TITLE:

In-situ measurement of metabolic status in three coral species from the Florida Reef Tract

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Abstract:
The goal of this study was to gain an understanding of intra-and inter-specific variation in calcification rate, lipid content, symbiont density, and chlorophyll *a* of corals in the Florida Reef Tract to improve our insight of *in-situ* variation and resilience capacity in coral physiology. The Florida Keys are an excellent place to assess this question regarding resilience because coral cover has declined dramatically since the late 1970s, yet has remained relatively high on some inshore patch reefs. Coral lipid content has been shown to be an accurate predictor of resilience under stress, however much of the current lipid data in the literature comes from laboratory-based studies, and previous *in-situ* lipid work has been highly variable. The calcification rates o three species were monitored over a seven-month period at three sites and lipid content was quantified at two seasonal time points at each of the three sites. *Montastraea cavernosa* had the highest mean calcification rate (4.7 mg cm^{-2} day^{-1}) and lowest mean lipid content (1.6 mg cm^{-2}) across sites and seasons. In contrast, *Orbicella faveolata* and *Porites astreoides* had lower mean calcification rates (2.8 mg cm^{-2} day^{-1} and 2.4 mg cm^{-2} day^{-1}, respectively) and higher mean lipid contents (3.5 mg cm^{-2} and 2.3 mg cm^{-2}, respectively) across sites and seasons. Given the recent Endangered Species Act (ESA) listing of *O. faveolata* and the relative persistence of *M. cavernosa* and *P. astreoides* on a population-scale, this study suggests that the hypothesis that coral lipids are good indicators of resilience may be species-specific, or more complex and interrelated with other environmental factors than previously understood. Additionally, coral lipid storage under benign thermal conditions may differ from lipid storage before, during, and after thermal stress events.

Introduction:

Corals reefs are biodiverse ecosystems with numerous cultural, economic, medical, and recreational values (Costanza et al. 1997). Today's coral reefs are facing multiple stressors including, but not limited to, anthropogenic pollution, nutrification, overfishing, habitat destruction, and climate change. The detrimental effects of these stressors on coral reefs are well-established, but the metrics and baselines that should be used to improve science-based policy decisions are still somewhat unclear. In order to help protect this important ecosystem and all of its resources, it is imperative to understand which coral species at which sites are going to be most resilient to stress. Resilience is the ability of an organism to return to its original state after experiencing a disturbance (Lewontin 1969), and thus resilience is about having the means to overcome stress. Following the disappearance of Acroporid corals in the Caribbean, massive coral species with slower growth rates, i.e. *Montastraea* species, have become primary reef builders, and weedy corals, i.e. *Porites* species, have started to increase in abundance (Alvarez-Filip et al. 2009). Specifically, *Montastraea cavernosa* and *Porites astreoides* were found to be some of the most abundant coral species on today's Caribbean reefs (Alvarez-Filip et al. 2011; Alvarez-Filip et al. 2013). Identifying coral species that will be "winners" and "losers" on reefs of the future, as well as sites to focus stronger conservation efforts on, have become major foci of the field of coral eco-physiology and conservation science.

Lipid content in reef-building corals represents an alternative source of fixed carbon that can be used to maintain vital processes under stress, i.e. calcification and daily metabolism (Grottoli et al. 2006; Rodrigues and Grottoli, 2007; Anthony et al. 2009). Different species may partition their resources (use for calcification vs. use for reproduction vs. general storage) differently and this allocation differential may affect resilience to bleaching and other stressors.

Due to the fact that stored lipids can serve as energy reserves during times of stress, measuring lipid content may be an accurate predictor of the potential resilience capacity of a certain species.

The density of a coral's symbiotic algal population is also a good proxy for overall coral condition and health because the symbiosis between the coral host and its zooxanthellae is the fundamental building block of reef-building coral success (Davy et al. 2012). Under normal, unstressed conditions, a coral may receive up to 95% of its daily metabolic requirements from the transfer of photosynthate from the symbiont to the coral (Muscatine 1990). Therefore, the amount of chlorophyll *a*, the major photosynthetic pigment of coral's symbiotic algae, is also a good indicator of the status of the symbiont. Lipids and zooxanthellae density have been shown to vary considerably by coral species, reef site, sampling season, and sampling year (Fitt et al. 2000; Teece et al. 2011; Pisapia et al. 2014), and thus trying to compare results between studies where one or more of these factors differ can be inconclusive. Due to the variability associated with these parameters, as well as the fact that many sites have changed since early observations were published, it is important to continue to monitor the parameters that could indicate capability for resilience or indicate a 'red flag' regarding sites or species in distress. Additionally, measuring these metabolic indicators could give us more insight into coral condition (and stressor-response mechanisms) than the typical population-level (percent live coral cover) monitoring programs do, i.e. it may be instructive to measure coral condition before the corals experience stress events instead of just measuring the loss of live colonies following disturbances.

