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Temporal and spatial variation in the $\delta^{15}N$ and $\delta^{13}C$ of coral tissue and zooxanthellae in *Montastraea faveolata* collected from the Florida reef tract

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Abstract

Tissues were collected from *Montastraea faveolata* at five locations on the Florida Reef tract representing both nearshore and offshore environments. The tissue and zooxanthellae were removed from the skeletons, separated, and subsequently analyzed for $\delta^{15}N$ and $\delta^{13}C$. The mean $\delta^{15}N$ value in the coral tissue was $+6.6$ (± 0.6‰) while the $\delta^{13}C$ was -13.3 (± 0.5‰) ($n = 197$). The $\delta^{15}N$ and $\delta^{13}C$ of the zooxanthellae were $+4.7$ (± 1.1‰) and -12.2 (± 1.0‰), respectively ($n = 147$). The differences in the $\delta^{15}N$ and $\delta^{13}C$ between the zooxanthellae and the tissue were statistically significant. No statistically significant differences were observed between nearshore and offshore stations in either $\delta^{15}N$ or $\delta^{13}C$. The absence of a difference casts doubt on both whether the $\delta^{15}N$ of the coral tissues is related to anthropogenic influences and/or whether the $\delta^{15}N$ value itself can be used as an indicator of sewage contamination in corals. Between 1995 and 1997, there was an increase of 1‰ in the $\delta^{13}C$ and a decrease of approximately 0.8‰ in the $\delta^{15}N$. The increase in the $\delta^{13}C$ of the organic material was mimicked in the $\delta^{13}C$ of the skeletal material from corals from two reefs in the area. There appears to be clear seasonal variations in the $\delta^{13}C$ of the coral tissue at certain locations with $\delta^{13}C$ of the coral tissues and the zooxanthellae becoming more positive between July and August. The difference between the $\delta^{13}C$ of the zooxanthellae and the coral tissue varies seasonally with the maximum difference occurring in July of each year. In contrast, the maximum $\delta^{13}C$ in the skeleton appears to occur later in the year, between September and November.

It is well established that certain scleractinian corals have symbiotic associations with dinoflagellate algae (zooxanthellae) that are beneficial to the host (Muscatine and Cernichiari 1969). The zooxanthellae are able to pass organic compounds to the coral, resulting in positive influences on the growth of the coral. Under shallow water conditions, the coral–zooxanthellae system is autotrophic (Muscatine and Cernichiari 1969). Evidence of the autotrophic nature of zooxanthellate corals is found in the difference in the $\delta^{13}C$ of the zooxanthellae and coral tissue at various water depths. At shallow depths, where light intensity is high, the $\delta^{13}C$ of the zooxanthellae and the coral tissue are relatively similar (Land et al. 1975; Muscatine et al. 1989) and the $\delta^{13}C$ of the coral tissue is significantly more positive (-10‰ to -14‰) than the supposed food source of the coral, zooplankton (~ -20‰). This indicates that sufficient photosynthate is being translocated so that the $\delta^{13}C$ values of the coral tissue and zooxanthellae are similar. With increasing depth, the $\delta^{13}C$ of the coral tissues become more negative and the $\delta^{13}C$ approaches that of the zooplankton. Such variations are taken as indicating a change from autotrophy to heterotrophy. Studies of the $\delta^{15}N$ of coral tissue have mainly concentrated on their potential as indicators of anthropogenic waste (Heikoop et al. 2000*a*), although Muscatine and Kaplan (1994) also investigated $\delta^{15}N$ as an indicator of autotrophic and heterotrophic responses. The study by Muscatine and Kaplan (1994) showed a slight decrease in $\delta^{15}N$ with increasing depth, although this pattern was not always consistent. In contrast with $\delta^{13}C$, the $\delta^{15}N$ value was generally enriched in the coral tissue compared with the zooxanthellae.

Common to all previous studies on the $\delta^{15}N$ and $\delta^{13}C$ of coral tissues is the fact that they have ignored any temporal variation in the isotopic composition of the soft tissues of the coral. Usually, such samples are taken during the summer months when weather conditions are more favorable. However, in the study of Swart et al. (1996), it was noticed that the $\delta^{13}C$ of the coral tissues, which were collected during the summer months (June–July 1990) were isotopically more positive (-15‰) than those measured in September 1990 (-17‰). The difference between the $\delta^{13}C$ of the zooxanthellae and coral tissue also changed from about $+3$‰ in June 1990 to $+7$‰ in September. Based on these data, the authors speculated that the changes might be induced by changes in the partitioning of the internal C pool. This pattern was replicated in data measured from another reef in South Florida (Swart et al. 2005). This paper reports on temporal and spatial variability in the $\delta^{13}C$ and $\delta^{15}N$ of the tissues and zooxanthellae of corals from nearshore and offshore reefs over a 2-yr period. The paper includes $\delta^{13}C$ data presented by Swart et al. (2005) in addition to data from four additional sites representing both inshore and offshore reefs.

Study site

The study sites chosen were five patch reefs off Key Largo in the Florida Keys (Fig. 1). At each site, small pieces of

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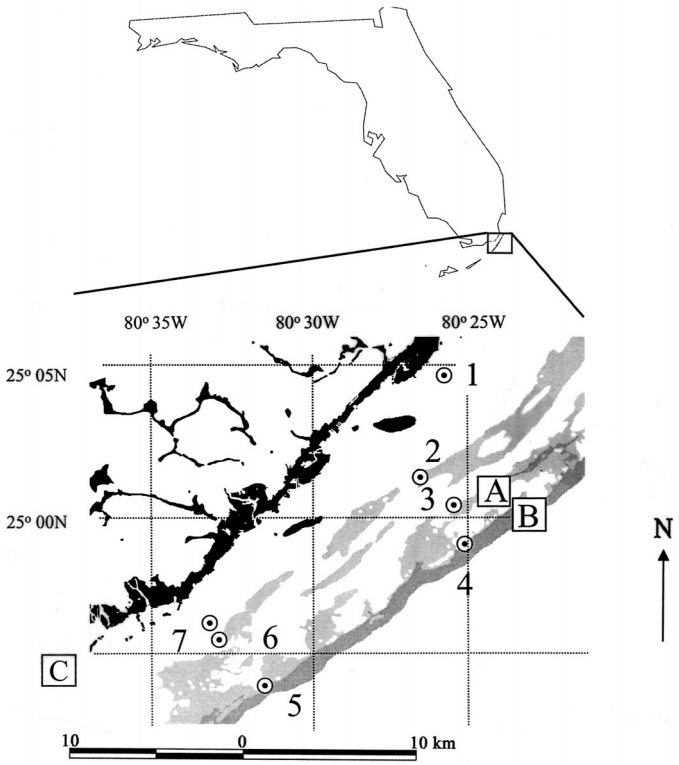

