Elevated maximum temperatures and high-magnitude thermal variability drive low coral diversity on nearshore lagoonal reefs in Belize

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ABSTRACT

**Aim** Coral reefs are increasingly threatened by interactions of global and local anthropogenic stressors, two of the most prominent being rising seawater temperature and nutrient enrichment. We aim to determine how spatiotemporal variations of environmental stressors across a reefscape determine which coral species are most successful during this climate change interval.

**Location** Belize, Central America

**Methods** Thirteen lagoonal reefs on the Belize Barrier Reef System (BBRS) were surveyed to investigate the influence of temperature and nutrient history on coral community structure across reefsapes. A novel metric was developed using ultra-high resolution sea surface temperature (SST) records to classify reefs as enduring low temperature parameters (lowTP), moderate temperature parameters (modTP), or extreme temperature parameters (extTP) based on four thermal parameters known to be important drivers of overall reef health.

**Results** Coral species richness, abundance, diversity, density, and percent cover were lower at extTP sites compared to lowTP and modTP sites, but these reef community traits did not differ between lowTP and modTP sites. Coral life history strategy analyses indicated that extTP sites were dominated by hardy stress-tolerant and fast growing weedy coral species, while lowTP and modTP sites included competitive, generalist, weedy, and stress-tolerant coral species.

**Main Conclusions** Coral community differences between extTP and lowTP/modTP sites were primarily driven by temperature differences. While the influence of nutrients on reef community traits was minimal, bulk nutrient concentrations likely affected percent coral cover. Lack of community scale differences between lowTP and modTP sites is likely driven by low-magnitude thermal variations in these reef locations. Dominance of weedy and stress-tolerant genera at extTP sites suggests that corals utilizing these two life history strategies may be better suited to cope with IPCC projected ocean warming conditions. Our results reveal that temperature is the primary driver of differences in coral community composition among these distinct reef environments.
INTRODUCTION

Coral reefs are threatened globally due to interactions of anthropogenic impacts such as warming from increasing greenhouse gas emission, excessive agricultural runoff, overfishing, and habitat destruction (Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Frieler et al., 2013). Of particular concern are increasing greenhouse gas emissions that are leading to significant warming of the oceans (Hughes et al., 2003; Donner et al., 2005). This warming trend is especially troubling in the Caribbean, where rates of warming are higher than in many other tropical basins (Chollett et al., 2012), and where coral cover has declined up to 80% in recent decades (Gardner et al., 2003). Elevated sea surface temperature (SST) is the major cause of the breakdown of essential coral-algal symbiosis, which can ultimately lead to mass coral bleaching (Jokiel & Coles, 1990; D'Croz et al., 2001) and these bleaching events are projected to increase in frequency and severity as the climate continues to warm (Donner et al., 2005; Wooldridge et al., 2005). The Caribbean Sea is expected to be severely affected by warming as corals are extremely sensitive to even small temperature increases of less than 1°C (McWilliams et al., 2005). In fact, the Caribbean is predicted to suffer bleaching events biannually within the next 20-30 years (Donner et al., 2007) with predicted annual bleaching events occurring as soon as 2040 (van Hooidonk et al., 2015). Caribbean-wide and global scale bleaching events are predicted to continue through the end of the century unless corals can increase their thermal tolerance at a rate of 0.2-1.0 °C per decade (Donner et al., 2005).

Annual or daily thermal variability have recently been identified as important factors in coral thermal tolerance (Oliver & Palumbi, 2011; Soto et al., 2011; Barshis et al., 2013). Indeed, previous exposure to thermal variability increases a coral’s tolerance to future stress events (Oliver & Palumbi, 2011; Carilli et al., 2012; Castillo et al., 2012; Pineda et al., 2013), and
research suggests that Pacific corals living in areas with a high annual average SST are less susceptible to bleaching (van Woesik et al., 2012; Fine et al., 2013). A recent study has also shown that coral from both the mildest and the most extreme thermal environments can escape mortality during a bleaching event (Pineda et al., 2013). Along the Belize Barrier Reef System (BBRS), corals historically exposed to less thermal variability exhibited slower growth rates and/or greater mortality in response to SST increases (Carilli et al., 2012; Castillo et al., 2012).

In the Florida Keys, coral growth rates and cover were found to be higher in nearshore environments with more variable temperatures than on deeper reefs with more stable temperatures, in spite of higher nutrient concentrations nearshore (Lirman & Fong, 2007). While many studies suggest that extreme temperature variability (prolonged summer warming or extreme daily fluctuation) leads to higher coral resilience (Oliver & Palumbi, 2011; Barshis et al., 2013; Pineda et al., 2013), there is also evidence that corals experiencing moderate long term temperature variability (either average annual or daily variation) are better able to cope with stress (Soto et al., 2011).

Temperature stress is not the only factor leading to Caribbean coral decline. Nutrient enrichment also plays a role and can lead directly to reef degradation (Fabricius, 2005; Kline et al., 2006; Wooldridge, 2009; Wiedenmann et al., 2013; DeCarlo et al., 2015). Specifically, increased dissolved inorganic nitrogen (DIN) has been linked to a reduction of bleaching thresholds (Wooldridge, 2009; Wiedenmann et al., 2013) and has been shown to increase disease and bleaching prevalence on Florida reefs (Vega Thurber et al., 2014). Additionally, macrobioerosion can occur up to 10 times faster in corals in high nitrogen (N) waters compared to corals in low N waters (DeCarlo et al., 2015). Kline et al. (2006) suggested that elevated levels of N, phosphorous (P), and ammonia did not cause substantial coral mortality in
Panamanian corals; instead, elevated levels of dissolved organic carbon (DOC) promoted coral mortality through acceleration of microbe growth on the surface layer of corals.

