



Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys USA

JAMES W. FOURQUREAN^{1,*} and JOSEPH C. ZIEMAN²

¹Department of Biological Sciences and Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA; ²Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, USA; *Author for correspondence (e-mail: fourqure@fiu.edu; phone: 305-348-4084; fax 305-348-4096)

Received 26 July 2001; accepted in revised form 18 October 2001

Key words: Carbonate, Nutrient limitation, Seagrass, Spatial pattern, Stoichiometry

Abstract. Between 1992 and 2000, we sampled 504 randomly chosen locations in the Florida Keys, Florida, USA, for the elemental content of green leaves of the seagrass *Thalassia testudinum*. Carbon content ranged from 29.4–43.3% (dry weight), nitrogen content from 0.88–3.96%, and phosphorus content from 0.048–0.243%. N and P content of the samples were not correlated, suggesting that the relative availability of N and P varied across the sampling region. Spatial pattern in C:N indicated a decrease in N availability from inshore waters to the reef tract 10 km offshore; in contrast, the pattern in C:P indicated an increase in P availability from inshore waters to the reef tract. The spatial pattern in N:P was used to define a P-limited region of seagrass beds in Florida Bay and near shore, and an N-limited region of seagrass beds offshore. The close juxtaposition of N- and P-limited regions allows the possibility that N loading from the suburban Florida Keys could influence the offshore, N-limited seagrass beds without impacting the more nearshore, P-limited seagrass beds.

Introduction

Elemental stoichiometry and the spatial pattern in elemental content of primary producers have been shown to be good integrators and indicators of ecological processes. The familiar Redfield ratio (Redfield 1958), for example, can be used as an indicator of the relative availability of essential plant nutrients for phytoplankton communities. The same technique can be applied to more structurally complex primary producers as well: deviations from a taxon-specific “Redfield ratio” have been used as proxies for relative nutrient availability for seagrasses and macroalgae (Atkinson and Smith 1983; Duarte 1990). Moreover, spatial pattern in elemental stoichiometry is caused by spatial variation in the environment of the primary producers. The spatial pattern in nutrient content can be used to generate hypotheses about the nature of spatial variation of ecosystem processes. For example, a strong gradient in the C:P of *Thalassia testudinum* leaves across Florida Bay was interpreted to indicate a spatial pattern in the degree of phosphorus limitation in the ecosystem (Fourqurean et al. 1992), an hypothesis later confirmed by experiments (Tomas et

al. 1999). In Tomales Bay, strong gradients in the C:N of *Zostera marina* leaves were interpreted to indicate both the N source and the importance of net denitrification within the bay (Fourqurean et al. 1997).

Indicators of nutrient availability for primary producers are necessary because of the difficulties of measuring nutrient availability directly. Water quality monitoring programs provide important data on concentrations of important nutrients, but rarely are the samples in such a program collected frequently enough to capture the temporal variability in nutrient concentrations. Additionally, concentration measures are not sufficient measures of nutrient availability because cycling rates control the supply of limiting nutrients (Howarth 1988). Seagrasses make excellent indicators of nutrient availability in marine ecosystems because they are fixed to the substratum, they often grow in nutrient-limited, clear-water areas, and the nutrient content of their leaves reflects relative availability (Atkinson and Smith 1983; Duarte 1990).

One of the world's most extensive seagrass beds (ca. 14,000 km²) surrounds the chain of islands known as the Florida Keys at the southern tip of the Florida Peninsula (Fourqurean et al. 2001, 2002). In the northern section of the Florida Keys, seagrass beds extend from just inside the fringing barrier reef 10 km offshore to the shallow intertidal zone of the islands. Seagrass beds also line the bottom of Florida Bay to the north and west of the islands (Figure 1). Increasing human population on the Florida Keys has raised concern about the potential for anthropogenic impacts on these seagrass resources. It has been demonstrated that nutrient impacts can alter the structure of seagrass beds in the region (Powell et al. 1989, 1991; Tomasko and Lapointe 1991; Fourqurean et al. 1995), and also that humans have altered nutrient availability in both groundwater and nearshore marine waters in the Florida Keys (Lapointe et al. 1990; Lapointe and Matzie 1996).

Because of work with macroalgae (Lapointe 1987) and seagrasses (Powell et al. 1989; Fourqurean et al. 1992) from Florida Bay, it has been generally assumed that phosphorus is the limiting nutrient for primary production in the Florida Keys. This is also the prediction made from the general model proposed by Short (1987) that seagrasses in carbonate sediments, like those that surround the Florida Keys, should be P- rather than N-limited. More recent work with tropical seagrass communities, however, indicates that seagrasses from carbonate environments can be N-limited if loading rates and organic matter diagenesis can supply more P than can be sequestered on carbonate sediment particles (Erfteimeijer and Middelburg 1993; Erfteimeijer 1994; Jensen et al. 1998).

Enhanced N:P in anthropogenic wastes and the supposition that P, not N, would be the nutrient to increase primary production in the shallow waters of the Florida Keys have until now partially placated the concerns of resource managers about general cultural eutrophication of the nearshore environments of the Florida Keys, since it has been shown that anthropogenic P injected into groundwater has limited mobility (Corbett et al. 2000). But evidence is beginning to accumulate that P may not be the limiting nutrient across all shallow benthic habitats in the Florida Keys. N:P ratios in sediments decrease from the Keys offshore to the reef (Szmant and Forrester 1996), likely as a result of pulsed intrusions of P-rich, recently upwelled

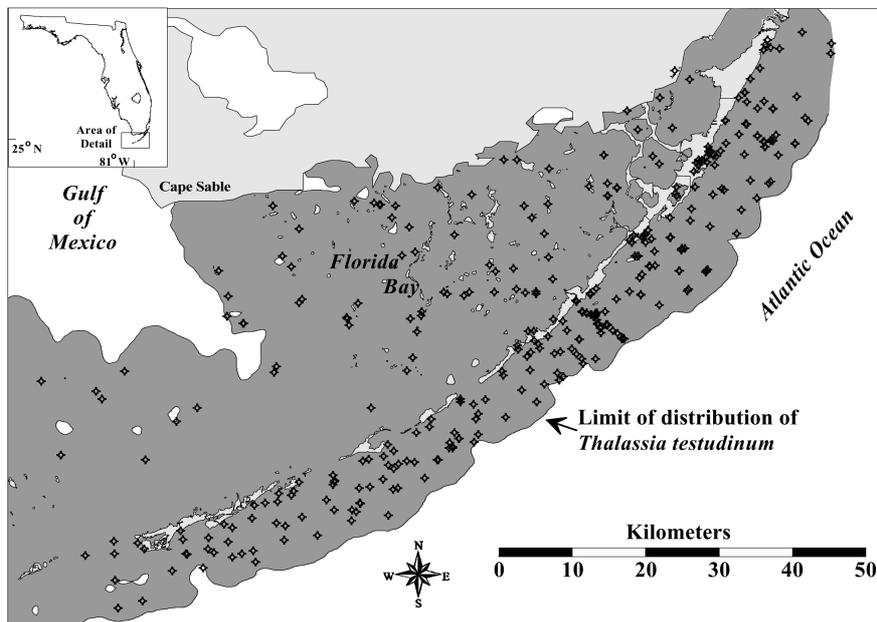


Figure 1. Map of study area, showing the limit of distribution of the seagrass *Thalassia testudinum* in south Florida (distribution information from Fourqurean et al. (2002). Sampling locations ($n = 504$) were randomly chosen across the study area, and are indicated by symbols

