RESPONSES TO *in situ* SHADING BY ZOOXANTHELLAE IN THE SCLERACTINIAN CORAL *Siderastrea radians*

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
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To my friends and family for all of their love, support, and encouragement

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
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By

Emily Mitchem

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Siderastrea radians colonies in the St. Martins Keys, Florida (SMK) were shaded for 10 days using artificial shading screens with targeted light reductions of 0, 25, 50, 75, and 100%. Corals were sampled and processed to yield equations for estimating surface area and number of polyps from diameters and heights. In combination with counts of zooxanthellae and analyses of chlorophyll *a* concentrations, these equations were used to estimate numbers of zooxanthellae per square centimeter, concentrations of chlorophyll *a* per square centimeter, and concentrations of chlorophyll *a* per zooxanthellae. On average, *S. radians* colonies had fewer zooxanthellae per cm and less chlorophyll *a* per square centimeter than has been reported for other coral species. Results suggest that zooxanthellae densities vary among plots within treatments, and the densities do not change in a consistent pattern as shading is increased. Similarly, chlorophyll *a* concentrations per square centimeter did not exhibit a consistent relationship with intensity of shading. In contrast, corals subjected to 50% light reduction had chlorophyll *a* concentrations per zooxanthellae that were 58.6% higher than concentrations in unshaded corals. However, corals subjected to 75% light reduction had only 3.6% higher concentrations than corals subjected to 50% light reduction. Thus, corals responded to shading in a 10-day period, but their response appeared to be constrained by their light compensation point, the amount of chlorophyll

a that can be contained in a single zooxanthellae, or the rate at which chlorophyll *a* can be produced. Assuming unshaded corals represent a reliable control, *S. radians* gained an estimated 0.1713 pg of chlorophyll *a* per zooxanthellae per day on average. *Siderastrea radians*' zooxanthellae, though "sun-loving", did show some adaptation to low light environments, by increasing chlorophyll *a* concentrations, suggesting that colonies of these corals from SMK have the ability to adapt to reduced light environments in a relatively short amount of time. This and future studies of *S. radians* and its responses to the myriad effects of eutrophication will be valuable when attempting to implement sustainable management of the St. Martins Keys and true coral reefs elsewhere.

CHAPTER 1
INTRODUCTION

As human populations grow, anthropogenic activities introduce increasing quantities of sediments, nutrients, and other pollutants into coastal waters (Roberts et al. 2002, Brun et al. 2003). In particular, increased nutrient delivery caused by industrial and domestic wastewater, deforestation, and agricultural and urban run-off often can result in changes in the production characteristics of estuarine and nearshore ecosystems that, in turn, alters their structure and function (Duarte 1995, Valiela et al. 1997). For example, eutrophication can result in a proliferation of phytoplankton, epiphytes, and drift macroalgae (Duarte 1995, Ruiz & Romero 2001, Brun et al. 2003, Lamote & Dunton 2006). One typical change in eutrophic waters is a shift from nutrient limitation to light limitation (Duarte 1995). Such a change can greatly affect sessile organisms that rely directly on photosynthesis because they cannot seek out a more suitable light environment.

Nearshore corals, whether reef-building or solitary, are affected by light availability because they rely on symbiotic algae known as zooxanthellae. In fact, photosynthetically active radiation (PAR; 400-700 nm) and short wavelength radiation (UVR; 290-400 nm) strongly influence both the distribution and physiology of corals because these forms of energy influence zooxanthellae (Hoegh-Guldberg 1999). The most common zooxanthellae are dinoflagellates in the genus *Symbiodinium* (Rowan 1998). *Symbiodinium* is a genetically diverse genus that seems to comprise a yet-to-be-defined number of ecologically distinct types, clades or species (LaJeunesse 2001). Zooxanthellae supply their hosts with energy and essential compounds by translocating up to 95% of their photosynthetic production in the form of leaked amino acids, sugars, complex carbohydrates and small peptides (Hoegh-Guldberg 1999). In return, the host supplies its symbionts with essential nutrients in the form of ammonia and phosphate from its

waste (Hoegh-Guldberg 1999). Factors that stress zooxanthellae can often impact their ability to photosynthesize and supply nutrients and other essential compounds to their Cnidarian host, which can cause deleterious changes in the host. Thus, tracking changes in zooxanthellae abundance and their chlorophyll content allows researchers and managers alike to understand and possibly predict how coral populations will react or adapt to environmental stressors.

In the waters surrounding the St. Martin's Keys (SMK), located near the Homosassa River, recent survey work has revealed a large population of the scleractinian coral, *Siderastrea radians*, previously unstudied by the scientific community (Lazar 2008). This species, however, is common in Florida, the Bahamas, and the Caribbean (Amos & Amos 1997, Bak & Meesters 1999, Humann & Deloach 2002), often inhabiting flat or rocky substrates, shallow reefs, and back reefs (Humann and Deloach 2002). Like most corals, *S. radians* has an intimate symbiotic relationship with a type of zooxanthellae, *Symbiodinium* type B5a. This type is known to tolerate temperatures up to 36 ^{o}C (Warner et al. 1999) and predominate in very shallow waters where irradiance is high. *Siderastrea radians* generally are a stress tolerant species (see Lirman et al. 2002, Lirman et al. 2003).

In the SMK, *Siderastrea radians*, is found primarily in relatively shallow (< 3 m) waters. In this region, a long-term monitoring program (Project COAST) has documented conditions in five coastal systems since 1997 (see Jacoby et al. 2008). The Homosassa River system, which is nearest the SMK, has been exhibiting changes that indicate the potential for detrimental eutrophication, including increased nutrient concentrations, increased periphyton loads and loss of submerged aquatic vegetation (Frazer et al. 2006a, 2006b). Such effects point to reduced light availability as a key concern in this region. Thus, an improved understanding of how *S. radians* colonies in the SMK respond to shading will assist local managers in making sustainable

decisions regarding nutrient loadings and provide insights that are likely to be applicable to other scleractinian corals.

A large number of shading studies have been conducted on vegetated habitats, including seagrass meadows (see Fitzpatrick & Kirkman 1995, Ruiz & Romero 2001, Brun et al. 2003, Fokeera-Wahedally & Bhikajee 2005) and kelp forests (Kennelly 1989). Fewer shading studies have been conducted on corals (but see Rogers 1979, Lirman et al. 2003), and of those, most were long term (i.e., 30 days or longer). In general, shading studies have shown that concentrations of chlorophyll *a* and other photosynthetic pigments within zooxanthellae, and other algal species, increase under low light intensity and decrease under high light intensity (Kirk 1994, Hoegh-Guldberg 1999). In this study, I experimentally manipulated the light environment of *Siderastrea radians* colonies in the shallow, coastal waters adjacent to the Homosassa River by installing shading screens for a period of 10 days. Though eutrophication is typically a longer, more gradual process, algal blooms are a common result (Duarte 1995). These algal blooms often last for weeks, significantly reducing available light penetrating to the bottom. Artificially shading *S. radians* for a short time should aid our understanding of how such algal blooms affect these corals, whose symbionts rely on light for photosynthesis. Although artificial shading is not equivalent to extreme turbidity or blooms of phytoplankton or macroalgae, any of these influences can lower light intensity below the relevant light compensation point and elicit similar responses in corals (Rowan 1998). Altering the amount of light penetrating to *S. radians* in the SMK can provide insights into how zooxanthellae react or adapt to reduced light in eutrophic environments. This research will augment our understanding of the effects of eutrophication and facilitate improved management and conservation of corals in eutrophic waters.

The objectives of this shading study were to quantify zooxanthellae densities, chlorophyll *a* concentrations per unit surface area, and concentrations of chlorophyll *a* per zooxanthellae in *Siderastrea radians* from the SMK before and after shading. The results will indicate if and how *S. radians* responds to reduced irradiance over a relatively short amount of time (10 days).

CHAPTER 2
MATERIALS AND METHODS

Study Site

The study was conducted in the waters surrounding the St. Martins Keys (SMK; 28^{o} 45.5' N, 82^{o} 37.1' W), located along the north-central Gulf coast adjacent to Citrus County, Florida. These islands are contained within the St. Martins Marsh Aquatic Preserve and the Chassahowitzka National Wildlife Refuge. The benthic habitat in the study area comprises a varying mixture of patchy, locally dense *Thalassia testudinum, Syringodium filiforme,* and *Halodule wrightii* on a limestone bed (Greenawalt-Boswell et al. 2007). *Penicillis* spp., *Halimeda* spp., and *Acetabularia* spp. are common macroalgae in the area (Mitchem, pers. obs.). The coral assemblage at SMK comprises a nearly monospecific assemblage of *Siderastrea radians*, with a few colonies of *S. siderea*. Corals are found in mean densities of 7 colonies m^{-2}, with maximum densities of 86 colonies m^{-2} (Lazar 2008).

The study area borders an extensive salt-marsh complex associated with the Homosassa River, a spring-fed, coastal stream approximately 14.5 km in length (Frazer et al. 2006a, 2006b) that discharges into the Gulf of Mexico. At two fixed sites that are monitored monthly in the immediate vicinity of the study site (see Jacoby et al. 2008), water clarity in an 8-year time period was generally good, allowing, on average, 40% of incident light to penetrate to the bottom (mean depth = 0.88 m, mean light extinction coefficient (K_d PAR) = 1.05 m^{-1}, mean Secchi depth = 0.87 m). Water temperatures ranged from 9.6 ^{o}C to 33.3 ^{o}C, with a mean of 23.1 ^{o}C, and salinities ranged from 11.95‰ to 36.39‰, with a mean of 25.06‰. The shallow coastal waters in the area are well-flushed as a consequence of a semi-diurnal tidal range of ca. 1 m (Glancy et al. 2003), driving, in large part, observed variations in salinity.

