The EVERGLADES, FLORIDA BAY, and CORAL REEFS of the FLORIDA KEYS

An Ecosystem Sourcebook

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28 The Influence of Nearshore Waters on Corals of the Florida Reef Tract

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CONTENTS

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INTRODUCTION

At the distal end of water flow through the South Florida hydroscape lies the Florida Reef Tract. This discontinuous group of reefs is at the interface between the nearshore environment of Hawk Channel and the oceanic conditions of the Florida Straits. Depending upon their location along the tract and temporally variable oceanographic conditions, the reefs are subject to various combinations of nearshore or oceanic water. Florida Bay has exerted an increasing influence on the waters of Hawk Channel since sea level rise allowed its waters to pass through the Keys archipelago (Ginsburg and Shinn, 1964; Shinn et al., 1994). (Influences that affect Florida Bay are discussed elsewhere in this volume.) In turn, the effects of Florida Bay water on the reefs have also increased, particularly in the Middle Keys (Lower Matecumbe to Big Pine Key) where broad channels permit considerable exchange of Florida Bay waters with those of Hawk Channel. Reefs are poorly developed offshore of these channels, although geological evidence indicates that Holocene reef development was considerable in these areas until broaching of the Keys approximately 4000 years BP (Shinn, 1963).

Summarizing previous literature, Chiappone (1996) stated that "...water exchange between Florida Bay and the Atlantic Ocean significantly impeded coral growth in certain areas, particularly the middle Florida Keys." Reefs found offshore of the Middle Keys are limited in development and are usually found where islands provide a barrier to direct Florida Bay influence (e.g., Sombrero Reef near Marathon). Tidal currents flow in and out of Florida Bay via channels through the Keys but with a net flow outward from Florida Bay (Smith, 1994). Within Hawk Channel, between the Keys proper and the Reef Tract, flows are generally southwest to westward (Pitts, 1994; *cf.* Figure 28.1). How much of the Florida Bay water actually reaches the Florida reef tract is uncertain and certainly varies with wind and current conditions; however, it appears clear that waters of Florida Bay have influence on the reef tract, particularly in the Middle and Lower Keys. Extensive development of reefs in the Upper Keys is likely due to low Florida Bay influence because of the barrier provided by the Keys in this region and the westward movement of bay water after entering Hawk Channel (Shinn et al., 1994).

So, why is Florida Bay water deleterious to reef development, especially in the Middle Keys? High turbidity (Roberts et al., 1982), variable temperature (Shinn, 1966) and salinity (Shinn et al., 1989), and elevated nutrients (Szmant and Forrester, 1994) of Florida Bay waters have been suggested as possible reasons for these "inimical effects" (Ginsburg and Shinn, 1964). Porter et al. (1999) have emphasized that these stressors are likely to act in concert in impacting the Florida Keys coral reef ecosystem. In this chapter, we consider these stressors in the context of known effects on reef corals and our own preliminary transplantation experiments in the Middle Keys.

Florida Bay has been documented as a source and sink for fine carbonate sediments, and these sediments are one cause of elevated turbidity in the Bay. Calcareous green algae, particularly *Penicillus* spp., produce fine carbonate particles which are normally trapped and stabilized as sediments by seagrass meadows. However, the extensive loss of *Thalassia testudinum* during the late 1980s and early 1990s (Robblee et al., 1991) has been largely responsible for increasing the turbidity of Florida Bay by allowing wind-driven resuspension of these unstabilized carbonate sediments and seagrass detritus (see Thayer et al., 1994). Extensive algal blooms (Smith and Robblee, 1994) have also increased turbidity in the bay in recent years.

Because of their shallow depth (<10 m), the waters of Florida Bay and the southeastern Gulf of Mexico that overlie the Southwest Florida Shelf are subject to large temperature and salinity fluctuations. Polar cold fronts during the winter can rapidly lower water temperatures to as low as 9°C during extreme events (Hudson, 1981; Porter et al., 1982). Summer insolation during periods of low wind velocities can raise temperatures up to 40°C (Schmidt and Davis, 1978). These extremes are well beyond the optimal range for reef corals (20 to 30°). Salinities can vary considerably, as well, particularly during the wet season in summer when evaporation can produce high salinities that can be quickly lowered by rainfall and runoff from the South Florida mainland. Management of upstream water supply has had considerable effects on the salinity of Florida Bay (Light and

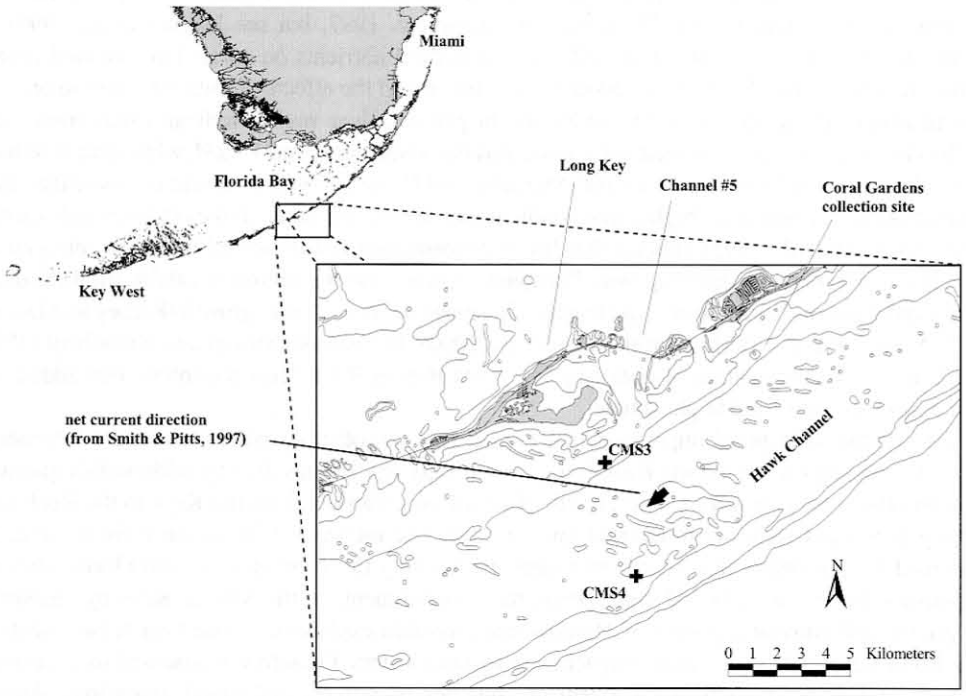

FIGURE 28.1 Collection site (Coral Gardens) and array sites at Long Key (CMS3 and CMS4) used in study. Broad arrow near Tennessee Reef shows location of current meter (deployed by N. Smith, Harbor Branch Oceanographic Institution) and net current direction over the period.