subthermocline water from offshore of the barrier reef (Leichter et al. 1996). This delivery of P from offshore may alleviate the P limitation of seagrasses offshore, leading to N- or light-limited seagrasses. If this were the case, then it is possible that N transported from naturally P-limited environments of Florida Bay and from the N-enriched anthropogenic waste from the Florida Keys could have an impact on benthic primary producers far offshore of the nearshore P-limited benthic communities.

In order to assess the potential limiting nutrient for seagrass growth in the upper Florida Keys, we sampled seagrass leaves from the most common seagrass, *Thalassia testudinum*, from randomly selected locations from the barrier reef tract through to Florida Bay. We hypothesized that nutrient stoichiometry would change predictably across the study area, from low N:P, potentially N-limited seagrasses just behind the barrier reef to very high N:P, potentially P-limited seagrasses adjacent to the Florida Keys and in Florida Bay. Such a pattern would indicate differences in the supply rates of nutrients across the ecosystem, and have important waste water management implications for the region.

Methods

The upper Florida Keys (Figure 1) are a nearly continuous chain of islands that were formed as a barrier coral reef during a Pleistocene higher stand in sea level (see Schomer and Drew (1982) for a review). The Keys separate Florida Bay, a shallow, seagrass-dominated lagoonal estuary (see Fourqurean and Robblee (1999) for a description) from a higher-energy shallow-water platform. Florida Bay is very shallow (generally < 2 m deep) and the bottom of the bay is covered with fine-grained carbonate sands and muds. About 10 km offshore from the Florida Keys, a barrier coral reef delineates a change in the shelf slope. Maximum water depths between the reef and the Florida Keys is 10 m. Inshore of the reef tract, unconsolidated carbonate sediments overlay a limestone bedrock. Seagrass beds, dominated by *Thalassia testudinum*, are the dominant benthic habitat type both in Florida Bay (Zieman et al. 1989) and the backreef environment (Fourqurean et al. 2001).

Between 1992 and 2000, we sampled 504 randomly chosen locations for the elemental content of seagrass (Figure 1). Sampling was restricted to summer (May–September) because the influence of nutrient availability on seagrass growth is most evident during times when seagrass growth rates are potentially high enough to outstrip nutrient supply rates (Thom and Albright 1990; Pedersen and Borum 1992; Fourqurean et al. 1997); seagrass growth rates peak during summer months in south Florida (Fourqurean et al. 2001). At each sampling site, 5 intact short shoots of *Thalassia testudinum* were haphazardly collected from a 10 m² area. These short shoots were returned to the lab, where all attached green leaves were cut from the short shoots and cleaned of adhering epiphytes by gently scraping with a razor blade. All leaves from a site were pooled and dried at 80 °C. Dried leaves were ground to a fine powder using a ceramic mortar and pestle. Powdered samples were analyzed in duplicate for carbon and nitrogen content using a CHN analyzer (Fisons NA1500). Phosphorus content was determined by a dry-oxidation, acid hydrolysis extraction followed by a colorimetric analysis of phosphate concentration of the extract (Fourqurean et al. 1992). Elemental content was calculated on a dry weight basis; elemental ratios were calculated on a mole:mole basis.

Results

There was substantial variation in the elemental content of leaves of *Thalassia testudinum* from the 504 samples (Table 1). Carbon content was less variable than nitrogen or phosphorus content. The Coefficient of Variation ($CV = s.d./\bar{x}$) for C was 6.7%, compared to 22.6% for N and 33.9% for P. The distributions of C and N content were symmetrical about the mean, but the distribution of P content was skewed to the right by infrequent samples with relatively high P content (Figure 2). The N and P content of the samples were not correlated (Pearson's $r = -0.52$, $p = 0.241$, $n = 504$; scatterplot not shown).

Table 1. Summary statistics for elemental composition of *Thalassia testudinum* from 504 samples. Elemental ratios were calculated on a mol:mol basis

Element	Minimum	Maximum	Median	Mean	S.D.
Carbon (% of dry wt)	29.4	43.3	36.6	36.9	2.5
Nitrogen (% of dry weight)	0.88	3.96	1.76	1.82	0.40
Phosphorus (% of dry weight)	0.048	0.243	0.110	0.113	0.037
C:N	11.1	47.1	24.5	24.6	5.2
C:P	373.4	1901.3	874.0	937.4	311.5
N:P	15.4	107.1	34.8	40.2	17.8

The distributions of the C:N, C:P and N:P of the samples were all skewed to the right by relatively infrequent samples with high nutrient ratios (Figure 3). Because of the relative constancy of C content of the samples, C:N and C:P ratios were less variable than the N:P ratio (CV of 21.2%, 35.6% and 51.1%, respectively). All three ratios had substantial range, from 11.1 to 47.1 for C:N, from 373.4 to 1901.3 for C:P, and from 15.4 to 107.1 for N:P (Table 1).

There was striking spatial pattern in the distribution of elemental ratios in *Thalassia testudinum* leaves. The lowest C:N (< 20) was observed in central Florida Bay, and the C:N generally increased from the Florida Keys seaward, with maximum C:N (> 30) observed at the seaward extent of the seagrass beds (Figure 4). Conversely, C:P showed the opposite trend (Figure 4): C:P was maximum in eastern Florida Bay (> 1200), and generally decreased in an offshore direction, reaching a minimum (< 600) near Cape Sable in western Florida Bay and at the furthest offshore seagrass beds. N:P was maximum in the eastern half of Florida Bay, where values > 80 were not uncommon (Figure 5). Within Florida Bay, N:P decreased westward, to values < 30 along the western edge of our study area. On the Atlantic Ocean side of the Florida Keys, there was a general pattern of decreasing N:P as distance from shore increased. When all of the Atlantic Ocean side data were analyzed together, there was a significant linear decrease in N:P in an offshore direction, with a slope of -2.32 km^{-1} (Figure 6). The strength of this general pattern varied from east to west along the Florida Keys: in the east, the offshore decrease was always observed.