Although much is known about the influence of temperature and nutrient enrichment on coral health, it is unclear exactly how these stressors interact to affect coral community structure. Community differences induced by anthropogenic stressors may lead to circumstances where reef calcification does not sufficiently counter reef erosion, leading to an overall flattening of reef structure, decline of coral reefs, and shifts from one dominant coral group to another, or from coral to algal dominance (Loya et al., 2001; McManus & Polsenberg, 2004; Alvarez-Filip et al., 2009; Alvarez-Filip et al., 2013). Due to the variety of coral life history strategies and differential response to stress, an overall decline in coral cover and abundance can also be coupled with an increase in abundance of certain coral species (Loya et al., 2001; Darling et al., 2012), as seen in the Caribbean with the recent increase in abundance of ‘weedy’ species, including *Porites astreoides* (Green et al., 2008). Brooding, small, opportunistic corals (weedy) and fast growing (competitive) corals recover faster from stress events, but are more impacted by bleaching events than more stress-tolerant, slower growing species (Darling et al., 2012; Darling et al., 2013). Taken together, this evidence suggests that differential responses between coral species to temperature and nutrient stressors may lead to community scale shifts in composition.

The purpose of the current study was to investigate the influence of temperature and nutrients on coral community composition of lagoonal reefs across the Belize Barrier Reef System (BBRS). A novel GIS-based metric was developed to characterize lagoonal reefs across the BBRS into three thermally distinct regions. Within these three regions, thirteen reef sites were identified and benthic surveys were conducted to quantify coral community composition. Quantifying coral community differences amongst these thermally distinct reefs may help predict
how coral community structure may respond to climate change. In addition, identifying which
areas and species are best able to cope with stress will allow for more targeted management
strategies and for increased protection of vital reef areas that would otherwise be left
unprotected.

MATERIALS AND METHODS

Novel Site Identification

SST Data Assembly

Daily 1-km horizontal resolution sea surface temperature (SST) data were acquired from
JPL’s Multi-Scale High Resolution Sea Surface Temperature (JPL MUR SST) via the Physical
Oceanography Distributed Active Archive Center (PO.DAAC) at the NASA Jet Propulsion
Laboratory, Pasadena, CA (http://podaac.jpl.nasa.gov). Conventional 1-km resolution satellite
SST measurements (infrared, IR) are contaminated by clouds, creating data-void areas.
Microwave (MW) data sets can penetrate clouds to gain better temporal coverage, but with a
much coarser spatial resolution (25 km) (Chin et al., 2013). MUR combines these two datasets to
present a more comprehensive and complete SST product. MUR uses the multi-resolution
variational analysis (MRBA) as an interpolation method to combine high resolution datasets with
more conventional datasets, producing a product that contains no cloud contamination (Chin et
al., 2013). MUR reports foundation SST, or SST at the base of the diurnal thermocline (~5-10m
depth). Comparison of in-situ temperature (recorded by HOBO® v2 data loggers) and MUR
revealed that MUR showed an average negative bias of -0.495±0.01°C relative to in-situ loggers
(Fig S1). Due to the comprehensive coverage, high resolution, range (2002-2012), and lack of
contamination in this dataset, it was ideal for use in the current study.
Site Classification

Multiple thermal parameters were calculated at different temporal resolutions and examined across the thirteen reef sites. In the end, four parameters produced distinct thermal environments across the BBRS: average annual maximum temperature (Fig S2A in Supporting Information), average annual temperature range (Fig S2B), average annual number of days above the regional bleaching threshold of 29.7°C (Aronson et al., 2002) (Fig S2C), and average annual consecutive days above the regional bleaching threshold (i.e., longest potential thermal stress events) (Fig S2D). A metric that combined all four thermal parameters was generated using ArcGIS© in order to assess thermal environments across the BBRS. Data from each of the four parameters in the metric were divided into 8-10 bins (0.5 standard deviations (SD) of the mean) and overlaid on a map of the BBRS (Table 1). Reefs were not present in areas where the value of any single variable was <1 SD below or >2 SD above the mean (across the entire data set from 2002-2012). For all four parameters, areas that were classified in bins ≥1 SD above the mean were designated extreme temperature parameter (ext$_{TP}$) sites (Fig.1A). Moderate temperature parameter (mod$_{TP}$) sites were classified as areas where all values were 0.5 to 1 SD above the average annual temperature range and average annual maximum temperature and within 1 SD of the average annual consecutive days and average annual number of days above the regional bleaching threshold (Fig 1A). Low temperature parameter (low$_{TP}$) sites were classified as bins that were 0.5 SD above the average to 2 SD below the average for annual temperature range and annual maximum temperature and below the average for consecutive and annual days above the regional bleaching threshold (Fig 1A). Using the metric presented in Fig 1A, 15 sites were selected. 13 of these sites were visited and surveyed in November 2014 (2 sites were not surveyed as no corals were located inside of the marked geographic area) (Table 1, Fig 1A).
Benthic surveys

In November 2014, benthic surveys were performed at the 13 sites described above. A team of three divers surveyed a total of 6 transects at each site following AGRRA methodology (AGRRA 2003). Genus and species of each coral was identified and the number and size of individual colonies of each species was recorded on underwater data sheets. After these data were collected, species diversity, abundance, species richness, and coral life history (following Darling et al., 2012) were calculated for each site.