Dineen, 1994). Reductions in water flow during the 1970s and 1980s generally raised salinity to levels where the bay had become significantly hypersaline (40 to 50‰; Boesch et al., 1993). This problem was addressed by the South Florida Water Management District in 1993 by increasing freshwater flow into the Everglades and thus Florida Bay. However, the effects of these salinity fluctuations on corals in the Florida Reef Tract are not clear. In one of the few published studies on the effects of salinity on coral physiology, Muthiga and Szmant (1987) found that changes of ±10‰ had little effect on photosynthesis and respiration of the coral *Siderastrea siderea*, although at 42‰ photosynthesis decreased by 25%. Porter et al. (1999) have demonstrated that coral productivity is reduced by the interactions of elevated salinity and temperature.

The role of elevated nutrient levels as a factor in the decline of coral reefs has been a subject of recent debate (Lapointe, 1997; Szmant, 1997; Hughes et al., 1999). Florida Bay has seen an increase in nutrient levels from the Gulf of Mexico and the South Florida watershed and the release of nutrients from sediments following seagrass dieoffs (Boesch et al., 1993). These processes have resulted in elevated nitrogen concentrations, so that phosphorus can be limiting in the bay, especially in the northeast portions (e.g., Fourqurean et al., 1993). The sources and effects of nutrients on coral reefs in the Florida Reef Tract have been subjects of considerable concern and debate. In the Middle Keys can be found a gradient of decreasing nitrogen concentrations from the bay to the reef tract (Szmant and Forrester, 1996), so that bay waters reaching the reefs during ebbing tides could deliver nutrients to the reef. Anthropogenic sources in the Keys proper increase dissolved nutrient levels in the inshore waters (Lapointe and Matzie, 1996), but the extent to which this input affects the offshore reef tract in the Keys is unclear (Szmant and Forrester, 1996). Other possible nutrient inputs to reef waters include upwelling, tidal bore events, and regeneration from sediments (Leichter et al., 1996; Szmant and Forrester, 1996). Typically, coral reef development is greatest in oligotrophic waters and is adversely affected by elevated nutrients.

Nutrient-related effects on reef corals may be indirect, as when macroalgae proliferate and outcompete corals under eutrophic conditions (Lapointe, 1997, but see Hughes et al., 1999), or direct. However, studies of the direct effects of dissolved nutrients on corals have yielded contradictory results. Ferrier-Pagès et al. (2000) have summarized the effects of nutrient addition on coral growth under laboratory and field conditions. In general, their review indicates that ammonium inhibits linear growth and calcification at concentrations between 2 and 15 μM, while nitrate reduces total calcification between 1 and 20 μM (Marubini and Davies, 1996). It should be noted that these concentrations are generally higher than ambient reef levels, and other studies (Meyer and Schultz, 1985; Atkinson et al., 1995) indicate that lower concentrations of dissolved inorganic nitrogen are associated with increased coral growth. Phosphate acts as a crystal poison in calcification (Simkiss, 1964), and most studies indicate that elevated phosphate depresses coral growth (Kinsey and Davies, 1979; Stambler et al., 1991; Ferrier-Pagès et al., 2000). In contrast, Steven and Broadbent (1997) found increased calcification of corals on the Great Barrier Reef when phosphate was added to a final concentration of 4 μM phosphate.

Despite the widespread impression that Florida Bay and other nearshore waters are detrimental to corals growing on the Florida Reef Tract, surprisingly few studies directly address this question. Hudson (1981) measured the linear growth of corals on a transect from the Keys to the Reef Tract starting at Snake Creek and found that linear growth rate increased with distance from shore. We examined the possibility that nearshore waters, particularly those emanating from Florida Bay, are responsible for decreased coral vigor (thus, reef development) in the Middle Keys by measuring the growth and nutrient exposure of *Montastraea faveolata* explants over one year at two locations near Long Key, a site of maximal impact from inshore waters. Growth was assessed by measuring changes in buoyant weight, areal extension, number of polyps, and radial extension. Nutrient exposure was assessed by physiological signals in the coral zooxanthellae (*Symbiodinium* sp.) that are commonly used to assess the nutrient sufficiency of marine algae and other plants (Flynn, 1990). These signals (elemental ratios, free amino acid content, and ammonium enhancement of dark carbon fixation) integrate both long-term nutrient history and nutrient inputs to corals from both dissolved and particulate (e.g., host-feeding) sources (Cook et al., 1997). We also examined the photosynthetic capability of the zooxanthellae, as calcification in corals is enhanced by symbiont photosynthesis (Vandermeulen and Muscatine, 1974).

METHODS

We used a pneumatic drill fitted with a diamond coring bit to obtain 24 cores (5.1-cm diameter; ~2.5 cm deep) from each of four colonies of *Montastraea faveolata* (Knowlton et al., 1992) at an inshore patch reef near Lower Matecumbe Key (Coral Gardens, 24°50.154′ N; 80°43.751′ W; Figure 28.1). Core holes in the donor colonies were later filled with pre-cast cement plugs and Portland Type 2 cement. The cores were imaged, stained with 10 mg l^{-1} Alizarin Red S for 24 hours, secured in PVC collars, and weighed using the buoyant weight technique (Mettler AT400 balance; 0.1-mg resolution). The explants were then deployed on two arrays such that all of the colonies were equally represented. The inshore array (CMS3; 4-m depth) was located near the shoreward edge of Hawk Channel (24°47.868′ N; 80°47.093′ W) and received direct flow from Florida Bay via Channel #5 on ebbing tides. The offshore array (CMS4; 5-m depth) was located on the outer edge of Hawk Channel near Tennessee Reef (24°45.475′ N; 80°46.370′ W). Based on information on net current speed and direction (Figure 28.1), it received less water flow from Florida Bay.