Millions of people visit coral reefs in the Florida Keys every year, and these reefs are estimated to have an asset value of $7.6 billion (Johns et al. 2001). Unfortunately, coral reefs in the Florida Reef Tract have experienced dramatic declines in coral cover since the late 1970s

(Dustan and Halas, 1987; Porter and Meier, 1992). This decline has continued after the 1997-1998 El Nino event and since then has been mainly due to the continued attrition in the *Orbicella annularis* species complex (Ruzicka et al. 2013; Toth et al. 2014). An exception to this trend is found on some inshore patch reefs of the Florida Reef Tract where coral cover and growth have remained relatively high (Lirman and Fong, 2007; Ruzicka et al. 2013; Manzello et al. 2015a, 2015b). These inshore reefs of the Florida Keys present an opportunity to study the physiology behind this observed resilience success. Possible hypotheses for resilience are coral thermal acclimatization/adaption to higher inshore temperatures and/or relatively high inshore aragonite saturation states due to proximity to seagrass beds (Lirman and Fong, 2007; Soto et al. 2011; Manzello et al. 2015a), or inshore turbidity helping to ameliorate bleaching stress via shading (Zepp et al. 2008; Ayoub et al. 2009). Previous work exploring other mechanisms for resilience, such as elevated lipid content given the potential for increased heterotrophy due to increased turbidity (Teece et al. 2011), have been inconclusive as lipid content can be highly variable for the same species due to differing nutrient levels and plankton abundance on reefs. However, using lipids as a metric for resilience may prove to be useful when comparing between a few dominant reef-building species at specific sites and time points. Many studies to date on coral calcification and lipids as indicators of resilience to stress have been assessed in laboratory settings. Less is known regarding *in-situ* inter- and intra-specific variation with respect to calcification and lipid content.

The purpose of this study was to quantify inter-and intra-specific variation in calcification, lipid content, zooxanthellae density, and chlorophyll *a* in three common species of corals in the Florida Reef Tract at three different sites in two sampling seasons (summer vs. winter). These data will provide an important updated and *in-situ* baseline for coral metabolic

indicators. This baseline will be useful for measuring future change and in comparison with laboratory results on climate change effects.

Methods:

Collection

Three species of scleractinian corals, *Porites astreoides*, *Montastraea cavernosa*, and *Orbicella faveolata*, were collected in August 2013 and March 2014 from three different sites throughout the Florida Reef Tract. The coral fragments used in this study were the same ones presented in Manzello et al. (2015b) and detailed information on sampling and collection can be found there. Briefly, coral fragments (9-16 cm^2) were obtained with hammer and chisel from healthy parent colonies in 2010. One to two fragments were collected per parent colony. The fragments had been previously affixed to cement plugs using All-Fix epoxy and were secured to the seafloor on PVC frames that were approximately 1 m L x 0.5 m W x 0.5 m H. PVC frames were affixed to rebar that had been hammered into the reef framework substrate and were maintained at these sites through the end of the present study (March 2014). The three sites were Lower Keys Inshore (LKI) by Marker 50A (24.59723N, 81.45505W), Upper Keys Inshore (UKI), also known as Tavernier Rocks (24.9398ºN, 80.56272ºW) and Upper Keys Offshore (UKO), also known as Little Conch Reef (24.94650ºN, 80.50207ºW). A map of the collection sites is shown in Figure 1. All sites were approximately four to six meters maximum depth. Approximately five individuals per species (x three) per site (x three) per season (x two) were collected totaling approximately 90 measurements per parameter, although there was some mortality over the seven month study. Corals were retrieved by SCUBA divers at each sampling point, cleaned of all non-coral flora and fauna, and transported on ice back to the University of Miami to be analyzed for calcification, total lipid content, zooxanthellae density, and chlorophyll

a content. HOBO loggers were deployed at all reefs sites during the seven month study to monitor sea temperature data, but unfortunately only the loggers at UKI and UKO were able to be retrieved. Molasses Reef (MLRF1) (25.012 N, 80.376 W) data from the Coastal Marine Automated Network (C-MAN) was obtained from www.ndbc.noaa.gov and used as a quality control reference to compare with the HOBO logger data from the upper keys sites.

Calcification, total lipid content, zooxanthellae density, and chlorophyll *a* content

Calcification was measured using the buoyant weight technique (Davies et al. 1989) in August 2013 and March 2014. Therefore, the calcification rate data shown is integrated over this seven month period. To analyze the other three parameters, coral tissue was removed from the skeleton using the air-brush technique (Szmant et al. 1990) and homogenized for 30 seconds. The aliquot for total lipids (three mL) was filtered onto a glass fiber filter (GF/A) and frozen at -80ºC until further analysis. Analysis followed that of Teece et al. (2011). Briefly, total lipids were extracted three times with two mL of 1:1 dichloromethane:methanol and five minutes of vortexing. The resulting organic extracts were collected, dried under a stream of nitrogen gas, weighed on an analytical balance (Mettler AE 200) and normalized to surface area.

One mL of total blastate was placed in a 1.5 mL Eppendorf tube filled with 50µL of Lugols solution to be used for manual zooxanthellae counts via microscopy. Samples were vortexed for ten seconds, and counted twice in independent replicate counts with a haemocytometer (Hausser Scientific) using a VistaVision compound microscope at 100× magnification. Zooxanthellae density was normalized to surface area. Lastly, one mL of total blastate was filtered onto a glass fiber filter (GF/A) for chlorophyll *a* analysis and frozen at -80ºC until further analysis following Holm-Hansen and Riemann (1978). Briefly, chlorophyll *a* samples were analyzed on a fluorometer (TD-700 Turner Designs) calibrated with purified

chlorophyll *a* (Sigma-Aldrich catalog no. C6144). Pigment content was normalized to coral surface area.

Surface area

Corals were scanned using a white light 3D scanner (HDI Advance R2, 3D3 Solutions) calibrated with a five mm glass calibration board following Enochs et al. (2014). Each coral sample was scanned from two different angles eight times while rotated 360 degrees around a central axis. The resulting sixteen scans were aligned and compiled into a single mesh using the FlexScan3D software package. Each mesh was exported as a .stl file and imported into Leios II, where surface area was calculated.