Six video transects (1 m x 20 m) were also performed at each site using GoPro® cameras attached to PVC stabilizing apparatuses allowing each diver to stabilize the camera while performing transects. Video transects were analyzed at UNC in a manner similar to the AGRRA method used in the field, except two additional parameters (percent coral cover and coral density) were calculated. Full details and a comparison of the methods employed are available in Appendix 1 of Supplementary Information.

Nutrient analysis

Chlorophyll a

Eight-day composite 4-km horizontal resolution chlorophyll a (chl a) measurements were obtained from NASA’s Moderate Resolution Imaging Spectroradiometer (AQUA MODIS) via NOAA’s Environmental Research Division’s Data Access Program (ERDDAP) (Simons, 2011). Eight-day composite data were selected in order to minimize gaps in data from cloud cover. Unlike the MUR SST data used for temperature calculations, there is no integrated, high-resolution product for chl a. Similar to temperature calculations, monthly and yearly average chl a values were calculated for each survey site (Fig 1B, 2C). Chl a is a widely used proxy for both primary productivity and nutrient content in seawater (Bell, 1992), as it is the main
photosynthetic pigment present in phytoplankton (which can often quickly deplete nutrient concentrations below detectable limits). It has been shown that remotely sensed data, such as chl \( a \) concentration, yields better metrics for water quality than traditional measures such as distance from shore and distance from the nearest river (Polónia et al., 2015). Here, chl \( a \) data are used as a proxy for bulk nutrient content across the BBRS. In addition to this reef scale coarse estimate of bulk nutrients, fine-scale in-situ nutrient sampling was conducted.

**In-situ nutrient sampling**

125ml water samples (n=3-10) were filtered and collected in acid washed bottles from each survey site (n=13), flash frozen on dry ice, and transported to UNC for analysis. Fine-scale nutrient dynamics were quantified from dissolved inorganic nitrogen [(DIN) = nitrate plus nitrite \( (NO_3^-) \) and ammonium \( (NH_4^+) \)] and dissolved organic carbon (DOC). See Appendix 2 of the supplementary information for measurement and instrumentation details.

**Statistical Analysis**

Standard deviations used for temperature bins and site classification were calculated in ArcGIS©. All other statistical analysis were carried out in R 3.2.2 (R Core Team, 2014). Transect averaged survey data for species richness, abundance, Shannon diversity, coral cover, coral density, DIN, DON, DOC, and log-transformed chl \( a \) data were analyzed using analyses of variance (ANOVA). Three fixed factors were included in the ANOVA (survey method, site, and site type) for species richness, abundance, Shannon diversity, DIN, DON, and DOC. Only two fixed factors (site and site type) were included in the ANOVA for coral cover and coral density, since only data from video surveys were used to calculate these averages, and also for chl \( a \)
concentrations since they were calculated using satellite measurements and survey type did not factor in.

If factors were significant ($p<0.05$), a post-hoc Tukey’s HSD test was used to evaluate the significance of each pair-wise comparison. To visualize coral community differences between site types non-metric multidimensional scaling (NMDS) ordination was implemented using Bray-Curtis similarity coefficients in the vegan package in R (Oksanen et al., 2013). An optimal stress test was performed to determine the optimal k value (k=20). Resulting NMDS scores were visualized in two-dimensional ordination space. A PERMANOVA test was performed to analyze the site type differences using the adonis function in the vegan package in R (Oksanen et al., 2013).

Linear mixed effects models with random intercepts, random slopes, or random slopes and random intercepts were created using the nlme package in R (Pinheiro et al., 2007), and were used to analyze the effects of site type and temperature parameters on ecological measurements (species richness, abundance, Shannon diversity, coral cover, and coral density). The model that best described the effect of site type or each temperature parameter on each ecological parameter was chosen based on the Akaike Information Criterion (AIC), which scales estimated differences between the model equation and the actual equation (Burnham & Anderson, 2002). This criterion is based on goodness of fit of the data as well as a correction term that increases the AIC value as number of predictors increases, which optimizes the model with the lowest AIC for both fit and simplicity (Burnham & Anderson, 2002). Once the best fitting model was chosen using best AIC procedure for each ecological parameter vs. temperature parameter across site types, marginal $R^2$ ($R^2_m$) and conditional $R^2$ ($R^2_c$) were calculated using the $r.squaredGLMM$ function of the MuMIn package in R (Nakagawa & Schielzeth, 2013). Marginal $R^2$ describes the proportion of
variance explained by fixed factors alone, while the conditional $R^2$ describes the variance explained by both random and fixed factors (Nakagawa & Schielzeth, 2013).

Linear models tested for the influence of temperature and nutrient parameters on the variation observed along NMDS1 and NMDS2 (within and between site type community variation) using the `lm` function in R (R Core Team, 2014). $R^2$ and $p$ values were calculated for each parameter based on each linear model (Table S11.) For NMDS1, data were also divided by site type in order to assess within site type variation (Table S9).