At approximately quarterly intervals over one year, 12 cores were retrieved from each of the arrays for assessment of growth and the nutrient status of the symbiotic zooxanthellae. Core numbers for collection at each interval were randomly selected at the start of the study so that each collection consisted of matched pairs from each site from the same colonies located at corresponding positions on the arrays. After thorough cleaning of the PVC collars to remove fouling organisms, buoyant weights were measured to determine total calcification (Jokiel et al., 1978). Tissues were removed

from the skeletons using 0.22-μm-filtered seawater (FSW) in a recirculating water-jet system (Annis, 1998) based on a Water-Pik™ design; the extracts were used for biomass and nutrient exposure assays. Surface areas of the cleaned skeletons were determined using the foil method (Marsh, 1970), as were counts of the number of polyps. For measurements of linear extension, cores were bisected transversely using a diamond sawblade. One half was roughly polished with 600 grit silicon carbide sandpaper, and images of the polished face were recorded using an Olympus SZH10 stereomicroscope with a Sony video camera and SVHS recorder. For each core section, five points within intercalyx regions were selected for vertical growth measurements by making measurements of the distance from the alizarin stain line to the uppermost dissepiment (Lamberts, 1978) directly from the monitor screen.

The nutrient exposure of the corals was assessed by determining the nutrient status of freshly isolated zooxanthellae. Physiological parameters such as elemental ratios (C:N:P), free amino acid pools, and the ammonium enhancement of dark carbon fixation is commonly used to assess the nutrient status of marine plants such as microalgae (Flynn, 1990) and seagrasses (e.g., Fourqurean et al., 1992). These parameters integrate nutrient exposure from all sources over time, as has been demonstrated for zooxanthellae in host tissue (Cook et al., 1997). In addition, biomass characteristics of coral tissue such as numbers of zooxanthellae and protein content also reflect the environmental history of the host (Muller-Parker et al., 1994b; Fitt et al., 2000). These integrating measurements are particularly important for multitrophic organisms such as reef corals that receive nutrient inputs from a variety of sources.

Host tissues and zooxanthellae were separated and prepared according to the protocol developed by Muller-Parker et al. (1994b). Measurements of the zooxanthellae included cell counts, chlorophyll *a* and c_2 content (Jeffrey and Humphrey, 1975), and elemental ratios (CNP). For the latter, frozen samples on pre-combusted GF/F filters were sent to the Analytical Services Laboratory of the University of Maryland (Chesapeake Biological Laboratory). C and N content was determined with an Exeter Analytical Model CE-440 elemental analyzer, and P content was determined by the method of Aspila et al. (1976). For analysis of the free amino acid (FAA) pools, zooxanthellae were collected on sterile 1.2-μm nylon syringe filters, rinsed with FSW and frozen. FAA were extracted from the filters in 2 ml of HPLC-grade distilled water for 1 hr at 70°C, derivatized with *o*-phthaldialdehyde (OPA) and separated by HPLC with a reversed-phase C18 column (Lindroth and Mopper, 1979; Ferrier, 1992). Protein content of animal supernatants was determined by the Lowry procedure (Muller-Parker et al., 1994b). In addition, suspensions of freshly isolated zooxanthellae were used for determination of photosynthetic rates and ammonium enhancement of dark carbon fixation (20 μ*M* NH_4Cl) with $^{14}CO_2$ (Cook et al., 1992). For photosynthesis, the algae were incubated with $NaH^{14}CO_3$ for 30 min under fluorescent lamps producing an irradiance of 200 μmol photon m^{-2} sec^{-1}.

For each quarterly sampling, we made between-sites comparisons of matched pairs (i.e., cores from the same colony at the same position on each array) with paired *t*-tests assuming unequal variances. For other statistical analyses (seasonal, colony, and overall effects), multi-way ANOVA and correlation analyses were used. *Post hoc* comparisons between groups were performed with Tukey's HSD procedure to examine seasonal and intercolony differences at each site. All datasets were normalized with the graphical procedures of Systat (SPSS, Inc.) prior to analysis.

RESULTS

Growth and Survival of Coral Explants

Coral Explant Survival

All 96 explants appeared to recover from the coring, handling, and alizarin treatment; however, over the one-year duration of the experiment, several explants suffered physical damage (breakage

or tissue abraded by buoy lines) and one lost tissue, possibly due to hydrogen sulfide-rich water emanating from under the core through a gap in the epoxy. We saw no evidence of disease. Damaged cores were excluded from the datasets, so that the final sample sizes were 43 at the inshore site and 47 at the offshore array. Incomplete pairs were eliminated from between-site, paired *t*-test comparisons, but healthy unpaired cores were included in overall comparisons. For the 12 explants on each array deployed for the entire experiment, the survival rates were 83.3% inshore (385 to 390 days) and 91.7% offshore (361 days).

Mass Accretion

Deposition of total $CaCO_3$ was greater at the offshore site (CMS4) during each of the quarterly samplings (Figure 28.2; paired *t*-tests; $p < 0.05$ for each interval). Corals at this site had accretion rates that were 25 to 46% greater than those at the inshore site (CMS3). Combining the rates for all sampling periods, the mean accretion rate of the offshore corals was 34.9 ± 11.9 mg $CaCO_3$ day^{-1} (mean ± SD), while that of corals at CMS3 was 21.1 ± 7.7 mg $CaCO_3$ day^{-1} ($p < 0.001$; two-sample *t*-test). The mean $CaCO_3$ accretion rate by all inshore corals was 39.7% lower than those offshore. The data in Figure 28.1 are not corrected for surface area. The area-corrected rates for offshore corals also exceeded those of the inshore corals during every sampling period (Table 28.1). Overall, the accretion rate per square centimeter of the offshore corals was 37.4% greater than that of the inshore corals.

Our measurements integrate growth from the time of deployment to the time of collection, so that any seasonal differences in calcification (e.g., decreased growth during winter months) may not be evident. A three-way ANOVA of the entire dataset for Figure 28.1 showed a strong effect of site ($p < 0.001$; *cf.* Figure 28.2) but no effects of sampling date or colony, We examined the data within each site for effects of sampling time and donor colony. Explants at the inshore site showed significant differences between dates ($p < 0.05$), with the October 1997 samples having slightly increased rates over the other samples. No effects of either sampling date or donor colony were found at the offshore site. The area-corrected data in Table 28.1 suggest decreased calcification rates of the offshore corals after the last sample (March 1997, after the winter period); however, this was more likely due to the increase in surface area of these corals during this period (Figure 28.3A), as no suggestion of decreased accretion rates of these corals can be seen in Figure 28.2.

