THE EFFECT OF SEASONAL TEMPERATURE CHANGES ON THE LIGHT-USE EFFICIENCY OF TWO CORAL COMMUNITIES

by

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A THESIS

Presented to the Department of Biology and Human Physiology
and the Robert D. Clark Honors College
in partial fulfillment of the requirements for the degree of
Bachelor of Science

June 2017

An Abstract of the Thesis of

Hannah Saraceno for the degree of Bachelor of Science in the Departments of Biology
and Human Physiology to be taken June 2017

Title: The Effect of Seasonal Temperature Changes on the Light-Use Efficiency of Two
Coral Communities

Approved:____

Dr. Kelly Sutherland

Coral reefs continue to decline due to threatening human-related activities. Despite a general awareness of mass coral bleaching, intervention efforts have not effectively targeted the causes of reef decline. In order to identify specific stressors on reefs, additional assessment methods are required. The proposed method in this study is determining coral condition through light-use efficiency (LUE). To develop this method for reefs and determine the effects of seasonal temperatures, two coral communities were collected from offshore Bermuda and placed in an indoor racetrack flume. The first community was collected in the summer and placed in 28°C seawater, while the second community was collected during fall and placed in 25°C seawater, the ambient temperatures of their environment. The daily LUE for each community was measured and compared to determine if seasonal temperatures affect LUE. Primary production and absorbed photosynthetically available radiation (APAR) were also measured in order to detect which component of LUE may have changed. The community in the 28°C seawater was found to have a significantly higher LUE than the community in the

25°C seawater ($p<0.01$). Primary productivity of the 28°C community was also an average of 1.5 times higher than the productivity of the 25°C community at the same levels of APAR. However, the LUE of the corals in 25°C had a significant linear increase over the eleven days they were studied ($p=0.016$), suggesting that the community was still acclimating to the flume. If the study had continued, it is possible there may not have been a significant difference in the LUE of the two communities. The results of this study suggested that temperature change from fall to summer increased the LUE and therefore influenced the primary productivity of the communities. It was hypothesized that this result only occurs until a threshold temperature is reached, at which point bleaching and coral mortality occurs. This has implications for projected temperature increases due to climate change and further studies can determine whether these changes will lead to coral bleaching or increased primary production. This study suggests that LUE has the potential for measuring the sub lethal effects of specific stressors on coral reefs in order to better target intervention efforts for impacts to coral reefs.

Acknowledgements

I would like to thank everyone that has helped me complete this work. Thank you to Dr. Eric Hochberg for the opportunity to participate in his ongoing research, as well as the experiences and insights that have resulted from it. Secondly, I would like to thank the other members of my thesis Committee, Professors Kelly Sutherland and Michelle Wood for their willingness to help me think about this research from a whole new perspective. Thanks to Michael Wooster, who was always there to answer my questions. Lastly, I would like to thank Professor Daryl Parkyn for everything he has done for me throughout my college career.

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Background

Coral Reef Assessment

Current studies estimate that 58-70% of coral reefs worldwide are threatened by these human-related activities (Hughes & Connell 1999; Downs et al. 2005). Reef decline has been thoroughly documented in scientific papers regarding human impacts to reefs; a few examples of these impacts include sedimentation, marine pollution, over-harvesting, calcium carbonate mining, oil spills, and climate change (Wilkinson 1998; Downs et al. 2005). These threats have lead to reef decline through incidence of disease, growth and regeneration rates, reproduction, and recruitment (Downs et al. 2005). Despite the implementation of interventions designed to protect reefs, they have continued to deteriorate (Hoegh-Guldberg et al. 2007). Therefore, it is important for methods of reef assessment to be improved to better pinpoint the exact causes of degradation for specific reefs in order to design more direct interventions that can lead to recovery of coral reefs.

The most common metric in reef assessment worldwide is proportional (or percent) cover of coral. This is based on the observation that healthy reefs typically increase in coral coverage during recovery periods. If reefs face ongoing disturbances, algae and rubble gradually dominate them, with little to no coral recovery (Connell 1997). Therefore, past and many current methods of reef assessment focused on quantitative assessment of coral cover over small spatial and temporal scales (Hughes & Connell 1999; Jokiel et al. 2004). An issue with assessing coral reefs based on abundance of organisms is that coral cover can vary both temporally and spatially (Hughes & Connell 1999).

In recent years, methods have been developed, such as video transects, fixed photo-quadrants, manta tow surveys and remote sensing to study coral reefs long term or over a large spatial area (Wilson & Green 2009). Methods for assessing the health of corals themselves have also been developed including determining the abundance of zooxanthellae, rate of photosynthesis through changes in oxygen using benthic enclosures or flow respirometry, and coral calcification (Gutasso et al. 1999). Although these forms of measurement are important for assessment of coral condition, quantitative reef assessment gives little time to implement mitigation or for determination of the type of mitigation required (Downs et al. 2005). Furthermore, these methods do not allow for monitoring the changes of important functions of reefs, such as productivity, which may occur before or without detectable declines in coral coverage. Primary production provides the energy for all the processes within the reef system, but an issue with directly measuring this is it can be highly variable for different reefs as well as within one reef throughout the day, mainly due to variations in irradiance (Odum & Odum 1955; Kinsey 1985; Gattuso et al. 1999; Atkinson & Falter 2003).

What is Light-Use Efficiency?

Measurement of light-use efficiency (LUE) can be used to correct for changes in primary production due to irradiance. LUE essentially normalizes primary productivity by the amount of light absorbed by a plant or community. Measuring primary productivity in this way removes the variability caused by fluctuations in light capture and allows for comparisons between reefs as well as within the same reef over time. Because LUE corrects for variations due to light, differences in LUE are due to changes in other factors affecting primary production. Evaluation of coral reef LUE will allow researchers to determine the effect of various stressors on primary productivity without needing to consider the light conditions of the day.