Fig. 1. Location of the reefs studied in the Florida Keys. Site 2 (triangles), site 4 (Pickles), site 5 (Crocker), site 6 (Hen and Chickens), and site 7 (The Rocks). In addition, water samples were collected from marker 2 (site 1) and Molasses Channel (site 3). The location of sites from which water samples are collected for the Florida Keys National Marine Sanctuary (FKNMS) water-quality network are shown in the squares (Molasses Channel (A) and Molasses Reef (B). The coral skeletons analyzed were collected from Crocker Reef (site 5) and Cheeca Reef (C). The shading denotes 20 ft depth contours. Land and semiemergent mudbanks are shown in the black shading.

skeletons with living coral tissue (~2 cm in diameter) were chipped off the sides of the heads. A total of 197 samples were analyzed for the δ^{15}N and δ^{13}C of the coral tissue and 147 for the δ^{15}N and δ^{13}C of the zooxanthellae. With the exception of Pickles Reef, the corals were collected at only one depth. At Pickles, corals were collected from water depths of 8.5 and 3–3.5 m, where typically between 4 and 6 corals were collected at this site each month. At Crocker Reef, the corals were collected from 6 m. The corals were never collected from the same individuals that had been sampled during previous visits. The initial rationale was to protect the corals, but it was later realized that continued sampling would not only eventually destroy the colony but also severely stress the individual and perhaps lead to changes in the δ^{13}C induced by stress. Water samples were also collected in order to check for seasonal variation in the δ^{13}C of the dissolved inorganic carbon (DIC) in the water from the same sites at which the corals were collected as well as two additional sites (site 1; marker 2) and site 3 (near Molasses Channel) (Fig. 1). In order to compare changes in the δ^{13}C of organic matter (OM) with changes in the δ^{13}C of coral skeletons, two corals were cored, a specimen of *Montastraea faveolata* at Crocker Reef (~10 m) and a specimen of *Siderastrea siderea* from Cheeca Rocks (~2 m) (Fig. 1).

Methods

Tissue removal—After collection, samples were placed on ice until removal of the tissues (within 24 h) by air brushing. The zooxanthellae and tissue samples were separated using the methods of Szmant et al. (1989). These are fully described in Swart et al. (2005). Previous work using this method has shown that there is only a small amount of cross-contamination by zooxanthellae in the coral tissue (<5%; Fitzgerald and Szmant 1997). In contrast, there can be significant contamination of the zooxanthellae by the coral tissue during separation (up to 50%; Fitzgerald and Szmant 1997).

Isotopic analyses—The isotopic composition (δ^{15}N and δ^{13}C) of organic coral samples were determined using a CN analyzer interfaced with a continuous-flow isotope-ratio mass spectrometer (CFIRMS) (Europa Scientific). Samples were measured in triplicate and the data presented as the mean of these analyses. External precision determined through the analysis of replicate standard material is 0.1‰ for C and 0.2‰ for N.

Analyses of the dissolved inorganic carbon—The CO_2 was removed from the sample by acidification in a stream of He gas and analyzed using a Europa 20-20 mass spectrometer by comparison with a pulse of injected reference gas. External precision for this method as determined by measuring replicate samples is ~0.08‰.

Analysis of the coral skeleton—Samples of skeletal material from colonies of *M. faveolata* at Crocker Reef (~10 m) and *S. siderea* at Cheeca Rocks (~2 m) were drilled from the slab using a hand-held drill at a resolution of approximately 20 samples per year. Material was analyzed using a Kiel III attached to a Finnigan Delta plus mass spectrometer.

Nutrient data—For comparison with changes in the concentration of inorganic N and salinity, we have used the data collected and analyzed by Florida International University-South East Environmental Research Center (FIU-SERC). The methods used and the errors on these analyses are discussed in Boyer et al. (1999).

Results

The δ^{15}N and δ^{13}C data are presented in Table 1 and Figs. 2 and 3 as the mean values of the separated zooxanthellate and coral fractions measured at each site during each month of the study. The values represent either the mean of several samples or the values of individual samples.

Nitrogen—The mean δ^{15}N of the coral tissues has a value of +6.6 (±0.6‰). In comparison, the δ^{15}N of the zooxanthellae has a mean value of +4.8 (±1.0‰). The zooxan-

Table 1. Mean C and N isotopic composition of coral tissue and zooxanthellae from all reefs studied (Fig. 1).

	Coral tissue					Zooxanthellae				
	δ^{15}N	SD	δ^{13}C	SD	*n*	δ^{15}N	SD	δ^{13}C	SD	*n*
Mar 95	7.00	1.04	−14.47	0.99	21	5.72	1.05	−13.63	0.83	21
Apr 95	6.57	0.89	−13.82	1.01	15	5.67	0.65	−12.83	0.94	11
Jun 95	6.83	0.83	−13.27	0.78	14	6.07	0.66	−12.01	0.85	14
Jul 95	6.11	0.95	−12.80	0.97	15	6.35	1.00	−12.11	1.26	15
Aug 95	6.70	0.43	−12.91	0.69	9					
Sep 95	7.18	0.85	−13.93	0.68	13	4.72	0.50	−13.92	0.79	7
Oct 95	7.07	0.83	−13.48	1.40	9	5.52	0.85	−12.49	0.93	9
Nov 95	6.25	0.40	−13.87	0.69	12	3.03		−12.17		1
Dec 95	7.83	0.46	−13.35	0.64	8	2.70	1.43	−9.02	0.32	2
Jan 96	5.77	0.40	−13.46	0.60	7	3.83	0.72	−12.71	0.46	7
Mar 96	6.68	0.27	−12.86	0.88	9	4.70	1.35	−10.90	2.35	3
May 96	6.30	0.42	−12.97	0.72	13	4.36	0.50	−11.40	1.16	13
Jun 96	6.95	0.58	−12.41	0.96	13	5.01	0.42	−10.99	1.71	8
Sep 96	5.90	0.80	−12.81	0.88	13	4.30	0.70	−12.78	0.98	13
Oct 96	6.00	1.36	−13.28	0.96	13	4.22	1.09	−12.00	2.46	13
Nov 96	5.62	1.43	−13.21	0.86	13	4.26	0.68	−12.02	1.11	10
Mean	6.55	0.75	−13.31	0.86	197	4.82	0.83	−12.06	1.15	147
SD	0.60	0.35	0.53	0.20		0.99	0.31	1.23	0.63	