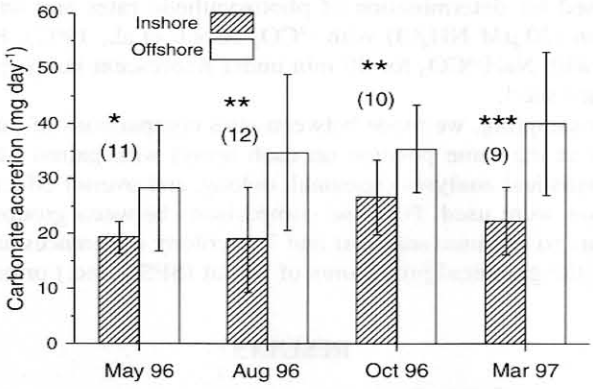

FIGURE 28.2 Rates of buoyant weight increase (carbonate accretion) between paired coral cores at the inshore (CMS3) and offshore (CMS4) sites during each sampling period. Rates are integrated over the time between the deployment and collection of cores. Significance levels are from paired *t*-tests of log-transformed data. The variances for the March 1996 dataset were not homogeneous following this transformation. Error bars represent ±1 SD; *n* value in parentheses. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

TABLE 28.1
Rates of Buoyant Weight Increase (Accretion Rates) from Figure 28.2 Normalized to Surface Area During Each of the Measurement Intervals

Collection Date	Accretion Rate (mg $CaCO_3$ day^{-1} cm^{-2}) CMS3	CMS4	*n*	*p*
May 1996	0.93 ± 0.17	1.45 ± 0.58	11	<0.05
August 1996	0.64 ± 0.19	1.29 ± 0.71	12	<0.01
October 1996	0.77 ± 0.15	1.17 ± 0.19	10	<0.01
March 1997	0.75 ± 0.24	0.92 ± 0.19	10	<0.001

Note: The data were transformed with an inverse square root transformation prior to comparisons between sites by paired *t*-tests. Variances were homogenous except for the May 1996 dataset. Data reported as mean ± SD.

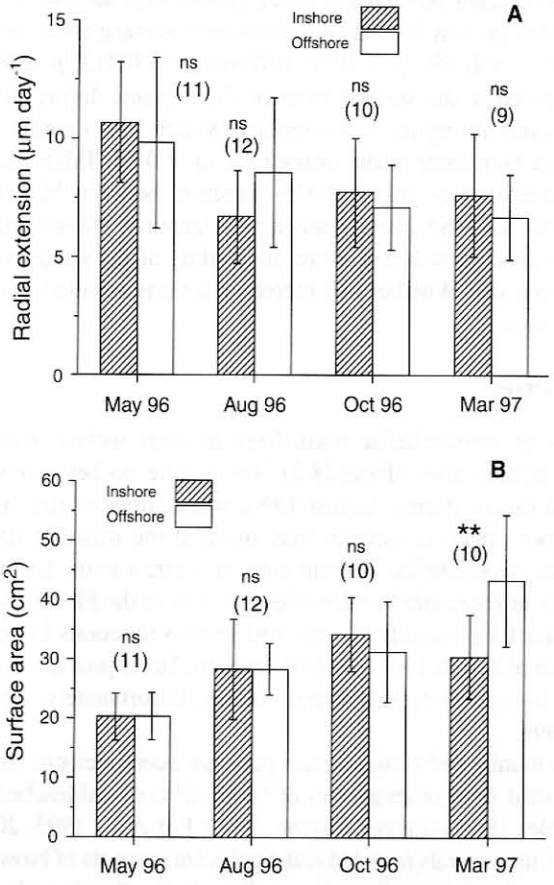

FIGURE 28.3 (A) Rates of linear increase (radial extension) of the coral cores in Figure 28.2, as determined from alizarin staining. Significance levels are from paired *t*-tests of log-transformed data (all variances homogeneous). Statistical conventions are the same as in Figure 28.2. (B) Surface areas of the corals shown in Figure 28.2. Significance levels from paired *t*-tests of log-transformed data (all variances homogeneous). Statistical conventions are the same as in Figure 28.2.

Radial Growth

In contrast to the mass accretion data, no differences were found in radial growth (linear extension) of corals at the two sites during any sampling period, as indicated by the deposition of new skeleton above the alizarin stain lines (Figure 28.3A). The mean rates of extension ranged from 7.0 to 10.7 μm day^{-1} (inshore) and 6.6 to 9.8 at the offshore site. Averaged over all corals in the study, these values correspond to extrapolated yearly growth rates of 3.02 ± 0.86 mm yr^{-1} at the inshore site and 2.92 ± 0.95 mm yr^{-1} at the offshore site (range 2.4 to 3.9 mm yr–^{1}). As expected from the paired comparisons, the ANOVA did not reveal any between-site differences. Taken together with the mass accretion and surface areal data (below), these results indicate that the inshore corals were producing less dense skeletons. For each sample we calculated the density of newly deposited skeleton by dividing the weight of $CaCO_3$ added during each interval by the extension of the skeleton (mg $CaCO_3$ μm^{-1} extension). For the offshore corals this value was 4.92 ± 2.18 ($n = 47$); for the inshore corals, 3.04 ± 2.00 ($n = 43$; $p < 0.001$). The analysis indicates a 38% decrease in the density of skeletal material added at the inshore site.

Areal Growth

Coral explants showed evident skeletal and tissue growth over the epoxy and PVC collars during the experiment, and this growth is evident as increased surface areas of the samples over time at both sites (inshore: $r = 0.460$, $p < 0.01$; offshore: $r = 0.713$, $p < 0.001$) No between-site differences were observed in the surface areas of the explants during the first three collections (Figure 28.3A). However, during the last sampling (March 1997) corals at the offshore site had 30% more surface area than those at the inshore site ($p < 0.05$; Table 28.2). The offshore corals more than doubled their surface area (a 100% increase) between May 1996 and March 1997, while the inshore corals at CMS3 showed only a 50% increase. We noticed that the inshore corals routinely had greater algal growth and other bio-fouling at the margins of the live tissue than did those at the offshore site. Whether this increased fouling resulted in inhibition or regression of coral tissue is not clear.

Zooxanthellae Biomasses

Overall, the densities of zooxanthellae normalized to coral surface area or per-milligram host protein were similar at both sites (Table 28.2). There were no between-site differences at each measurement interval except during August 1996, when corals at the inshore site (CMS3) had more zooxanthellae per square centimeter than those at the offshore site. ANOVA showed no seasonal differences in zooxanthellae per unit area, in contrast to the findings of Fitt et al. (2000), who reported a decline in zooxanthellae densities of corals in the Florida Keys during late summer and autumn. Our values for zooxanthellae per host protein for corals in October 1996 were lower than those in May 1996 or March 1997 ($p < 0.05$ for both; Tukey *post hoc* comparisons), suggesting that there might have been a fall decline in these values. Unfortunately, we had no protein samples for the summer of 1996.