This spatial variation in N:P of seagrass leaves can be interpreted as an indicator of the spatial pattern in the relative availability of N:P for *Thalassia testudinum*. Using 30 as the "Redfield" N:P for seagrass that indicates a balance between N and P availability (Atkinson and Smith 1983), there were broad areas of both N- and P-limited seagrass beds (Figure 7). All of Florida Bay except the western margin had *T. testudinum* N:P consistent with P-limitation. Along the western margin of Florida Bay, the N:P indicated N-limitation. In general, there was also a signal of P-limitation in the near-shore along the Atlantic Ocean side of the Florida Keys. In more offshore regions, however, the N:P was consistent with N-limited *T. testudinum*. In the western half of the study area, there were regions of apparent P-limi-

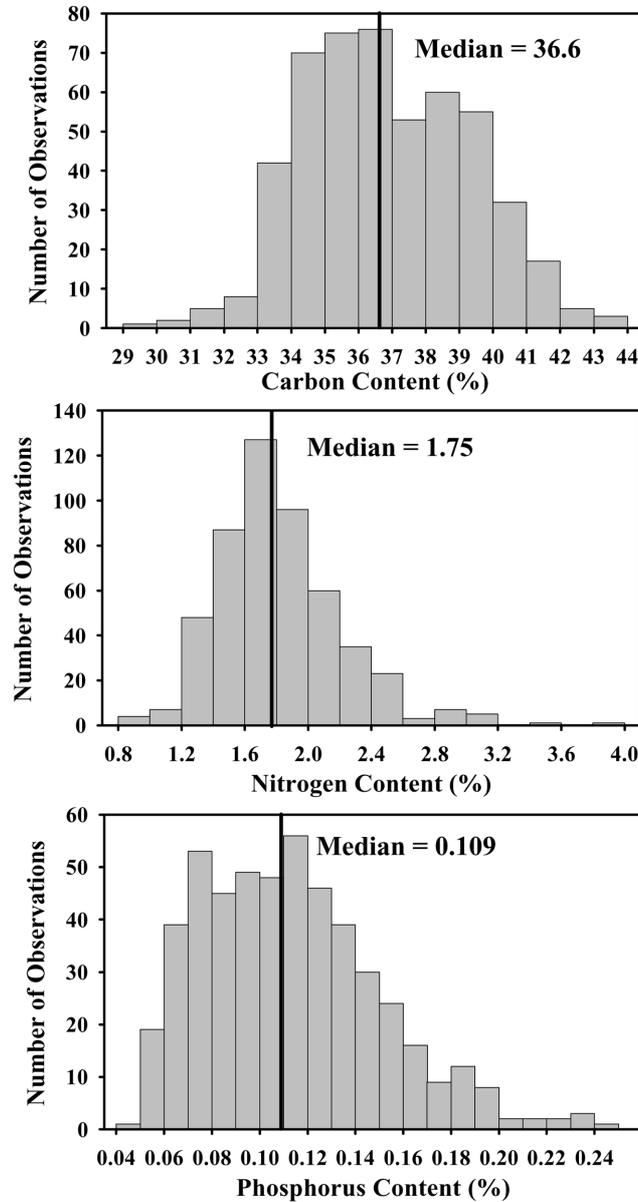


Figure 2. Frequency histograms of C, N and P content of 504 samples of *Thalassia testudinum* leaves collected in the upper Florida Keys, FL, USA. The mean values for each element are indicated by solid vertical lines

tation that extended offshore of the Florida Keys to the edge of the seagrass bed at the barrier reef tract.

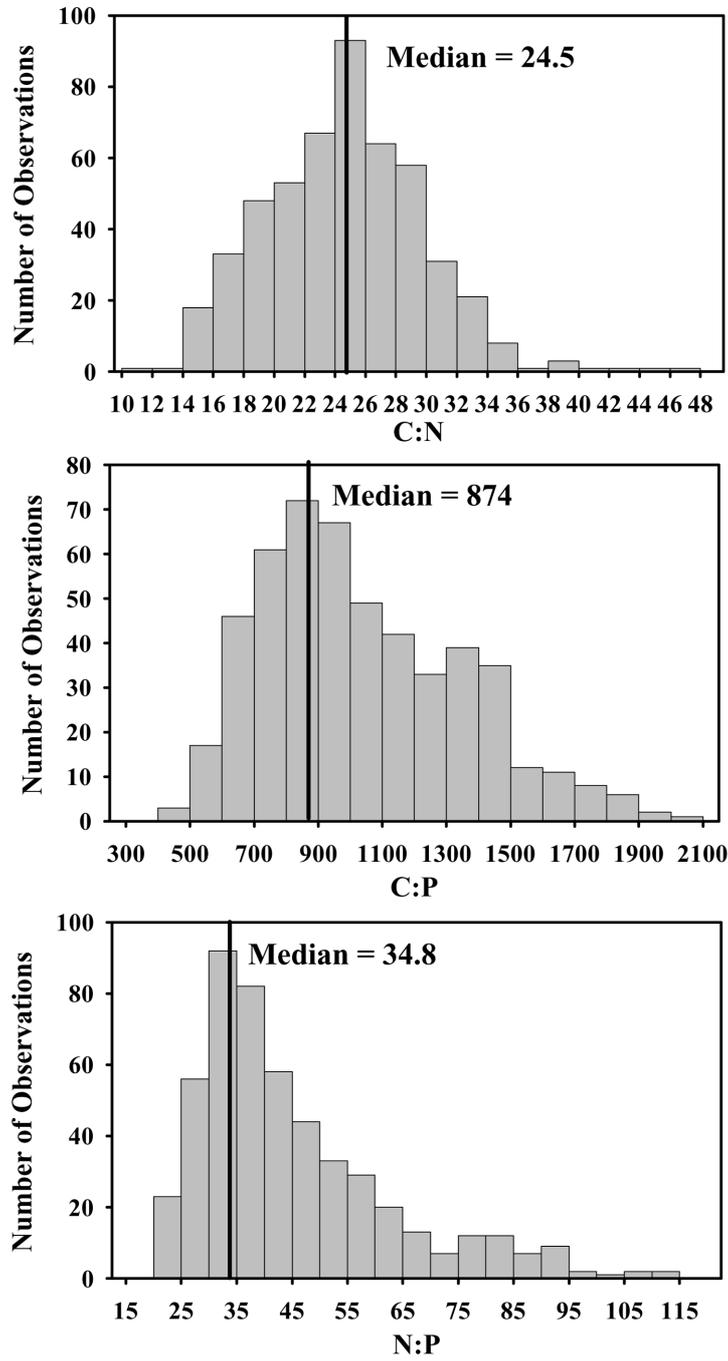


Figure 3. Frequency histograms of C:N, C:P, N:P of 504 samples of *Thalassia testudinum* leaves collected in the upper Florida Keys, FL, USA. The mean values for each element are indicated by solid vertical lines