Statistics

All statistical analyses were completed in the program JMP version 12.0.0. Because it is well-established that calcification rates vary by species, rather than run a two-way ANOVA of site x species for calcification rate, we chose to run a one-way ANOVA with site as the main factor for each species separately. Season was not tested as a main factor for calcification due to the fact that calcification rate was integrated over the seven month period. Full-factorial two-way ANOVAs (site, season, and the interaction between site and season) were run for the dependent variables lipid content, zooxanthellae density and chlorophyll *a* for each species. Normality and homoscedasticity were ascertained prior to testing each dependent variable using a Shapiro-Wilk test and Levene's test, respectively, and all assumptions were met prior to running ANOVA models. If significant differences were found, a *post-hoc* test (Tukey's HSD) was run to determine where the differences were. Alpha for all tests was set at 0.05.

Results:

Calcification rate was significantly affected by site in *M. cavernosa* and *P. astreoides*, but not in *O. faveolata* (Table 1, ANOVA, $p<0.05$). For *M. cavernosa*, UKO calcification rates (6.9

mg cm^{-2} day^{-1}) were significantly higher than LKI rates (2.5 mg cm^{-2} day^{-1}) (Fig. 2a). For *P. astreoides*, LKI rates (4.0 mg cm^{-2} day^{-1}) were significantly higher than UKI rates, which were essentially zero (Fig. 4a). *M. cavernosa* had the highest combined mean calcification rates of the three species pooled across sites and seasons (4.7 mg cm^{-2} day^{-1}, Table 3). *O. faveolata* and *P. astreoides* had lower mean calcification rates pooled across all sites and seasons (2.8 and 2.4 mg cm^{-2} day-1, respectively, Table 3).

Lipid content was significantly affected by season in *P. astreoides*, the interaction between site and season in *O. faveolata*, and was not significantly affected by any factors in *M. cavernosa* (Table 2, ANOVA, $p<0.05$). *M. cavernosa* had the lowest mean lipid value of the three species pooled across sites and seasons (1.6 mg cm^{-2}, Table 3), whereas *O. faveolata* and *P. astreoides* had higher mean lipid values across all sites and seasons (3.5 mg cm^{-2} and 2.3 mg cm^{-2}, respectively, Table 3). *O. faveolata* lipids had significant differences whereby UKI summer levels were significantly greater than UKI and LKI levels in winter (Fig. 3b, Tukey's HSD, $p<0.05$). In *P. astreoides*, lipid levels tended to be higher in winter than in summer across all sites (Fig. 4b).

Zooxanthellae density was not significantly affected by site or season for any of the three species (Table 2, Fig. 2c, 3c, 4c). Chlorophyll *a* was significantly affected by site for *M. cavernosa*, and by the interaction between site and season for *O. faveolata* (Table 2, ANOVA, $p<0.05$). Generally chlorophyll *a* values at the LKI site were higher than the UKO site for *M. cavernosa* (Fig. 2d). *O. faveolata* had the highest chlorophyll *a* levels in winter at LKI, which were significantly higher than levels at UKI in the summer, as well as UKO in the winter (Fig. 3d).

Mean temperature data are summarized for each month of the study in Table 4 for UKI and UKO. Temperatures at the UKI and UKO sites, as well as the 'quality control' for the Upper Keys (Molasses Reef Buoy) never exceeded local bleaching threshold (30.4°C, Manzello et al. 2007) during the seven month study. Unfortunately, temperature data from LKI were not available over this seven month period. However, historical data from the LKI site indicated that temperatures often exceed 30.4°C in the summer, as they did in 2010 and 2011 (Manzello, In Review, Table 5).

Discussion:

This study quantified the calcification rates of three common coral species in the FRT over a seven month period at three sites in the upper and lower Florida Keys. Calcification rates measured here were comparable to rates of the same three species measured on other reefs in Jamaica, the FL Keys, the Western Atlantic, and Bermuda. Mallela and Perry (2007) found the calcification rates of *M. cavernosa*, *O. faveolata*, and *P. astreoides* in Jamaica were approximately 2.4 mg cm^{-2} day^{-1}, 2.3 mg cm^{-2} day^{-1}, and 1.0 mg cm^{-2} day^{-1}, respectively. These calcification values from Jamaica were lower than values obtained in this study for *M. cavernosa* (4.7 mg cm^{-2} day^{-1}), *O. faveolata* (2.8 mg cm^{-2} day^{-1}) and *P. astreoides* (2.4 mg cm^{-2} day^{-1}). The mean calcification rate for *O. faveolata* colonies from this study was the same as the mean calcification rate from *O. faveolata* cores from the Upper Keys (2.8 mg cm^{-2} d^{-1}) (Manzello et al. 2015a) and very similar to mean rates from the Western Atlantic (2.7 mg cm^{-2} d^{-1}) (Carricart-Ganivet et al. 2012). However, the mean calcification rate in this study for *P. astreoides* colonies *(*2.4 mg cm^{-2} d^{-1}) was higher than calcification rates from *P. astreoides* cores from comparable Upper Florida Keys sites (1.9 mg cm^{-2} d^{-1} at an inshore upper keys site, 1.5 mg cm^{-2} d^{-1} at the same UKO site used in this study, (Manzello et al. 2015b), Bermuda sites, (1.9 mg cm^{-2}

d^{-1}, Venti et al. 2014), and sites in the Western Atlantic off of Cuba and Mexico, (1.5 mg cm^{-2} d^{-1}, Elizalde-Rendon et al. 2010). The summer of 2013 that preceded the time points taken in this study (August 2013 and March 2014) was the coolest since 1996 at Molasses Reef (Manzello, In Review), therefore conditions were theoretically favorable for growth (Manzello et al. 2015a). These favorable conditions may partially explain why *M. cavernosa* and *P. astreoides* had higher growth rates compared to other field studies, and is also consistent with population level trends indicating that *M. cavernosa* and *P. astreoides* are doing well in the FRT (Green et al. 2008; Edmunds et al. 2014). Comparable growth rates for *O. faveolata* in this study compared to those reported from previous Caribbean studies provide a glimmer of hope that calcification has not dramatically declined over the last few years at these specific study sites, despite population level trends indicating drastic declines of *O. faveolata* in this region (Ruzicka et al. 2013).