Our values for the numbers of zooxanthellae per square centimeter of coral surface are generally lower than those reported from other species of "normal" (i.e., unbleached) corals in the *Montastraea annularis* complex (Szmant and Gassman, 1990; Fitt et al., 1993, 2000; Cook et al., 1994). Sectioned skeletons of these corals revealed that significant amounts of brown coral tissue remained, indicating that the removal of tissue from these relatively large (<20 cm^2) pieces of coral was less than 100%. While our values for the total numbers of zooxanthellae (particularly per unit area) are underestimates, subsequent data normalized to cell numbers in this chapter refer to determinations made on final cell suspensions and do not depend on the efficiency of tissue recovery.

TABLE 28.2
Between-Site Comparisons for All Parameters of Zooxanthellae Measured in this Study, Without Regard to Time of Sampling

Parameter	CMS3 Mean ± SD	CMS3 *n*	CMS4 Mean ± SD	CMS4 *n*	*p*
10^6 zooxanthellae cm^{-2}	0.80 ± 0.50	39	0.67 ± 0.40	41	ns
10^6 zooxanthellae mg $protein^{-1}$	0.60 ± 0.31	28	0.50 ± 0.24	31	ns
Chlorophyll *a* per cell[a]	4.17 ± 1.67	41	2.98 ± 1.49	45	<0.001
Chlorophyll *c* per cell	1.31 ± 0.61	41	1.02 ± 0.55	43	ns
Chlorophyll *a* / chlorophyll c_2	3.45 ± 0.84	41	3.19 ± 0.83	43	ns
C:N ratios	6.50 ± 0.51	36	6.81 ± 0.49	47	<0.01
N:P ratios	33.52 ± 5.58	36	28.71 ± 4.75	47	<0.001
C:P ratios	220.57 ± 45.07	36	194.99 ± 31.89	47	<0.001
gln:glu	1.15 ± 0.81	37	1.17 ± 0.69	46	ns
Basic FAA/total FAA[b]	0.22 ± 0.09	37	0.22 ± 0.08	46	ns
Ammonium enhancement[c]	1.17 ± 0.18	23	1.07 ± 0.16	28	< 0.05
Photosynthesis per cell (pg C $cell^{-1}$ h^{-1})	5.64 ± 3.86	31	5.296 ± 3.86	33	ns
Photosynthesis per chlorophyll *a* (pg C µg chlorophyll a^{-1} h^{-1})	1.21 ± 0.68	31	1.641 ± 0.77	32	<0.05

Note: Comparisons by two-sample *t*-tests assuming unequal variances; data were log-transformed except where indicated; ns = not significant ($p > 0.05$).

[a] Data transformed as y = chlorophyll $a^{0.2}$.
[b] Data transformed as $y = (\text{basic/total})^{0.6}$.
[c] Data transformed as $y = (NH_4 \text{ enh})^{0.5}$.

Indices of Nutrient Sufficiency of Zooxanthellae

Elemental Ratios

C:N ratios of zooxanthellae from both sites were consistently low during every sampling, clustering around the N-sufficient Redfield ratio of 6.6:1 (Figure 28.4A). No between-site differences in C:N were observed, except in the October samples, for which ratios of zooxanthellae from the offshore corals were slightly higher than those from CMS3 ($p < 0.05$). The N:P ratios of zooxanthellae from both sites were generally elevated, roughly double the Redfield ratio of 16:1. N:P ratios of zooxanthellae from the inshore corals were greater than those of the offshore corals in the summer samples ($p < 0.01$), and possibly in the autumn ($p < 0.06$; Figure 28.4B). The winter and spring samples showed no between-site differences. As with the N:P ratios, C:P ratios for zooxanthellae from both sites were generally twice the Redfield ratio for P-sufficient phytoplankton (Figure 28.4C). C:P values were higher at the inshore site than offshore in the August samples (Figure 28.4C; $p < 0.01$); no other between-site differences were observed.

The overall pattern of the elemental data indicates that zooxanthellae at both sites were N sufficient throughout the year and probably were P limited. P limitation was greater at the inshore site in the summer, and a seasonal analysis revealed that both N:P and C:P ratios in the August samples were greater than other samples at this site (Tukey, $p < 0.05$). P limitation in Florida Bay waters also is most pronounced during the summer months (Fourqurean et al., 1993).

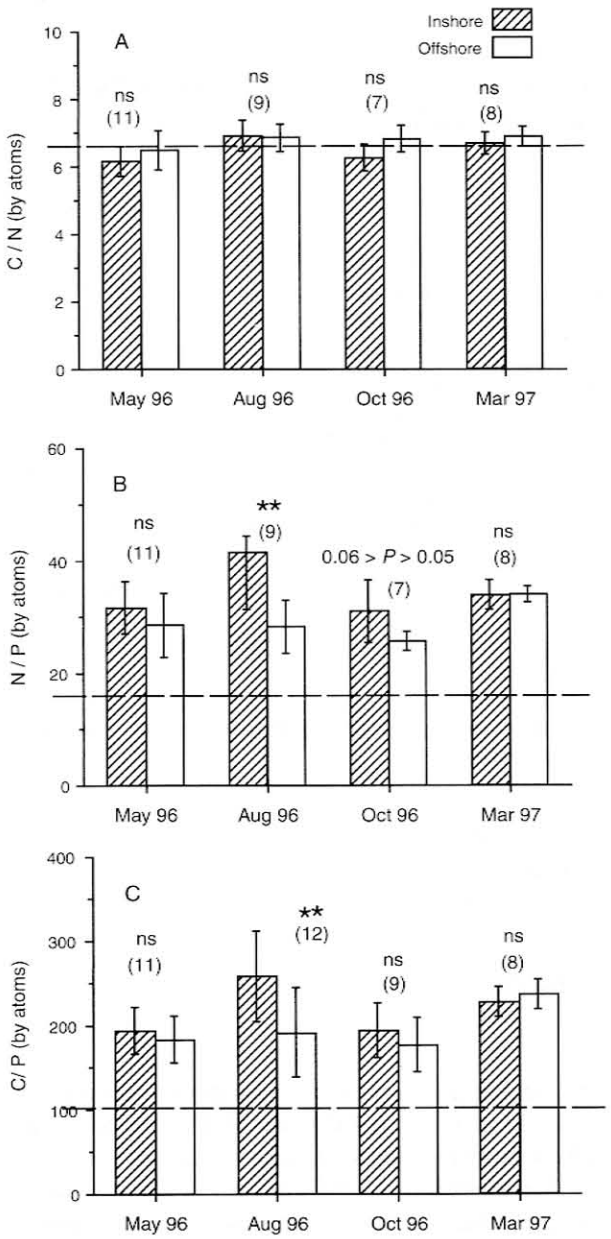

FIGURE 28.4 Elemental ratios of zooxanthellae isolated from the corals in Figure 28.2. (A) C:N; (B) N:P; (C) C:P. Significance levels are from paired *t*-tests of log-transformed data (all variances homogeneous).