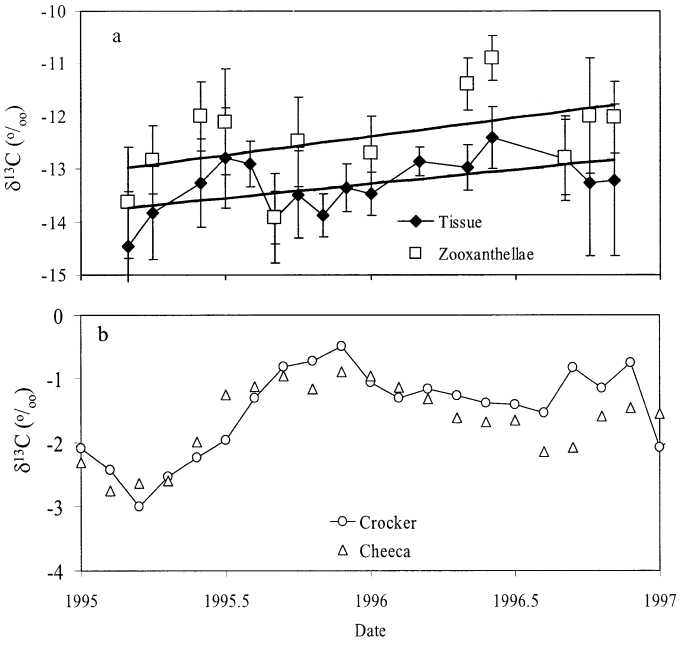

Fig. 2. (a) Changes in the δ^{13}C of the coral tissues and the zooxanthellae over the time period January 1995 to December 1996. There is an increase in the δ^{13}C of both the zooxanthellae (r^2 = 0.10) and the coral tissue (r^2 = 0.29) over this time period. The change in the δ^{13}C of the coral tissues is statistically significant at the 95% level ($p < 0.05$, $n = 16$). (b) Changes in the δ^{13}C of the coral skeleton of *M. faveolata* collected from Crocker Reef and *S. siderea* collected from Cheeca Rocks over the same time period as measurement of the δ^{13}C of the coral tissue and zooxanthellae. These two records both exhibit a small increase during the experimental period superimposed on an overall decrease in the δ^{13}C of the skeleton as a result of the ^{13}C Suess effect (see Fig. 7). Data measured on zooxanthellae from December 1995 and March 1996 have been omitted for scaling reasons (see Table 1).

thellae are statistically significantly more negative than the coral tissues at the 95% confidence limits.

Carbon—The mean δ^{13}C of all the coral tissue, −13.3 (±0.5‰), is statistically more negative than that in the zooxanthellae, −12.2 (±1.0‰), at the 95% confidence limits.

Spatial variation—Average δ^{15}N and δ^{13}C values of the coral tissues and zooxanthellae from the inshore and offshore sites are shown in Fig. 4 and Tables 2–5. At the 95% confidence limits, there are no statistical differences in either the δ^{15}N or δ^{13}C of the coral tissue or zooxanthellae between different reefs.

Depth variation—Changes in δ^{13}C and δ^{15}N relative to depth were studied only at site 4 (Pickles Reef). Although the δ^{15}N of the coral tissue of the deeper samples was slight-

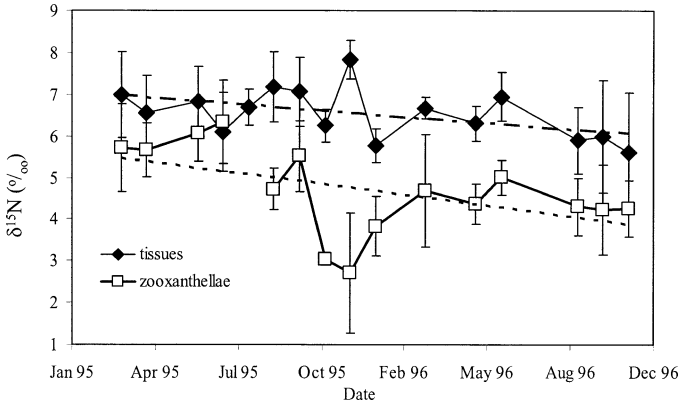

Fig. 3. Changes in the δ^{15}N of the coral tissues and the zooxanthellae over the time period January 1995 to December 1996. There is a statistically significant decrease in the δ^{15}N of both the zooxanthellae and the coral tissue. The r^2 of the coral tissue and the zooxanthellae are 0.25 ($n = 16$) and 0.34 ($n = 14$), respectively.

Table 2. Nitrogen isotopic composition tissue and zooxanthellae from inner reef corals (see Fig. 1). Data represent the mean of individual corals collected at each site.

	Tissue					Zooxanthellae				
Inner	2	6	7	Mean	SD	2	6	7	Mean	SD
Mar 95	6.91	7.10	8.01	7.34	0.59	5.62	5.79	5.84	5.75	0.11
Apr 95	6.69	7.06	7.28	7.01	0.30	4.28	5.34	5.71	5.11	0.75
Jun 95	6.88	7.62	6.44	6.98	0.60	6.06	7.11	6.31	6.49	0.55
Jul 95	6.50	5.40	6.35	6.08	0.60	5.63	6.73	3.06	5.14	1.89
Aug 95		7.01	6.21	6.61	0.56					
Sep 95		6.94	5.74	6.34	0.84		4.87	5.03	4.95	0.11
Oct 95	4.82	7.36		6.09	1.80	4.86	6.50		5.68	1.16
Nov 95		6.45		6.45						
Dec 95		8.26	7.72	7.99	0.38					
Jan 96	5.79	5.06	6.35	5.73	0.65	3.95	3.87	4.15	3.99	0.14
Mar 96		6.36	6.71	6.54	0.25		3.82	4.55	4.18	0.52
May 96	6.36	6.26	6.77	6.46	0.27	4.16	4.46	4.12	4.25	0.18
Jun 96	6.55	6.83	7.47	6.95	0.47		4.59	4.98	4.79	0.28
Sep 96	5.52	5.29	6.60	5.81	0.70	4.00	3.96	4.03	4.00	0.03
Oct 96	5.78	7.55	7.36	6.90	0.97	3.88	3.43	2.99	3.43	0.45
Nov 96	6.85			6.85		3.78			3.78	
Mean	6.24	6.70	6.85	6.63		4.62	5.04	4.61	4.73	
SD	0.67	0.91	0.67	0.58		0.85	1.25	1.09	0.89	

ly enriched in both the tissue and the zooxanthellae fraction, there were no statistically significant differences between the samples collected from 8.5 and 3 m. The $\delta^{13}C$ values of the tissues and the zooxanthellae were slightly more negative in the deeper corals, although the differences were not statistically significant at the 95% confidence limits (Fig. 4).

