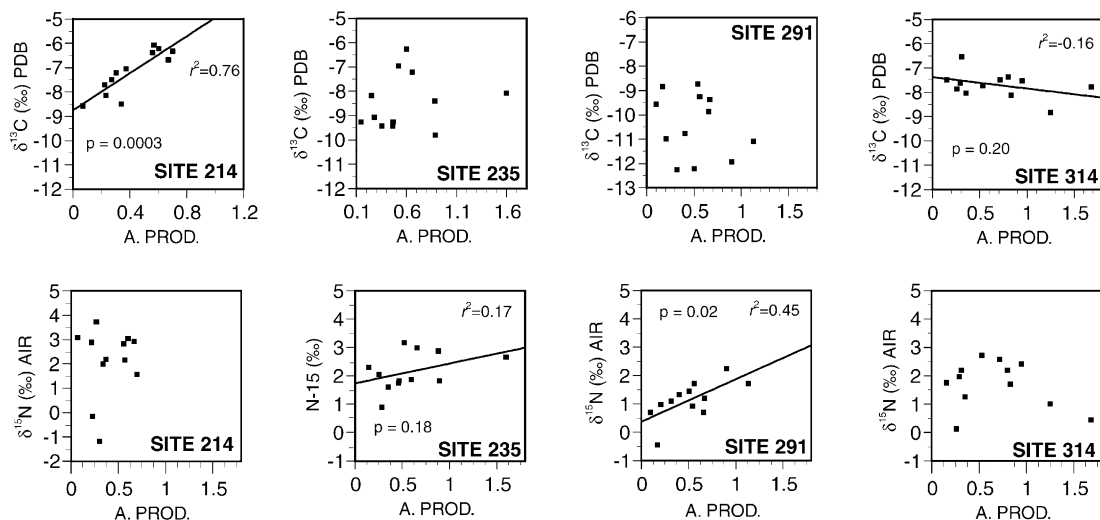
Table 2
Complied ^{15}N (‰) *Thalassia testudinum* values from all stations

Station	n	Mean	S.E.	Min	Max	Range
214	12	2.08	0.41	−1.2	3.7	4.9
235	12	2.15	0.19	0.9	3.2	2.3
291	12	1.14	0.20	−0.4	2.3	2.7
314	12	1.70	0.24	0.1	2.7	2.6

Fig. 3. *Thalassia testudinum*: (A) comparison of ^{13}C values from all stations and C:P ratios with (B) comparison of $\delta^{15}N$ values from all stations and C:N rations. Dashed lines indicate the 95% confidence level.

erogeneous. Most of the stations' isotopic data did not show strong correlations with the productivity data (Fig. 4), and owing to small sample size and natural variability in this preliminary data set, we had limited power to detect significant relationships between variables. Therefore, we have chosen a benchmark of $P = 0.15$ as our indication of significant relationships. The $\delta^{13}C$ values from station 214 did have a positive relationship with aerial productivity ($r^2 = 0.76$,