FAA Ratios of Zooxanthellae

Typically nitrogen-replete algae store N as free basic amino acids with high N content (lysine, arginine, glutamine). As with the C:N ratios, neither ratios of glutamine to glutamate (gln:glu) nor basic to total FAAs showed any between-site differences in our samples; overall values are given in Table 28.2. Gln:glu ratios greater than 0.5 generally indicate N-sufficient microalgae (Flynn, 1990), as do basic-to-total ratios over 0.25. Our gln:glu data were well in excess of 0.5, with the overall mean for both sites greater than 1 (more glutamine than glutamate in the free amino acid pool), and the basic-to-total ratios approached 0.25. These ratios generally indicated N sufficiency at both sites throughout the study.

Ammonium Enhancement of Dark Carbon Fixation

The addition of ammonium typically increases dark carbon fixation by nitrogen-limited microalgae, while it has little effect on N-sufficient ones (Flynn, 1990; Cook et al., 1992). We only assayed ammonium enhancement in three samples (May, August and October), but as with the C:N and FAA data, no differences in ammonium enhancement ratios (ammonium dark rates/seawater dark rates) between the two sites could be found at these times, although the overall dark enhancement ratio at the inshore site was slightly higher than the offshore site. In general, ratios at both sites were very low (Table 28.2), and there actually was no overall effect of ammonium addition on dark carbon fixation in these samples (*t*-test). These data complement those for C:N and FAA ratios in demonstrating N sufficiency for zooxanthellae at both sites in our Long Key study.

Chlorophyll Content

Figure 28.5 summarizes the data on chlorophyll content of the zooxanthellae. During every sampling, zooxanthellae from corals at the inshore site contained more chlorophyll *a* than did those at the offshore site (Figure 28.5A). Overall, zooxanthellae from the inshore corals had 25% more chlorophyll *a* ($p < 0.001$; Table 28.2). Chlorophyll c_2 content at the inshore site was also greater during two of the sampling periods (Figure 28.5B). The ratios of the two pigments (chlorophyll *a*/chlorophyll c_2) generally ranged between 3 and 4 throughout the study, and showed no between-site differences (Figure 28.5C). The pigment content of zooxanthellae in corals can be influenced both by nitrogen supply and light conditions (Hoegh-Guldberg and Smith, 1989; Muscatine et al., 1989). Given the apparent similarity in nitrogen exposure of corals at the two sites, the differences in chlorophyll *a* content were probably the result of differing light conditions at the two sites.

Fitt et al. (2000) have demonstrated a seasonal pattern of pigment content of zooxanthellae from corals in the Keys, with samples taken in the summer having consistently less chlorophyll than winter samples. Our samples did not show this trend; chlorophyll *a* values at both sites were highest in October 1996 and lowest in March of 1997 (Tukey HSD, $p < 0.05$). The pigment ratios showed no effects of sampling date.

Photosynthetic Rates of Isolated Zooxanthellae

Photosynthetic rates were only compared for the May, August, and October samples. Pooling data for all of the sites revealed no differences in per-cell photosynthetic rates, but photosynthesis per unit chlorophyll *a* was 26% greater at the offshore site ($p < 0.05$; Table 28.2). Comparisons of matched pairs of corals at each sampling time showed this pattern only in the August samples ($p < 0.05$), with no between-site differences in the other samples.

DISCUSSION

We chose the Long Key area as a site for this work in part because the influence of Florida Bay on the inshore waters (and possibly the Reef Tract) is greatest in this part of the Middle Keys (e.g., Szmant and Forrester, 1996). Without replicated sites, our results are inconclusive with respect to the general influence of Florida Bay on reef corals. However, our study produced four significant findings comparing these inshore and offshore sites: (1) total calcification, but not skeletal extension, was reduced in inshore corals; (2) corals at both sites were exposed to sufficient, if not excessive, sources of nitrogen; (3) corals at both sites were probably phosphorus limited, and this limitation was probably greater at the inshore site in the summer; (4) zooxanthellae from the inshore site had higher chlorophyll *a* content and lower photosynthetic rates (per μg chlorophyll *a*) than those from the offshore site.

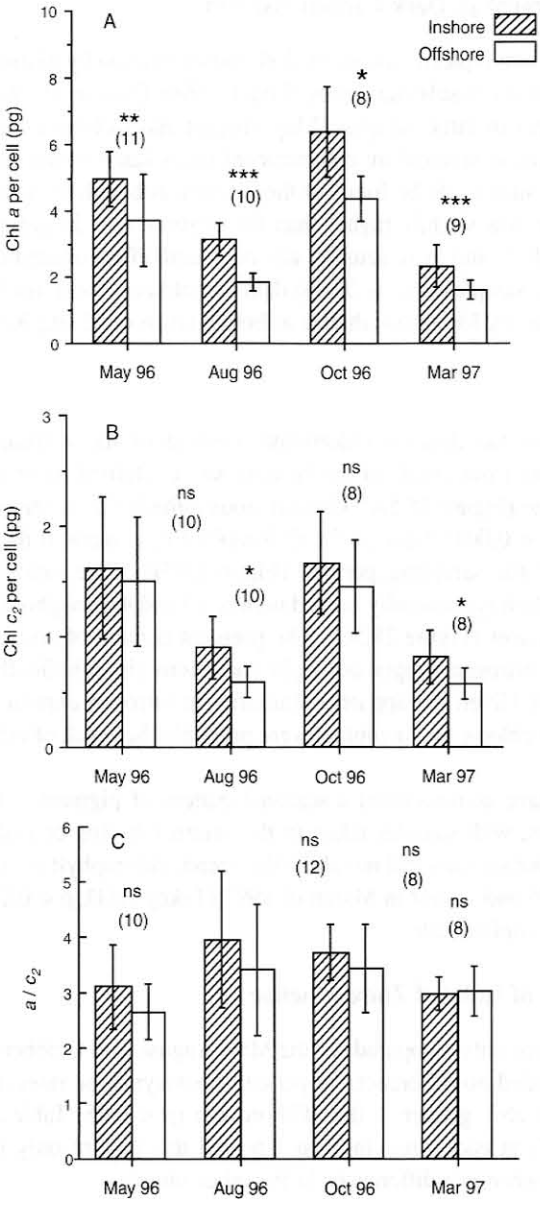

FIGURE 28.5 Chlorophyll *a* content of zooxanthellae isolated from the corals in Figure 28.2. Significance levels are from paired *t*-tests of log-transformed data (all variances homogeneous). Statistical conventions are the same as in Figure 28.2.