RESULTS

Coral Community Composition

Combined results of AGRRA diver surveys and GoPro® video surveys of all 13 sites revealed that coral species richness varied as a function of site location as well as site type (low$_{TP}$, mod$_{TP}$, or ext$_{TP}$) (Table 3A). Coral species richness was significantly lower at ext$_{TP}$ sites compared to low$_{TP}$ and mod$_{TP}$ sites, but was not significantly different between low$_{TP}$ and mod$_{TP}$ sites (Table 3B, Fig 3A). Coral abundance, Shannon diversity, percent coral cover, and coral density also followed these same trends (Table 3A, 3B; Fig S3 in Supporting Information).

Nonmetric multidimensional scaling (NMDS) analysis showed the same patterns. Community structure was significantly different (stress=0.018, adonis test $p$ value=0.006) between ext$_{TP}$ sites and low$_{TP}$/mod$_{TP}$ sites along the NMDS2 axis, but was not different between low$_{TP}$ and mod$_{TP}$ sites (Fig 3B).

Linear modeling of temperature and nutrient parameters against NMDS1 and NMDS2 revealed that average annual maximum temperature, average annual temperature range, average annual days above the bleaching threshold, average annual consecutive days above the bleaching
threshold, DOC, and DON all had significant effects on the NMDS1 variation and all four temperature parameters, as well as DON and chl a, also had significant effects on NMDS2 variation (S11; Fig S6). The parameter that explained the most variation for NMDS1 was DON ($R^2=0.3414$, $p$ value=$1.18 \times 10^{-15}$) and average annual consecutive days above the bleaching threshold explained the most variation in NMDS2 ($R^2=0.6039$, $p$ value=$2 \times 10^{-16}$, S11; Fig S6).

Linear regressions of temperature and nutrients parameters within site types along NMDS1 revealed significant effects ($p <0.05$) of average annual maximum temperature, average annual days above the bleaching threshold, average annual consecutive days above the bleaching threshold, DOC, DIN, and DON for all site types, average annual temperature range for mod$_{TP}$ and ext$_{TP}$ sites, and chl a for ext$_{TP}$ sites only (Table S9; Fig S5). Average annual days above the bleaching threshold yielded the highest $R^2$ for low$_{TP}$ and mod$_{TP}$ sites, while average annual temperature range yielded the highest $R^2$ for ext$_{TP}$ sites (Table S9; Fig S5).

Linear mixed effects models of ecological parameters for species richness, abundance, Shannon diversity, coral cover, and coral density by site type reveal that random intercepts models best fit the trends in species richness, abundance, Shannon diversity, and coral cover the best (best AIC), while a random slopes and intercepts model works best for coral density (Table S10A). Models with the best AIC showed no significant difference between low$_{TP}$ and mod$_{TP}$ sites for any parameters, but a significant difference between low$_{TP}$ and ext$_{TP}$ sites for species richness, abundance, Shannon diversity, and coral density (Table S10B).

Further linear mixed effects modeling of ecological parameters vs. temperature and nutrient parameters revealed that variation in species richness and coral density across sites was best explained by the number of consecutive days above the bleaching threshold per year, while total days above the bleaching threshold per year best explained the variation in coral abundance and
Shannon diversity. Variation in coral cover was best explained by \textit{chl} \textit{a} concentration (Table S5 in Supporting Information). Each model selected as best AIC (model that explains the variation the best) had a significant \textit{p} value (<0.05) (Table S6 in Supporting Information). A similar modeling approach completed for transects from low\textsubscript{TP} sites only showed that average annual temperature range best explains the variation for all five ecological parameters, however \textit{p} values are only significant for coral cover and coral density (Tables S7, S8 in Supporting Information).

**Coral Life History**

Coral life history proportions varied by site and differences were observed between site types (Table 3A). These trends, while not statistically significant across all sites (\textit{p}=0.055), may still be ecologically interesting (Table 3A). low\textsubscript{TP} sites and ext\textsubscript{TP} sites had significantly different life history distributions (Table 3B, Fig 4). mod\textsubscript{TP} sites did not differ significantly from low\textsubscript{TP} or ext\textsubscript{TP} sites. Overall, these data suggest a decrease in competitive and generalist species at ext\textsubscript{TP} sites compared to low\textsubscript{TP} and mod\textsubscript{TP} sites (Fig 4).

**Nutrients**

\textit{Chlorophyll a}

\textit{Chl} \textit{a} concentrations varied by year and differed by site and site type (Table 2A), but were consistently lowest at low\textsubscript{TP} sites and highest at ext\textsubscript{TP} sites regardless of year (Table 2B, Fig 2A). 13-year average \textit{chl} \textit{a} concentrations were significantly different between all three site types. low\textsubscript{TP} sites had the lowest average \textit{chl} \textit{a} concentrations, mod\textsubscript{TP} sites had average \textit{chl} \textit{a} values significantly higher than low\textsubscript{TP} sites, but significantly lower than ext\textsubscript{TP} sites, and ext\textsubscript{TP}
sites had significantly higher average chl a values than both low<sub>TP</sub> and mod<sub>TP</sub> sites (Table 2B, Fig 2B).