Temporal variation—There were no statistically significant seasonal variations in the $\delta^{15}N$ of either the coral tissues or zooxanthellae at any of the sites. There was a decrease in the $\delta^{15}N$ from the start of the measurements throughout 1995 and 1996, which was statistically significant at the 95% confidence limits. This decrease was greater in the zooxanthellae than in the coral tissue (Fig. 3). In contrast, the $\delta^{13}C$'s of the coral tissue show statistically significant seasonal patterns at some sites but not at others. The most striking intra-annual variation occurred at Pickles. Carbon isotopic data from the Pickles site were presented in Swart et al. (2005) undifferentiated by depth. Although statistically significant variations were observed in these data, the patterns are much more pronounced if only specific depths are considered (Fig. 5). The values of the tissues become more positive during the summer months. and the differences between the $\delta^{13}C$ of the tissue and the zooxanthellae ($\Delta t - z$) are larger during

Table 3. Nitrogen isotopic composition tissue and zooxanthellae from outer reef corals (see Fig. 1). Data represent the mean of individual corals collected at each site.

	Coral tissue				Zooxanthellae			
	4	5	Mean	SD	4	5	Mean	SD
Mar 95	7.03	5.99	6.51	0.74	6.81	5.99	6.40	0.58
Apr 95	6.28	6.18	6.23	0.07	5.99	5.76	5.88	0.17
Jun 95	7.06	6.68	6.87	0.27	5.73	5.86	5.79	0.09
Jul 95	5.92	6.49	6.20	0.41	6.35	7.07	6.71	0.51
Aug 95	6.85	6.81	6.83	0.03				
Sep 95	7.86	7.28	7.57	0.42	4.89	4.39	4.64	0.35
Oct 95	6.98	7.69	7.34	0.50	5.18	5.02	5.10	0.12
Nov 95	6.15	6.01	6.08	0.09	4.32		4.32	
Dec 95	7.91	7.56	7.74	0.25	3.07	1.57	2.32	1.07
Jan 96	5.83	6.31	6.07	0.34	3.32	4.31	3.81	0.70
Mar 96	6.68		6.68			5.73	5.73	
May 96	6.14	6.57	6.36	0.30	4.48	4.85	4.67	
Jun 96	7.08	6.18	6.63	0.64	4.75	4.84	4.80	0.07
Sep 96	6.28	5.37	5.83	0.64	4.49	4.73	4.61	0.17
Oct 96	7.25	7.78	7.51	0.37	4.60	4.68	4.64	0.06
Nov 96	5.00		5.00		4.50		4.50	
Mean	6.64	6.64	6.59		4.89	4.98	4.93	
SD	0.77	0.72	0.72		1.06	1.29	1.09	

Table 4. Carbon isotopic composition tissue and zooxanthellae from inner reef corals (see Fig. 1). Data represents the mean of individual corals collected at each site.

	Tissue					Zooxanthellae				
Inner	2	6	7	Mean	SD	2	6	7	Mean	SD
Mar 95	−14.80	−15.24	−14.10	−14.72	0.58	−12.63	−13.37	−11.71	−12.57	0.83
Apr 95	−13.54	−13.40	−13.60	−13.51	0.10	−12.30	−10.30	−13.53	−12.05	1.63
Jun 95	−13.26	−12.72	−13.21	−13.06	0.29	−10.79	−11.74	−12.91	−11.82	1.06
Jul 95	−12.82	−13.48	−12.76	−13.02	0.04	−12.41	−12.97	−13.63	−13.01	0.61
Aug 95		−12.52	−12.57	−12.55	0.04					
Sep 95		−14.70	−13.46	−14.08	0.88		−14.26	−13.93	−14.10	0.23
Oct 95	−11.42	−11.16		−11.29	0.18	−11.19	−9.29		−10.24	1.35
Nov 95		−13.82		−13.82						
Dec 95		−12.98	−12.50	−12.74	0.34					
Jan 96	−12.68	−12.78	−14.19	−13.22	0.84	−12.29	−12.41	−11.56	−12.09	0.46
Mar 96		−14.36	−14.08	−14.22	0.20		−8.99	−13.53	−11.26	3.21
May 96	−11.60	−12.93	−11.94	−12.16	0.69	−10.95	−11.26	−12.41	−11.54	0.77
Jun 96	−11.04	−12.85	−10.73	−11.54	1.15		−10.25	−10.78	−10.51	0.37
Sep 96	−12.14	−12.50	−12.48	−12.37	0.20	−12.24	−14.42	−10.87	−12.51	1.79
Oct 96	−13.33	−13.30	−12.42	−13.02	0.52	−10.58	−10.91	−11.94	−11.14	0.71
Nov 96	−13.31	−13.50	−11.15	−12.65	1.30	−12.16	−10.86		−11.51	0.92
Mean	−12.72	−13.27	−12.80	−13.00		−11.75	−11.62	−12.44	−11.87	
SD	1.10	0.97	1.06	0.94		0.78	1.77	1.14	1.04	

this period. At the end of the summer, the $\delta^{13}C$ of the tissue becomes more negative and the $\Delta t - z$ becomes smaller. The differences between adjacent $\delta^{13}C$ values at Pickles were statistically significant at the 95% confidence limits. Such clear seasonal patterns were not observed at any of the other sites.

Dissolved inorganic carbon—The $\delta^{13}C$ of the DIC showed no long-term variation throughout the length of the experiment. However, significant seasonal variation was present (Fig. 6). Although there was considerable overlap in the $\delta^{13}C$ of the DIC between sites, the inner locations, such as marker 2 and The Rocks, possessed lower mean $\delta^{13}C$ values than the more ocean sites. These differences were not statistically different at the 95% confidence limits.

Carbon isotopic composition of the coral skeleton—The $\delta^{13}C$ was measured in the skeleton of one corals collected from Crocker Reef as well as an additional coral from a site outside the study area (Cheeca Rocks; Fig. 1). Over the period of measurements of the OM (January 1995–December 1996), the $\delta^{13}C$ of both the coral skeletons showed an increase, similar in magnitude to that observed in the OM (Fig. 2b).

Table 5. Carbon isotopic composition tissue and zooxanthellae from outer reef corals (see Fig. 1). Data represent the mean of individual corals collected at each site.