Field Work

Eight 2.25-m^2 plots were established in a qualitatively homogenous section of the study area. At each plot, 1.5-m x 1.5-m shading screens of dark gray fiberglass (Phifer Wire Products, Inc., Tuscaloosa, AL, USA) were set at 60 cm above the limestone bottom following methods reported by Calleja et al. (2006). Shade treatments targeted 0%, 25%, 50%, 75%, and 100% light reduction, with 0%, 50%, and 100% treatments duplicated, yielding a total of eight study plots. Shading plots were designed to cover at least 30 corals that were not within 0.25 m of the plot's border. Shades remained in place for 10 days, beginning 18 June 2008. Weather permitting, water temperatures, salinities, water depths, dissolved oxygen concentrations, pH values, and light attenuation coefficients were measured every day at noon (± 1 hour). In addition, screens were examined and fouling organisms that might affect the light field were removed.

Actual light attenuation under the screens was assessed by measuring photosynthetically active radiation (PAR, 400-700 nm) at the bottom using a LI-COR sensor (model LI-192SA) and comparing this measurement with similar measures obtained with the sensor positioned above the substrate in five different positions along a transect under each screen (outer left, inner left, center, inner right, and outer right; Figure 2-1). The outer positions were approximately 0.5 m from the center, and the inner positions were 0.25 m from the center. All measurements were taken at noon on clear days under calm conditions.

On the 11th day (28 June 2008), 30 corals within each shading regime were harvested with a hammer and chisel. Whenever possible, only corals more than 0.25 m from the edges of the shades were collected. Harvested corals were immediately wrapped in tin foil and double-bagged in Ziploc™ freezer bags (Broadbent et al. 2002). These bags were placed in a styrofoam cooler with dry ice to freeze the corals as quickly as possible. Once a cooler was filled, its lid was sealed with duct tape. Additionally, on the day the plots were assembled, 30 corals were taken

from the surrounding waters to serve as a baseline for the condition of all corals at the start of the experiment. These corals, labeled ambient corals, were harvested and frozen in the same way as the shaded corals. In total, 270 corals were harvested.

Sample Processing

Tissue was removed from the coral skeletons using the Waterpik™ method (see Johannes & Wiebe 1970; Falkwoski & Dubinsky 1981; Broadbent et al. 2002; Edmunds & Gates 2002). Filtered seawater was used to prevent cytolysis of zooxanthellae (Johannes & Wiebe 1970). The seawater and tissue mixture was collected in a beaker and sieved, sequentially, through 40-µm and 20-µm mesh sieves to remove debris and mucus. Three separate 2-ml samples were taken from the mixture and preserved in Lugol's for enumeration of zooxanthellae. The remaining solution was vacuum filtered onto Whatman GF/F glass filters (nominal pore size = 0.7 µm) for determination of chlorophyll *a*. The diameter and height of each coral skeleton also was measured.

Chlorophyll samples were extracted in 90% ethanol for 24–72 hours. Extracted samples were centrifuged, and chlorophyll *a* was measured using a spectrophotometeric technique, with acidification and correction for phaeophytin (Sartory & Grobbelaar 1984).

Zooxanthellae densities were estimated by pouring each 2-ml sample into a settling chamber and allowing the algal cells to settle for at least four hours. Samples in the settling chambers were examined with the aid of an inverted microscope at 400x magnification. Zooxanthellae were counted using a 250 x 250 µm grid, with each square in the grid measuring 25 x 25 µm. At least 100 cells were counted per sample, for a total of at least 300 cells per coral colony. A conversion factor (CF) was obtained using Equation 2-1.

$$CF = \frac{283.385}{0.0625(\text{Number of grids counted})(\#\text{ ml settled})} \qquad (2\text{-}1)$$

The CF obtained in Equation 2-1 was multiplied by the total number of cells counted per sample to calculate the number of zooxanthellae per ml. This value was multiplied by the total volume of the coral tissue and seawater mixture to obtain the total number of zooxanthellae per colony.

Formulae for converting diameters and heights of corals to surface areas and numbers of polyps were created using the tin foil method (see Marsh 1970; Fagoonee et al. 1999; Edmunds & Gates 2002). The tin foil method required weighing 10 replicate squares for each of five surface areas (i.e., 1 cm^2, 4 cm^2, 16 cm^2, 36 cm^2, and 64 cm^2). A least-squares linear regression was fit to the data, including the origin, to obtain a weight to surface area relationship. Next, tin foil was wrapped around a sub-sample of 88 corals, with as little wrinkling as possible, and cut around the bottom of the colony. These pieces of tin foil were weighed, and the surface areas of the colonies were estimated using the regression equation created above. A least-squares linear regression of the square roots of the estimated surface areas versus the square roots of the products of the appropriate heights and radii was forced through the origin to yield an equation for converting heights and/or diameters to surface areas. Polyps were counted on the 88 corals, and a least-squares linear regression of number of polyps versus estimated surface area was forced through the origin to provide an equation for converting surface area to number of polyps.

Data Analysis

The relative amount of shading and its consistency under the shades was tested by converting irradiance measurements obtained during the experiment to proportion of the light available at the bottom. Data were balanced by randomly selecting one of the two duplicate values for the 0%, 50% and 100% treatments. The resulting data were arcsin transformed. A Ryan-Joiner test for normality, a Cochran's test for homoscedasticity and a nested analysis of variance (ANOVA) were conducted on the transformed data. The ANOVA had levels of shading

as a fixed factor and position under the shade as a nested factor. A Tukey's test was conducted to determine differences among levels within a significant factor. Type I error rates for the ANOVA and Tukey's test were chosen according to the results of Ryan-Joiner and Cochran's tests. Means and 95% confidence limits were calculated, back-transformed and plotted.

Chlorophyll and zooxanthellae data were transformed into µg chl *a* cm^{-2} (or µg chl *a* $polyp^{-1}$) and cells cm^{-2} (or cells $polyp^{-1}$), respectively. These standardized measures allow physiological data to be compared among corals of different types, shapes and sizes (Edmunds & Gates 2002).

For all analyses, zooxanthellae densities, chlorophyll *a* concentrations cm^{-2}, and concentrations of chlorophyll *a* $zooxanthellae^{-1}$ were tested for normality using a Ryan-Joiner test and tested for homoscedasticity using Cochran's test. The data were transformed if necessary. A nested ANOVA was conducted using the data from the replicated 0%, 50% and 100% treatments, with plots nested within the fixed factor treatments. Based on the results from this analysis, data were either pooled (no significant variation between replicate plots) or balanced by randomly selecting one replicate for inclusion in a one-way ANOVA with treatment as a fixed factor, with five levels. Tukey's tests were conducted to detect differences among levels in significant factors. Type I error rates for the ANOVAs and Tukey's tests were chosen according to the results of Ryan-Joiner and Cochran's tests. Means and 95% confidence intervals were calculated, back-transformed and plotted.

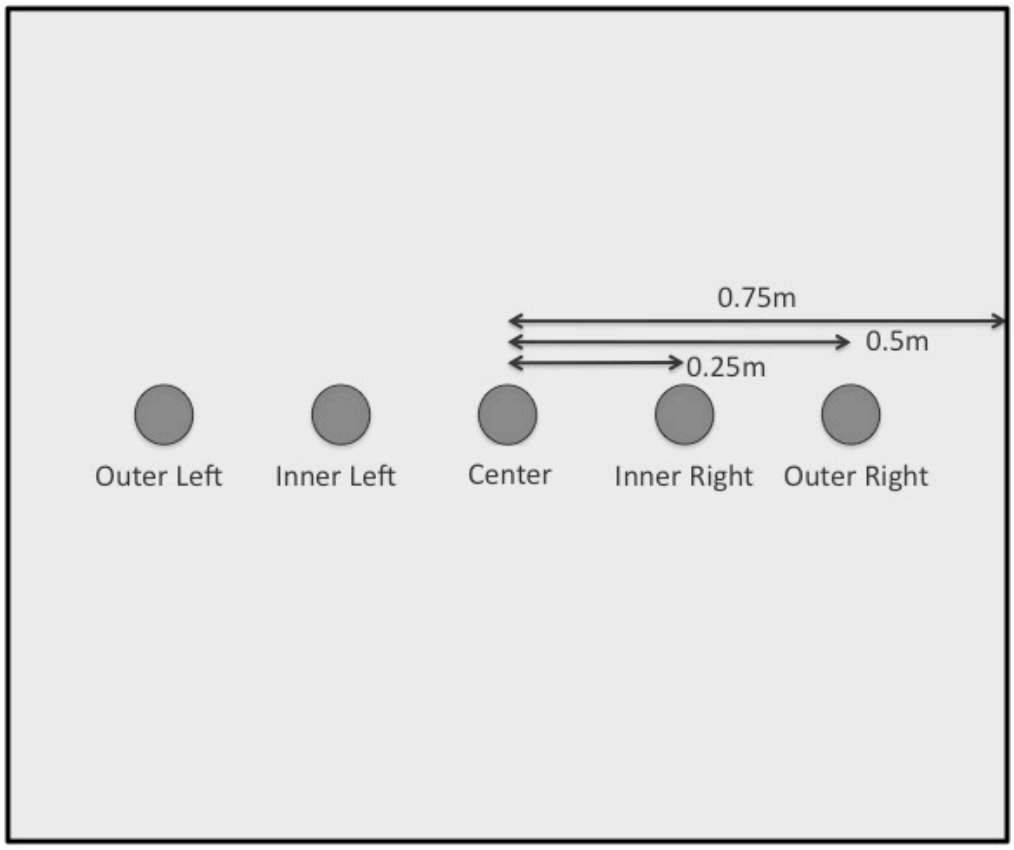

Figure 2-3. Locations under each shading treatment (1.5 x 1.5-m plots) where light was measured.