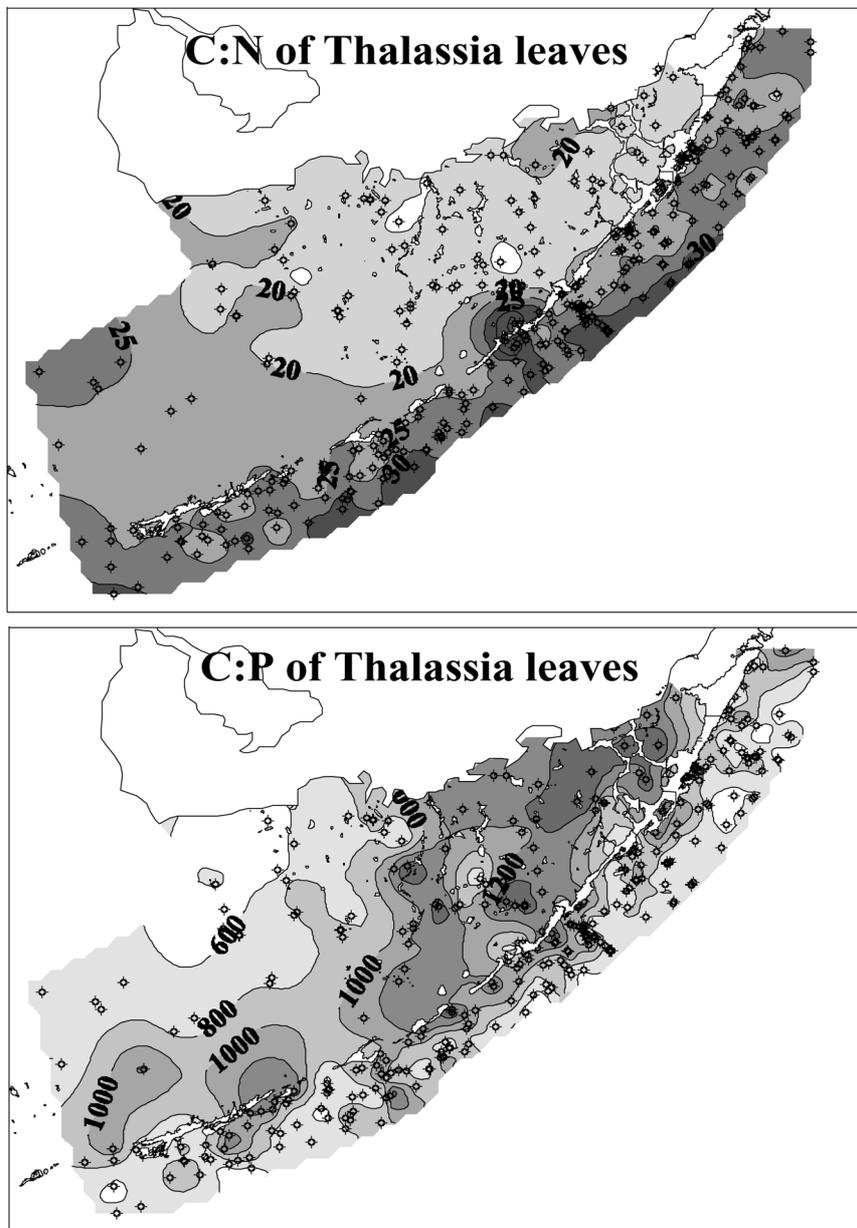


Figure 4. Spatial pattern in the C:N (top) and C:P (bottom) of *Thalassia testudinum* leaves in south Florida. C:N contour lines are separated by increments of 5, C:P contour lines are separated by increments of 200. The darkness of the shading increases with the ratio. Symbols indicate sampling locations

Discussion

There was a broad range in the N and P content of *Thalassia testudinum* leaves from across our study area. Elemental content did not vary randomly; rather there was a strong spatial pattern in the relative amounts of N and P in the samples. The spatial pattern suggested two main trends. The first trend was a decrease in the availability of P from the Gulf of Mexico eastward into Florida Bay, as has been documented previously (Fourqurean et al. 1992; Frankovich and Fourqurean 1997). The second pattern was an increase in relative P availability as distance from shore increases on the Atlantic Ocean side of the Florida Keys. This second pattern is consistent with the documented trend in sediment nutrient ratios (Szmant and Forrester 1996). Our data adds to these previously established trends by documenting that changes in ratios of sediment nutrients are reflected in primary producers, and analysis of the seagrass leaf N:P data suggest that there is a qualitative shift from P-limitation to N-limitation of the seagrasses in different regions of our study area. This shift in the limiting nutrient to seagrasses occurs despite the similarity in the mineralogy of the sediments in which the seagrasses are growing—we found evidence for both P- and N-limited seagrass growth on carbonate sediments, contrary to the predictions of Short (1987).

Data from this study expand the range of nutrient content reported for *Thalassia testudinum* from south Florida. Previous investigations (Powell et al. 1989; Fourqurean et al. 1992; Frankovich and Fourqurean 1997) have reported nutrient ratios mostly consistent with P-limitation, with N:P generally greater than 30 except in areas locally influenced by nutrient additions. For example, N:P of *T. testudinum* leaves decreased from a background value of ca. 60 to 29 adjacent to bird rookery islands in the eastern part of Florida Bay (Fourqurean et al. 1992). Experimental application of bird feces caused the N:P of *T. testudinum* leaves to decrease from 48 to 28 in the central part of Florida Bay (Powell et al. 1989). Note that in neither of these two cases were N:P ratios much lower than 30 recorded, suggesting that nutrient addition in Florida Bay led to amelioration of P-limitation, but did not produce much N-limitation. In the wider geographic scope of the data presented in this paper, there were many samples with N:P less than 30, and 23 samples had $N:P < 25$. Such low N:P values for *T. testudinum* are rare across the geographic range of this species. Patriquin (1972) reported a mean N:P of 32 for 9 samples from Barbados, and Gallegos et al. (1993) reported N:P of 29 at two back reef sites and 47 from a shallow lagoon in the Mexican Caribbean.