**In-Situ Nutrient Concentrations**

In-situ values for DIN, DON, Total N, DOC, and C:N varied by site (Table S2, S4). However, there were no significant differences between site types in terms of average DON and C:N, while concentrations of DOC and Total N were significantly elevated at ext<sub>TP</sub> sites compared to low<sub>TP</sub> and mod<sub>TP</sub> sites (Table S3 in Supporting Information, Fig S4A-E in Supporting Information). DIN concentrations were significantly higher in mod<sub>TP</sub> sites compared to low<sub>TP</sub> sites, but concentrations at low<sub>TP</sub> and mod<sub>TP</sub> were not significantly different than ext<sub>TP</sub> sites (Table S3, Fig S4A).

**DISCUSSION**

Surveys revealed that ext<sub>TP</sub> sites had lower species richness, abundance, diversity, coral cover, and coral density than low<sub>TP</sub> and mod<sub>TP</sub> sites, which did not significantly differ from one another (Fig 3A, 3B, S3). Differences between ext<sub>TP</sub> sites and low<sub>TP</sub>/mod<sub>TP</sub> sites were largely driven by the temperature parameters used to define the three thermal environments (Table S6, S11; Fig S6). Ext<sub>TP</sub> sites were dominated by weedy and stress tolerant coral species while corals of all four life history strategies (Darling *et al.*, 2012) were found at low<sub>TP</sub> and mod<sub>TP</sub> sites (Fig 4). Our data suggest that these coral community differences across site types are likely driven by temperature parameters and, to a lesser extent, nutrients. Higher bulk nutrient concentrations in ext<sub>TP</sub> sites may play a role in observed decreased in coral cover (Table S6), while DOC, DON, and DIN appear to play roles in community differences within, but not among, site types (Table S11, Fig S5).
Coral community composition differed between extTP sites and lowTP/modTP sites

Coral species richness, abundance, diversity, coral cover, and coral density were all lower at extTP sites compared to lowTP and modTP sites, (Fig 3A, S3) suggesting that the coral community at extTP sites is different from the community at lowTP and modTP sites. This finding was further supported by NMDS and linear mixed effects models (Fig 3B, Table S10B) and is contrary to the results of Soto et al. (2011) which shows that sites with moderate temperature variability (modTP) have higher coral cover than sites at either extreme and Lirman and Fong (2007) which showed that nearshore reefs (ExtTP) had higher coral cover than offshore reefs in the Florida Keys. ExtTP sites were subjected to higher annual maximum temperatures, more extreme annual temperature variations, a higher number of days above the bleaching threshold per year, more consecutive days above the bleaching threshold per year, and higher chl a concentrations than lowTP and modTP sites. As variation between site types occurred along the NMDS2 axis (Fig 4), linear modeling of these parameters against NMDS2 revealed that temperature parameters had a much more significant effect on community differences between site types than did nutrient parameters (Table S11, Fig 3B). The average annual number of days above the bleaching threshold ($R^2 = 0.5644$) and the average annual consecutive days above the bleaching threshold ($R^2 = 0.6039$) (S11, Fig S6) were especially important in driving the observed community differences. Interestingly, these same two temperature parameters best explain the trends seen in coral species richness, abundance, diversity, and density between site type (Table S5, S6). This evidence suggests that coral community composition is strongly influenced by time spent above the regional thermal maximum. Chl a concentration was also significant, but produced an $R^2 = 0.0434$ (S11; Fig S6), indicating that while chl a may have some impact on coral community differences between site types; it is unlikely to be a primary driver. Taken
together with the fact that other nutrient parameters do not explain a significant proportion of the variation in NMDS2 (S11; Fig S6), it seems likely that nutrient parameters play a lesser role in determining overall differences in community structure between these three thermally distinct site types. Reef flattening may also play a role in decreased species richness between site types (Newman et al., 2015), however in the current study 3-dimensional reef complexity was not quantified. Previous research shows that climate change has resulted in increased thermal stress, declines in coral cover, and shifts in coral community composition (Hughes et al., 2003; Hoegh-Guldberg et al., 2007). These results suggest that even without causing actual coral bleaching locally, thermal parameters have a strong influence on coral community composition.

In contrast, variation within site types appeared to be dependent upon both temperature and nutrient parameters and varied based on site type. In low\textsubscript{TP}, mod\textsubscript{TP}, and ext\textsubscript{TP} sites, average annual days above the bleaching threshold explained the most variation within site types ($R^2>0.95$) (Table S9; Fig S5). Average annual maximum temperature explains 86% of variation at ext\textsubscript{TP} sites, but only 11% at low\textsubscript{TP} sites (Table S9; Fig S5), indicating that annual maximum temperature is more of a factor at warmer sites. Average annual consecutive days above the bleaching threshold showed a similar trend. However, nutrient parameters, such as DIN and DON appeared to play significant roles within site type variation at mod\textsubscript{TP} and especially ext\textsubscript{TP} sites (Table S9; Fig S5). Interestingly, linear mixed effects models of ecological parameters (species richness, abundance, diversity, coral cover, and coral density) among low\textsubscript{TP} sites show that patterns within all of these parameters were most likely driven by annual temperature range (Table S7, S8). Overall, within site variation is different based on site type, but both temperature and nutrient parameters play a role. Variation among sites classified as low\textsubscript{TP} was best explained by temperature parameters, however at mod\textsubscript{TP} and ext\textsubscript{TP} sites both temperature and nutrient
parameters show reasonably high $R^2$, suggesting that both play a role in variation within site type.