CHAPTER 3
RESULTS

General Site Characteristics

The weather during the experiment varied (Table 3-1). On 5 days, the weather at the site was sunny to partly sunny and calm. On the other 5 days, however, the area experienced heavier cloud cover, severe thunderstorms and rain. On three days, rain fell at nearby locations but not at the study site, and on two days, rain was not recorded in the area.

In contrast to rainfall, conditions in the nearshore waters were relatively constant throughout the experiment. Means ± standard deviations (SD) for water temperatures and salinities were 28.99 ± 0.76 ^{o}C and 30.92 ± 1.05‰, respectively. Mean water depth at the study site during the experiment was 1.66 ± 0.31 m, with bottom Secchi measurements on all days. Mean dissolved oxygen concentration was 4.77 ± 1.00 mgL^{-1}, and mean pH was 7.88 ± 0.12 during the experiment. The mean light attenuation coefficient (K_d PAR) measured on five days during the experiment was 0.512 ± 0.130 m^{-1}, which indicated that approximately 43% of incident light penetrated to the bottom.

Confirming Light Reduction Treatments

Arcsin transformed proportions of light penetrating under the shades were found to be non-normal ($p < 0.01$) and homoscedastic ($p > 0.05$), suggesting that significant results should be interpreted cautiously. A nested ANOVA indicated that there were significant differences in light levels under different shading treatments ($F = 315.15$, $df = 3, 8$, $p < 0.001$; Table 3-2), but not among the outer, inner, and center measurement points under each treatment ($F = 0.33$, $df = 8, 78$, $p = 0.950$; Table 3-2). A Tukey's test (Type I error rate = 0.001; Figure 3-1) indicated that significantly less light penetrated under the 100% and 75% treatment than under the 50% and

25% treatments, which were not significantly different. Overall, mean proportions were within 5–17% of their relative target values.

Light reductions under the various shading treatments also were compared with monthly light data from two Project COAST stations (see Jacoby et al. 2008) near the experimental area (Homosassa Stations 6 and 7). Irradiance (μE m^{-2} s^{-1}) under all treatments was less than the mean irradiance in June or any other month of the year, as calculated with data from eight years (1999-2007; Figure 3-2). Light reaching corals in the 0% shade treatment was similar to the mean light reaching the bottom during the months of June in the eight years.

The mean diameter (± SD) of *Siderastrea radians* colonies was 38.6 ± 13.8 mm, and the mean height was 22.8 ± 8.8 mm. The smallest diameter measured was 14.6 mm, and the largest was 80.4 mm. The smallest height measured was 4.8 mm, and the largest was 49.7 mm.

The linear regression of foil surface areas to weights was significant ($r^2 = 0.99$, $n = 50$, $p < 0.001$; Figure 3-3). The weight of tin foil (mg) was related to surface area (cm^2) by Equation 3-1.

$$\text{Surface area} = 230.6\ (\text{Weight of foil}) \quad (3\text{-}1)$$

The weights of pieces of foil wrapped around 88 *Siderastrea radians* colonies were regressed against their expected surface area, obtained using Equation 3-1. The surface areas of *S. radians* colonies were similar to those of hemispheres, and a significant linear regression of square roots of estimated surface areas versus square roots of the products of the appropriate heights and radii ($r^2 = 0.84$, $n = 88$, $p < 0.001$; Figure 3-4) was converted to Equation 3-2 for calculating surface area (cm^2) from height (cm) and diameter (cm).

$$\text{Surface area} = 6.2071(\text{Height} \times 0.5\text{Diameter}) \quad (3\text{-}2)$$

A significant linear regression ($r^2 = 0.92$, $n = 88$, $p < 0.001$; Figure 3-5) related estimated number of polyps per colony to surface area (cm^2) according to Equation 3-3.

Number of polyps = 7.212(Surface area) (3-3)

Changes in Zooxanthellae Densities

Counts of zooxanthellae cm^{-2} were tested for normality and homoscedasticity using a Ryan-Joiner test and Cochran's test, respectively. The results from these tests indicated that the data were non-normal and had unequal variances. To correct for this, zooxanthellae cells cm^{-2} were log_{10}-transformed. After transformation, a Ryan-Joiner test for normality and a Cochran's test for homoscedasticity indicated that data remained non-normal ($p < 0.01$) and variances remained unequal ($p < 0.01$), which suggests cautious interpretation of significant results. A nested ANOVA indicated significant differences between duplicate plots ($F = 7.17$, $df = 3, 173$, $p < 0.001$; Table 3-3), but not among treatments ($F = 0.93$, $df = 2, 3$, $p = 0.484$; Table 3-3).

Given these results, counts of zooxanthellae cm^{-2} were balanced by randomly selecting 30 corals from the duplicate 0%, 50%, and 100% light reduction treatments. The log_{10}-transformed data were non-normal ($p < 0.01$) and variances were unequal ($p < 0.01$), so results of the ANOVA were interpreted cautiously. A one-way ANOVA indicated significant differences among shading treatments ($F=13.84$, $df = 5, 263$, $p < 0.001$; Table 3-4; Figure 3-6). Results of an ANOVA using zooxanthellae cells $polyp^{-1}$ were the same because the ANOVA is not affected by linear scaling. A Tukey's test (Type I error rate = 0.001) indicated that fewer zooxanthellae cm^{-2} were found in corals from the 25% light reduction treatment (Figure 3-6).

Changes in Chlorophyll *a* Concentrations

Due to a malfunctioning spectrophotometer, chlorophyll *a* samples from one plot of the 0% shading treatments and all of the 25% and 100% shading treatments were lost. Therefore, no nested ANOVAs were performed on chlorophyll data per unit surface area, per polyp, or per zooxanthellae. Log_{10}-transformed chlorophyll *a* concentrations were normal ($p > 0.10$) and homoscedastic ($p > 0.05$). A one-way ANOVA indicated that concentrations of chlorophyll *a*

cm^{-2} differed significantly among shading treatments ($F = 6.44$, $df = 3, 146$, $p < 0.001$; Table 3-5; Figure 3-7). Results of an ANOVA using concentrations of chlorophyll *a* $polyp^{-1}$ were the same since the ANOVA is not affected by linear scaling. A Tukey's test (Type I error rate = 0.05) indicated that ambient *Siderastrea radians* colonies, i.e., those collected at the start of the experiment, had less chlorophyll *a* per unit area or polyp than those from all other treatments, which were not significantly different.

Changes in Chlorophyll *a* Per Zooxanthellae

Chlorophyll concentrations expressed as $\log_{10}$-transformed pg chl *a* $zooxanthellae^{-1}$ were normal ($p > 0.10$) and homoscedastic ($p > 0.05$). A one-way ANOVA indicated that concentrations of chlorophyll *a* $zooxanthellae^{-1}$ were significantly different among shading treatments ($F = 23.64$, $df = 3, 146$, $p < 0.001$; Table 3-6). A Tukey's test (Type I error rate = 0.05) indicated that colonies from the 0% treatment yielded the least concentrations of chlorophyll *a* $zooxanthellae^{-1}$, with ambient colonies yielding intermediate concentrations, and 50 % and 75 % shading treatments yielding the highest concentrations, which were not significantly different (Figure 3-8). Mean chlorophyll *a* concentrations $zooxanthellae^{-1}$ increased by 58.6% between corals from the 0% and 50% treatments, but there was an increase of only 3.6% between corals from the 50% and 75% treatments.

Table 3-1. Weather during the experiment.

Day	Date	Site Weather 28° 45'30" N 82° 37'6" W	Daily Rainfall (mm) Ozello Station #1160 28° 51'12" N 82° 35'45" W	Daily Rainfall (mm) Chassahowitzka Station #6113 28° 43'18" N 82° 33'5" W
1	18 June 2008	Stormy 100% cloud cover	1.016	6.858
2	19 June 2008	Sunny 75% cloud cover	2.032	2.794
3	20 June 2008	Sunny 0% cloud cover	0.000	0.000
4	21 June 2008	Stormy 100% cloud cover	11.176	4.318
5	22 June 2008	Stormy 100% cloud cover	10.922	6.858
6	23 June 2008	Stormy 100% cloud cover	1.524	0.254
7	24 June 2008	Sunny 75% cloud cover	0.000	0.000
8	25 June 2008	Sunny 0% cloud cover	6.096	8.382
9	26 June 2008	Sunny 55% cloud cover	0.254	8.890
10	27 June 2008	Stormy 100% cloud cover	0.254	0.254

Rainfall data obtained from the Southwest Florida Water Management District (http://bkvscadasrv03.swfwmd.state.fl.us/public/)

Table 3-2. Nested ANOVA testing for differences in proportion of light at the bottom for various locations under shading treatments.

Source	DF	SS	MS	*F*	p
Treatment	3	3.84548	1.28183	315.15	<0.001
Location (Treatment)	8	0.03030	0.00379	0.33	0.950
Error	78	0.88490	0.01134		

Light data were arcsin(√proportion) transformed.