	Tissue				Zooxanthellae			
Outer	4	5	Mean	SD	4	5	Mean	SD
Mar 95	−13.39	−14.40	−13.90	0.71	−14.43	−10.73	−12.58	2.62
Apr 95	−13.63	−15.44	−14.53	1.28	−10.47	−10.46	−10.46	0.01
Jun 95	−12.98	−13.95	−13.46	0.69	−11.57	−12.40	−11.98	0.59
Jul 95	−12.04	−13.71	−12.87	1.18	−10.33	−11.48	−10.90	0.81
Aug 95	−13.04	−14.36	−13.70	0.93				
Sep 95	−13.17	−13.74	−13.46	0.41	−9.28	−12.63	−10.95	2.37
Oct 95	−13.52	−13.91	−13.72	0.27	−12.61	−15.13	−13.87	1.78
Nov 95	−14.44	−13.58	−14.01	0.61				
Dec 95	−13.49	−13.25	−13.37	0.17	−10.51	−8.66	−9.59	1.31
Jan 96	−13.77	−13.59	−13.68	0.12	−12.60	−13.43	−13.02	0.59
Mar 96	−12.56		−12.56			−10.17	−10.17	
May 96	−13.13	−13.62	−13.37	0.35	−11.64	−9.72	−10.68	1.35
Jun 96	−12.66	−13.06	−12.86	0.28	−11.26	−12.38	−11.82	0.80
Sep 96	−13.06	−13.18	−13.12	0.08	−12.10	−14.02	−13.06	1.36
Oct 96	−13.39	−11.43	−12.41	1.39	−11.84	−10.70	−11.27	0.81
Nov 96	−13.33	−13.11	−13.22	0.15	−11.29	−11.60	−11.45	0.22
Mean	−13.22	−13.62	−13.39		−11.53	−11.68	−11.56	
SD	0.55	0.86	0.55		1.29	1.78	1.23	

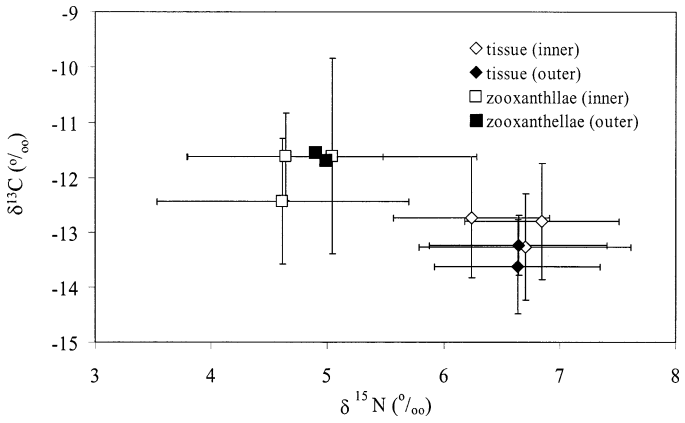

Fig. 4. Mean $\delta^{13}C$ and $\delta^{15}N$ of coral tissue from all sites. Note the absence of significant differences in the $\delta^{13}C$ and $\delta^{15}N$ between the inner and out reef sites.

Discussion

Anthropogenic influences—The $\delta^{15}N$ of OM in the marine environment has been used to distinguish N derived from fertilizers (0‰) (Shearer et al. 1974; Kreitler 1979), NO_3^- produced from the oxidation of waste (+10 to +22‰) (Kreitler 1979), and NO_3^- produced from the oxidation of organic N in the soil (+4 to +9‰) (Mariotti 1974; Gormly and Spalding 1979). Numerous papers have been published that report the use of $\delta^{15}N$ in benthic organisms in order to distinguish sewage (Sammarco et al. 1999; Heikoop et al. 2000*a*,*b*; Risk and Erdmann 2000; Costanzo et al. 2004). Simplistically, these authors have interpreted positive $\delta^{15}N$ values (>+7 to +10‰) as reflecting input of sewage. However, there are other workers who have shown convincingly that sewage-derived N has more negative $\delta^{15}N$ values compared with normal planktonic N (Wada and Hattori 1975; Rogers 2003; Savage and Elmgren 2004). For example, in the study by Wada and Hattori (1975), the $\delta^{15}N$ of the sewage effluent only had a value of +2.5‰ while the planktonic $\delta^{15}N$ was greater than +9‰. Similar positive planktonic $\delta^{15}N$ values have also been reported by other workers (Wada and Hattori 1978; Sweeney and Kaplan 1980; Peterson and Howarth 1987; Harrigan et al. 1989; Goering et al. 1990) and appear not to be related to anthropogenic sources, but rather a result of the uptake of isotopically positive NO_3^-, which is, in turn, a result of fractionation during the process of assimilation or denitrification. Hence, based on the literature, there appears to be an apparent significant discrepancy in the interpretation of $\delta^{15}N$ values in marine organisms. In the case of the corals themselves, Heikoop et al. (2000*a*,*b*) examined the $\delta^{15}N$ in coral tissue from a number of reefs. Muscatine and Kaplan (1994) and Muscatine et al. (1989) also examined a number of species of corals from different depths from Discovery Bay in Jamaica. Note that the data presented by Heikoop et al. (2000*a*,*b*) are for bulk coral organic sam-

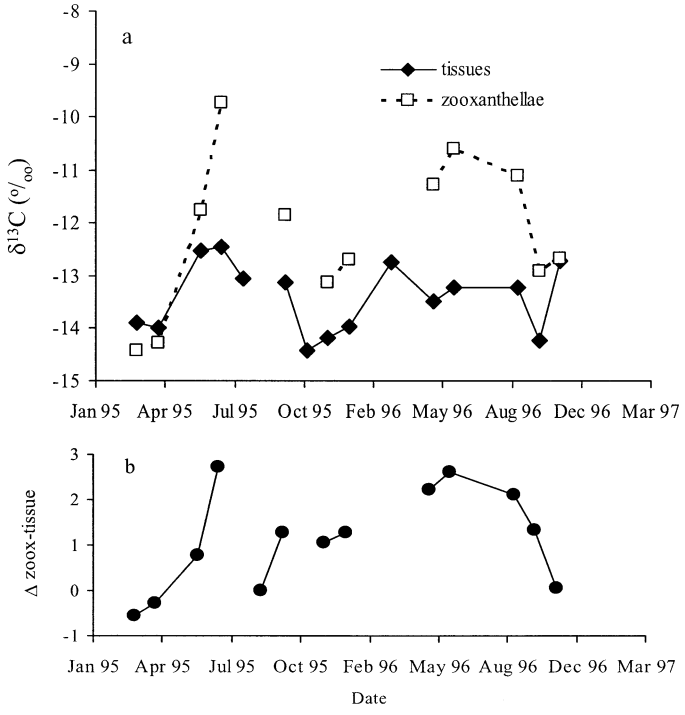

Fig. 5. (a) Seasonal changes in the $\delta^{13}C$ of the coral tissue and the zooxanthellae in the corals from ~8 m at Pickles Reef. This site show a very clear seasonal change in the $\delta^{13}C$ of both the fractions as well as a seasonal difference between the $\delta^{13}C$ of the zooxanthellae and the coral tissue. (b) Changes in the difference between the zooxanthellae with respect to season. Maximum difference between the zooxanthellae and the coral tissue occur during the summer months.