LUE as a model was first suggested by Monteith (1972) for tropical and sub-tropical crop plants. Monteith observed the effects of stressors on crop LUE, such as water, temperature and solar radiation. He determined that there was a substantial loss in crop efficiency during dry summers (Monteith 1977). The method of measuring crop primary productivity based on LUE is now widely used in terrestrial remote sensing (Hochberg & Atkinson 2008). However, this model has not yet been implemented for measurement of primary productivity on coral reefs and there are currently no published measurements of LUE for reefs. LUE in combination with remote sensing is potentially an extremely useful tool for measurement over large and inaccessible areas. In a previous study by Hochberg and Atkinson (2008), LUE was estimated based on image processing as well as data from previous studies and results suggested that LUE increases with depth.

The equation for determining productivity based on LUE for the present study conducted in a flume mesocosm is

$$P = \varepsilon \int_{400}^{700} E_d(\lambda; H) A(\lambda) d\lambda \qquad \textbf{Equation 1}$$

where spectral downwelling plane irradiance [$E_\text{d}(\lambda;H)$] represents the amount of light reaching the coral community at a given wavelength (λ) and distance from the bottom of the flume (H), spectral absorptance [$A(\lambda)$] describes the percentage of light absorbed by the coral community (non-dimensional), and community photosynthetic light-use efficiency (ε) is the capacity for the community to convert light energy to fixed carbon. Since corals use light in the wavelengths of 400 to 700nm for photosynthesis, the irradiance and absorptance are only integrated over these wavelengths (Hochberg & Atkinson 2008). Rearranging the equation illustrates that LUE is simply primary productivity normalized by absorbed phothosynthetically available radiation (APAR):

$$\varepsilon = \frac{P}{\int_{\lambda=400}^{700} E_d(\lambda;H)A(\lambda)d(\lambda)} = \frac{P}{APAR}$$

Equation 2

“Superleaf” Hypothesis

Another important consideration for improving reef condition assessment is studying the reef as a whole instead of focusing on individual coral colonies. A solution to improve whole reef evaluation was found in remote sensing of land plants, referred to as the “Superleaf” hypothesis (Field 1991). This hypothesis effectively views an entire canopy as a giant leaf and is based on the Functional Convergence Hypothesis, which states that the resources necessary for carbon fixation are allocated to areas that will maximize carbon gain because there is a high energy demand for the biocapacity to fix carbon (Field 1991). In the “Superleaf” hypothesis, the ecological considerations that apply to leaves also apply to canopies, or multiple coral colonies comprising of communities. Multiple organisms can be viewed as a single community with a capacity for CO_2 fixation that is dependent on absorbed light and resource availability (Field 1991). Therefore, the net gains and losses for a single community can be a useful measure for an ecosystem (Kinsey 1985).

The “Superleaf” hypothesis can also be applied to coral and other reef communities in order to measure changes in primary productivity over time from factors such as acidity, salinity, or temperature. Measuring the LUE for a community is useful because it can determine the net effect of stressors on the reef, without interference from smaller details, such as which species are more resistant to certain stressors. Furthermore, it is important to consider photosynthesis and LUE on a community scale because these can help determine how the productivity of the entire ecosystem will be affected. However, because there are slight variations in photosynthesis rates throughout the day, it is important to measure LUE over a larger time scale, integrating at least for an entire day.

Past Studies on Coral and Temperature Variations

The stressors considered in this study were seasonal temperatures. Early studies in coral research determined that temperature could have lethal effects on coral. One of the earliest studies, in 1928, examined the effect of steadily increasing the temperature to 40°C for various species (Edmondson 1928). Colonies were determined to be alive or dead after a given interval. By the time the temperature of the water reached 40°C all the coral species were determined to be dead (Fig. 1). However, there were no specific processes measured in this experiment and therefore it was unknown what physiological changes occurred leading to coral death.

TABLE 4. COMPARATIVE RESISTANCE OF HAWAIIAN CORALS TO A SLOW RISE OF TEMPERATURE (2°C. PER HOUR) TO 34°C., TO 35°C. AND TO 38°C.—40°C.

At 34°C. and 35°C., which experiments were distinct from each other and from that ranging from 38°C. to 40°C., the temperature was maintained for 1 hour, while there was a steady rise from normal temperature to 38°C. and continuing to 40°C. D = specimen dead, A = alive at the end of the specified period.

Corals	34° C.	35° C.				38° C.	38.5° C.	39° C.	40° C.
	60 min.	15 min.	30 min.	45 min.	60 min.				
Pocillopora meandrina var. nobilis	D	A	D			D			
Pocillopora ligulata	A	A	A	D		D			
Pocillopora cespitosa	A	A	A	A	D	D			
Porites evermanni	A	D				D			
Porites lobata forma lacera	D	D				D			
Porites lobata forma centralis subforma alpha	A	D							
Porites lobata forma centralis subforma beta	A	D							
Porites lobata forma centralis subforma gamma	?	D							
Porites compressa forma granimurata	A	D				D			
Porites compressa forma angustisepta	D	D				D			
Montipora verrucosa	D	D				D			
Montipora flabellata	A	A	D			A	A	D	
Montipora verrilli	A	A	A	D					
Montipora patula	A	D							
Pavona varians	A	A	A	A	D	D			
Pavona duerdeni	A	A	A	A	?				
Cyphastrea ocellina	D	D				D			
Stephanaria stellata	A	A	A	A	A	D			
Stephanaria brighami	A	A	D			A	A	A	D
Favia hawaiiensis	A	A	A	A	A	A	A	A	D
Leptastrea agassizi	A	A	A	A	A				
Fungia scutaria	A	A	A	.A	A	?	?	D	

Figure 1: The effect of the slow rise in temperature to 40°C on the mortality of Hawaiian coral species. Reprinted from “The Ecology of an Hawaiian Coral Reef,” by C. H. Edmondson, 1928, *Bulletin of Bernice P. Bishop Museum, 45*, 18.