Factors other than changes in the supply rate of N and P can affect the nutrient content of seagrasses. Nutrient limitation can only occur when seagrass growth rate is potentially high enough to outstrip the nutrient supply rate (Thom and Albright 1990; Pedersen and Borum 1992), hence any factor that limits growth rate can also influence the degree of nutrient limitation and therefore elemental content. For example, variation in light availability can cause changes in C:N of seagrasses, so areas of low light availability have low C:N (Abal et al. 1994; Grice et al. 1996). However, environmental gradients other than relative nutrient availability were not consistent with the spatial pattern in elemental ratios of *Thalassia testudinum* leaves

(Figures 4 and 5). There are spatial patterns in water clarity and light availability in the region; water clarity generally increases from onshore to offshore on the Atlantic Ocean side of the Florida Keys (Boyer and Jones 2002), and benthic light availability is a function of water clarity and water depth. Water depth does not increase on average from onshore to offshore on the ocean side of the Keys until the seaward side of the reef tract, and all our samples were collected inside the reef tract. In addition, while it is clear that light availability can affect C:N and C:P in a similar manner (Abal et al. 1994; Grice et al. 1996), the divergent patterns in C:N and C:P (Figure 4) suggest factors other than light availability are responsible for the observed spatial patterns.

The hypothesis that seagrasses found in carbonate environments should be P-limited (Short 1987), and hence have a high N:P, is based upon the geochemistry of phosphate uptake onto carbonate particles (de Kanel and Morse 1978) and the high rates of nitrogen fixation measured in tropical, carbonate seagrass beds (e.g. Capone et al. (1979)). As pointed out by Erftemeijer (1994), however, the real determinant of which element limits seagrass production is a function of a more complicated budget of gains and losses of N and P. Respiration and other oxidative processes in the rhizosphere of seagrasses in carbonate environments create hydrogen ions that will cause the dissolution of carbonate mineral phases (Ku et al. 1999), thereby releasing sorbed phosphate into the porewater and making it available to seagrasses (Jensen et al. 1998). Were these releases greater than the rate of phosphate uptake onto carbonate particles, P supply could be quite high. Organic matter content of the sediments, potentially an indicator of respiration rate, is very high (> 20% of dry weight) in the center of Florida Bay (J. W. Fourqurean, unpublished data), but the N:P data do not indicate a maximum in P availability in the center of the bay. Further, the sorption of phosphate onto carbonates is a surface-area phenomenon, so that smaller particles with a higher surface area to volume ratio, should sorb more P than larger particles. Relatively high P availability in tropical seagrass beds occurring in coarse sands has been ascribed to this grain-size effect (Erftemeijer and Middelburg 1993; Erftemeijer 1994). Differences in grain size across our study area are partly coincident with the pattern of N:P of *T. testudinum* leaves (Figure 5). Florida Bay, where the N:P of *T. testudinum* was largely indicative of P limitation, is underlain by very fine sediments (Bosence 1989). On the ocean side of the Florida Keys, coarser carbonate sediments are found in the back-reef seagrass beds, where fines (< 62 μ) make up less than 5 % of the sediment (Enos and Perkins 1977). But, fines make up the largest fraction (> 50%) of the sediment mid-way between the Florida Keys and the reef tract, where water depth is maximum; the fine fraction decreases shoreward. If grain size were the only determinant of P availability, then N:P should exhibit a maximum midway between the Keys and the reef, instead of the decreasing reefward pattern we observed (Figure 5).

The most likely explanation of the spatial pattern in N:P is a spatial pattern in loading rates across our study area. The low N:P of seagrass leaves from samples from the western margin of Florida Bay and the back reef areas suggest that the major sources of P for primary producers in our study are the Gulf of Mexico for Florida Bay and the Atlantic Ocean for the ocean side of the Florida Keys. Surface

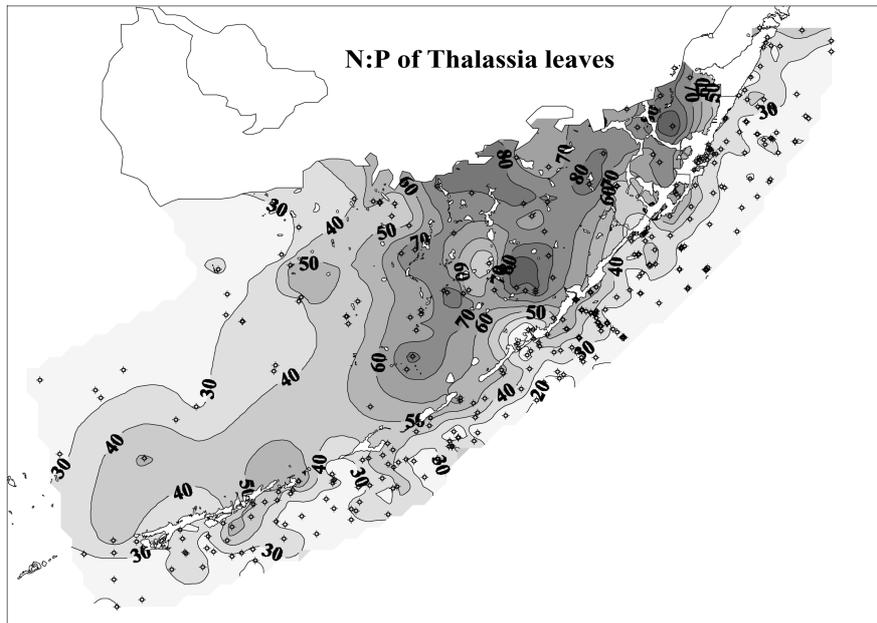


Figure 5. Spatial pattern in the N:P of *Thalassia testudinum* leaves in south Florida. Contour lines are separated by increments of 10 in N:P, the darkness of the shading increases with N:P. Symbols indicate sampling locations

waters of the Gulf of Mexico receive N and P from river runoff; analysis of spatial pattern (Fourqurean et al. 1993; Boyer et al. 1997) and nutrient budgets (Rudnick et al. 1999) of Florida Bay confirm the importance of the Gulf as a P source for Florida Bay. On the Atlantic side of the Keys, upwelling of nutrient rich water has been shown to be a source of nutrients for the reef tract (Leichter et al. 1996); we propose that P in this upwelled water is transported across the 10 km distance between the reef and the Keys by tidal action. This transport would lead to a decrease in P loading from this upwelled water from the reef to the Keys as the tidal bore is attenuated and P is taken up by primary producers and carbonate sediments. Such a pattern in P loading is evident in the accumulation of N and P in the sediments of the back-reef environment (Szmant and Forrester 1996); and this gradient is apparently great enough to cause a shift in the limiting nutrient for seagrass growth from N near the reef to P close to shore (Figure 6).