Looking just within the FL keys, the trend for *M. cavernosa* was that calcification was higher in the upper keys compared to the lower keys. This trend may be partially explained by previous research on the FRT showing that coral calcification in the middle keys is reduced due to the influence of water input from Florida Bay, referred to as the "Inimical Water Hypothesis" (see: Kuffner et al. 2013; Manzello et al. 2015b). Coral growth is thought to be impeded here because Florida Bay water has high turbidity levels (Roberts et al. 1982), variable temperature and salinity (Shinn 1966; Shinn et al. 1989), and elevated nutrients (Szmant and Forrester, 1996). In contrast, the upper keys is characterized by water with a low influence from Florida Bay (Cook et al. 2002), which could explain more favorable growth in the upper keys. The upper keys have a low influence from FL bay waters because flow out of the bay through Hawk Channel generally flows in a southwest direction (Pitts 1994), i.e. toward the lower keys. The water exiting FL Bay is very hot with high salinity in the summer, and very cold in the winter

(Manzello et al. 2012, 2015b). These data may support the inimical water hypothesis to explain why growth at the LKI site was lower for *M. cavernosa,* but still do not explain why calcification in *P. astreoides* at the UKI site was poor. Still, based on comparisons to other field study calcification rates, these data agree with previous hypotheses that *M. cavernosa* and *P. astreoides* may be "winners" in the FRT and larger Caribbean region.

Lipid content in this study was affected by season in *P. astreoides*, and by the interaction between site and season in *O. faveolata*. An interesting pattern may have emerged with respect to lipids and reproduction, as brooding *P. astreoides* had higher lipid content during the March sampling, right before they theoretically should be getting ready to spawn in April and May (McGuire 1998). Similarly, lipids were elevated in broadcast spawner *O. faveolata* in the summer at UKI, theoretically right before spawning in August and September (van Veghel and Bak 1994). This data for *O. faveolata* is generally consistent with Harland et al. (1992, 1993) and Oku et al. (2003) who found lower coral lipid values in winter months, which they attributed to reduced temperatures and light conditions, reducing photosynthetic activity of the coral symbiont, and thereby reducing the amount of photosynthate transferred to the coral as lipids. Cruz-Piñón et al. (2003) also found that tissue layer thickness, a proxy for lipid content, was lower in *O. faveolata* in the winter (February) compared to the summer (August). This data suggests that *in-situ* lipids may largely be driven by the reproductive status of the coral.

While reproductive status certainly appears to affect lipid content, it is also important to consider the potential contribution of heterotrophic feeding to lipids. Although many essential fatty acids, the building blocks of lipids, can be translocated to the coral from its symbionts, heterotrophic feeding on zooplankton and/or particulate organic matter can also provide significant amounts of lipids and fatty acids for the coral host (Imbs et al. 2010; Teece et al.

2011). Edmunds (1986) hypothesized that low lipid levels in corals could be attributed to the species being largely autotrophic as opposed to heterotrophic, suggesting that larger lipid levels may be indicative of greater usage of heterotrophy. Therefore, the higher mean lipid levels found in this study for *O. faveolata* and *P. astreoides* may be attributed to greater usage of heterotrophy. In contrast, lower lipid levels in *M. cavernosa* and lack of seasonal or site changes may suggest that *M. cavernosa* is not a species that uses a great degree of heterotrophic feeding. Heterotrophic feeding is contingent on the immediate area surrounding a coral i.e. turbidity, nutrient, and light levels, and possibly reproductive status (Lirman and Fong, 2007; Teece et al. 2011), and is also highly species-specific (Ferrier-Pagès et al. 2010). These data showing higher mean lipid content in *O. faveolata* and *P. astreoides* indicate that they may exhibit greater plasticity in their ability to switch from autotrophic to heterotrophic nutritional inputs. This hypothesis agrees with Teece et al. (2011), who asserted that heterotrophy may provide up to 50% of the fatty acids found in *O. faveolata* and *P. astreoides*, which may become important when a coral experiences bleaching, whether from thermal stress or natural seasonal changes in symbiont parameters.

In this study, zooxanthellae density and chlorophyll *a* levels tended to be higher in the winter time than in the summer time. Fitt et al. (2000) noted that symbiont parameters tend to peak in the winter because in summer corals often undergo seasonal "bleaching" events where symbiont populations are reduced due to exposure to higher temperatures and irradiance levels, even when those bleaching events are not fatal. The symbiont and chlorophyll data from this study were largely consistent with Fitt et al. (2000); however, certain species did experience peaks in these parameters in summer at certain sites. This finding may be due to the fact previously mentioned that the summer that preceded the first time point of this study (August

2013) was the mildest summer in nearly 20 years (Manzello, In Review). Summer 2013 in the FRT was not characterized by any major bleaching events, and thus perhaps symbiont parameters were not reduced during the summer due to lack of severe thermal stress, but were reduced in winter in some cases due to reduced light and temperature, etc. This data highlights the importance of continued monitoring, as trends from older FRT field work papers may no longer provide generalizable baseline values.