As the study of coral reef ecology continued, researchers began to analyze the effects of smaller changes in temperature on processes such as photosynthesis and respiration. In Kinsey’s 1985 review, he examined studies measuring differences in photosynthesis and respiration between the summer and winter months (Fig. 2). A general trend noted was that photosynthesis and respiration increased during the summer months and decreased during the winter. Temperature differences from winter to summer in the sites where coral productivity was measured ranged from about 1.4°C to 5°C. However, the rate of primary productivity was approximately doubled in the summer as compared to the winter at each of the sites despite the varied temperature differences between sites. Therefore, it is uncertain whether the differences in primary productivity were simply due to changes in light or whether temperature also played a role. Other studies have explored this question and found that primary productivity tends to increase with increasing temperatures up to a threshold, at which point the corals began to bleach and die (Jorkiel & Coles 1977; Howe & Marshall 2001; and Fujimura et al. 2008). However, Jorkiel & Coles' (1977) study was conducted outdoors and therefore light intensity was not controlled for, while Howe & Marshall (2001) and Fujimura et al.'s (2008) studies had twelve-hour light periods followed by twelve-hour dark periods, leading to an underestimation of gross primary productivity because respiration rates decrease at night (Kinsey 1985).

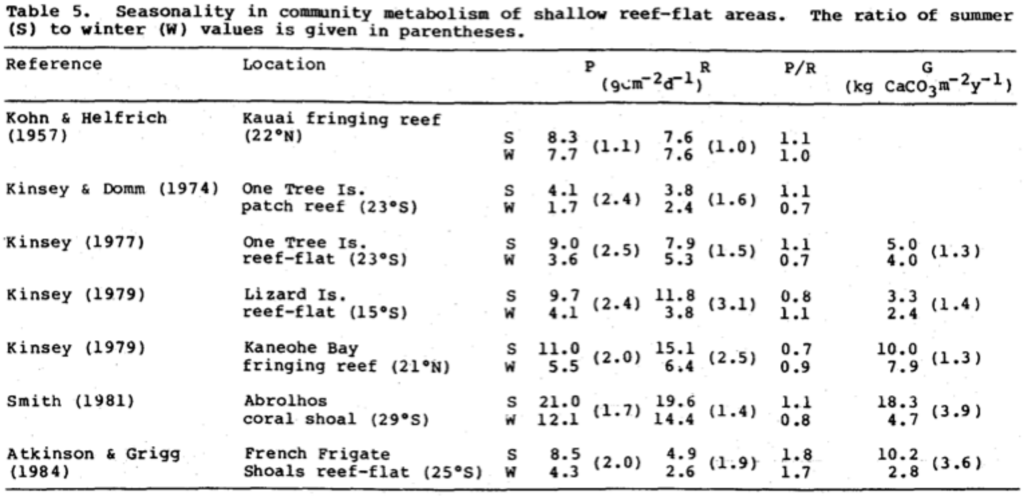

Table 5. Seasonality in community metabolism of shallow reef-flat areas. The ratio of summer (S) to winter (W) values is given in parentheses.

Reference	Location		P $(gcm^{-2}d^{-1})$		R $(gcm^{-2}d^{-1})$		P/R	G $(kg\ CaCO_3m^{-2}y^{-1})$	
Kohn & Helfrich (1957)	Kauai fringing reef (22°N)	S	8.3	(1.1)	7.6	(1.0)	1.1		
		W	7.7		7.6		1.0		
Kinsey & Domm (1974)	One Tree Is. patch reef (23°S)	S	4.1	(2.4)	3.8	(1.6)	1.1		
		W	1.7		2.4		0.7		
Kinsey (1977)	One Tree Is. reef-flat (23°S)	S	9.0	(2.5)	7.9	(1.5)	1.1	5.0	(1.3)
		W	3.6		5.3		0.7	4.0	
Kinsey (1979)	Lizard Is. reef-flat (15°S)	S	9.7	(2.4)	11.8	(3.1)	0.8	3.3	(1.4)
		W	4.1		3.8		1.1	2.4	
Kinsey (1979)	Kaneohe Bay fringing reef (21°N)	S	11.0	(2.0)	15.1	(2.5)	0.7	10.0	(1.3)
		W	5.5		6.4		0.9	7.9	
Smith (1981)	Abrolhos coral shoal (29°S)	S	21.0	(1.7)	19.6	(1.4)	1.1	18.3	(3.9)
		W	12.1		14.4		0.8	4.7	
Atkinson & Grigg (1984)	French Frigate Shoals reef-flat (25°S)	S	8.5	(2.0)	4.9	(1.9)	1.8	10.2	(3.6)
		W	4.3		2.6		1.7	2.8	

Figure 2: A comparison of photosynthesis and respiration rates of Hawaiian and Australian corals in studies from 1957 to 1984. Reprinted from "Metabolism, Calcification and Carbon Production," by D. W. Kinsey, 1985, *Proceedings of the Fifth-International Coral Reef Congress, 4,* 515.

The goals of the present study were to develop a method for reef assessment on a reef-wide scale that could detect sub-lethal variations, as well as determining whether seasonal temperatures influence the LUE of a coral community. This study also aimed to determine whether potential increases in LUE were due to increased ability to absorb light or the ability perform photosynthesis from a given amount of light. Prior to the study, it was hypothesized that temperature does affect primary productivity and a natural increase in temperature will increase the LUE of the coral community, as has been observed for primary productivity in previous studies (Jorkiel & Coles 1977; Kinsey 1985; Howe & Marshall 2001; Fujimura 2008).

Materials and Methods

Experimental Communities

The experimental communities each consisted of six *Porites astreoides* and four *Diploria labyrinthiformis* colonies, as these species are abundantly available on reefs surrounding Bermuda. The communities were collected from natural reefs offshore Bermuda at an average depth of approximately 3.5 meters. *P. astreoides* is a colonial stony coral species commonly found in the western Atlantic and Caribbean Sea. It typically grows in water less than 15 meters deep, but occasionally in up to 50 meters (Rowland 2007). *D. labyrinthiformis* is also a stony coral, commonly known as grooved brain coral, found in tropical areas of the West Atlantic Ocean. Some members of this species exhibit strong green fluorescence by coral-host pigments (as opposed to those of the zooxanthellae), which is measurable in reflectance measurements (Rossi-Snook 2005).