$P = 0.0003$). On the other hand, station 314 had a weakly negative correlation between aerial productivity and ^{13}C, but its p values feel below our significance criteria at $P = 0.20$. The correlation the $\delta^{15}N$ values from station 291 yielded positive relationships with aerial productivity. Yet, site 235 displays a positive relationship between $\delta^{15}N$ values and aerial productivity, but this is a weak correlation ($P = 0.18$). The comparison of the different stations' $\delta^{13}C$ and $\delta^{15}N$ values with specific
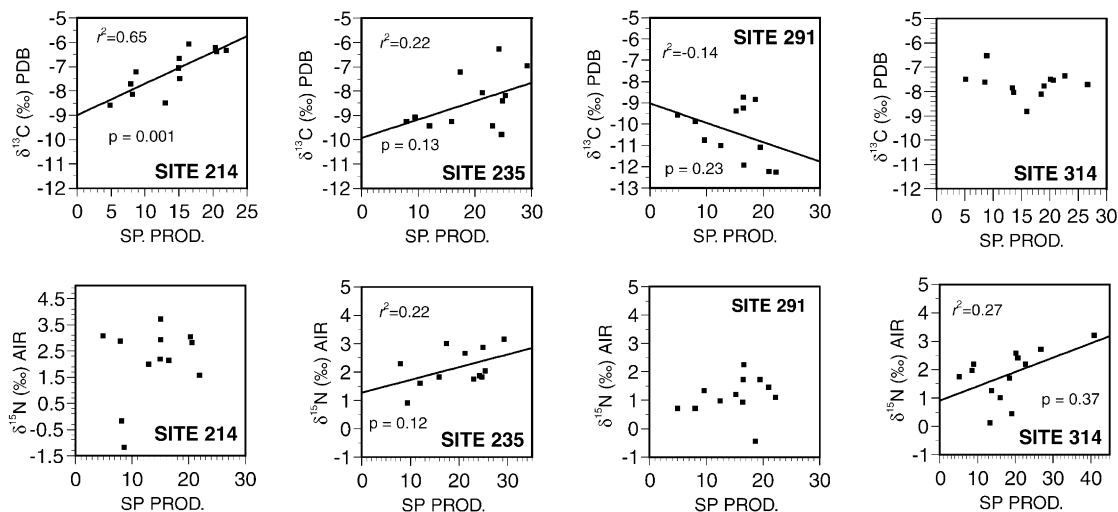

Fig. 4. Multiple plots of all sites' isotopic data with the two measures of productivity; aerial and specific productivity. Productivity data are from Fourqueran et al. (2001).
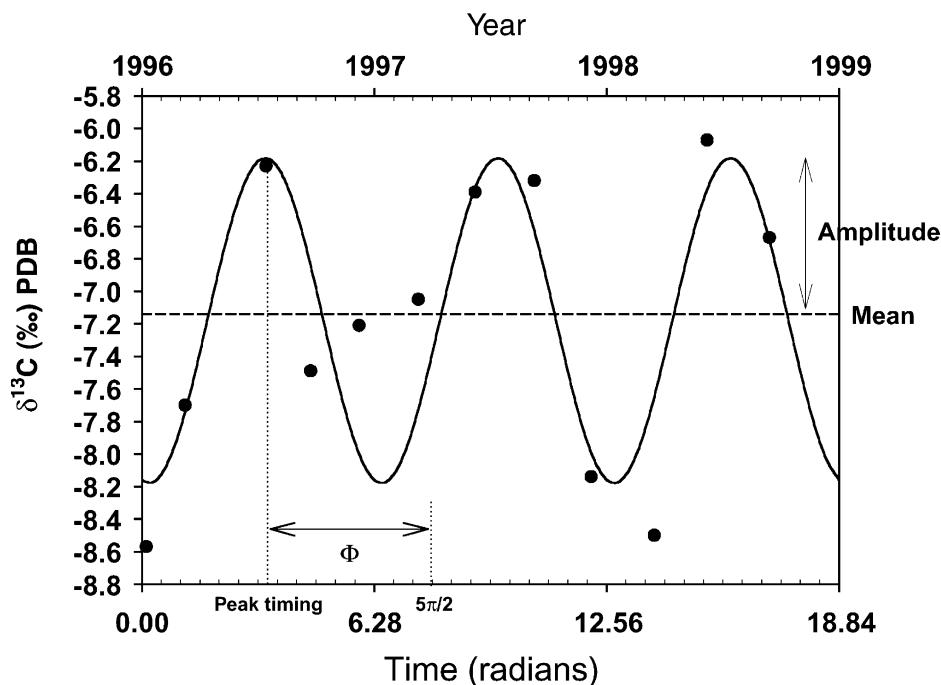
Fig. 5. An example of a sine model based on station 214's $\delta^{13}C$ values. Data for all stations are tabulated in Table 3.

productivity (Fig. 4) proved to have one more significant correlation than with aerial productivity. For carbon, stations 214 and 235 yielded positive relationships with specific productivity.