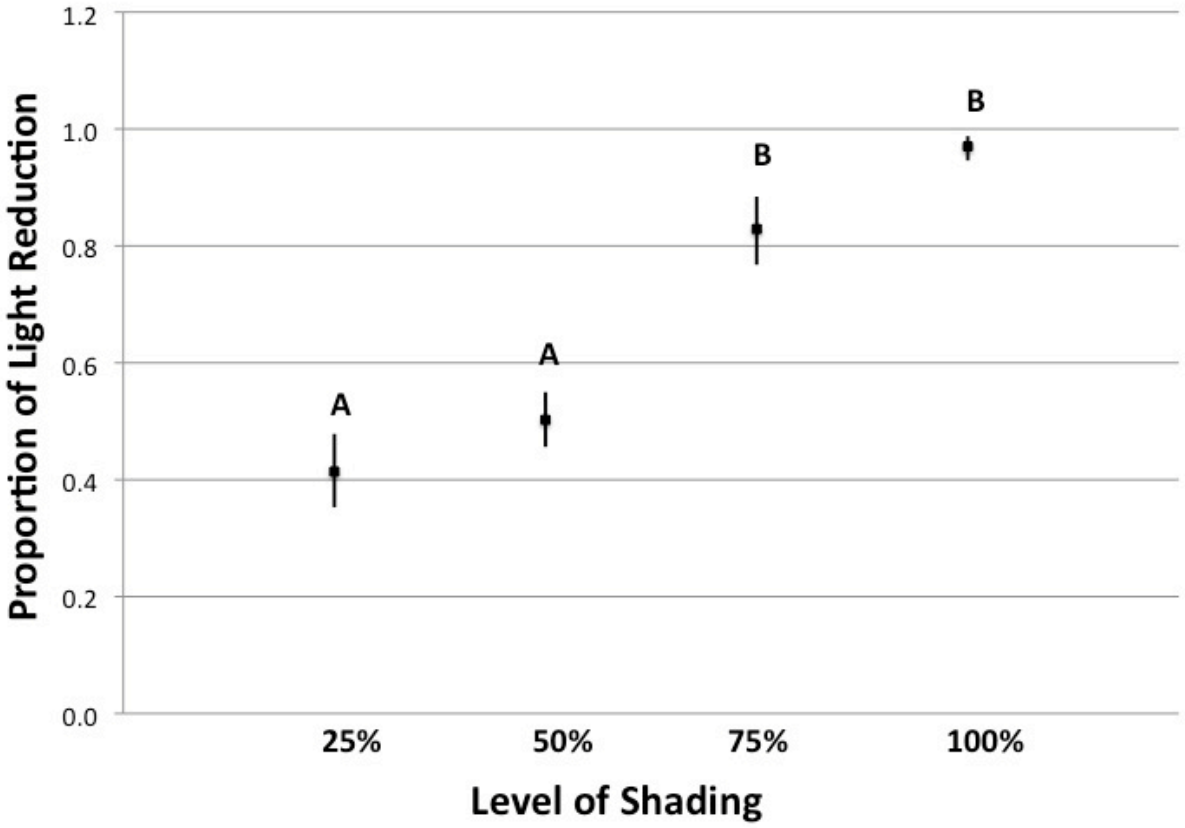

Figure 3-1. Back-transformed mean proportions of light penetrating under shading treatments with 95% confidence limits. Different letters indicate significantly different means according to a Tukey's test.

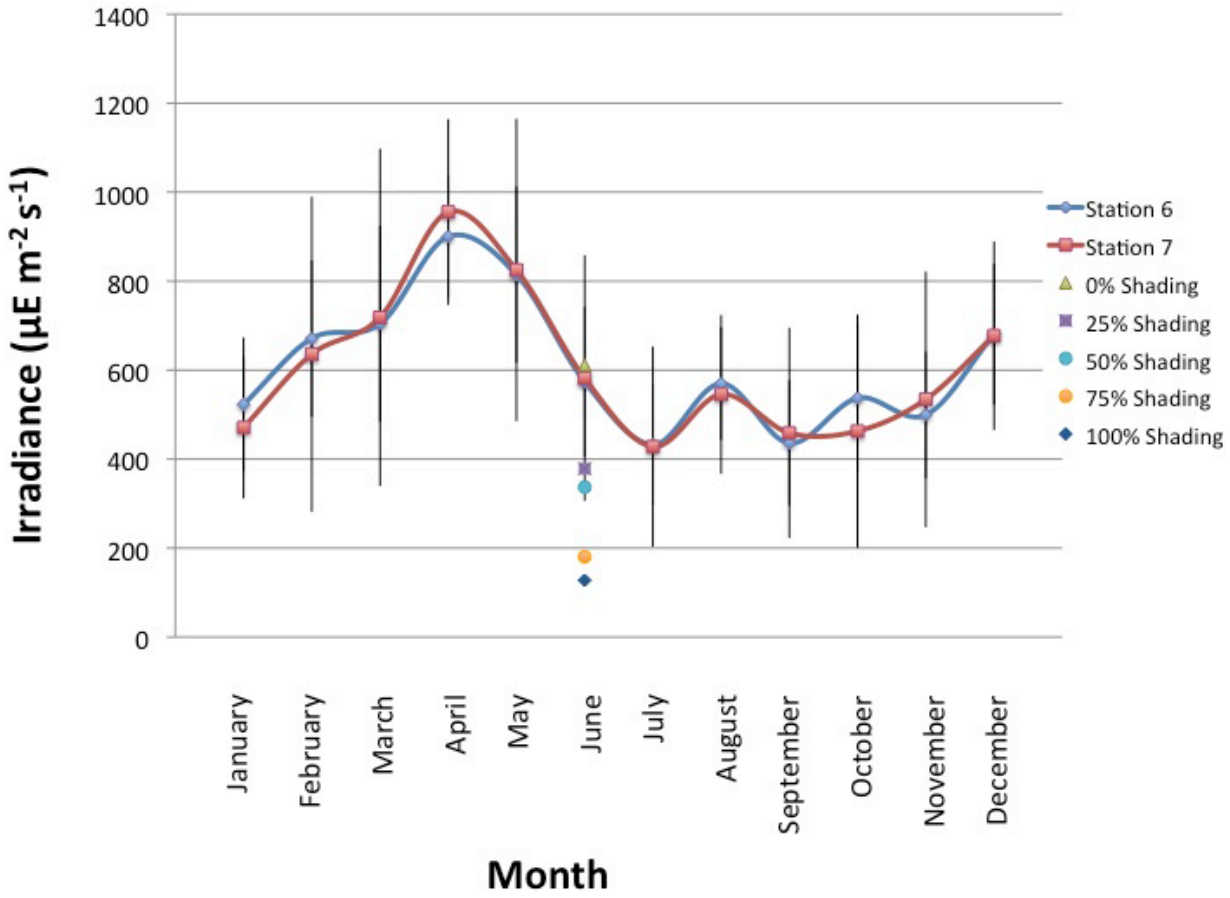

Figure 3-2. Mean irradiances measured at the bottom at two stations for Project COAST (Stations 6 and 7) and in all treatments during the experiment.

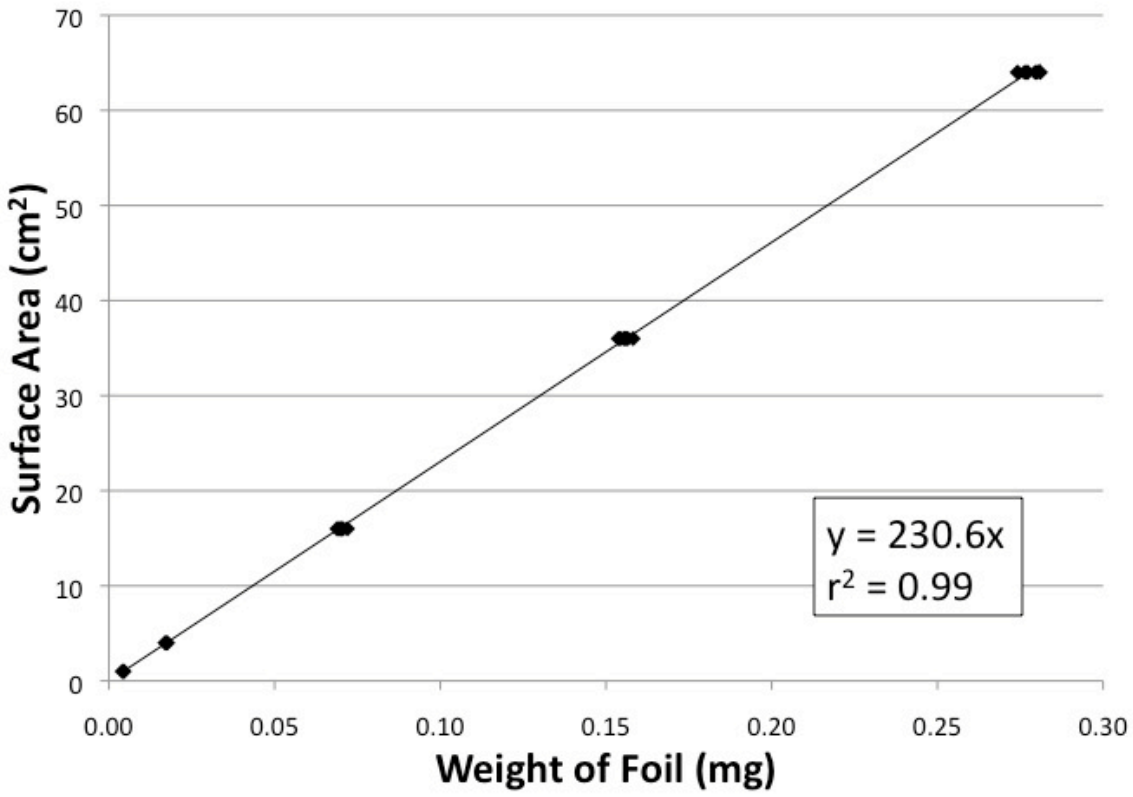

Figure 3-3. Linear regression of surface area (cm^2) vs. weight of tin foil (mg) for 5 standard surface areas (1cm^2, 4 cm^2, 16 cm^2, 36 cm^2,and 64 cm^2). Y = Surface area (cm^2); X = Weight of foil (mg)