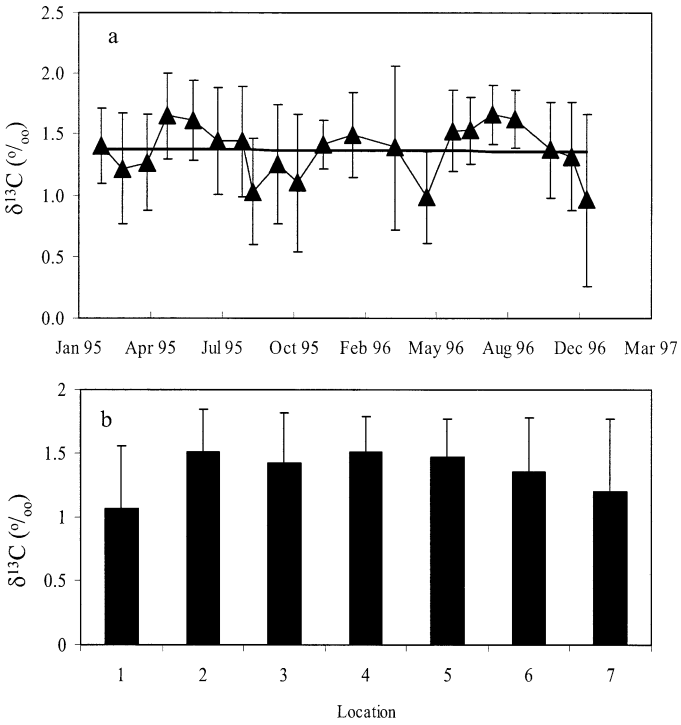

Fig. 6. (a) Changes in the $\delta^{13}C$ of the DIC at sites shown in Fig. 1. Note that there are only 2 yr worth of data yet there are four cycles in the $\delta^{13}C$ DIC data. These multiple changes also appear to be present in the $\delta^{13}C$ signal in the coral skeleton. (b) The mean and standard deviation (error bars) of the $\delta^{13}C$ of the DIC from all seven sites studied during this investigation are shown.

ples (including the coral tissue and zooxanthellae). This is in contrast with studies by Muscatine et al. (1989), Muscatine and Kaplan (1994), and this investigation, in which the zooxanthellae and coral tissue were separated prior to analysis. Heikoop et al. (2000*a*) divided their reefs into two categories, those that were and were not affected by sewage. The sewage-affected reefs possessed slightly more positive δ^{15}N values (+6 to +10‰) compared with the unaffected reefs (+4 to +6‰). Based on this comparison, the corals from South Florida would fall in the category that was unaffected by anthropogenic waste. Note that the δ^{15}N values for coral tissue of +6.6‰ would be considered to be influenced by anthropogenic sources if one applied the recent guidelines of Lapointe et al. (2004). These workers claimed that values for macroalgae above +4‰ are indicative of having been influenced by sewage.

Of relevance to the issue of whether the corals in this study are influenced by sewage is the comparison of the δ^{15}N in the tissues and zooxanthellae between the nearshore and offshore environments. Our data indicate that there is no statistical significance difference between these reefs. The nearshore reefs occur less than 5 km offshore and often experience extremely turbid waters. Although waters close to the Florida Keys tend to be slightly elevated in their nutrient concentrations and, based on the studies by Shinn et al. (1994) and Lapointe et al. (1990), might be expected to be affected by sewage derived from the Florida Keys, by 0.5 km, it has been shown that the nutrient concentrations of the reefal water are close to open marine conditions (Szmant and Forrester 1996). If the δ^{15}N of organisms, such as corals, can be considered to be valid indicators of anthropogenic influence on the marine environment, then the data presented in this paper would suggest that the Florida reefs are relatively unaffected by anthropogenic N. Such results are in contrast with the study by Sammarco et al. (1999), which examined a number of reefs stretching from the coast of Australia to the Great Barrier Reef, a distance of 120 km. That study showed more positive values close to the coast of Australia, a decrease in the midshelf reefs, followed by an increase in the corals farthest away from land. They interpreted these changes as a reflection of the input of isotopically positive N from anthropogenic sources near the coast and from upwelling of N with positive δ^{15}N values at the shelf break. In a recent publication, Lapointe et al. (2004) measured δ^{15}N values from a number of different macroalgae in the Lower Florida Keys during July 2000 and March 2001. During the July sampling period, which corresponded to the wet season, the δ^{15}N values ranged between +1 and +3‰, while during the March sampling period, the values were approximately +6‰. These workers concluded that the elevated values indicated the input of sewage-derived nutrients. Data from the SERC water-quality monitoring network over the same time period indicate that there was little change in the concentrations of NH_4^+ or NO_3^- over this time period, suggesting that perhaps parameters other than sewage are influential in causing the observed differences.

One of the more striking patterns in our data is the long-term decrease in the δ^{15}N over the 2 yr during which samples were taken. While we have no definitive explanation for this trend, it is possible that it is related to variations in the concentrations of various inorganic-bearing species, which in turn may be related to changes in the regional circulation and oceanography. The decrease in the δ^{15}N corresponds to a decrease in the concentration of NH_4^+ and NO_2^- at all the sites, as is evident in the data of SERC-FIU (Fig. 7). For example, at Molasses Reef (close to Pickles Reef), the concentration of NH_4^+ decreased from approximately 0.5 μmol L^{-1} at the start of 1995 to 0.2 μmol L^{-1} by September of 1996. The decrease in NO_2^- disappears if the first data point in 1995 is omitted, but the change in NH_4^+ is still present. Apart from a spike in the NH_4^+ concentration of 0.8 μmol L^{-1} in December 1997, the concentration of NH_4^+ continued to decrease to below 0.05 μmol L^{-1} by the end of 1997. The concentration of total organic N (including the particulate material) was approximately a factor of two higher at the