Coral collections adhered to Bermuda laws and regulations, as well as Bermuda Institute of Ocean Sciences (BIOS) Collecting and Experimental Ethics Policy. The community collected in July from an ambient seawater temperature of 28.2°C was placed in 28°C ±1°C seawater and acclimated to the indoor flume for approximately three months prior to the study. The second community was collected from 25.5°C seawater in October and acclimated for five days to the flume in 25°C ±1°C seawater. The temperatures were chosen based on seasonal averages, approximately 24.4°C in the fall months and 27.4°C in the summer months (NOAA 2016).

Flume Mesocosm

The corals were placed in an indoor “racetrack” flume mesocosm with a volume of approximately 0.3 m^3. The flume was constructed of fiberglass-reinforced plastic with an outer layer of gelcoat. It had two 2.5-meter long straightaways with semicircular fins at the ends to guide the flow of the water as it rounded the turns. The straightaways and semicircular ends were 40 cm wide and 60 cm tall. There was a constant water flow provided by a water pump and two temperature groups, one at 28°C ±1°C and the second at 25°C ±1°C, controlled by a PolyScience 6000 series chiller/heater. The water input was seawater from the BIOS system and the flume was filled with a volume of approximately 0.3 m^3 of seawater. While the coral communities acclimated, there was constant input of water and water flow.

A Tailored Lighting Solar Simulator D50 Ten Light Array provided the lighting for the experimental communities. A twelve-hour light period was used with ten-minute dark periods intermittently every 110 minutes. The light was raised and lowered haphazardly each day. The typical above-water, 100% irradiance levels in St. George’s, Bermuda are ~48 mol photos m^{-2} d^{-1} in the summer and ~24 mol photons m^{-2} d^{-1} in winter (Frouin et al. 2007). The irradiance levels within the flume achieved 30-80% of these values, to account for depth and variably cloudy conditions.

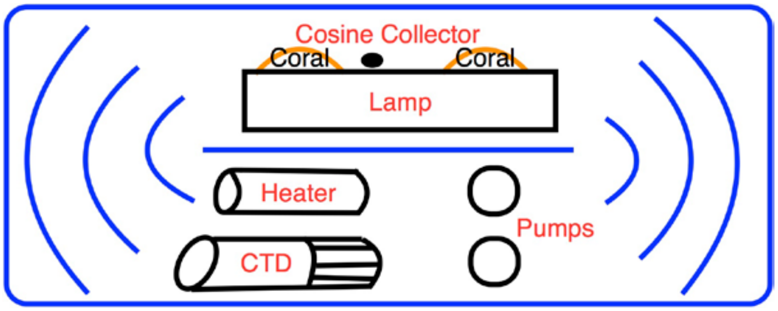

Figure 3: Illustration of Flume Setup, consisting of an automatic heater, CTD, pumps to create water flow, solar simulator lamp, and cosine collector located at the same depth as the coral community.

Oxygen Air-Water Flux

Photosynthesis and respiration were determined by measuring changes in dissolved oxygen, with photosynthesis and respiration producing and consuming oxygen, respectively. However, oxygen also diffuses across the air-water surface, which can affect the gain and loss terms. Therefore, it was necessary to estimate how much of the changes in dissolved oxygen were due to the air-water flux. Clear coral skeletons were placed in the flume, and the flume water was supersaturated with oxygen by bubbling in through aquarium stones. Then the rate of efflux was monitored as the gas returned to saturation. This baseline rate, which changed depending on the saturation level of the flume, was then applied to the measurements from the actual experiments with live corals.

Primary Production Measurements

During experiments, the water in the flume re-circulated and pumps provided water flow over the coral colonies, allowing oxygen changes due to photosynthesis to be measured. The water flow rate was measured at 0.1 m/s, at the low end of in situ measurements of 0.05-0.5 m/s (Munk and Sargent 1954; Odum and Odum 1955; Falter et al. 2004), but a closer simulation to natural coral conditions than aquariums (Atikinson and Cuet 2008). A YSI 6600 Sonde CTD was placed in the flume to measure dissolved oxygen, temperature, and pH. The Solar Simulator automatically turned on each morning at 7 AM and turned off every 110 minutes for 10 minutes until 7 PM. The amount of dissolved oxygen and the oxygen saturation of the flume were measured each minute throughout the twelve-hour period. After correcting for air-water gas flux, changes in oxygen during the 110-minute light periods were used to calculate net photosynthesis (gross photosynthesis minus respiration), and changes in oxygen during the ten-minute dark periods were used to estimate light respiration. This model of calculating coral community photosynthesis is advantageous compared to models in which respiration is calculated during twelve-hour dark periods because daytime respiration rates are higher than nighttime rates (Kinsey 1985). This allowed for the determination of oxygen usage during daytime respiration.

The derivative of the dissolved oxygen was determined in order to find the rate of the net community primary productivity. This rate was integrated to find the rate of primary productivity per hour. The change in dissolved oxygen was then divided into net community primary productivity and respiration. Net primary productivity was the amount of oxygen produced during the 110-minute periods the light was on, while respiration was the amount of oxygen used while the light was off for ten minutes. The oxygen used per hour during respiration was then added to the net amount of oxygen produced per hour when the light was on and both photosynthesis and respiration occurred in order to determine daily gross primary production.