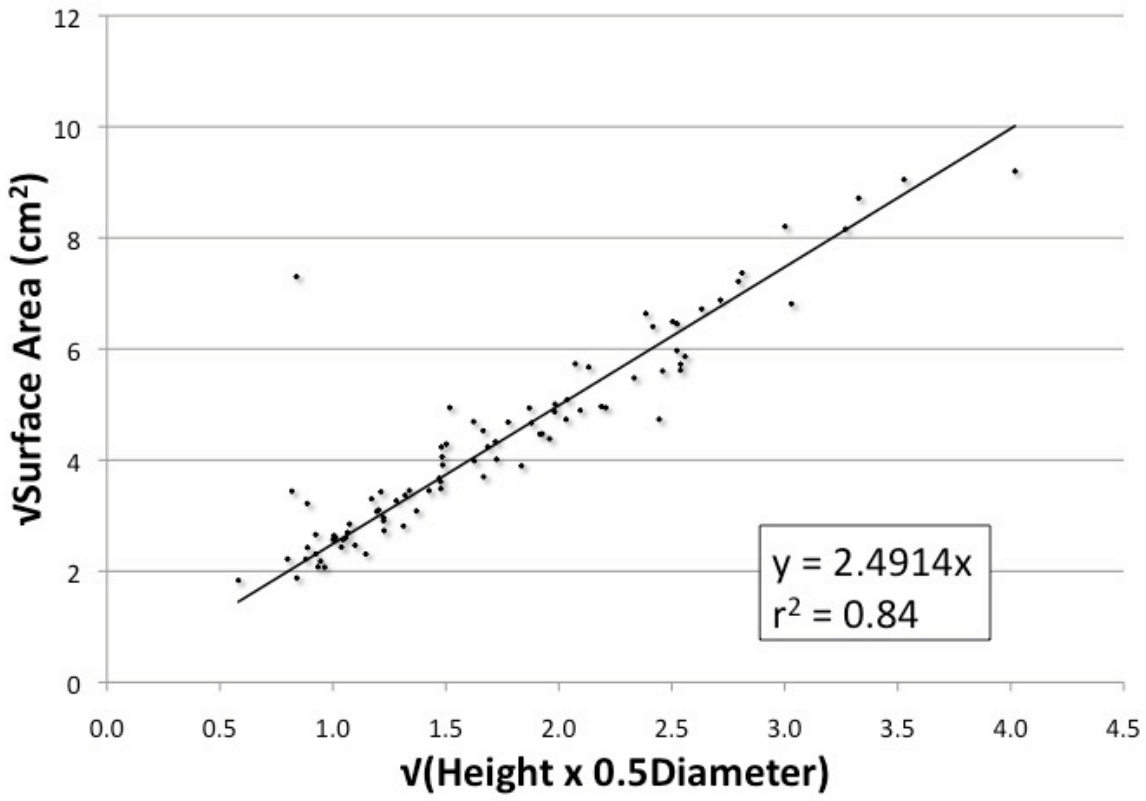

Figure 3-4. Linear regression of *Siderastrea radians* √(Surface area (cm^2) vs. √[Height(cm) x 0.5Diameter(cm)]. Y = √(Surface area (cm^2); X = √[Height(cm) x 0.5Diameter(cm)]

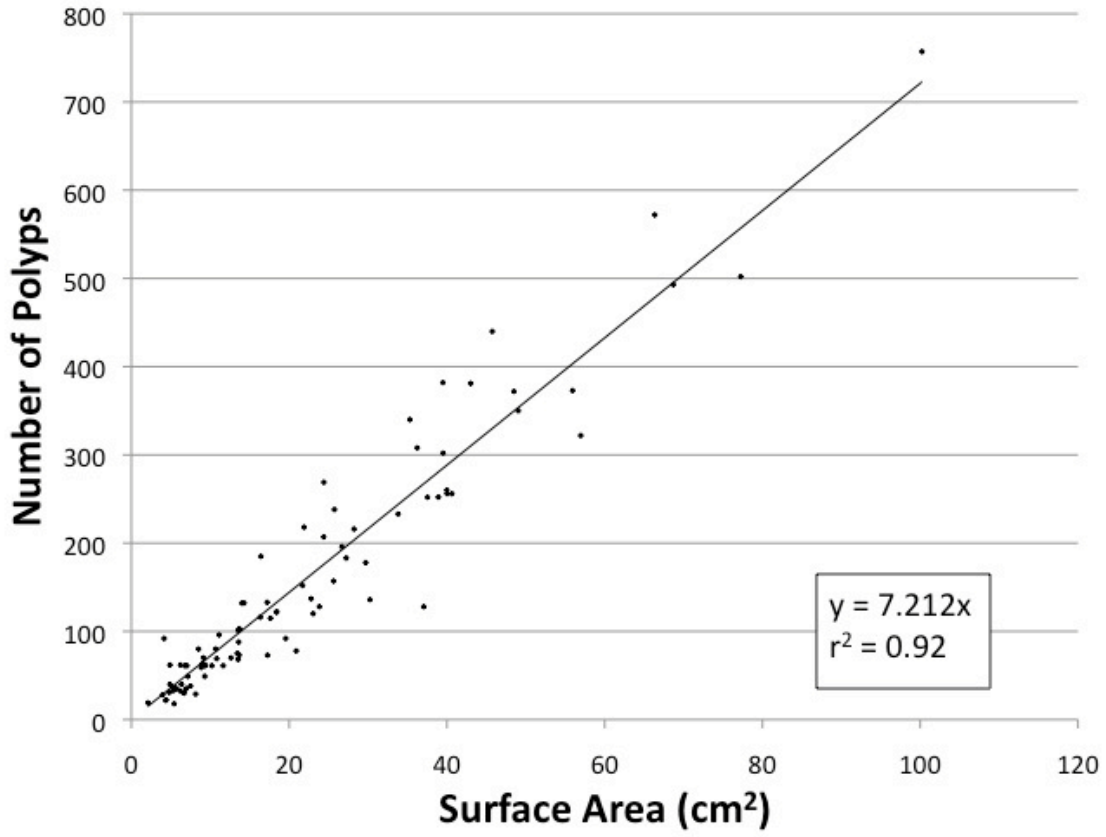

Figure 3-5. Linear regression of number of polyps vs. *Siderastrea radians* estimated surface area (cm^2). Y = Number of polyps; X = Surface area (cm^2)

Table 3-3. Nested ANOVA testing for differences in zooxanthellae densities among *Siderastrea radians* colonies from shading treatments.

Source	DF	SS	MS	*F*	p
Treatment	2	0.74964	0.37482	0.93	0.484
Plot (Treatment)	3	1.20600	0.40200	7.17	<0.001
Error	173	9.70575	0.05610		

Cells cm^{-2} were log_{10}-transformed.

Table 3-4. One-way ANOVA testing for differences in zooxanthellae densities among *Siderastrea radians* colonies from shading treatments.

Source	DF	SS	MS	*F*	p
Treatment	5	4.9976	0.9995	15.73	<0.001
Error	263	16.7143	0.0636		

Cells cm^{-2} were log_{10}-transformed.

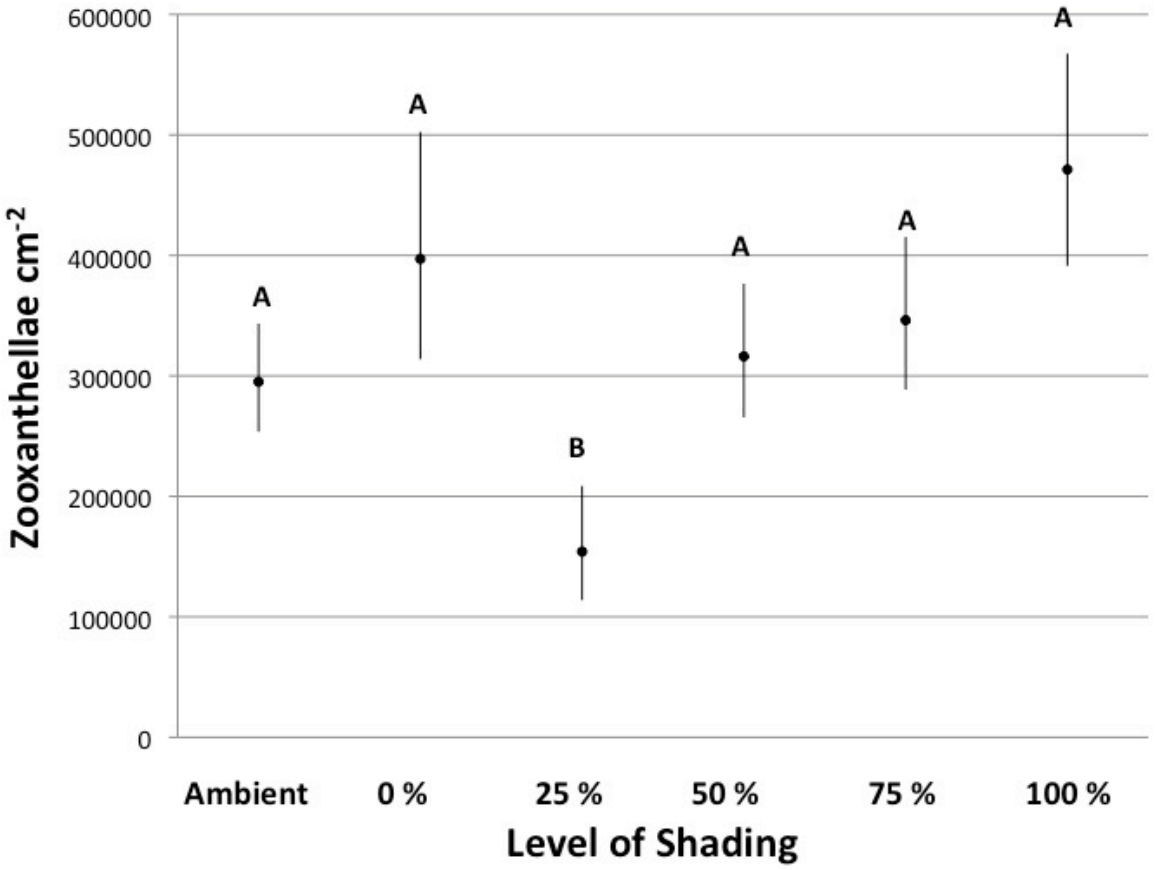

Figure 3-6. Back-transformed mean densities of zooxanthellae (cells cm^{-2}) with 95% confidence intervals for *Siderastrea radians* colonies from different shading treatments. Different letters indicate significantly different means according to a Tukey's test.