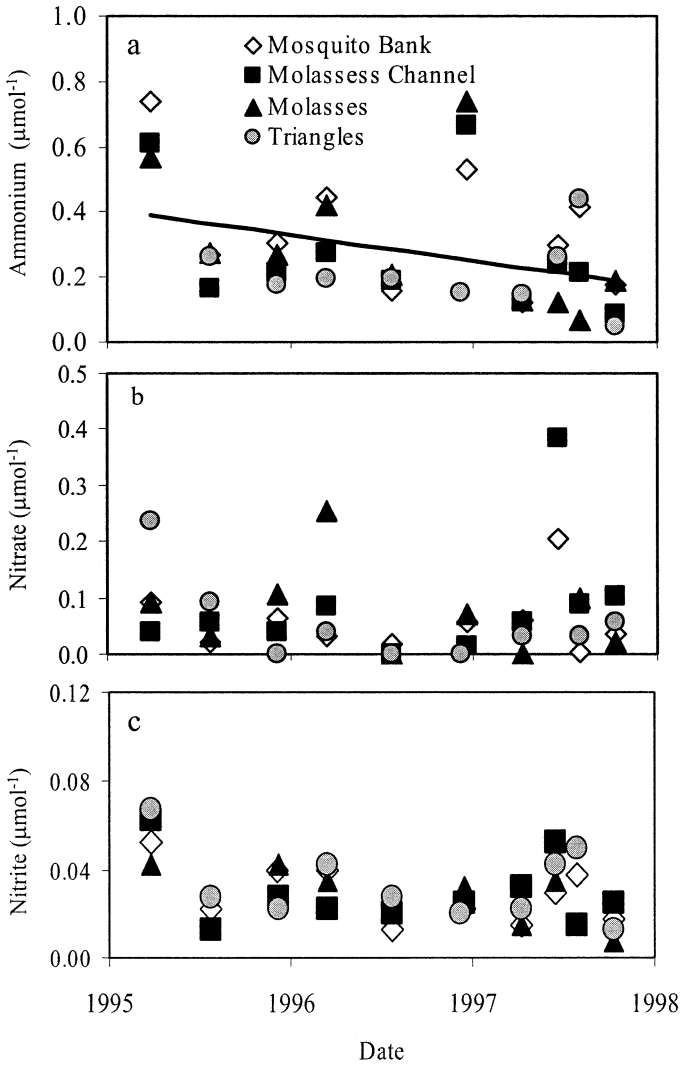

Fig. 7. Changes in the concentration of (a) NH_4^+, (b) NO_3^-, and (c) NO_2^- from locations near the collection sites of the coral tissue during the time period of the study (data are from FIU-SERC). The trend line in (a) shows the decrease in the concentration of NH_4^+ at Molasses Reef. Although the decrease is not statistically significant at the 95% confidence limits ($r^2 = 0.13$, $n = 10$), the change mirrors decreases in the δ^{15}N of the coral tissues over the same time period.

inshore sites (~10 μmol L^{-1} compared with 5 μmol L^{-1}) and showed no variation over the time period of the investigation. A decrease from 0.04 to 0.01 μmol L^{-1} in the concentration of NO_2^- was noticed over the same time period. As the $\delta^{15}N$ of NH_4^+ tends to be isotopically positive as a result of fractionation during conversion to NO_2^- and NO_3^-, it might be speculated that the decrease in the $\delta^{15}N$ and the change in the concentration of the inorganic species might be related. However, this is speculative, as no $\delta^{15}N$ measurements were made on the different species in this study. The isotopic effect could be translated to the coral tissue either through direct uptake of NH_4^+ by coral–zooxanthellae or indirectly through assimilation by phytoplankton, which are in turn predated by zooplankton and eventually corals. Changes in the concentration of dissolved inorganic nitrogen (DIN) species and $\delta^{15}N$ might also be related to variations in the regional oceanography and climatology. For example, there was a major El Niño Southern Oscillation (ENSO) in 1997 at the end of the experimental period. It is possible that this influenced the dynamics of the Florida coral reef, although our data do not cast any definitive information upon this hypothesis.

Anthropogenic effects: carbon—The $\delta^{13}C$ of coral tissue has also been shown to change relative to the proximity to the coast line and has been suggested to reflect contributions from terrestrial C sources (Risk et al. 1994). However, as in the case of $\delta^{15}N$, the $\delta^{13}C$ revealed no statistically significant differences at the 95% confidence limits between the inner and outer reefs.

Resource partitioning: nitrogen—The $\delta^{15}N$ of coral tissue and associated zooxanthellae has been suggested to be an indicator of the translocation of photosynthate from the zooxanthellae to the coral animal. The observation that the $\delta^{15}N$ of the coral animal is approximately 1.5‰ more positive than the zooxanthellae supports the notion of isotopic enrichment associated with changes in trophic levels. As corals are in essence feeding on material supplied by the zooxanthellae, and as there is a well-established isotopic enrichment with respect to trophic level, the difference is not unexpected. The more negative $\delta^{15}N$ values of the coral tissues compared with the $\delta^{15}N$ of the particulate OM (+2‰ to +8‰; Lamb et al. 2002) suggest that this source does not contribute substantially to the budget of the coral organisms. If a trophic effect is the correct explanation for the difference between the coral tissues and the zooxanthellae, then it might be expected that the difference would change with increasing depth as corals become more reliant on zooplankton for their energy source. However, in this study, we did not investigate corals over a wide range of depths and the deeper corals (~8.5 m) were only marginally more positive than the corals from shallower depths (~3 m). In the study by Muscatine and Kaplan, the $\delta^{15}N$ of the coral tissue and the zooxanthellae tended to decrease with depth, although the trends were extremely inconsistent, perhaps reflecting a variety of food sources and changing ratios of photosynthesis to respiration with respect to increasing depth.

Although the intra-annual patterns in $\delta^{15}N$ are weak, there appears to be a consistent decrease in the $\delta^{15}N$, consistent with the end of the warm season, when it has been shown that symbiont densities and tissue biomass are at their lowest (Fitt et al. 2000).

Resource partitioning: carbon—The observation that the $\delta^{13}C$ of the coral tissue and zooxanthellae at one of the sites (Pickles Reef) exhibited significant intra-annual variations over the 2-yr period of the study supports the previous observation (Swart et al. 1996) that significant variation in the $\delta^{13}C$ of the coral tissues and zooxanthellae occurs on an intra-annual basis and that there are consequent seasonal variations in the $\delta^{13}C$ of the respiratory CO_2 (Swart et al. 2005). These variations were observed in both the shallow (~3 m) and deeper corals (~8 m), although they were more pronounced in the deeper corals. The causes of the intra-annual variations in the $\delta^{13}C$ are believed to be related to C limitation and increased fractionation of the inorganic C pool during the early summer months (Swart et al. 2005). It is postulated that, during high rates of photosynthesis, the fractionation of the CO_2 during photosynthesis is reduced as the zooxanthellae struggles to supply the CO_2 necessary for photosynthesis. During conditions of high P:R ratio, the fractionation factor (α) exerted during the fixation of CO_2 by RuBP has been shown to decrease (Swart et al. 2005), an observation that supports the notion of CO_2 limitation. During this process, the $\delta^{13}C$ of the zooxanthellae increases, as observed in this study. This change in the $\delta^{13}C$ of the zooxanthellae in turn drives changes in the $\delta^{13}C$ of the coral tissue as photosynthate is translocated to the coral host. During the late summer, when the zooxanthellae densities are at their lowest (Fitt et al. 2000), the $\delta^{13}C$ of the tissues and the zooxanthellae fall to their most negative values and the difference between the tissue and the zooxanthellae is at a minimum (Fig. 5). The host does not exactly mimic the changes seen in the zooxanthellae, as the coral derives part of its food from zooplankton. The larger seasonal amplitude in the deeper corals might be a result of a greater variation in light availability at depth and its consequent impact on the carbon isotopic dynamics of the coral.