It is of interest to note that symbiont data reported herein were lower than previously published studies. While many Caribbean studies report mean symbiont density and chlorophyll *a* values ranging from 1.0-3.0 x 10^6 cells cm^{-2} (Gleason 1993; Fitt et al. 2000) and 4-6 µg cm^{-2} (Meyers et al. 1999; Lesser et al. 2000), respectively, lower values are not necessarily abnormal and certainly in the range of previous published literature, especially in degraded reef areas such as the FRT. There is precedent for *M. cavernosa* chlorophyll *a* levels ranging from 0.6-1.0 µg cm^{-2} (Costa et al. 2004), and symbiont densities on the order of 6.0 x 10^5 cells cm^{-2} (Cruz et al. 2015). Inshore reef sites tend to be more turbid with less light availability than offshore sites (Lirman and Fong, 2007; Wagner et al. 2010), contributing to lower symbiont densities on inshore relative to offshore sites. Given that two of the three study sites were inshore, this may partially explain low values for both symbiont density and chlorophyll *a*. However, it is important to note that the low values presented here are indicative of corals in less than ideal ranges for symbiont parameters, which should continue to be monitored in the FRT.

Summary in context with population-level trends

This study implies that lipid content may not necessarily be an accurate predictor of *in-situ* inshore resilience in the context of population level trends in the FRT. Anthony et al. (2007, 2009) found that lipid content below 1.0 mg cm^{-2} in the Pacific coral *Acropora intermedia* was a

threshold level below which triggered high mortality following a bleaching event. Based on previous studies and models showing that lipids are good indicators of resilience, our data would suggest that *O. faveolata* and *P. astreoides* would be more resilient following thermal stress than *M. cavernosa*. However, *M. cavernosa* and *P. astreoides* are more stress and heat tolerant than the *Orbicella annularis* species complex, which has undergone such a drastic, recent decline that it is now an ESA-listed species (Bruckner and Bruckner, 2006; Edmunds and Elahi, 2007; Bruckner and Hill, 2009; Ruzicka et al. 2013; Edmunds et al. 2014; National Marine Fisheries Service 2014). The relative abundance of *P. astreoides* has significantly increased in the Caribbean (Green et al. 2008). Cover, both absolute and relative, of *M. cavernosa* has not changed on the FRT or across the wider Caribbean (Ruzicka et al. 2013; Edmunds et al. 2014). Therefore, lipid content as an indicator of resilience may need to be examined on a species-specific basis, or *in-situ* lipid content may simply be driven by the reproductive cycle, and thus multiple years of data would be necessary to sort out the annual variation in lipid storage and how that relates to environmental variables.

Additionally, the metabolism of coral lipid content during benign thermal conditions like those that coincided with this study may differ from what occurs before, during, and after warm-water bleaching and other stress events. Recent evidence indicates that elevated lipid reserves can protect corals from climate change stress by allowing them to maintain their calcification rates (Rodrigues and Grottoli, 2007; Towle et al. 2015). It is important to put these data in context because in this study we observed that under *in-situ* non-stress scenarios, a low lipid content (1.6 mg cm^{-2}) appeared to favor high calcification rates in *M. cavernosa*. Compare this finding to the idea that when a coral is undergoing a laboratory-induced stress, increasing its lipid stores can provide it with the extra energy it needs to maintain daily calcification and

metabolism on the shorter-term. The two findings are not mutually exclusive, but rather, may shed light on an important and contextual balance between calcification and lipids. Under normal non-stressed conditions, a coral might benefit from a moderate balance between growing enough and storing enough lipid reserves. However, when stressed, the coral may benefit from increasing lipid reserves to use when calcification is suffering due to bleaching and/or acidification stress. Future research is needed to improve our understanding of how coral lipids are metabolized under ambient *in-situ* conditions versus under metabolic stress scenarios, especially with respect to the potential to confer resilience in the FRT.

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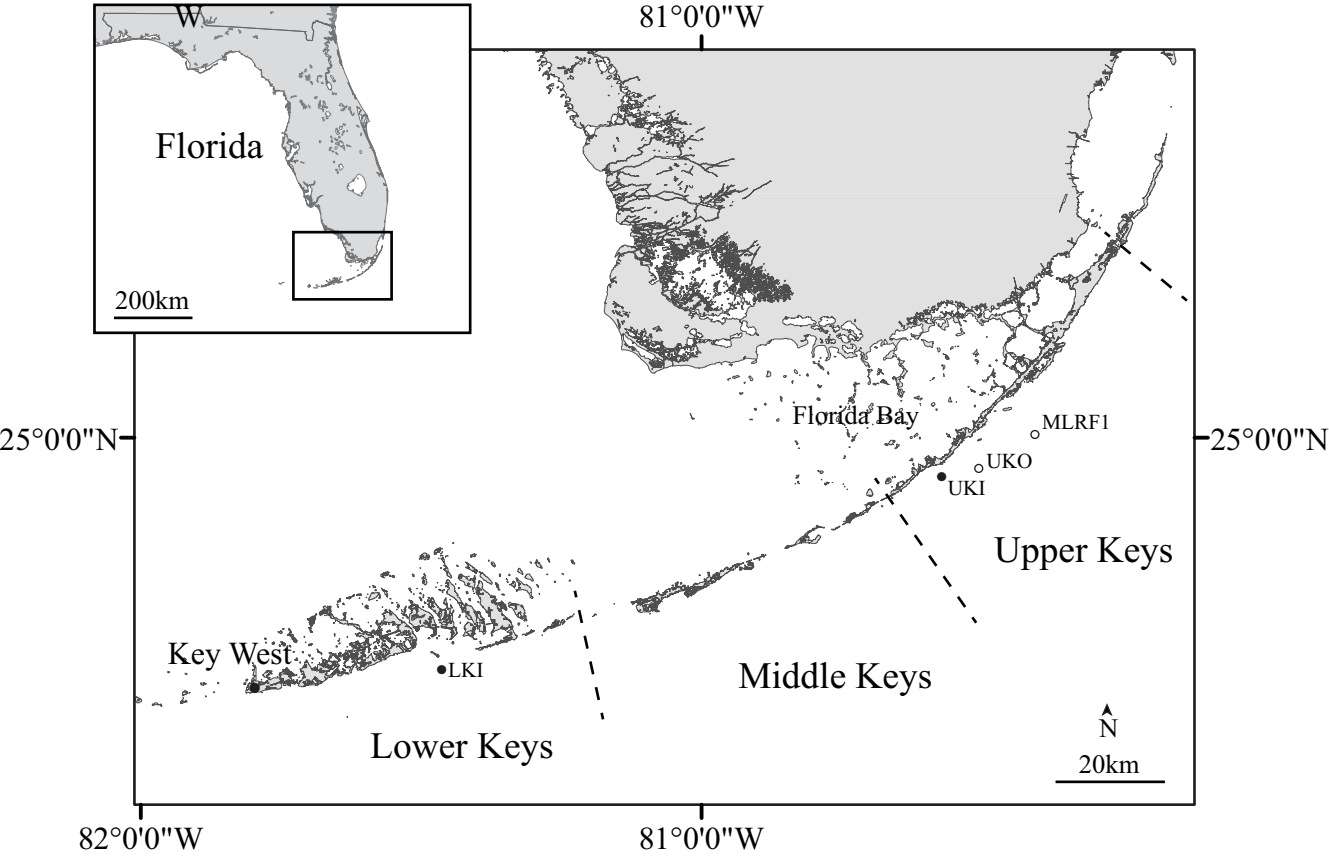
Figure Legends:

Figure 1: Map of the Florida Keys portion of the Florida Reef Tract adapted from Manzello et al. 2012. Study sites are depicted by black dots and labeled with site acronym.

Figure 2: *Montastraea cavernosa* a.) Calcification rates at each of the three sites over the course of the seven month study, and b.) Lipid content, c.) Zooxanthellae density, and d.) Chlorophyll *a* level at each site in each season. Dark grey bars represent winter sampling, while light grey bars represent summer sampling. Bars marked with dissimilar letters are statistically different based upon Tukey's HSD *post-hoc* test. Error bars represent ± 1 S.E and n = 5 coral fragments per bar.

Figure 3: *Orbicella faveolata* a.) Calcification rates at each of the three sites over the course of the seven month study, and b.) Lipid content, c.) Zooxanthellae density, and d.) Chlorophyll *a* level at each site in each season. Dark grey bars represent winter sampling, while light grey bars represent summer sampling. Bars marked with dissimilar letters are statistically different based upon Tukey's HSD *post-hoc* test. Error bars represent ± 1 S.E. and n = 5 coral fragments per bar.

Figure 4: *Porites astreoides* a.) Calcification rates at each of the three sites over the course of the seven month study, and b.) Lipid content, c.) Zooxanthellae density, and d.) Chlorophyll *a* level at each site in each season. Dark grey bars represent winter sampling, while light grey bars represent summer sampling. Bars marked with dissimilar letters are statistically different based upon Tukey's HSD *post-hoc* test. Error bars represent ± 1 S.E. and n = 5 coral fragments per bar.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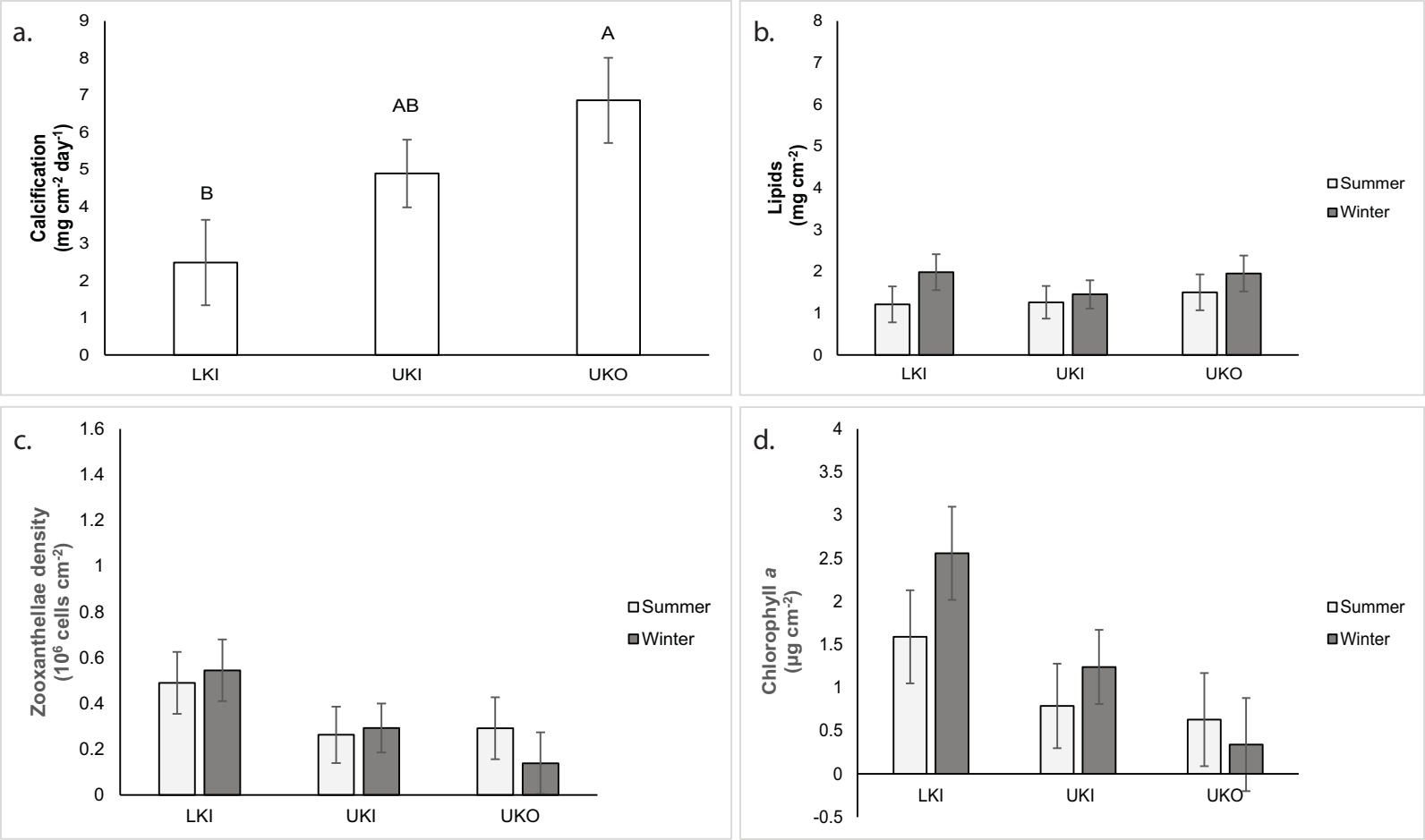
a.
Calcification (mg cm-2 day-1)
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Lipids (mg cm-2)
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UKI
UKO
c.
Zooxanthellae density (10^6 cells cm-2)
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d.
Chlorophyll a (µg cm-2)
Summer
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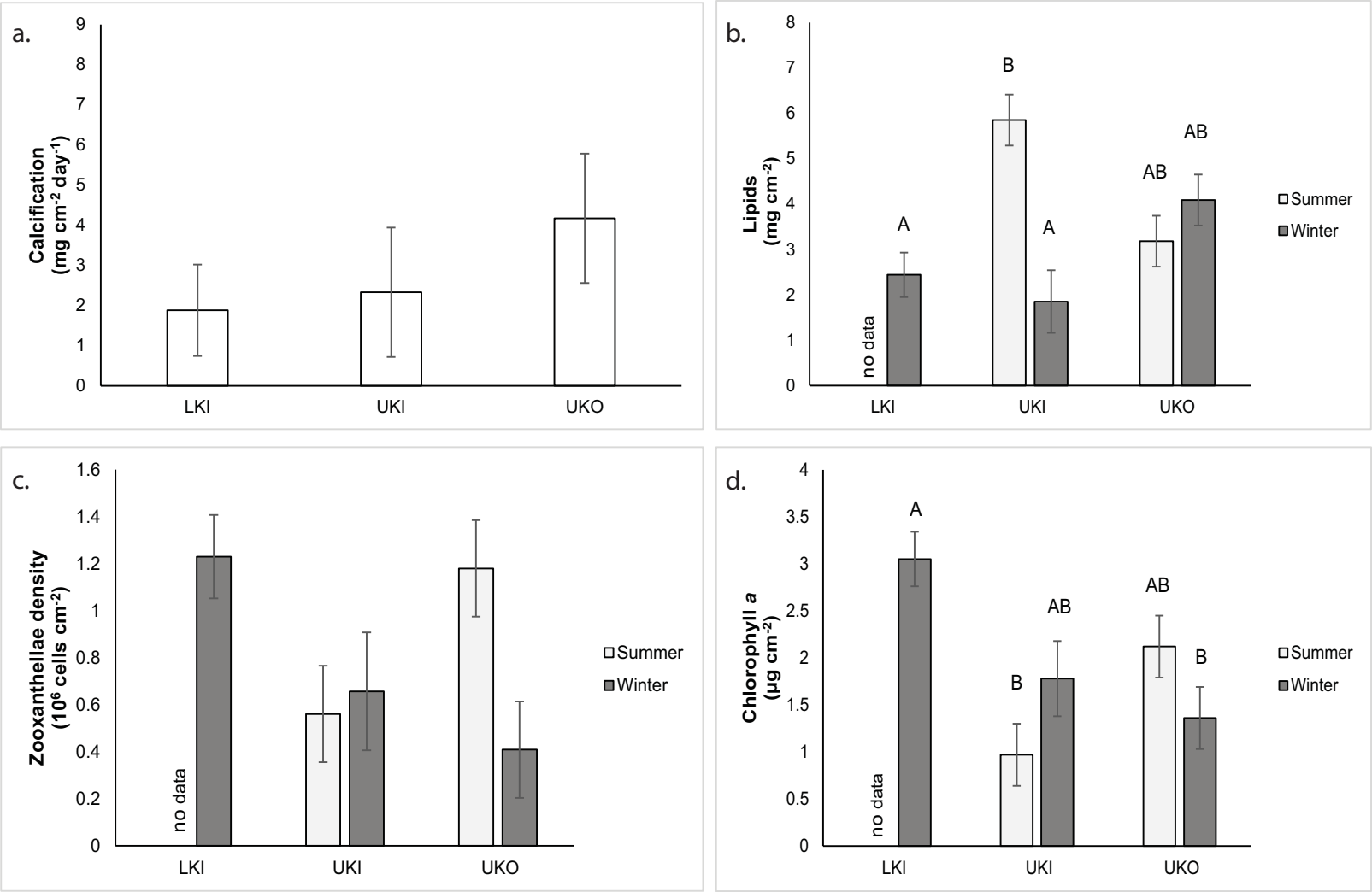
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Calcification (mg cm-2 day-1)
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LKI
UKI
UKO
b.
Lipids (mg cm-2)
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1