Coral Growth: Linear Extension

Two other studies of the growth of corals transplanted between inshore sites and offshore sites in the Florida Keys have been conducted. Shinn (1966) transplanted colonies of *Acropora cervicornis* from the Reef Tract off Key Largo to two locations: (1) on a pinnacle in Hawk Channel, and (2) in shallow water 300 ft from Key Largo Island. Linear extension, as determined by a banding technique, was twice as great at the donor site as at the two other sites. While the sites differed in a number of respects, temperature extremes were considered to be a major reason for the decreased growth (and increased mortality) at the inshore sites. However, it is not clear that the inshore corals were exposed to water from Florida Bay, as there are no major passes in this area of Key Largo.

Using alizarin staining techniques, Hudson (1981) measured skeletal extension rates of *Montastraea annularis* transplants along a transect from Snake Creek Channel (inshore) to Crocker Reef (offshore) in the Upper Keys. These are sites that would be affected by flow through Snake Creek and Whale Harbor Channels. He found a gradient in the rate of skeletal extension with nearshore corals growing more slowly than those offshore, and be correlated this result with increasing temperature stress near shore. We made no temperature measurements in our study. While our inshore corals very likely experienced a wider range of temperatures than the offshore corals, these differences in temperature exposure were not expressed as effects on skeletal extension rates. We did find evident differences in coral growth in regard to total carbonate deposition, which is also temperature dependent (Clausen and Roth, 1975). For reasons discussed below, we believe that water clarity was an important factor affecting total calcification at Long Key.

Comparison of our extension data with those of Hudson (1981) and other studies suggests that inshore waters affected corals at both of our sites. Corals at Hudson's most inshore site had mean extension rates of 2 mm yr^{-1}, while transplants on offshore reefs added 8 to 9 mm yr^{-1}. The extension rates that we measured at Long Key were similar to his inshore rates at both the inshore and offshore sites (2.4 to 3.9 mm yr^{-1}) and were lower than those reported for the *M. annularis* species complex in shallow waters elsewhere in the Florida Keys (Vaughan, 1915; Hudson, 1981) or from the Caribbean (Dustan, 1975; Graus and Macintyre, 1982; Tomascik and Sander, 1985). As temperature has been implicated in the reduction of extension rates of corals in the Keys, this may be a stress experienced by corals on reefs in the Middle Keys due to tidal exchange through the passes.

Coral Growth: Total Calcification

Our finding that offshore corals deposited more total CaCO3 than inshore corals while exhibiting no differences in extension rate indicates that the inshore corals had produced a less dense skeleton (37% reduction). We are aware of no comparable studies for reef corals in the Florida Keys. Risk and Sammarco (1991) found increasing skeletal density in *Porites lobata* on the Great Barrier Reef with greater distance from shore and suggested that this was due either to increased light penetration offshore or to the inhibition of calcification inshore due to elevated nutrients. Foster (1979) examined the density of skeletons of *M. annularis* from a variety of habitats in Jamaica and found that corals from lagoonal environments had more porous skeletons than did those from patch or offshore reefs. Reciprocal transplants between lagoonal and other environments resulted in the skeletons of transplants taking on the morphology characteristic of the new environment. The lagoonal environment was characterized as having higher sedimentation rates and lower light levels than the other sites, and Foster (1980) suggested that differences in light levels were largely responsible for the growth differences in *M. annularis* at these sites. Similar results were reported by Dodge and Brass (1984), who measured both extension rates and total mass accretion of *M. annularis* at various sites in St. Croix. They found that corals from Christiansted Harbor, historically exposed to dredging activities and sewage effluent, exhibited reduced mass accretion compared to corals at more pristine sites, although extension rates were similar.

At Long Key there is a decreasing gradient of both dissolved nutrients and suspended material from Florida Bay to the Reef Tract (Szmant and Forrester, 1994, 1996). While we made no irradiance measurements at our sites, the patterns of chlorophyll *a* content of zooxanthellae in our study indicated lower light levels at the inshore site. Zooxanthellae in corals typically respond to lower light levels by increasing pigment content (e.g., Falkowski and Dubinsky, 1981). Because these corals were at comparable depths and showed no differences in zooxanthellae density (thus eliminating self-shading as a factor), reduced light penetration of the water column at the inshore site was most likely responsible. Increased turbidity inshore was supported by our own qualitative observations during dives and by subsequent field measurements (Jones and Boyer, 1999; Szmant, pers. comm.). Thus, the effects of nearshore waters in decreasing bulk calcium deposition by reef corals, but not skeletal extension, appear to be related to reduced water clarity. In South Florida this appears to be due to the increasing turbidity of Florida Bay, associated with seagrass dieoffs (Robblee et al., 1991).

It appears that calcification by reef-building corals involves at least two phases. Skeletal extension (constructing the "flimsy scaffolding" of Barnes and Crossland, 1980) occurs largely at night and does not require light (Barnes and Crossland, 1980; Gladfelter, 1983; Vago et al., 1997). Bulk deposition of calcium carbonate as an "infilling" process takes place during the day and may represent the light-enhanced calcification that is typical of zooxanthellate corals (Gladfelter, 1983). We suggest that increased turbidity of inshore waters inhibits this light-enhanced bulk calcification and has a lesser effect (or none) on skeletal extension. In contrast, the wider temperature ranges of inshore waters are likely to affect both processes, perhaps linked through the interacting effects of salinity and temperature on coral productivity (Porter et al., 1999).