Table 3-5. One-way ANOVA testing for differences in chlorophyll *a* concentrations among *Siderastrea radians* colonies from shading treatments.

Source	DF	SS	MS	*F*	p
Treatment	3	0.7201	0.2400	6.44	<0.001
Error	146	5.4434	0.0373		

Concentrations (µg chlorophyll *a* cm^{-2}) were log_{10}-transformed.

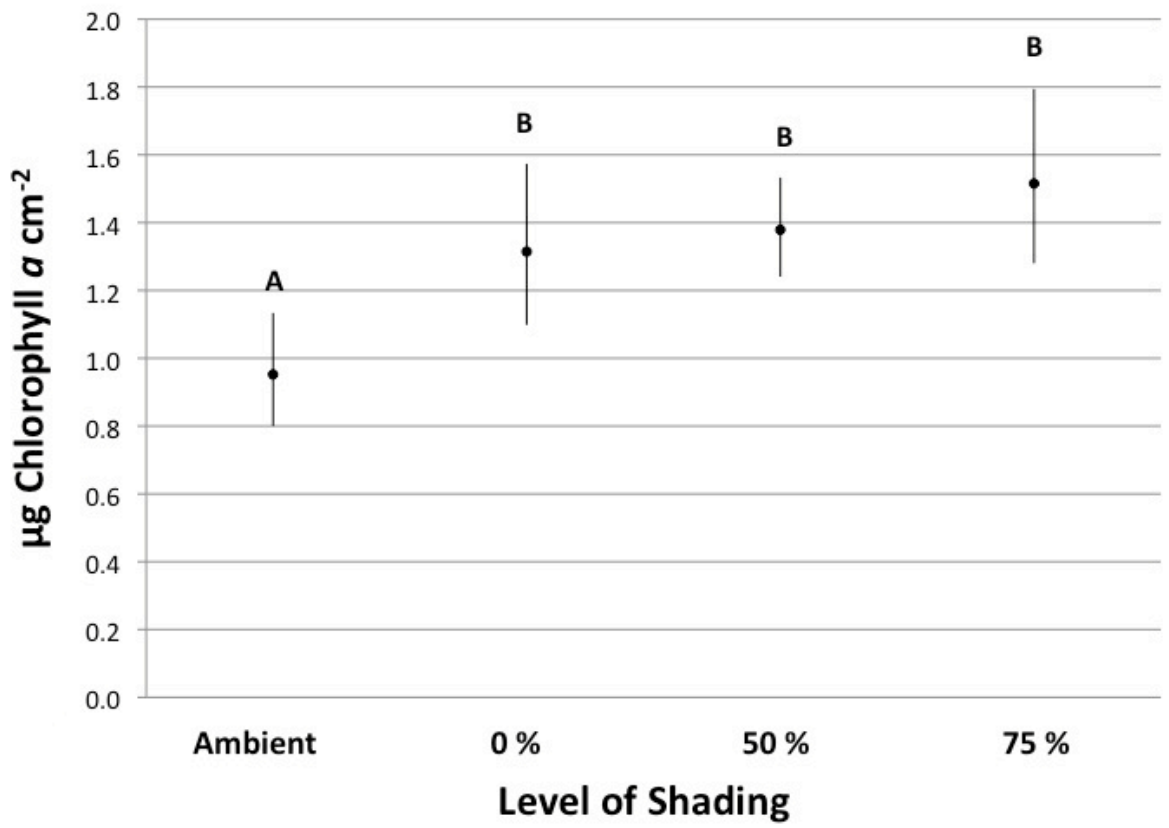

Figure 3-7. Back-transformed mean concentrations of chlorophyll *a* (µg cm^{-2}) with 95% confidence intervals for *Siderastrea radians* colonies from different shading treatments. Different letters indicate significantly different means according to a Tukey's test.

Table 3-6. One-way ANOVA testing for differences in chlorophyll *a* concentrations within zooxanthellae from shaded *Siderastrea radians* colonies.

Source	DF	SS	MS	*F*	p
Treatment	3	1.0746	0.3582	23.63	<0.001
Error	146	2.2136	0.0152		

Concentrations (pg chlorophyll *a* zooxanthellae^{-1}) were $\log_{10}$-transformed.

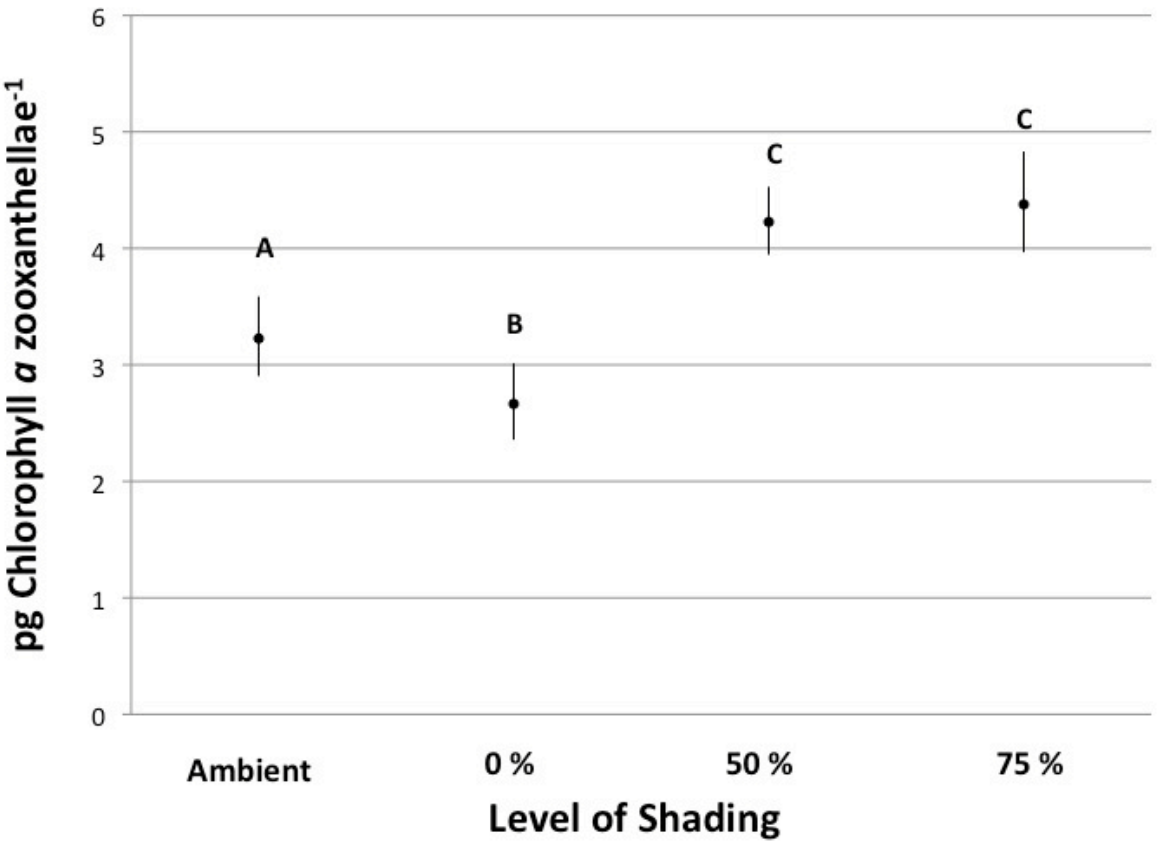

Figure 3-8. Back-transformed mean concentrations of chlorophyll *a* (pg zooxanthellae^{-1}) with 95% confidence intervals for *Siderastrea radians* colonies from different shading treatments. Different letters indicate significantly different means according to a Tukey's test.

CHAPTER 4
DISCUSSION

Light Reduction Treatments

ANOVA results indicated that light reduction treatments performed in the expected rank order (25% < 50% < 75% < 100%). Actual light reduction under shading treatments, however, differed from the target values. The 25% shading treatment was closer to 40% light reduction, making this treatment statistically equal to the light reduction in the 50% shading treatments, which achieved an actual mean of 50% light reduction. The 75% shading treatment reduced the available light by 83% on average. Therefore, the 75% light reduction treatment was statistically equal to the 100% light reduction treatment, which reduced light penetrating under the screen by 97%. Results also indicate that light was reduced consistently underneath each shading treatment, so corals harvested closer to the edge of the plots experienced the same light regime as corals harvested from the center of each plot.

Irradiance ($\mu E\ m^{-2}\ s^{-1}$) penetrating under all shading treatments was less than the mean irradiance penetrating to the bottom in any month for eight years (1999-2007). On sunny days, light reaching corals in the 0% shading treatment was similar to light reaching the bottom during June for the same eight years. It is unclear how event-driven light reduction, such as the storms during the experiment, affected the irradiance penetrating to the bottom.

Surface Area and Polyps

Results of a regression using height and diameter of *Siderastrea radians* colonies suggest these parameters can be used to predict the surface area of colonies with high accuracy. The results of the linear regression indicated that *S. radians* surface area was an accurate predictor of the number of polyps $colony^{-1}$. Surface area estimations suggest that *S. radians* in the SMK are roughly hemispherical. Thus, by simply measuring the diameter of these colonies, surface areas,

numbers of polyps per colony and heights (see Lazar 2008) can be estimated. These results could allow researchers to estimate a variety of parameters from diameters measured in the field without having to harvest colonies. Additionally, linear scaling meant that analyzing data expressed in terms of surface area was equivalent to analyzing data expressed in terms of polyps.