Interestingly, and in contrast to our results, coral growth and coral cover were found to be higher in nearshore (ext$_{TP}$-like) environments in the Florida Keys than cooler and less thermally variable (low$_{TP}$-like) offshore reefs (Lirman & Fong, 2007). This difference may be due to the fact that corals living in warmer (Williams et al., 2010; van Woesik et al., 2012; Fine et al., 2013) or more variable areas (Oliver & Palumbi, 2011; Barshis et al., 2013) are less susceptible to bleaching stress due to adaptation/acclimatization to local conditions. However, here we observe that corals living in ext$_{TP}$ environments were not visibly less healthy than corals at low$_{TP}$ and mod$_{TP}$ sites (data not shown). In fact, *Siderastrea siderea* in nearshore (ext$_{TP}$) environments have been shown to have higher growth and calcification rates than those on the forereef (low$_{TP}$) (Castillo et al., 2011; Carilli et al., 2012; Castillo et al., 2012), suggesting that this species is locally adapted/acclimatized to more extreme temperature conditions and/or nutrients. These more extreme conditions may not be suitable for other coral species, which can lead to failed recruitment or inability of juveniles from more moderate sites to survive in these more extreme environments due to the influence of thermal history on limiting acclimatization (Howells et al., 2013). Lack of differences in community variables between low$_{TP}$ and mod$_{TP}$ sites (Fig 3A, S3) indicates that although reefs subjected to moderate temperature variation have been shown to have higher coral cover (Soto et al., 2011) differences in temperature and nutrient variables between these site types (Table 1) may not have been significant enough to elicit a community level response.

**Influence of nutrients on coral community composition and life history strategies**
Overall, bulk nutrients (chl a) increase with increasing temperature parameters, as chl a is highest at extTP sites and lowest at lowTP sites (Table 2B, Fig 2 A, B). As nutrient concentrations are highest in extTP environments, it is possible that nutrients are at least partially responsible for lower species richness, abundance, diversity, cover, and density at extreme sites compared to lowTP and modTP sites. In fact, linear mixed effects models show that chl a is a better explanatory variable for the change in percent coral cover across site types than any measured temperature parameter (Table S4). However, linear modeling of temperature and chl a against the NMDS2 axis was used to tease apart the independent contributions of temperature and chl a between sites and revealed that temperature is the primary driver of overall community composition between site types (Table S11, Fig 3B).

Preliminary in-situ nutrient sampling shows that concentrations of DOC and total N are higher in extTP sites relative to lowTP and modTP sites (Fig S4C, S4D). It is likely that these two nutrient types are responsible for driving the increase in bulk nutrients at extreme sites. Therefore, it is possible that accelerated microbe growth on corals (due to elevated DOC) (Kline et al., 2006) and/or increased macrobioerosion (correlated with high N) (DeCarlo et al., 2015) may play a role in lower coral species richness, abundance, diversity, cover, and density at extTP sites. However, based on linear modeling, it is unlikely that DOC or chl a play a large role in changing coral community ecology between site types (S11, Fig S6). Elevated chl a concentrations at modTP sites compared to lowTP sites were likely driven by DIN (Fig S4A). Increased DIN has been shown to cause a reduction in the bleaching threshold and induce a higher incidence of mortality (Wooldridge, 2009; Vega Thurber et al., 2014). In this case, the above effect is unlikely to have occurred, as coral community composition did not differ between these site types. More frequent and consistent seawater nutrient sampling and manipulative
experiments are needed to fully understand the impacts of both bulk and individual nutrient pools on the dynamics of coral communities and individual coral physiology.

**Extreme sites are dominated by weedy and stress tolerant coral species**

Corals have previously been classified into 4 life history groups (Darling *et al.*, 2012). Competitive corals are large, quick growing, broadcast spawning, branching and plating species (i.e. *Acropora cervicornis*). These corals are dominant in ideal conditions and shade out competitors, but are sensitive to breakage. Weedy corals (i.e. *Porites sp.*) reproduce by brooding, have small colony sizes, and are opportunistic colonizers of recently disturbed habitat. Stress tolerant corals (i.e. *Siderastrea siderea*) are slow growing, massive, broadcast spawning species with long generation times and high fecundity. Generalists (i.e. *Orbicella sp.*) show overlap between these three groups (Darling *et al.*, 2012). In the current study, ext$_{TP}$ sites were dominated by stress tolerant and weedy genera, while low$_{TP}$ sites and mod$_{TP}$ sites contained all 4 life history types (Fig 4). Low$_{TP}$ sites contained all four life history strategies in mostly equal proportions, mod$_{TP}$ sites were similar but with fewer competitive species than low$_{TP}$ sites, and ext$_{TP}$ sites had comparatively fewer of all four life histories, but were dominated by weedy and stress tolerant genera. Shifts toward weedy and stress tolerant genera under climate change conditions were predicted by Darling *et al.* (2012) and have been recorded in many areas of the world, including the Caribbean (Loya *et al.*, 2001; Aronson *et al.*, 2004; Green *et al.*, 2008; Alvarez-Filip *et al.*, 2011). Even in the face of region-wide decline in coral cover and competitively dominant species (Gardner *et al.*, 2003), some weedy species, such as *Porites astreoides*, are actually increasing in prevalence in the Caribbean (Green *et al.*, 2008). This weedy species is likely able to succeed under recent stressors due to its ability to brood and mature quickly, which allow it to quickly colonize a recently disturbed area. In contrast, stress-
tolerant species such as *S. siderea* are likely able to survive in extTP environments due to its slow growth rates and massive size, which allow them to be resistant to stress. These two contrasting strategies seem most effective in extTP environments, and are likely to be most effective in future conditions as the oceans continue to warm.