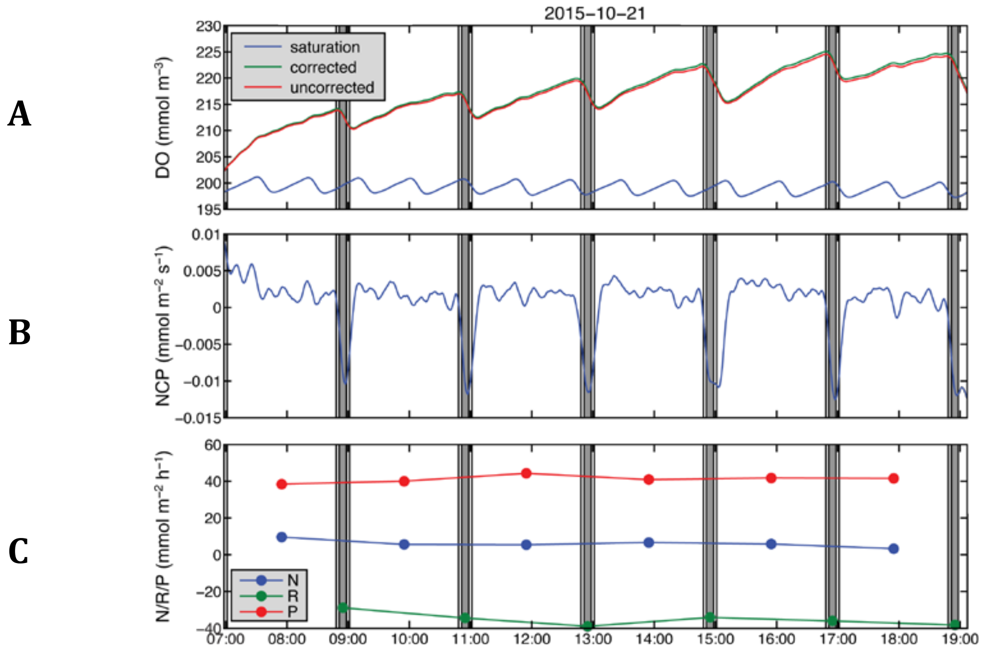

Figure 4: Changes in dissolved oxygen, associated primary productivity and respiration over a 10-hour period. (A) shows the oxygen saturation in the flume (blue) for each minute of the day as well as the dissolved oxygen (red). The green line shows the dissolved oxygen after atmospheric flux was corrected for. (B) shows the derivative of the corrected dissolved oxygen data, giving the rate of net community primary productivity for each minute of the day. (C) shows net primary productivity (blue) during light periods, respiration (green) during the dark periods and gross primary production (red) after the respiration rate was added back into the net primary productivity for October 21, 2015.

Absorbed Photosynthetically Available Radiation (APAR)

The irradiance of the lamp was measured each minute using an Ocean Optics USB4000 spectrometer attached to a fiber optic cable with a 3.9 mm-diameter cosine corrector connected to the sampling end. Each morning the spectrometer was calibrated against an LS-1-CAL Ocean Optics tungsten halogen light source. After the spectrometer was calibrated, the fiber was placed in the flume and the operating software (Spectra Suite) recorded the spectral irradiance for each minute throughout the twelve-hour period.

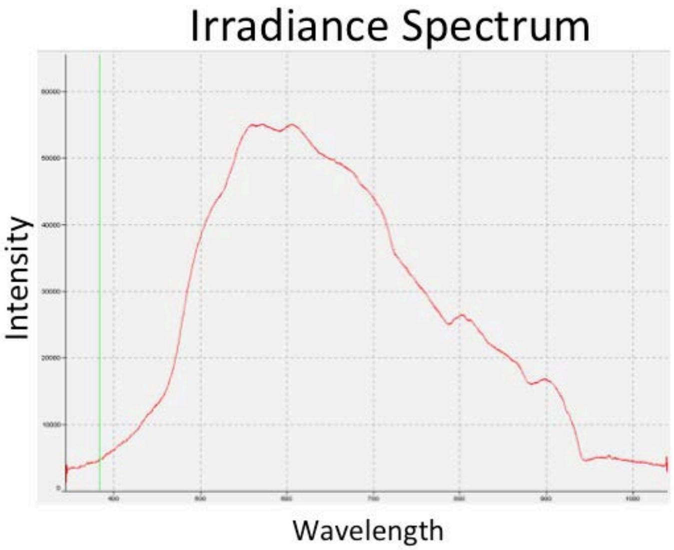

Figure 5: Irradiance Spectrum of the Tailored Lighting Solar Simulator D50 Ten Light Array measured in the present study with the Ocean Optics USB4000 spectrometer attached to 3900 mm fiber optic cable and cosine collector on the sampling end.

Once a day, the reflectance of the corals was measured during the ten-minute dark periods using OOIPS2000 software and Thorlabs’ OSL2 150 Watt broadband halogen fiber optic illuminator and Fiber Optic Reflection/Backscatter probe connected to an Ocean Optics USB2000. A Spectralon was used as a reference for the reflectance measures. The reflectance spectra were analyzed in Matlab and the outliers were discarded to account for changes in reflectance due to variations in the distance between the fiber optic illuminator and coral colonies. The percent reflectance measures were then used to find the percent absorptance of the coral community, according to the equation

$$1 - R = A \qquad \textbf{Equation 3}$$

where R is the percent reflectance, and A is the percent absorptance. Then, the average spectral absorptance for the coral community for the wavelengths 400 to 700 nm was determined. This spectrum was then multiplied by the spectral irradiance values for each minute throughout the day and integrated over the wavelengths 400 to 700 nm to produce APAR, according to the equation

$$APAR = \int_{400}^{700} E_d(\lambda; H) A(\lambda) d\lambda \qquad \textbf{Equation 4}$$

Finally, APAR was integrated over each minute of the day to provide the daily total APAR.