Previous work by Fourqurean et al. (2001) has shown that a sine function can be used to describe the intra-annual patter of growth and abundance of seagrasses in south Florida (Fig. 5). With this approach, the average annual cycles and their timing at each station may be better defined. Here we tested whether a similar approach with the isotopic time series would yield a similar sinusoidal pattern (Table 3). Our analysis indicates that the sine model did not produce a satisfactory fit for the nitrogen isotope time series data from all the sites, because of differences in the timing of the peak value from year to year ($F_{3,8}$ for all models < 0.19, $P > 0.22$). In contrast, the sine model applied to the carbon isotope time series did have a significant relationship at three of the four sites, 214, 235, and 291 (all

relationships at these sites where above the 95% confidence interval). The sine model of the carbon data showed that calculated averages are all within error of the actual means (Tables 1 and 3). Station 291 showed the highest amplitude of 1.52‰; note that a full seasonal cycle results in a > 3‰ change. Station 314 had the lowest amplitude of 0.44‰. Timing of the ^{13}C cycles did change with respect to station location. The stations (291 and 314) on the Bay side of the Keys had peaks in October, compared the Atlantic side, where the peaks occurred 1–2 months earlier.

5. Discussion

The $\delta^{13}C$ and $\delta^{15}N$ values of seagrass from our four sites in the FKNMS show a large amount of temporal variability. However, all the measurements fall within previously collected values. The more negative $\delta^{13}C$

Table 3
Sine model information for all stations including ^{13}C (‰) records, regression coefficients, mean values calculated from the model, amplitude, and timing of the maximum peak (see Fig. 5)

Station	Mean	Amp	Peak	r^2	$F_{3,8}$	p
214	−7.18±0.15	1.00±0.22	July 31 ±13 days	0.70	6.16	0.018
235	−8.45±0.19	1.25±0.27	Sept 17±13 days	0.71	6.70	0.014
291	−10.42±0.21	1.52±0.29	Oct 7±11 days	0.75	8.04	0.008
314	−7.71±0.14	0.44±0.02	Oct 29±25 days	0.36	1.15	0.280

values measured at Site 291 might be caused by increased terrestrial or mangrove OM, which when mineralized would drive down the local isotopic composition of dissolved inorganic carbon (DIC). A similar effect was observed by Lin et al. (1991) in South Florida. Mangroves are typical terrestrial C_3 plants, and have $\delta^{13}C$ values around -27‰ (Harrigan et al., 1989; Loneraga et al., 1997). Locally mineralized mangrove OM can cause the $\delta^{13}C$ of DIC to become more negative. Inputs of terrestrial OM can have similar affects too.

The observed variations in seagrass ^{13}C content do not appear to be random, but occur with a seasonal pattern. The carbon isotope enrichment–depletion pattern starts in the winter months, followed by a maximum value near late summer to fall with minimum values occurring in typically in the winter. These cycles for the $\delta^{13}C$ time series typically have a total magnitude change of more than 2‰. Many studies have documented this decrease in carbon isotopic discrimination with regard to seasonal changes in productivity and/or blooms that decrease available CO_2 for photosynthesis (Hollander and McKenzie, 1991; Laws et al., 1995; Ostrom et al., 1997). Lack of pervasive significant correlations between isotope values and productivity in our data sets may have been a result of low statistical power, small-scale spatial variability, or temporal variation in the isotopic composition of the source pools of DIC and DIN. Additionally the potential use of isotopically light HCO_3^- by the plants as a carbon source would cause isotopic changes not necessarily related to productivity (Laws et al., 1995). Assuming atmospheric CO_2 has a $\delta^{13}C$ value of near -8.0‰ (Francey and Allison, 1996), the carbon isotopic composition of HCO_3^- at 25 °C would be -0.1‰ and $CO_{2(aq)}$ would be -9.1‰ (Mook et al., 1974). We are addressing these questions in current work that will be presented elsewhere.