**Implications for conservation and management of reefs in the face of climate change**

Lower coral community diversity and percent cover at extTP sites compared to lowTP and modTP sites are likely driven by temperature parameters (particularly the number of days and number of consecutive days above the bleaching threshold per year, as well as average annual temperature range and max temperature). While ecological differences between sites may be mainly driven by temperature parameters, bulk nutrients may still play a role. Lack of community scale differences between lowTP and modTP sites suggests that low magnitude variations in temperature (and nutrient) parameters are less likely to cause measureable, community-wide changes. The change in community structure between extTP and lowTP/modTP sites was accompanied by a change in the dominant coral genera. LowTP and modTP sites contain all 4 coral life histories (competitive, generalist, weedy, and stress-tolerant) (Darling *et al.*, 2012), but extTP sites are dominated almost entirely by weedy and stress-tolerant species, suggesting that genera utilizing these two life history strategies may be better suited for survival under more extreme conditions. Future research is needed to examine the relative acclimatization/adaptation potential of corals at each of these site types as well as the relative contributions of thermal and nutrient stressors on coral health. Additionally, extTP sites may warrant further protection as they potentially harbor the coral genera and individuals that are most likely to thrive as the ocean continues to warm. These sites are not often protected and should be considered in future conservation management decisions.
ACKNOWLEDGEMENTS

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REFERENCES


**DATA ACCESSIBILITY**

Data will be archived on PANGAEA after acceptance and a DOI will be included here.

**BIOSKETCH**

Justin Baumann is a PhD student at the University of North Carolina at Chapel Hill working with Dr. Karl Castillo. His research focuses on the impacts of temperature and nutrients on coral reef ecosystems and the physiological response of the coral host and endosymbionts to climate change.
Table 1: Parameters used in Site Classification

<table>
<thead>
<tr>
<th>Factor</th>
<th>Min</th>
<th>Mean</th>
<th>Max</th>
<th>Standard Deviation</th>
<th>low&lt;sub&gt;TP&lt;/sub&gt; Sites</th>
<th>mod&lt;sub&gt;TP&lt;/sub&gt; Sites</th>
<th>ext&lt;sub&gt;TP&lt;/sub&gt; Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Annual Temp Range</td>
<td>4.35°C</td>
<td>5.168°C</td>
<td>7.065°C</td>
<td>0.692°C</td>
<td>4.350-5.514 °C</td>
<td>5.514-5.860 °C</td>
<td>5.860-7.065 °C</td>
</tr>
<tr>
<td>Mean Annual Days Above Bleaching Threshold</td>
<td>20.000 days</td>
<td>40.105 days</td>
<td>78.4 days</td>
<td>14.333 days</td>
<td>20.000-40.105 days</td>
<td>40.105-54.439 days</td>
<td>54.439-78.400 days</td>
</tr>
<tr>
<td>Mean Consecutive Days Above Bleaching Threshold</td>
<td>3.000 days</td>
<td>4.758 days</td>
<td>7.500 days</td>
<td>0.921 days</td>
<td>3.000-4.750 days</td>
<td>4.750-5.680 days</td>
<td>5.680-7.500 days</td>
</tr>
</tbody>
</table>

1 No corals below 30.352
2 No corals above 31.169
3 No corals below 4.476
4 No corals above 6.552
5 No corals below 25.772
6 No corals above 68.772
7 No corals below 3.837
8 No corals above 6.600

Table 1: Values for the four factors included in site selection metrics. Values are all averages from 2002-2012 and include measurements for minimum, mean, maximum, and standard deviation for each factor. The range at which each factor was classified as low<sub>TP</sub>, mod<sub>TP</sub>, or ext<sub>TP</sub> site is also shown. Note that these ranges vary for each factor because at both low and high extremes coral reefs were not present. Superscripts indicate ranges in which corals are not present.
Table 2A: Effects of site and site type on 13 year average (2002-2015) *Chl a* concentration

<table>
<thead>
<tr>
<th>Site Variable</th>
<th>df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>12</td>
<td>1350</td>
<td>112.75</td>
<td>131.5</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Site Type</td>
<td>2</td>
<td>288</td>
<td>144.00</td>
<td>166.7</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Table 2A: Results of analysis of variance (ANOVA) of the effect of site and site type on *chl a*. Significant effects are in bold (*p*<0.05). df= degrees of freedom.