There have been only a few studies that have examined whether the corals are autotrophic throughout the year or whether the corals derive less of their energy needs from their zooxanthellae during particular times of the year. Porter (1985) determined that specimens of *Montastraea annularis* showed higher P:R ratios during the summer than winter, implying a greater reliance on heterotrophic sources during the winter. Clearly, there is opportunity for variation in the amount of autotrophy experienced, as many corals can lose their zooxanthellae seasonally (Fitt et al. 2000) and during periods of stress. During these periods, it might be expected that corals would become more heterotrophic and, perhaps as a result, the $\delta^{13}C$ of the coral tissue would become more negative. In this regard, a further explanation for the changes in the $\delta^{13}C$ of the organic tissues may be that, during periods of more negative $\delta^{13}C$, the corals derive more of their food as a result of heterotrophy. Such an interpretation is supported by the experiments of Grottoli and Wellington (1999), in which the $\delta^{13}C$ of coral skeletons changed between coral that were denied zooplankton and those that were exposed to ambient levels. In these situations, the $\delta^{13}C$ of the respi-

ratory coral tissue would be closer to that of the zooplankton, which, in the Florida Keys, is approximately −20‰ to −22‰. In contrast, during periods of autotrophy, the tissues would become more positive in their $\delta^{13}C$ values, as they incorporated material translocated from the zooxanthellae.

At the other sites, the annual cycles visible in the $\delta^{13}C$ of the tissues were less pronounced. Although there are several explanations for the absence of agreement between the various sites, the most probable is that, because the corals at each site (see Methods) were not collected from the same colonies, the variation at Pickles represented a fortuitous example of random sampling of the population while random sampling of different colonies at the other sites, each with slightly different inherent physiology, masked the intra-annual variation.

Variations in the $\delta^{13}C$ of the coral skeleton—Over the time period during which the $\delta^{13}C$ in the coral tissue were examined, the $\delta^{13}C$ increased by approximately 1‰, a change that was mirrored in the skeleton. The change in the skeleton appeared to be lagged by several months relative to changes in the zooxanthellae and the tissue, a feature to be expected as a portion of the carbon that composes the skeleton is derived from and influenced by metabolic processes. Clearly, the change in the $\delta^{13}C$ is related to variations in the composition of the coral tissues, but are such changes related to the $\delta^{13}C$ of the ambient DIC or are they related to some other environmental parameters, such as insolation? In order to attempt to assess the continuing discussion as to the origin of $\delta^{13}C$ changes in coral skeletons, we examined the changes in the $\delta^{13}C$ of the DIC over the same time period, which, in contrast with the $\delta^{13}C$ of the coral tissue and skeleton, did not exhibit a gradual change between 1995 and 1997. Although the possibility exists that our $\delta^{13}C$ measurements of the DIC are not actually representative of changes over the experimental period, the data would support another origin for the long-term changes, such as some relationship to changes in insolation, which has been long suggested as an explanation for variations in the $\delta^{13}C$ of coral skeletons (Fairbanks and Dodge 1979; Swart 1982; Grottoli and Wellington 1999). The $\delta^{13}C$ of the DIC shows seasonal variations (Fig. 6), with two minima, one occurring early in the year (February–March) and one between August and October. We believe that the origin of these patterns reflect the amount of respiration relative to photosynthesis that is occurring in the reef environment. During the late summer, when temperatures are high, the overall amount of respiration in the coral reef waters increases while photosynthesis decreases. This leads to a decrease in the $\delta^{13}C$ of the DIC, which in turn is translated to the $\delta^{13}C$ of the plankton and the coral tissue. These general patterns do not appear to be reflected in the $\delta^{13}C$ of the coral tissue but show a remarkable similarity to variations in the skeleton over this time period (Fig. 2b). While this may reflect a true decoupling between the $\delta^{13}C$ of the DIC and the tissue, it is also possible that our sampling did not reflect the true temporal changes in the $\delta^{13}C$. We believe this because the $\delta^{13}C$ of water in the coral reef shows a significant amount of diurnal variability depending on the tidal range and whether the timing of low tide coincides with daytime or nighttime. During the daytime, the $\delta^{13}C$ of the waters are likely to become enriched when photosynthesis preferentially removes ^{12}C. If low tide coincides with maximum rates of photosynthesis, the changes are likely to be greater than if high tide occurs during the daytime. Conversely, during the nighttime, respiration adds $^{12}CO_2$, and, therefore, $\delta^{13}C$ of the DIC may preferentially decrease if low tide occurs during at night. Hence, it is possible that the absence of the trend in the $\delta^{13}C$ of the DIC (which was seen in the skeletal and tissue data) may be a result of inadequate sampling.

This study has measured the $\delta^{13}C$ and $\delta^{15}N$ of coral tissues from over 150 specimens of *M. faveolata* collected from five different reefs representing inshore and offshore localities situated off the Key Largo on the Florida reef tract over a 2-yr period. Based on a comparison with previously published $\delta^{15}N$ data on coral tissues that classified coral reefs into sewage influenced and pristine, the data presented in this article would place these corals in the unaffected-by-sewage category. Furthermore, we observed no statistically significant differences in $\delta^{13}C$ and $\delta^{15}N$ between the inner reefs, likely to be more susceptible to pollution, and the outer reefs. Statistically significant seasonal variations in the $\delta^{13}C$ of the coral tissue and zooxanthellae were observed at one of the sites investigated. The seasonal signal is believed to be a result of CO_2 limitation during the summer. The absence of similar signals at all the sites investigated may, in part, be a result of the use of different individuals and therefore may represent interspecimen variability. A long-term decrease in the $\delta^{15}N$ of the OM was observed, which was correlated with a decrease in the concentration of NH_4^+ and NO_2^- in the water column. We speculate that perhaps components of the food chain (phytoplankton–zooplankton) on which the corals are feeding are utilizing NH_4^+, which is perhaps being isotopically enriched during its conversion to NO_2^- and NO_3^-.

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