The onshore-offshore pattern in relative availability in N and P is quite strong in the eastern half of our study area, but breaks down in the western half (Figures 4 and 5). We propose that this breakdown is caused by the influence of water from the Gulf of Mexico that flows between the wide separations between the Keys in the western part of our study area. Owing to a tidal asymmetry, there is a net transport of water from the Gulf of Mexico to the Atlantic through these major passes (Smith 1994); this transport moves water, suspended particles and dissolved constituents in a region called the "Sluiceway" (Schomer and Drew 1982). It has long

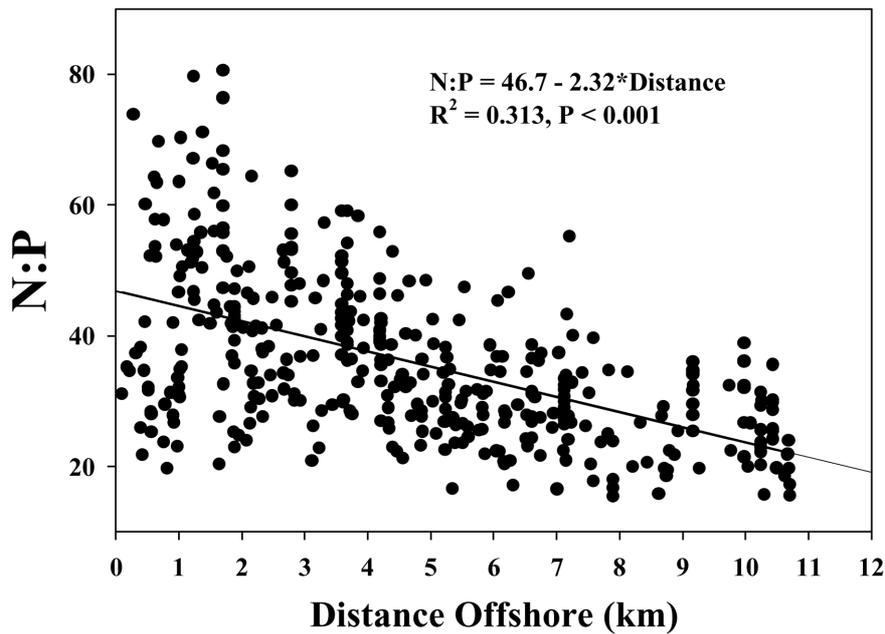


Figure 6. The relationship between the distance offshore and the N:P of leaves of *Thalassia testudinum* collected from the Atlantic Ocean side of the Florida Keys. The solid line represents the statistically significant regression (n = 405)

been reported that flow of water through passes in the Middle Florida Keys has a depressing effect on coral growth (Ginsburg and Shinn 1964; Hudson et al. 1976; Marszalek et al. 1977). Arguing from sedimentary petrology evidence, it has been suggested that elevated nutrients from Florida Bay and the Gulf of Mexico are responsible for this deleterious effect (Lidz and Hallock 2000). It is likely that the extension of the region of P limitation from of seagrass growth the Keys to the Reef in this area (Figure 7) is also a consequence of water transport from the Gulf of Mexico.

There are potential management implications of the spatial pattern in nutrient limitation. The P-limited nature of the benthos in most of Florida Bay and near-shore on the ocean side of the Keys illustrates the need to control P loading to the nearshore environment. P loading would be expected to cause eutrophication of these P-limited seagrass communities. Eutrophication of seagrass communities in south Florida follows a predictable pattern (Powell et al. 1989; Tomasko and Lapointe 1991; Duarte 1995; Fourqurean et al. 1995): first, an increase in the biomass of the dominant seagrass species (*Thalassia testudinum*), followed by increased epiphytization, then by a replacement of *T. testudinum* by faster growing macrophytes, and eventually a loss of benthic macrophytes because of competition from microalgae. Experimental evidence has shown that the spatial scale of eutrophication of seagrass communities in south Florida is generally limited to ca. 100 m from the point source at present (Powell et al. 1991; Fourqurean et al. 1995)

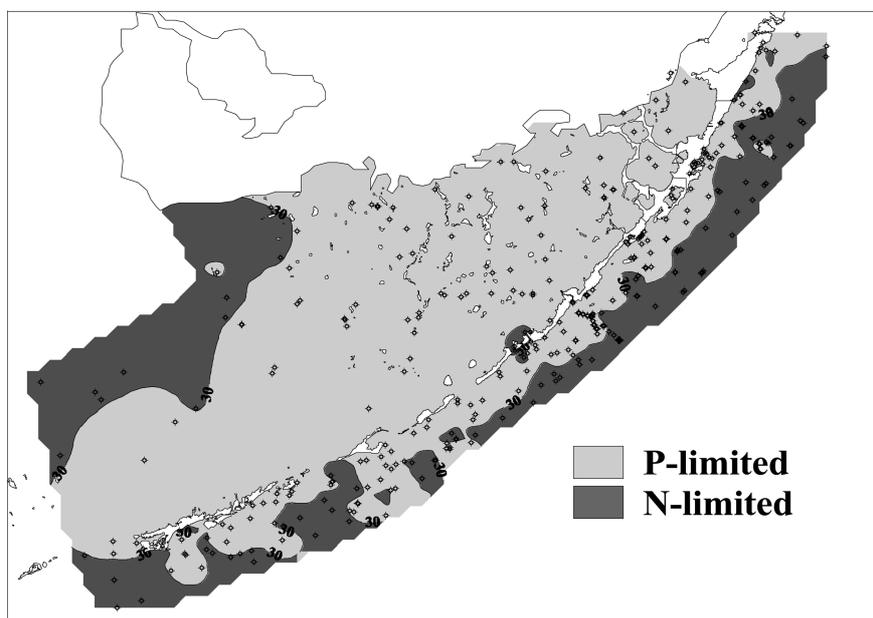


Figure 7. Zones of N- and P-limited seagrass communities in south Florida. The N:P contour of 30 (Figure 5) was used to delineate N-limited ($N:P < 30$) from P-limited ($N:P > 30$) regions

as a result of the very rapid nutrient uptake and assimilation rates of oligotrophic nature of the shallow water marine ecosystem. While previous studies have documented eutrophication-induced changes in seagrass beds very close to developed shorelines in the Florida Keys (e.g. Tomasko and Lapointe (1991)), effects of cultural eutrophication on seagrass beds more than 100 m from the shoreline have not been demonstrated. The ability of the benthic community to remove nutrients from the water is finite, however, and when these communities become sufficiently eutrophic the effects of eutrophication will surely increase in spatial scale.