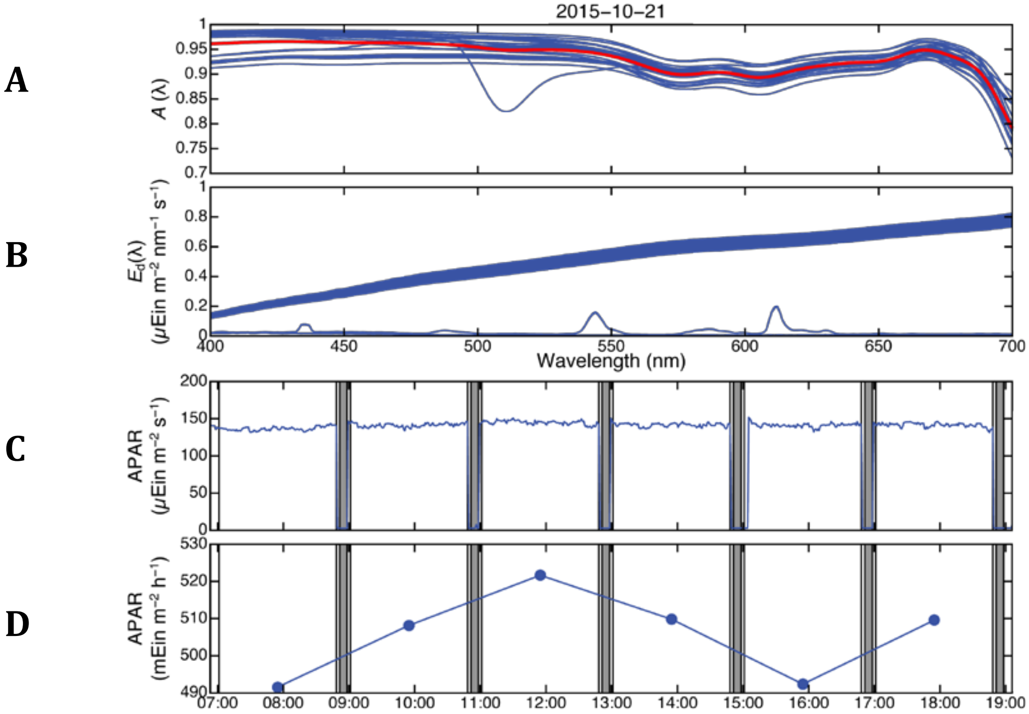

Figure 6: Measured absorptance and APAR for one day. (A) shows the absorptance over the wavelengths 400 to 700nm, determined from reflectance measurements in blue, with the average absoprtance in red. (B) shows the irradiance measures taken each minute of the day. (C) shows APAR after the absorptance has been integrated with the irradiance measures from each minute, and then this was integrated further to produce (D), which shows the hourly rate of APAR for October 21, 2015.

Data Analysis

Once oxygen saturation, irradiance and reflectance were measured, the data were analyzed statistically using MatLab to create Fig. 4 and Fig. 6 for each day. Data from the CTD were also analyzed to verify that temperature, pH, and salinity were kept constant each day. Then, the daily gross primary productivity was divided by the daily APAR to calculate the LUE value for each day according to Equation 2. The statistical significance of the difference between LUEs of the warmer and colder community was determined in Matlab using an independent two-sample t-test. The LUE values over time for both communities were also plotted and the statistical significance of each was determined with a linear regression.

Results

Daily Measurements

Table 1 shows rates of primary production for each day for the 28°C community, while Table 2 shows the results for the 25°C community. The average primary productivity of the 28°C community was about 1.5 times higher than the average primary productivity of the 25°C community. The APAR for both communities ranged from 4.4 to 10.4 mol photons/m^2/d. LUE for the 28°C community ranged from 0.0353 to 0.0907 with an average of 0.605. For the 25°C community, LUE ranged from 0.0252 to 0.0578, with an average of 0.0364. These results were then further analyzed to determine whether correlations existed between the constituents.

P (mmol C/m^2/day)	**APAR (mmol photons/m^2/d)**	**LUE**
351.43	5961.50	0.0589
356.29	9407.00	0.0379
350.39	7194.60	0.0487
374.62	6874.30	0.0545
432.98	8553.60	0.0506
399.63	4406.90	0.0907
425.10	7039.00	0.0604
414.30	5413.00	0.0765
368.42	10434.00	0.0353
400.01	6200.60	0.0645
381.68	4528.60	0.0843
423.81	6714.20	0.0631

Table 1: Primary Productivity, APAR and Light-Use Efficiency values for the 28°C Community.

P (mmol C/m^2/day)	**APAR (mmol photons/m^2/d)**	**LUE**
262.85	9478.20	0.0277
287.41	9815.10	0.0293
248.68	9869.80	0.0252
212.00	4874.90	0.0435
259.52	7940.10	0.0327
197.17	7619.10	0.0259
226.33	7422.10	0.0305
278.33	5653.60	0.0492
283.11	7955.50	0.0356
285.43	6564.30	0.0435
305.72	5292.60	0.0578

Table 2: Primary Productivity, APAR and Light-Use Efficiency values for the 25°C Community.

Light-Use Efficiency

LUE for the coral community in the 28°C seawater was significantly higher than that of the community in the 25°C seawater ($p<0.01$). The difference in the average LUE for the two groups was 0.024. However, LUE values of the community in 28°C seawater had a larger range than the community in 25°C seawater (Fig. 7).

The LUE of both the 28°C community and the 25°C community had positive trends over time (Fig. 8). There was a significant positive linear relationship for the 25°C community ($p=0.016$). However, this trend was not significant for the 28°C ($p=0.17$).

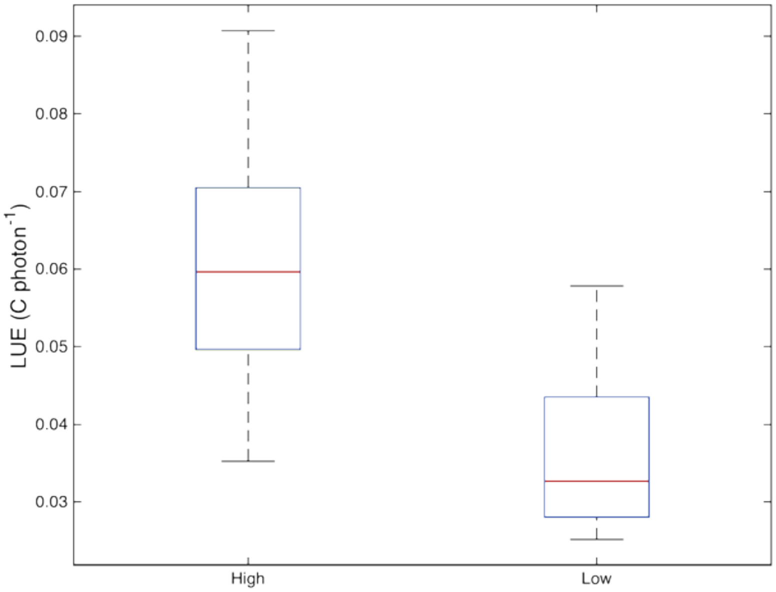

Figure 7: The light-use efficiency of the 28°C (High) compared to the 25°C (Low) communities (p<0.01).