Changes in Zooxanthellae Densities

Results suggest that zooxanthellae densities vary spatially, i.e. between plots within treatments. Therefore, data from replicate treatments were not pooled. The results of a balanced ANOVA indicate that increased shading did not yield consistent changes in densities of zooxanthellae. Only colonies from the 25% treatment had significantly lower densities. This result could be due to experimental factors, such as the 25% treatment being closer to 40% shading than 25% (Figure 3-1) or a variety of untested natural factors.

One *post hoc* hypothesis was that *S. radians* in 25% light reduction treatments were consistently smaller or larger than colonies in other treatments. Cumulative size frequency distributions based on diameters of corals from each shading treatment were similar, except ambient corals were larger (Figure 4-1). Thus, size was not likely to be a cause of the differences in the corals from the 25% shading treatment.

The lack of change in zooxanthellae densities among shaded *Siderastrea radians* from SMK is not unexpected. In one study, Falkowski and Dubinsky (1981) collected *Stylophora pistillata* from the Gulf of Eilat and transplanted colonies from high to low light environments. *Stylophora pistillata* zooxanthellae densities did not change with exposure to reduced light conditions. Producing more cells is thought to be more energy intensive than increasing the amount of photosynthetic pigments per cell. In fact, it is common for unicellular algae to increase the concentration of their photosynthetic pigments under reduced light conditions rather than investing energy in cell division (Kirk 1994).

Zooxanthellae densities in *Siderastrea radians* from the SMK were lower than reported for other coral species (Table 4-1). It has been suggested, however, that there is considerable variation in density within a coral colony throughout the year (0.5×10^6 to 5×10^6 cm^{-2}), with fluctuations over three orders of magnitude among coral colonies (Fagoonee et al. 1999). For example, Fagoonee et al. (1999) also found that zooxanthellae densities in *Acropora formosa* were lower in the spring and summer months, possibly due to the high levels of irradiance in the summer and spring, compared to the lower light levels in fall and winter. Although at the SMK, there is less light penetration in the summers, the days are longer. Corals may be responding to a longer duration of light in the summer, rather than increased light intensity. Therefore, *S. radians* taken from the SMK in June may be expected to have lower zooxanthellae densities than colonies collected in the winter. Additionally, there is evidence of a regulatory mechanism governing zooxanthellae densities, because zooxanthellae densities have been shown to depend on densities measured in the previous week (Fagoonee et al. 1999). This relationship suggests that the zooxanthellae may take longer than a week to adjust their numbers in response to environmental variations and stressors.

Further research, in the form of long-term monitoring and shading studies, would help clarify the questions related to lowered zooxanthellae densities in *Siderastrea radians* from SMK. Two types of studies should be conducted. First, a long-term monitoring of *S. radians* in the SMK could elucidate natural cycles in zooxanthellae densities over months, seasons, and even years to determine if densities vary through time. The second study, a long-term shading project, could further investigate if the non-significant difference in densities between the 0% and 100% shading treatments might continue as a trend and result in an adaptation, given enough time. A long-term shading study would prolong stress, which would give *S. radians* more time

to alter their zooxanthellae densities. For example, the difference between the zooxanthellae densities in corals from the 100% and 0% shading treatments would translate into an increase of 7400 zooxanthellae d^{-1} if unshaded corals acted as a reliable control.

Changes in Chlorophyll *a* Concentrations

Siderastrea radians colonies from SMK not exposed to shading had lower concentrations of chlorophyll *a* than four species of *Porites*, *Stylophora pistillata*, and three species of *Montastraea* (Table 4-1). Thus, *S. radians* colonies in the SMK may have lower chlorophyll *a* concentrations under normal conditions than some other species of coral. This is not unexpected for algae, both unicellular and multicellular, living in high light environments (Kirk 1994). In fact, the type of zooxanthellae found in *Siderastrea radians*, *Symbidinium* type B is known as a "sun-specialist" and predominates in corals living in very shallow water (Rowan 1998).

Ambient corals that were taken before the experiment started (Day 0) had lower chlorophyll *a* concentrations than corals from 0% shade treatments harvested at the end of the experiment (Day 11). This suggests that something unrelated to the shading experiment may have altered light in the SMK between Day 0 and Day 11, such as the large amount of rain the area received during the experiment.

Chlorophyll *a* concentrations from 50% and 75% shading treatments were not significantly different from the 0% treatment. These results combined with the results for zooxanthellae density suggest that chlorophyll *a* concentrations $zooxanthellae^{-1}$ may be the key to understanding how *S. radians* in SMK adapt to reduced light availability.

Changes in Chlorophyll *a* Per Zooxanthellae

Results indicate that concentrations of chlorophyll *a* per zooxanthellae were lowest in *Siderastrea radians* colonies in the 0 % shading treatment, with ambient (Day 0) colonies having slightly higher concentrations. Colonies from the 50% and 75% shading treatments exhibited the

highest concentrations, which were statistically equal. From the 0% to the 50% light reduction treatment, chlorophyll *a* concentrations per cell increased 58.6%, but from 50% to 75% light reduction, there was an increase of only 3.6%. These results are not unexpected. Many species of algae increase the amount of photosynthetic pigments they contain when exposed to reduced light intensity. Some species of algae are even known to increase their pigment concentrations two- to five-fold (Kirk 1994). Algal species that are successful in low light environments can increase their pigment concentrations in one of two ways. They can either increase the number of photosynthetic units per cell or increase the size of existing photosynthetic units (Richardson et al. 1983). For example, in most green plants, including algae, it appears that the increase in chlorophyll content during shade adaptation is largely due to an increase in the number of photosynthetic units, rather than their size (Kirk 1994). Shade adaptation in zooxanthellae, however, is seemingly due to an increase in the size of photosynthetic units, rather than the number of photosynthetic units per cell (Falkowski & Dubinsky 1981, Kirk 1994). In fact, Richardson et al. (1983) argued that increasing the size of the photosynthetic unit was more energetically efficient. As a consequence of increasing the size of photosynthetic units in cells, shade-adapted algae have higher photosynthetic rates per unit biomass than their high light-adapted counterparts (Falkowski & Dubinsky 1981, Kirk 1994). It is unclear which tactic *S. radians* in SMK used to increase their chlorophyll *a* concentrations per cell, but it is reasonable to conclude that they probably increased the size of their photosynthetic units, as this is typically how zooxanthellae respond to reduced irradiance.

The 58.6% increase in chlorophyll *a* per zooxanthellae in *Siderastrea radians* subjected to 50% shading, relative to unshaded corals, combined with the 3.6% increase in chlorophyll *a* per zooxanthellae between corals subjected to 75% shading and those subjected to 50%, suggests

that zooxanthellae may be reaching the point at which they can no longer increase the chlorophyll *a* concentrations in their cells and maintain basic metabolism. Exactly when zooxanthellae reach the compensation point where photosynthesis cannot keep up with respiration is not clear and not every species or type of *Symbiodinium* necessarily has the same compensation point. For example, Rogers (1979) shaded 10 species of coral for 5 weeks. During that time, *Acropora cervicornis* was the first to respond to shading stress, bleaching after only 3 weeks. At the end of 5 weeks, *Diploria labyrinthiformis* and *Montastrea annularis* were pale, but not white, indicating a negative stress response, but no coral death. The other 7 species of coral shaded during the 5 weeks had some pale areas, but remained fairly healthy. Of these healthy species, one was *Acropora agaricites*, indicating that even corals in the same genus can have very different stress responses. *Siderastrea siderea*, a close relative of *S. radians*, recovered from shading stress better than all other species in the experiment (Rogers 1979). This result may be related to the fact that *S. sidera* colonies harbor *Symbiodinium* type C1 (LaJeunesse 2001), a known shade-adapted type (Rowan 1998). As the zooxanthellae in *S. radians* are notoriously "sun-loving" (Rowan 1998), they may have a lower light compensation point. However, because the zooxanthellae in the experiment were subjected to a high level of shading relatively quickly, they may not have had enough time to adjust their light compensation point.

In addition, the capacity for zooxanthellae to accumulate pigments must be finite. Zooxanthellae are typically small, 5–10 µm in diameter, and type B zooxanthellae, those found in *Siderastrea radians*, are among the smallest (LaJeunesse 2001). Because the rate of increase in chlorophyll *a* per cell was less from 50% to 75% light reduction, the maximum chlorophyll *a*

per zooxanthellae for *S. radians* could be around 4.3 pg chlorophyll *a*, which was the mean concentration across the two treatments.

Lastly, *Siderastrea radians* zooxanthellae are evolutionarily adapted to high levels of irradiance, and they might not change chlorophyll *a* concentrations quickly. Both 50% and 75% light reduction treatments were of the same duration – 10 days. If the experiment had been continued for another 10 days, the chlorophyll *a* concentrations per zooxanthellae for corals in the 50% light reduction treatment may have stayed constant and the concentrations for corals in the 75% treatment may have increased. Assuming 0% shading treatments acted as a reliable control, *S. radians'* zooxanthellae had an estimated gain of 0.1713 pg chlorophyll *a* day^{-1}, which is faster than the rate reported for *Styphora pistillata* (0.1567 pg chloropyll *a* day^{-1}; Falkowski & Dubinsky 1981). Thus, *S. radians* may be increasing their chlorophyll *a* per zooxanthellae at their maximum rate, and colonies subjected to light reductions greater than 50% may require longer than 10 days to adapt completely.