The data presented in this paper do not allow for determination of whether regional-scale eutrophication is indeed occurring, because we have not analyzed time series of nutrient contents at fixed locations. The data presented in this paper were collected over an 8 year span, but there was no regional pattern to the timing of our sampling during this span. Hence, our observed spatial pattern was not an artifact of temporal change. There are reasons to suspect that there has been change in nutrient availability in the region. Human populations in south Florida have continued to grow, and recent changes in the importance of benthic versus pelagic primary production in Florida Bay (Fourqurean and Robblee 1999) are consistent with an increase in nutrient availability in Florida Bay. However, it is important to note that the spatial pattern in N and P content of seagrasses in Florida Bay was identical in 1994, following the dieoff of seagrasses, to the pattern observed in the late 1980's, prior to this event (Frankovich and Fourqurean 1997). But, such change analyses based on interpolated fields of broadly spaced data are made difficult by

small scale heterogeneity in nutrient availability. We are currently analyzing data collected routinely from fixed stations to determine whether there have been changes in nutrient content of *Thalassia testudinum* over time; these analyses will be presented elsewhere.

Most anthropogenic nutrients generated in the Florida Keys are disposed of in on-site sewage disposal systems (OSDS), which release these nutrients into the shallow groundwater. This shallow groundwater is pumped through the keys via tidal action, and pollutants disposed of in these OSDS can migrate rapidly to the marine surface waters (Lapointe et al. 1990; Paul et al. 1997; Dillon et al. 1999). The carbonate formations that underlie the Florida Keys are efficient at retaining phosphorus (Corbett et al. 2000), so anthropogenic nutrient inputs to the coastal zone are enriched with N compared to P. In the P-limited nearshore environments, the effects of N addition would be much reduced. But, cross-shelf transport of N towards the reef tract has the potential of causing eutrophication in the N-limited regions of our study area. These N-limited regions are generally removed by several kilometers from the possible source of anthropogenic nutrients. It is feasible, then, that uncontrolled anthropogenic N input to the system could cause changes to the benthic plant communities in areas several kilometers removed from the loading site, while having no effect near the loading site. Cross shelf transport of nutrients from the Keys to the reef has as yet not been adequately studied to allow for a definitive judgement about the magnitude of Keys-based N loading to the offshore shallow benthic communities (but see Szmant and Forrester (1996); Boyer and Jones (2002)). A recent evaluation of the patterns in seagrass species composition and growth rate did not find evidence of degradation of offshore seagrass beds in south Florida (Fourqurean et al. 2001), but the potential exists for these offshore seagrass communities to be influenced by N loading from the Florida Keys.

Acknowledgements

This research was funded by a grant from the National Oceanic and Atmospheric Administration's National Undersea Research center at the University of North Carolina at Wilmington and by grant X994620-94-5 from the Environmental Protection Agency as part of the Florida Keys National Marine Sanctuary Water Quality Protection Program. Many students and technicians have helped in the field collection and laboratory processing of these samples. In this regard, C.D. Rose and S.P. Escorcia have been particularly helpful. This is contribution number 167 of the Southeast Environmental Research Center at FIU.

References

- Abal E.G., Loneragan N., Bowen P., Perry C.J., Udy J.W. and Dennison W.C. 1994. Physiological and morphological responses of the seagrass *Zostera capricorni* Ascher. to light intensity. *J. Exp. Mar. Biol. Ecol.* 178: 113–129.
- Atkinson M.J. and Smith S.V. 1983. C:N:P ratios of benthic marine plants. *Limnol. Oceanogr.* 28: 568–574.
- Bosence D. 1989. Surface sublittoral sediments of Florida Bay. *Bull. Mar. Sci.* 44: 434–453.
- Boyer J.N., Fourqurean J.W. and Jones R.D. 1997. Spatial characterization of water quality in Florida Bay and Whitewater Bay by multivariate analyses: zones of similar influence. *Estuaries* 20: 743–758.
- Boyer J.N. and Jones R.D. 2002. View from the bridge: external and internal forces affecting the ambient water quality of the Florida Keys National Marine Sanctuary. In: Porter J.W. and Porter K.G. (eds), *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An ecosystem sourcebook*. CRC Press, Boca Raton, pp. 609–628.
- Capone D.G., Penhale P.A., Oremland R.S. and Taylor B.F. 1979. Relationship between productivity and N_2 (C_2H_2) fixation in a *Thalassia testudinum* community. *Limnol. Oceanogr.* 24: 117–125.
- Corbett D.R., Kump L., Dillon K., Burnett W. and Chanton J. 2000. Fate of wastewater-borne nutrients under low discharge conditions in the subsurface of the Florida Keys, USA. *Mar. Chem.* 69: 99–115.
- de Kanel J. and Morse J.W. 1978. The chemistry of orthophosphate uptake from seawater onto calcite and aragonite. *Geochim. Cosmochim. Acta* 42: 1335–1340.
- Dillon K.S., Corbett D.R., Chanton J.P., Burnett W.C. and Furbish D.J. 1999. The use of sulfur hexafluoride (SF₆) as a tracer of septic tank effluent in the Florida Keys. *J. Hydrol.* 220: 129–140.
- Duarte C.M. 1990. Seagrass nutrient content. *Mar. Ecol. Prog. Ser.* 67: 201–207.
- Duarte C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87–112.
- Enos P. and Perkins R.D. 1977. Quaternary Sedimentation in South Florida. Vol. 147. The Geological Society of America Inc, Boulder.
- Erfteimeijer P.L.A. 1994. Differences in nutrient concentrations and resources between seagrass communities on carbonate and terrigenous sediments in South Sulawesi, Indonesia. *Bull. Mar. Sci.* 54: 403–419.
- Erfteimeijer P.L.A. and Middelburg J.J. 1993. Sediment-nutrient interactions in tropical seagrass beds: a comparison between a terrigenous and a carbonate sedimentary environments in South Sulawesi (Indonesia). *Mar. Ecol. Prog. Ser.* 102: 187–198.
- Fourqurean J.W., Durako M.J., Hall M.O. and Hefty L.N. 2002. Seagrass distribution in south Florida: a multi-agency coordinated monitoring program. In: Porter J.W. and Porter K.G. (eds), *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An ecosystem source book*. CRC Press, Boca Raton, pp. 497–522.
- Fourqurean J.W., Jones R.D. and Zieman J.C. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, FL, USA: inferences from spatial distributions. *Estuarine Coastal Shelf Sci.* 36: 295–314.
- Fourqurean J.W., Moore T.O., Fry B. and Hollibaugh J.T. 1997. Spatial and temporal variation in C:N:P ratios, $\delta^{15}N$, and $\delta^{13}C$ of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. *Mar. Ecol. Prog. Ser.* 157: 147–157.
- Fourqurean J.W., Powell G.V.N., Kenworthy W.J. and Zieman J.C. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* 72: 349–358.
- Fourqurean J.W. and Robblee M.B. 1999. Florida Bay: a history of recent ecological changes. *Estuaries* 22: 345–357.
- Fourqurean J.W., Willsie A.W., Rose C.D. and Rutten L.M. 2001. Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Mar. Biol.* 138: 341–354.