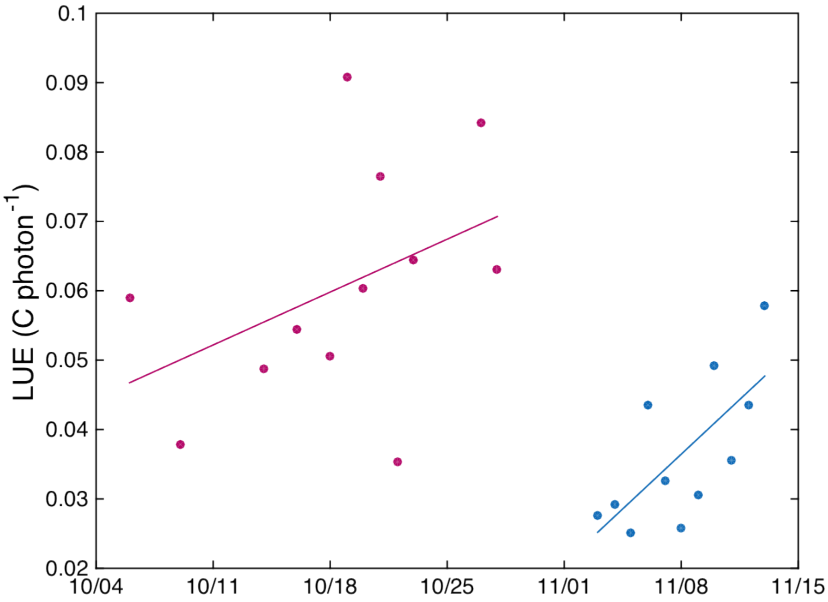

Figure 8: The change in light-use efficiency over time for the 28°C in red (p=0.17) and the 25°C in blue (p=0.016) communities.

Primary Productivity and APAR

There was no trend found in the relationship between primary productivity and APAR between 4,000 and 11,000 mmol photon m^{-2} d^{-2} (Fig. 9). However, the primary productivity values for the community in the 28°C seawater were higher than those of the 25°C community. The primary productivity of the 28°C group ranged from 350.39 to 432.98 mmol C/m^2/day, whereas the primary productivity of the 25°C group ranged from 197.17 to 305.72 mmol C/m^2/day.

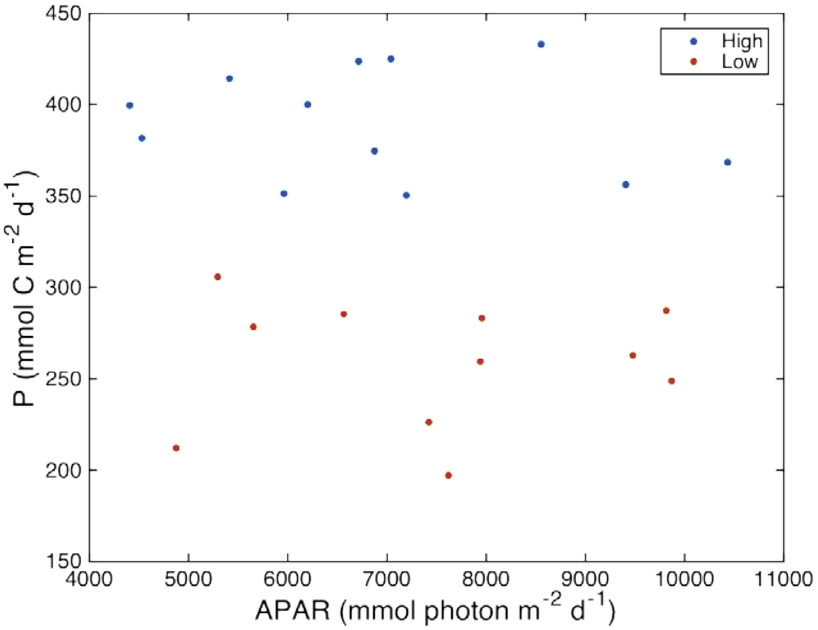

Figure 9: The relationship between gross primary productivity (P) and APAR for the 28°C (blue) and 25°C (red) communities.

Discussion

Higher Temperature, Higher LUE

The LUE of the coral community in the 28°C seawater was significantly higher than the LUE of the coral community at 25°C. This suggests that the photosynthetic machinery of the coral have an elevated ability to operate at higher temperatures. Therefore, during warmer months, it is predicted that a larger portion of their energy demand is supported through autotrophic mechanisms, which is consistent with previous studies (Coles and Jokiel 1977, Jacques et al. 1983; and Muthiga and Szmant 1987). However, because LUE is comprised of both primary productivity and absorbed light available, it is unclear based on LUE values alone if this is due to increased ability to absorb the light available or increases in primary productivity with a similar amount of available light absorbed. To determine the cause of increased LUE, APAR, and productivity values were further examined.

Upon examination of APAR values, there was not a trend established between APAR and difference in temperature, suggesting that temperature does not affect the amount of available radiation absorbed by a coral community. This was expected because the amount of APAR has been found to be largely dependent on the pigmentation of the colony (Enriquez et al. 2005). The reflectance of the community was not measured during any events of noticeable bleaching or pigment changes and as predicted, APAR was not associated with changes in temperature. Decreases in pigmentation have been noted at low growth temperatures, however this was not measured in the present study (Jokiel and Coles 1977; Raven and Geider 1988). Therefore, in this study, absorptance is independent of temperature. This statement is in agreement with previous studies except for in cases of extreme, prolonged temperature changes in which case bleaching events have been found to occur, leading to decreased light absorption (Raven and Geider 1988; Lesser et al. 1990; Fine et al. 2005).