2
3
4
5
6
7
8
no data
A
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AB
LKI
UKI
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Summer
Winter
c.
Zooxanthellae density (10^6 cells cm-2)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
no data
LKI
UKI
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Summer
Winter
d.
Chlorophyll a (µg cm-2)
0
0.5
1
1.5
2
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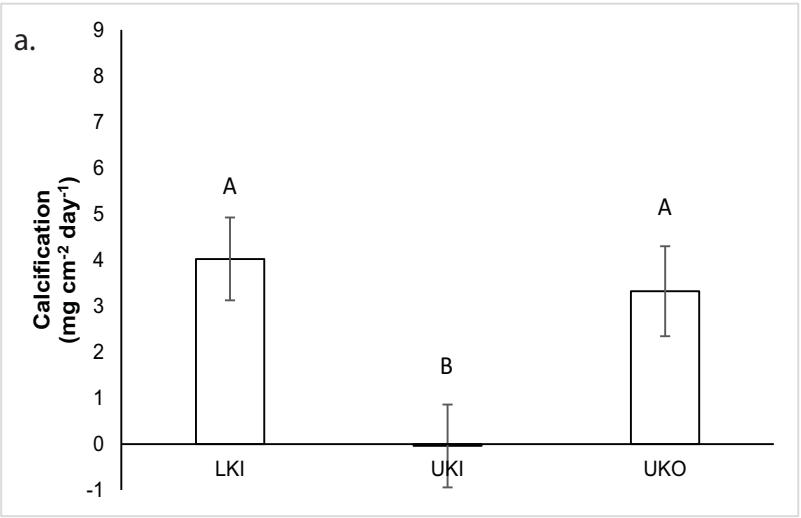
Summer
Winter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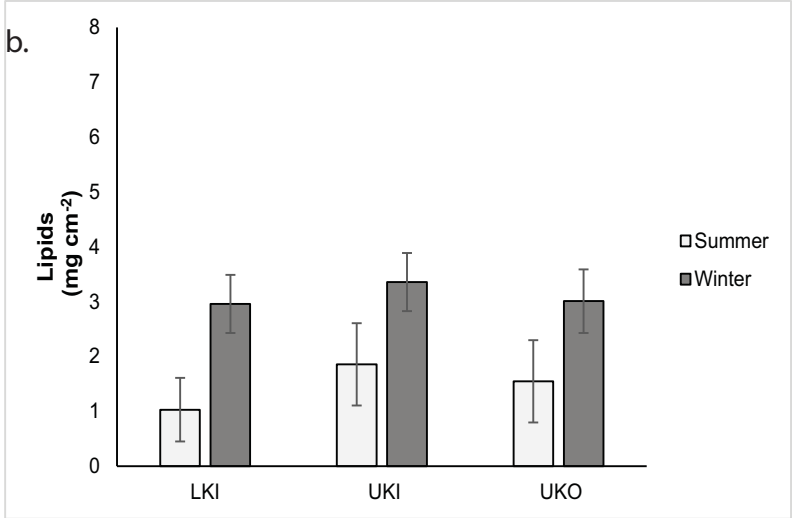
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Lipids (mg cm-2)
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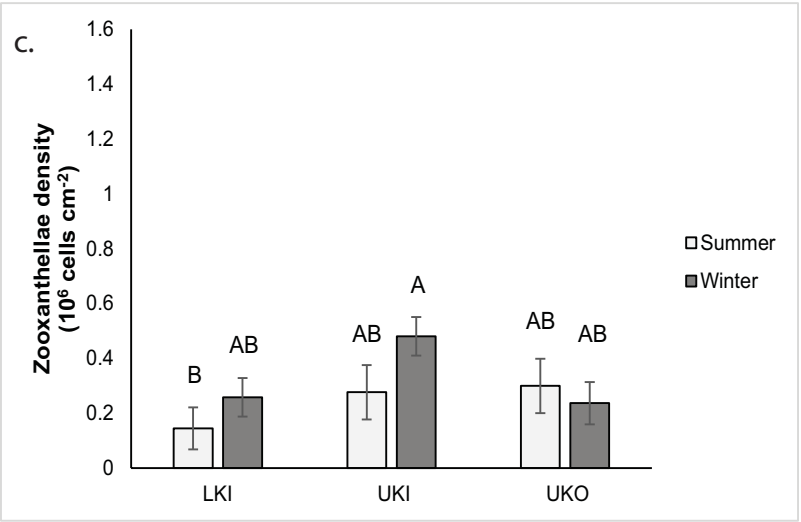
c.
Zooxanthellae density (10^6 cells cm-2)
1.6
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Summer
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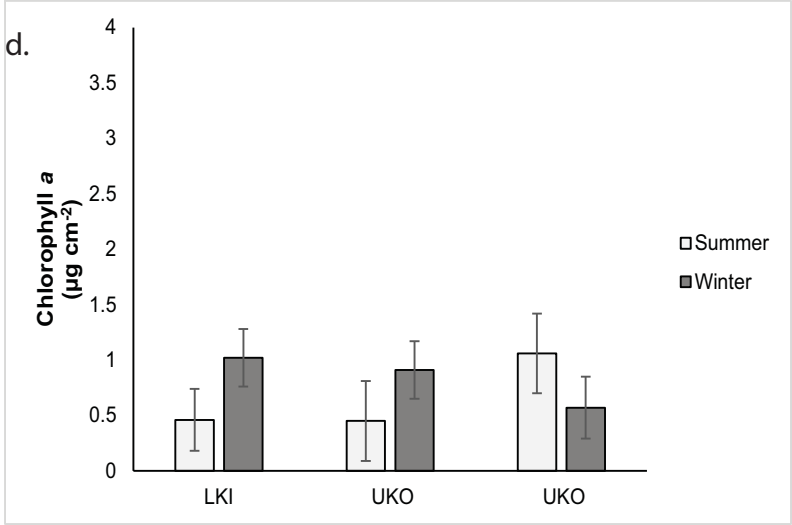
d.
Chlorophyll a (µg cm-2)
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1
0.5
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Summer
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