Table 2B: Pair-wise comparisons of effects of site type on 13 year (2002-2015) *Chl a* concentration

<table>
<thead>
<tr>
<th>Comparison</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-mod&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>mod&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Table 2B: Results of Tukey’s HSD tests evaluating the significance of the pair-wise comparisons of factors that had a significant effect on *chl a* concentration. Only significant pairwise comparisons (*p*<0.05) are included.
Table 3A: Effects of Survey Method, Site, and Site Type on Species Richness, Abundance, Shannon Diversity, Percent Coral Cover, Coral Density, and Life History

<table>
<thead>
<tr>
<th>Community Parameter</th>
<th>Site Variable</th>
<th>df</th>
<th>Sum sq</th>
<th>Mean sq</th>
<th>F value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species Richness</td>
<td>Survey Method</td>
<td>1</td>
<td>20.30</td>
<td>20.35</td>
<td>0.508</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>12</td>
<td>918.4</td>
<td>76.53</td>
<td>15.7</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>2</td>
<td>414.9</td>
<td>207.4</td>
<td>8.41</td>
<td>0.002</td>
</tr>
<tr>
<td>Abundance</td>
<td>Survey Method</td>
<td>1</td>
<td>16500</td>
<td>16500</td>
<td>1.37</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>12</td>
<td>238500</td>
<td>19890</td>
<td>3.80</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>2</td>
<td>116100</td>
<td>58010</td>
<td>7.06</td>
<td>0.004</td>
</tr>
<tr>
<td>Shannon Diversity Index</td>
<td>Survey Method</td>
<td>1</td>
<td>0.3010</td>
<td>0.3012</td>
<td>0.786</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>12</td>
<td>8.775</td>
<td>0.7312</td>
<td>13.1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>2</td>
<td>5.274</td>
<td>2.637</td>
<td>14.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Percent Coral Cover</td>
<td>Survey Method</td>
<td>1</td>
<td>0.5666</td>
<td>0.04721</td>
<td>15.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Site</td>
<td>12</td>
<td>0.1172</td>
<td>0.05859</td>
<td>6.68</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>2</td>
<td>0.1172</td>
<td>0.05859</td>
<td>6.68</td>
<td>0.002</td>
</tr>
<tr>
<td>Coral Density</td>
<td>Site</td>
<td>12</td>
<td>263.5</td>
<td>21.96</td>
<td>20.7</td>
<td>&lt;0.0001</td>
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<tr>
<td></td>
<td>Type</td>
<td>2</td>
<td>142.1</td>
<td>71.07</td>
<td>39.8</td>
<td>&lt;0.0001</td>
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<tr>
<td>Life History</td>
<td>Site</td>
<td>12</td>
<td>904.0</td>
<td>75.37</td>
<td>4.40</td>
<td>&lt;0.0001</td>
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<td></td>
<td>Type</td>
<td>2</td>
<td>4311</td>
<td>2156</td>
<td>2.92</td>
<td>0.06</td>
</tr>
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</table>

Table 3A: Results of three-way analysis of variance (ANOVA) of the effect of site variables on coral community parameters. Significant effects are in bold (p<0.05). df= degrees of freedom.

Table 3B: Pair-wise comparisons of effects of Site Type on Species Richness, Abundance, Shannon Diversity, Percent Coral Cover, Coral Density, Life History

<table>
<thead>
<tr>
<th>Community Parameter</th>
<th>Factor</th>
<th>Comparison</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species Richness</td>
<td>Type</td>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>mod&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.02</td>
</tr>
<tr>
<td>Abundance</td>
<td>Type</td>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>mod&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.02</td>
</tr>
<tr>
<td>Shannon Diversity Index</td>
<td>Type</td>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>mod&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.0001</td>
</tr>
<tr>
<td>Percent Coral Cover</td>
<td>Type</td>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>mod&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.003</td>
</tr>
<tr>
<td>Coral Density</td>
<td>Type</td>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Type</td>
<td>mod&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Life History</td>
<td>Type</td>
<td>low&lt;sub&gt;TP&lt;/sub&gt;-ext&lt;sub&gt;TP&lt;/sub&gt;</td>
<td>0.049</td>
</tr>
</tbody>
</table>

Table 3B: Results of Tukey’s HSD tests evaluating the significance of the pair-wise comparisons of factors that had a significant effect on species richness, abundance, Shannon diversity index, percent coral cover, coral density, or life history. Only significant pairwise comparisons (p<0.05) are included.
Figure Legends

**Figure 1:** The Belize Barrier Reef System (BBRS) classified by site type (A), and 13 year average log-transformed \([chl \, a]\) (B). Stars indicate survey and sampling sites. Numbers represent site labels (see statistical tables below).

**Figure 2:** Annual (2003-2015) average \(chl \, a\) concentration by site type (+/− SE) (A). Panel B shows overall average \(chl \, a\) (D). The letters a, b, and c indicate results of post hoc Tukey tests that show significant differences between site types \((p<0.05)\).

**Figure 3:** Species Richness (# of species present) at each site type (A). Statistically significant differences \((p<0.05)\) are marked with an *. This trend is consistent among other community variables, including: coral abundance (# of corals), percent coral cover, Shannon diversity, and coral density (# of coral/ m\(^2\)) (Fig S2). B. Nonmetric multidimensional scaling (NMDS) plot of coral community differences clustered by site type (B).

**Figure 4:** Abundance of coral (±1 SE) grouped by life history (Darling et al. 2012). Letters a and b indicate results of post hoc Tukey tests that show significant differences between site types \((p<0.05)\).
Figures

Figure 1: Site location, temperature parameter, and chl a maps
Figure 2: Average chl a by site type

[Graph showing annual average Chl a concentration by site type for different years and site types.]
Figure 3: A.) Average coral species richness by site type and B.) NMDS of coral community variables by site type
Figure 4: Coral life history strategy by site type

![Bar chart showing coral life history strategy by site type](chart.png)