Primary productivity was higher in colonies incubated at summer temperatures (350.39-432.98 mmol C/m^2/day) when compared to those incubated at fall temperatures (197.17-305.72 mmol/m^2/day) (Fig. 9). Although summer temperatures were compared to fall temperatures in the present study, previous studies measuring gross primary productivity for coral communities in summer versus winter temperatures have similar increases in photosynthesis with the higher temperature group (Howe and Marshall 2001; Anthony et al. 2008; Fujimura et al. 2008). It is hypothesized that this increase in primary production is due to the Q_{10} effect, or the doubling of an organism's metabolic rate with each 10°C rise in temperature due to increased kinetic energy (Sherwood et al. 2013). The results suggest that a significant portion of the increased LUE with temperature can be explained by an increase in the coral community's primary production.

Climate Change & Coral Bleaching

It is expected that this increase in LUE only occurs until a threshold temperature because studies have also shown that a temperature increase 2-3°C above ambient summer temperatures results in gradual to moderate bleaching by expulsion of zooxanthellae (Lesser et al. 1990; Jorkiel and Coles 1977). However, further research is needed to determine the point at which decreased LUE begins to occur. This has implications with respect to the projected sea surface temperature changes due to climate change. Within the past thirty years, winter sea surface temperatures in Bermuda have increased by 1.6°C ± 0.4 °C (Fig. 10). For this reason, it is important to continue measuring coral productivity over gradually increasing summer temperatures for a prolonged period of time to determine if coral are able to acclimate to these higher temperatures.

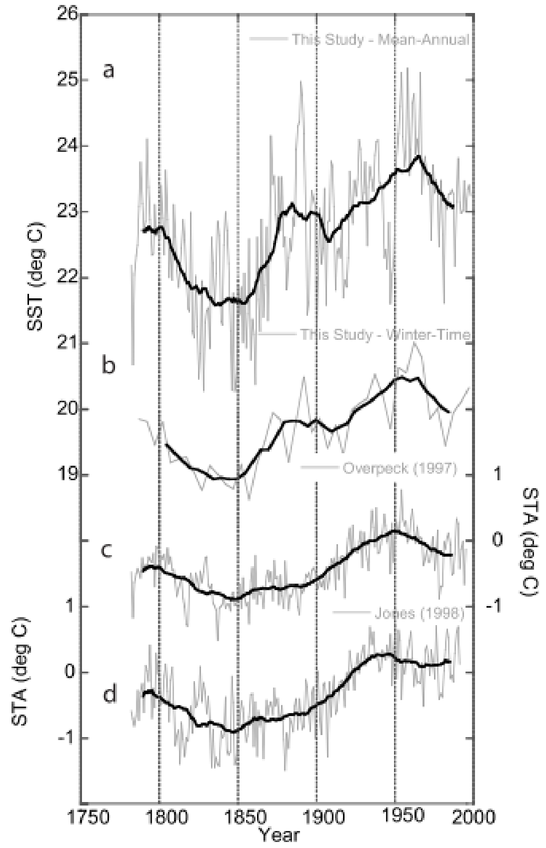

Figure 10: Mean annual and winter Sea Surface Temperature for 5 years reconstructed from coral skeleton strontium to calcium ratio (a and b), filtered records of Artic (c) (Overpeck et al. 1997) and Northern Hemisphere (d) (Jones et al. 1998) reconstructed surface temperatures. The temperature findings from coral skeleton agreed with the records from Overpeck and Jones. By N.F. Goodkin et al., 2008, Sea surface temperature and salinity variability at Bermuda during the end of the Little Ice Age. *Paleoceanography 23*, 3.

Higher LUE as a Result of More Primary Production

The increase in productivity with temperature, rather than a decreased APAR, partially explains the increased LUE for summer temperatures. Although the results suggest temperature does not affect corals’ ability to absorb light, it does affect the capacity to use it. This suggests that lower temperature cause stress to the photosynthetic machinery of the zooxanthellae, while summer temperatures allow the machinery to operate at a higher level. However, previous studies have measured that moderate thermal stress causes coral to expel an increased proportion of damaged zooxanthellae (Lesser et al. 1990; Weis 2008; Fujise et al. 2014). The present study did not directly measure specific enzyme activity within the zooxanthellae and therefore it is unknown the exact process by which the LUE was increased in the higher temperature treatment.

There was also a significant increase in LUE values for the lower temperature group over the eleven days in which this was measured (Fig. 8) and an observable increase in the higher temperature group (Fig. 8). As the temperature was held constant at the ambient temperature on the reef at the time of collection, this may have been caused by continued acclimation to the low light environment of the flume. The coral communities used in the study were collected from an average of 3.5 meters. At this depth in October the irradiance was an estimated 20 mol photons/m^2/day (Frouin et al. 2007). The irradiance in the flume was an average of 8 mol photons/ m^2/day. Although both communities had increases in LUE over time, the higher temperature group was acclimated for a longer period of time prior to the experiment (3 months as compared to 5 days), which may explain why the increase in LUE was not significant. It is possible that if the study had continued the LUE may have increased for both groups as they continued enhancing their ability to photosynthesize in the flume.

LUE & Remote Sensing

LUE appears to be a useful measure of coral condition, however adaptation of its use in remote sensing will require further studies on the effects of various environmental influences. Measuring LUE under various stressors in the lab will help determine whether there are predictable trends in the changes in LUE under variation in pH, temperature, or nutrients, which can accelerate the process of evaluation through remote sensing, as has been previously studied with land plants (Monteith 1977; Osmond et al. 1987; Field 1991). Knowing how certain factors impact LUE will be useful for observation of the effects of climate change and allow detrimental effects to be detected before additional ones occur. Much of the current research for measuring coral condition through remote sensing will be highly beneficial for determining LUE of reefs, such as mapping the composition of the reef to determine the areas that are relevant for measuring productivity (Hochberg & Atkinson 2008; Hochberg 2011). Until LUE has been further developed, remote sensing studies will continue to provide invaluable information about the status of coral reefs throughout the world.

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