- Fourqurean J.W., Zieman J.C. and Powell G.V.N. 1992. Phosphorus limitation of primary production in Florida Bay: Evidence from the C:N:P ratios of the dominant seagrass *Thalassia testudinum*. *Limnol. Oceanogr.* 37: 162–171.
- Frankovich T.A. and Fourqurean J.W. 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Mar. Ecol. Prog. Ser.* 159: 37–50.
- Gallegos M.E., Merino M., Marbà N. and Duarte C.M. 1993. Biomass and dynamics of *Thalassia testudinum* in the Mexican Caribbean: elucidating rhizome growth. *Mar. Ecol. Prog. Ser.* 95: 185–192.
- Ginsburg R.N. and Shinn E.A. 1964. Distribution of the reef-building community in Florida and the Bahamas. *Am. Assoc. Petroleum Geologists Bull.* 48: 527.
- Grice A.M., Loneragan N.R. and Dennison W.C. 1996. Light intensity and the interactions between physiology, morphology and stable isotope ratios in five species of seagrass. *J. Exp. Mar. Biol. Ecol.* 195: 91–110.
- Howarth R.W. 1988. Nutrient limitation of net primary production in marine ecosystems. *Ann. Rev. Ecol. Syst.* 19: 89–110.
- Hudson J.H., Shinn E.A., Halley R.B. and Lidz B. 1976. Sclerochronology: a tool for interpreting past environments. *Geology* 4: 361–364.
- Jensen H.S., McGlathery K.J., Marino R. and Howarth R.W. 1998. Forms and availability of sediment phosphorus in carbonate sand of Bermuda seagrass beds. *Limnol. Oceanogr.* 43: 799–810.
- Ku T.C.W., Walter L.M., Coleman M.L., Blake R.E. and Martini A.M. 1999. Coupling between sulfur recycling and syndepositional carbonate dissolution: evidence from oxygen and sulfur isotope composition of pore water sulfate, South Florida platform, USA. *Geochim. Cosmochim. Acta* 63: 2529–2546.
- Lapointe B.E. 1987. Phosphorus- and nitrogen-limited photosynthesis and growth of *Gracilaria tikvahiae* (Rhodophyceae) in the Florida Keys: an experimental field study. *Mar. Biol.* 93: 561–568.
- Lapointe B.E. and Matzie W.R. 1996. Effects of stormwater nutrient discharges on eutrophication processes in nearshore waters of the Florida Keys. *Estuaries* 19: 422–435.
- Lapointe B.E., O'Connell J.D. and Garrett G.S. 1990. Nutrient couplings between on-site sewage disposal systems, groundwaters, and nearshore surface waters of the Florida Keys. *Biogeochem.* 10: 289–307.
- Leichter J.J., Wing S.R., Miller S.L. and Denny M.W. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol. Oceanogr.* 41: 1490–1501.
- Lidz B.H. and Hallock P. 2000. Sedimentary petrology of a declining reef ecosystem, Florida Reef Tract, USA. *J. Coast. Res.* 16: 675–697.
- Marszalek D.S., Babashoff G., Noel M.R. and Worley D.R. 1977. Reef distribution in south Florida. In: *Third International Coral Reef Symposium*. Rosenstil School of Marine and Atmospheric Sciences. University of Miami, Miami, FL, USA, pp. 223–229.
- Patriquin D.G. 1972. The origin of nitrogen and phosphorus for growth of the marine angiosperm *Thalassia testudinum*. *Mar. Biol.* 15: 35–46.
- Paul J.H., Rose J.B., Jiang S.C., Zhou X.T., Cochran P., Kellog C. et al. 1997. Evidence of groundwater and surface marine water contamination by waste disposal wells in the Florida Keys. *Water Res.* 31: 1448–1454.
- Pedersen M.F. and Borum J. 1992. Nitrogen dynamics of eelgrass *Zostera marina* during a late summer period of high growth and low nutrient availability. *Mar. Ecol. Prog. Ser.* 80: 65–73.
- Powell G.V.N., Fourqurean J.W., Kenworthy W.J. and Zieman J.C. 1991. Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. *Estuarine Coastal Shelf Sci.* 32: 567–579.
- Powell G.V.N., Kenworthy W.J. and Fourqurean J.W. 1989. Experimental evidence for nutrient limitation of seagrass growth in a tropical estuary with restricted circulation. *Bull. Mar. Sci.* 44: 324–340.
- Redfield A.C. 1958. The biological control of chemical factors in the environment. *Am. Sci.* 46: 205–221.
- Rudnick D.T., Chen Z., Childers D.L., Boyer J.N. and Fontaine T.D.I. 1999. Phosphorus and nitrogen inputs to Florida Bay: the importance of the Everglades watershed. *Estuaries* 22: 398–416.

- Schomer N.S. and Drew R.D. 1982. An ecological characterization of the lower Everglades, Florida Bay and the Florida Keys. U.S. Fish and Wildlife Service. Office of Biological Services, Washington, DC, USA, pp 246.
- Short F.T. 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. *Aquat. Bot.* 27: 41–57.
- Smith N.P. 1994. Long-term Gulf-to-Atlantic transport through tidal channels in the Florida Keys. *Bull. Mar. Sci.* 54: 602–609.
- Szmant A.M. and Forrester A. 1996. Water column and sediment nitrogen and phosphorus distribution patterns in the Florida Keys, USA. *Coral Reefs* 15: 21–41.
- Thom R.M. and Albright R.G. 1990. Dynamics of benthic vegetation standing-stock, irradiance, and water properties in central Puget Sound. *Mar. Biol.* 104: 129–141.
- Tomas C.R., Bendis B. and Johns K. 1999. Role of nutrients in regulating plankton blooms in Florida Bay. In: Kumpf H., Steidinger K. and Sherman K. (eds), *The Gulf of Mexico Large Marine Ecosystem*. Blackwell Science, Malden, Massachusetts, USA, pp. 323–337.
- Tomasko D.A. and Lapointe B.E. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: field observations and experimental studies. *Mar. Ecol. Prog. Ser.* 75: 9–17.
- Zieman J.C., Fourqurean J.W. and Iverson R.L. 1989. Distribution, abundance and productivity of seagrasses and macroalgae in Florida Bay. *Bull. Mar. Sci.* 44: 292–311.