Conclusions

A long-term shading and monitoring approach, as previously described, could help answer questions as to how zooxanthellae respond and adapt to reduced irradiance. Long-term monitoring and shading studies could utilize underwater fluorometers (i.e. DIVING-PAM; Hoegh-Guldberg & Jones 1999; Winters et al. 2003; Hoogenboom et al. 2006) to detect changes in photosynthetic capacity, *in situ*, and these measurements could be converted to chlorophyll concentrations using a calibration curve developed by sampling some colonies. The required surface areas, numbers of polyps, and heights, could be estimated from simple diameter measurements that could be taken in the field, without harvesting colonies. Such studies would provide insights into the light compensation point for corals.

Despite the unanswered questions remaining at the end of this study, insights were gained into how *Siderastrea radians* in the SMK adapt to shading stress. Importantly, *S. radians*' zooxanthellae, though "sun-loving," did respond to lowered light conditions, by increasing chlorophyll *a* concentrations zooxanthellae^{-1}. This suggests that *S. radians*, along with being unusually tolerant of high and low temperatures (Macintyre 2003) and burial (Rice & Hunter 1992, Lirman et al. 2002, Lirman et al. 2003), has the ability to adapt to reduced light environments in a relatively short amount of time (~10 days). Eutrophication is usually a gradual process, occurring stepwise over time. The short-term response of *S. radians*' zooxanthellae to reduced irradiance suggests that these corals can respond quickly enough to cope with the gradual reduction in light availability caused by eutrophication.

Along with being gradual, reductions in light availability as a result of eutrophication are typically long-lasting, often reducing irradiance for all attached photosynthetic organisms over months or years. Whether the zooxanthellae in *Siderastrea radians* can continue to adapt and cope with long-term shading is unclear. Further research, including a long-term shading study of *S. radians* in SMK is needed to elucidate their responses.

Increased shading is not the only effect that eutrophication has on coastal environments. Eutrophication also causes major changes in submerged vegetation, including increased growth of algae that can overgrow corals (Duarte 1995, Valiela et al. 1997). Another relevant consequence of eutrophication are changes in benthic biogeochemical processes (Duarte 1995, Nixon 1995). By definition, eutrophication causes an increase in organic matter (Nixon 1995), which often results in increased remineralization of organic matter in the sediments and reduced oxygen concentrations in bottom waters. Hypoxic and often anoxic conditions can, in turn, decrease survivorship of benthic organisms (Duarte 1995). In addition, in eutrophic waters,

seagrasses are often lost, which can promote resuspension of sediments (Duarte 1995) and harm corals by further reducing light, burying colonies, or preventing coral larvae from settling and surviving. The consequences of eutrophication are diverse and more research is needed to fully understand how corals, including *S. radians* from the St. Martins Keys, will adapt or cope with such environmental changes.

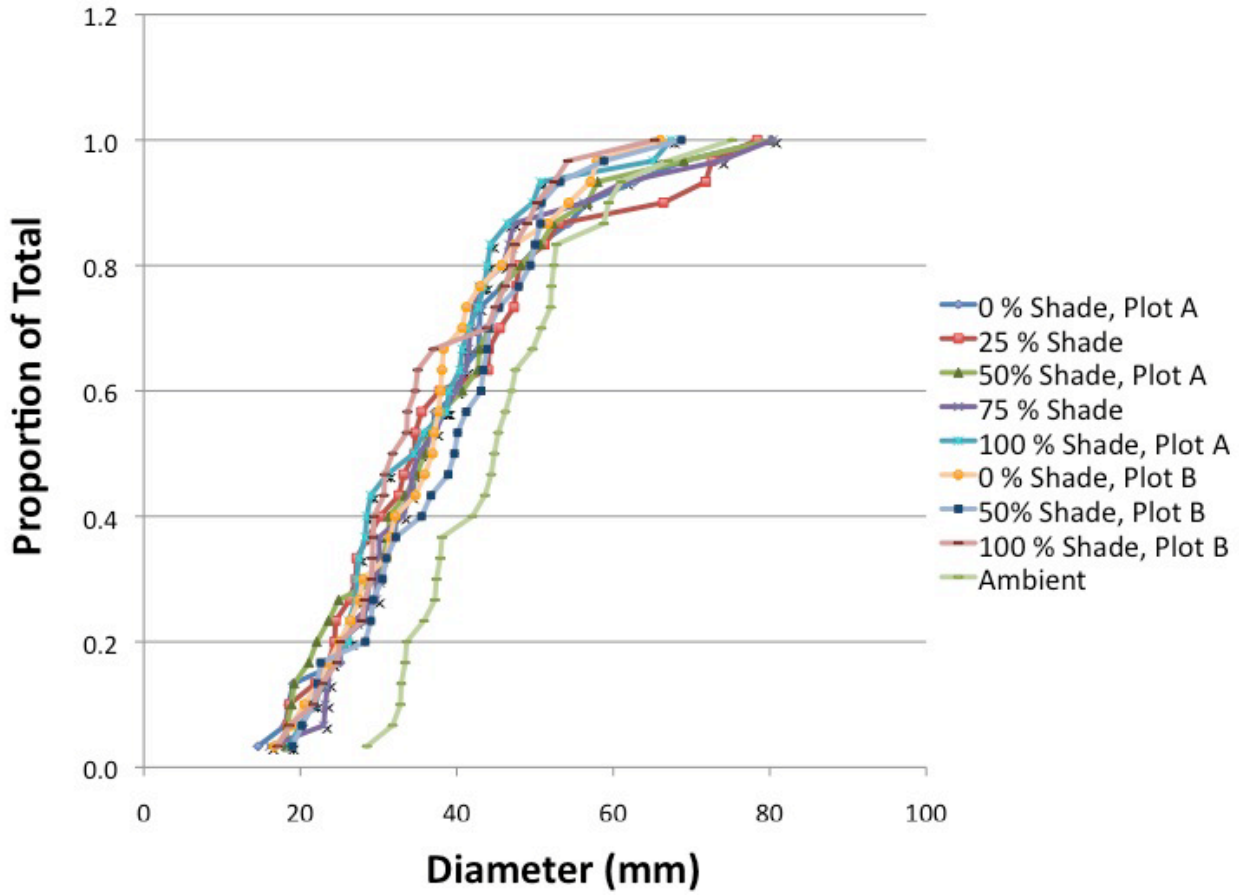

Figure 4-1. Cumulative size frequency distributions for diameters of *Siderastrea radians* colonies (n = 30) from different shading treatments.

Table 4-1. Zooxanthellae cells cm^{-2}, µg chlorophyll *a* cm^{-2}, and pg chlorophyll *a* $zooxanthellae^{-1}$ for various coral species.

Species	Depth (m)	10^6 cells cm^{-2}	µg chl *a* cm^{-2}	pg chl *a* $cell^{-1}$	Reference
Siderastrea radians (Ambient)	2	0.3 ± 0.1	1.1 ± 0.6	3.4 ± 1.0	This Study
Siderastrea radians (0 % Shade)	2	0.5 ± 0.3	1.5 ± 0.7	2.8 ± 1.0	This Study
Stylophora pistillata	–	1.6 ± 0.3	3.6 ± 1.1	2.2 ± 0.3	Falkowski and Dubinsky 1981
Porites lobata	0–2	1.5–6.9	9.3–47.5	4.5–16.7	Apprill et al. 2007
Porites lutea	0–2	2.3–5.6	17.3–29.3	4.4–9.8	Apprill et al. 2007
Porites astreoides	4–5	–	4.7 ± 2.0	2.2 ± 0.4	Myers et al. 1999
Porites porites	4–5	–	4.2 ± 2.3	3.7 ± 1.8	Myers et al. 1999
Acropora cervicornis	4–5	–	0.9 ± 0.8	0.9 ± 0.6	Myers et al. 1999
Agaricia tenuifolia	4–5	–	1.2 ± 0.8	1.6 ± 1.0	Myers et al. 1999
Favia fragum	4–5	–	0.9 ± 0.2	0.5 ± 0.5	Myers et al. 1999
Montastraea annularis	4–5	–	3.6 ± 0.8	1.1 ± 0.5	Myers et al. 1999
Montastraea cavernosa	4–5	–	5.4 ± 2.0	2.4 ± 1.2	Myers et al. 1999
Montastraea faveolata	10	–	5.4 ± 0.1	–	Lesser et al. 2000
Montastraea cavernosa	10	–	6.8 ± 0.4	–	Lesser et al. 2000

Values represent means ± standard deviations or ranges. A dash (–) indicates no data reported.

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BIOGRAPHICAL SKETCH

Emily L. Mitchem was born in 1984 in Atlanta, Georgia. She lived in Naples, Florida until 1998, when she moved to Rincon, Georgia, a suburb of Savannah, Georgia, with her parents. Emily ran cross-country in high school and was often outside running. She attended school in Georgia until she graduated in May 2002 from South Effingham High School, and left that same summer to attend the University of Florida. At first, Emily wanted to be a doctor and majored in microbiology. She soon learned that being a doctor involved being around numerous sick people and changed her major to zoology, with plans of becoming a marine biologist. Emily took "Doc" Maturo's marine biology class during summer 2001 under Dr. Patrick Baker and realized she had made the right choice in not becoming a doctor. With Dr. Shirley Baker under the University Scholar's Program, Emily completed an undergraduate thesis titled, "Native Florida Crustacean Predators Preferences Regarding the Non-Indigenous Green Mussel, *Perna viridis.*" In fall 2005, Emily received her Bachelor of Science in zoology (summa cum laude). Immediately, Emily began working in Dr. Thomas Frazer's lab doing lab and field work, with the anticipation of starting her master's degree in the fall. After two-and-a-half years of working with Dr. Thomas Frazer, Emily received the Master of Science degree from the University of Florida Fisheries and Aquatic Sciences Program in December 2008. After graduation, Emily plans to teach high school biology.