Effects of Nutrients

Another cause of decreased calcification at inshore reef sites could be elevated nutrients, especially nitrate, which can reduce calcification by corals at concentrations as low as 1 μM (Marubini and Davies, 1996). Nitrate levels at Long Key decrease along a gradient from Florida Bay to the reef tract (Szmant and Forrester, 1996). However, nitrate concentrations both inshore and offshore at Long Key typically are less than 0.5 μM (Szmant and Forrester, 1996; Jones and Boyer, 1999), and it not clear that nitrate concentrations in this range affect coral calcification.

It is generally thought symbiotic dinoflagellates in reef corals are limited by the availability of inorganic nutrients, especially nitrogen (e.g., Muscatine et al., 1989). All of the parameters of nitrogen sufficiency that we measured indicated that zooxanthellae from corals at both Long Key sites were nitrogen sufficient throughout the period of study. These included C:N ratios between 6.5 and 7.0, high levels of basic amino acids in the free amino acid pool, and the lack of significant enhancement of dark carbon fixation by ammonium. Our C:N values are lower than those found for coral zooxanthellae from the Red Sea (Muscatine et al., 1989), Hawaii (Muller-Parker et al., 1994a), Bermuda (Muller-Parker and Cook, unpub. data), and corals from the northern end of the Florida Reef Tract (McGuire and Szmant, 1997). Zooxanthellae from *M. annularis* in Bermuda typically exhibited significant enhancement of dark carbon fixation by ammonium with higher ammonium enhancement ratios, (Cook et al., 1994) in addition to higher C:N values. These comparisons all indicate that the corals at both of our Long Key sites were exposed to higher levels of nitrogen than those from other reef sites.

The sources of this elevated nitrogen are not clear, particularly for corals located at our offshore site. Dissolved and particulate nitrogen is clearly higher in Florida Bay (Szmant and Forrester, 1996), and dissolved N is elevated in the canals and other inshore waters in the Keys (Lapointe and Matzie, 1996). How much of this nutrient-enriched water actually impinges on the Florida Reef Tract is not clear (Porter et al., 1999). Current meter studies have shown a net transport along Hawk Channel, such that at least some of the tidal flow from inshore is diverted to the southwest (Pitts, 1994; Smith and Pitts, 1998). Our findings of P limitation of coral zooxanthellae, particularly in the summer at the inshore site indicate that some Florida Bay water reached this site, and possibly the offshore site as well. The waters of the eastern part of the bay typically are P limited in the summer (Fourqurean et al., 1992), and the P signals in the algae appear to reflect this. Other sources of dissolved nitrogen for corals on the Reef Tract could be upwelling events (Lee et al., 1992, 1994; Leichter et al., 1996) and particulate sources supplying nitrogen to coral zooxanthellae via host feeding (e.g., Cook et al., 1994). Regardless of the sources of these nutrients, it does not appear as though any evidence exists to date that elevated nutrients have a direct effect upon corals in the Florida Reef Tract.

Productivity

The calcification of reef corals is intimately associated with symbiont productivity, although the linkages between them are still unclear and controversial (Gattuso et al., 1999). Numerous authors

have noted that gross productivity of corals is stimulated by the addition of inorganic nutrients, primarily through the increase in symbiont numbers (Hoegh-Guldberg and Smith, 1989; Muscatine et al., 1989; Marubini and Davies, 1996; Ferrier-Pagès et al., 2000). In one of the few studies examining both the effects of long-term nutrient exposure on calcification and productivity of corals, Ferrier-Pagès et al. (2000) found an inverse relationship between the stimulation of productivity (P/R ratios) by nutrients and the inhibition of calcification. We measured photosynthesis, but not respiration, by isolated zooxanthellae from our corals. Carbon fixation per cell did not differ between inshore and offshore sites, although photosynthesis per unit chlorophyll *a* was greater at the offshore site (Table 28.2). The similar symbiont densities (Table 28.2) suggest that total photosynthesis by corals at the two sites was comparable under identical light conditions. As noted above, we believe that increased turbidity at the inshore site depressed productivity by reducing irradiance, thus total calcification by these corals, despite the elevated chlorophyll *a* content of the zooxanthellae. A related effect of turbidity on coral productivity would be increased respiratory rates (Telesnicki and Goldberg, 1995), which would further divert host energy from calcification processes. These possibilities should be examined by the use of *in situ* coral respirometry.

Other Effects of Inshore Waters on Corals

We found that the areal growth of corals at the inshore site was depressed in the latter stages of our study (Figure 28.3B). We noted increased bio-fouling of the coral maintenance structure at the inshore site during every sampling period. The attached epibionts included algae, hydroids, and other organisms that grew at the periphery of the growing edges of the coral explants. This bio-fouling may have inhibited both areal increase and polyp formation at this site. Longer-term effects on coral growth are suggested by our finding that the inshore corals produced skeletons of lower density. Coral skeletons with decreased density are structurally weaker and would be more susceptible to mechanical breakage from storm waves and other physical forces. A related consequence of weaker skeletons might be increased susceptibility to bio-erosion. Sammarco and Risk (1990) reported increased bio-erosion of *Porites lobata* at inshore sites on the Great Barrier Reef, where skeletal density was low (Risk and Sammarco, 1991). However, bio-erosion has also been reported to increase in coral skeletons of higher density (Highsmith, 1981).

CONCLUSIONS

Coral reefs of the Florida Reef Tract receive variable inputs of inshore waters and those of Florida Bay. Reef development is typically greatest where islands of the Florida Keys impede exchange of these waters and is least where passes permit such exchange. Temperature, salinity, turbidity, and elevated nutrient levels have been cited as "inimical effects" of inshore waters that inhibit coral growth. Previous work has indicated that temperature extremes reduce linear growth by corals in the Florida Reef Tract and operate with elevated salinity to reduce productivity. We performed transplant experiments using the major reef-building coral *Montastraea faveolata* at Long Key in the Middle Keys, where reefs are maximally affected by tidal exchange through passes. Corals at inshore and offshore sites exhibited no differences in linear growth rates, but skeletal deposition of $CaCO_3$ was 40% greater in offshore corals. We ascribe this effect to increased turbidity at the inshore site, as reported in other studies. Assays of nutrient exposure of coral zooxanthellae (elemental ratios, free amino acid pools, dark carbon) indicated no differences in nitrogen exposure at the two sites: symbionts were N sufficient, if not saturated, at both sites. Zooxanthellae from both sites had elevated N:P and C:P ratios, indicative of P limitation. Turbidity and temperature appear to be the major characteristics of inshore waters that affect corals on the Florida Reef Tract; to date, little evidence exists that elevated nutrients have a direct effect.

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