In contrast, the $\delta^{15}N$ time series constructed from the different stations did not display the same regular seasonal trend as observed in the carbon data. The nitrogen data did have intra-annual variability, but the timing of the enrichment and depletion varied among years and stations. One the best examples of this variability in the nitrogen time series can be observed at station 214, which has an almost 6‰ depletion in 1996 during the transition from late summer to fall. The nitrogen isotopic composition aquatic plants is controlled by two processes: (1) the isotopic composition of DIN and (2) the fractionations that occur during uptake and transformation (McCusker et al., 1999). The isotopic composition of DIN can change as proportions of NO_3^- and NH_4^+ change. Ostrom et al.'s (1997) work in a coastal cold-ocean embayment, Conception Bay, Newfoundland, indicated that $\delta^{15}N$ of NH_4^+ was 3.5–6.1‰ more enriched than the local NO_3^-. Denitrification can also

result in a relative isotopic enrichment of the residual NO_3^-. The time series data from our sites generally display trends that show enrichment during the summer to late fall, followed by a depletion during the winter. These trends also match changes in intra-annual DIN composition from different locations in Florida Bay, where NO_3^- concentrations increase 2-fold from the summer to winter months, with maximum values greater than 2 µM (Boyer et al., 1999). NH_4^+ shows the opposite trend, with elevated levels occurring during the summer months, varying between 0.5 and 10 µM (Boyer et al., 1999). Concentrations of NH_4^+ above 0.3 µM can inhibit the utilization of NO_3 by phytoplankton (Probyn, 1988; Wheeler and Kokinakis, 1990).

Our intra-annual nitrogen isotopic variability can be interpreted using the conceptual models of Ostrom et al. (1997) and McCusker et al (1999), where uptake of NH_4^+ by plants results in relatively enriched $\delta^{15}N$ values during the late summer to fall months. The more depleted values occurring during the winter months can be caused by the utilization isotopically depleted NO_3^-. Additionally, these trends also correspond with previously identified changes in DIN concentrations, where NO_3^- levels are highest in the winter, and NH_4^+ levels are highest in the summer. The lack of correlation between the nitrogen and carbon isotope time series indicates that perhaps a decoupling has occurred between the production and utilization of nutrients at out sites (Karl et al., 1998).

In total, these data indicate that seasonal and intra-annual variability must be taken into account when conducting food web work in similar areas. Not only does the carbon isotopic composition of *T. testudinum* change, but $\delta^{15}N$ values change by more than 4‰ between two seasons. In fact, the seasonal changes observed in our data set match in magnitude many of the isotopic changes observed in the Phanerozoic.

6. Conclusion

The isotopic composition of marine plants can provide important information about the environmental conditions in which those plants grew. This information may be used to infer productivity changes and/or changes in the nutrient cycling affecting a particular area. The variability in each of the four stations presented here indicates that more time series will be needed from more locations to understand fully the spatial and temporal variability of the carbon and nitrogen cycle within south Florida coastal environments. This increased resolution will help to define which areas are changing during different seasons. All of the study areas were located at similar water depths, but with different oceanographic conditions may have affected their carbon and nitrogen pools at different times. For example, DIC

from terrestrial runoff originating out of Shark River Slough might affect the Bay side, but this can also affect the Atlantic reef side as well. Even changes in upwelling from the reef side can affect the Bay side, in a delayed mode (Leichter and Miller, 1999). Therefore external forcing of local carbon and nitrogen pools can be affected by changes oceanographic controls. Furthermore, future evaluation of this isotopic time series with more water quality data will hopefully constrain how the composition of DIN is changing and its impact on the plants $\delta^{15}N$ values. It is possible our negative winter $\delta^{15}N$ data are the result of an increased importance of recently remineralized ammonium as an N source during winter.

Additionally, the variability of the seasonal isotopic response in our data set indicates that isotope based food-web studies should consider these patterns when analyzing primary producers. A 4‰ change can potentially have a large affect on an interpretation and trophic level assignment. Each study area will have its own unique forcing and controls (climate, oceanographic, community structure, etc.), and with higher resolution sampling the causes of variability may be further understood through time series analysis.

Acknowledgements

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