REPORT

High-resolution *in situ* thermal metrics coupled with acute heat stress experiments reveal differential coral bleaching susceptibility

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Abstract The relationship between thermal stress and coral bleaching has been a topic of study for decades, yet there is still a mismatch between remotely sensed bleaching predictors and population-specific bleaching responses. Recent studies have linked greater amounts of thermal variability to coral bleaching resistance over small spatial scales, yet in some sites, this variability appears to push corals beyond their thermal limits. Here, we performed a 12-month reciprocal transplant and acute heat stress experiments in populations of *Porites lobata* from an American Sāmoan backreef: the Highly Variable (HV), the Moderately Variable, and the Less Variable pools of Ofu to investigate how natural and experimental stress across different thermal environments related to coral bleaching responses during the 2016–2017 thermal anomaly. We also compared various sea surface satellite versus *in situ* temperature data to determine which metrics were most aligned with observed bleaching responses. We found ~ 0.6 °C higher maximum monthly means for *in situ* versus remotely sensed data, which resulted in fewer degree heating weeks. Although greater thermal variability and heat loading did not have a strong relationship with the onset of natural bleaching responses, acute heat stress revealed differences in sublethal stress responses that aligned with *in situ* thermal metrics. We suggest greater thermal spikes and heat loading in the HV pool, detected only in the high-resolution *in situ* data, best explain the decreased thermal performance seen in HV corals; demonstrating the utility of *in situ* data (both environmental and experimental) for understanding bleaching responses at population-specific spatial scales (< 5 km).

Keywords Coral bleaching · Thermal variability · Degree Heating Weeks · *Porites lobata* · Thermal tolerance · Physiology

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Introduction

As climate change intensifies, rising temperatures and temperature variation are increasing the magnitude and frequency of thermal anomalies (Pachauri et al. 2014; Stillman 2019). Marine heatwaves, prolonged periods of anomalously high sea surface temperatures (Hobday et al. 2016), are becoming more severe, especially in tropical coral reef regions (Lough et al. 2018). Reef-building corals live within a relatively narrow temperature range close to their upper thermal limits (Jokiel and Coles 1990; Berkelmans and Willis 1999) and are particularly vulnerable to increased sea surface temperatures (SST) associated with anthropogenic climate change. As such, summertime heatwaves are projected to cause annual mass coral bleaching on more than 90% of coral reefs worldwide by the end of the century (Frieler et al. 2013; Hughes et al. 2017).

The link between coral bleaching events and increased SST formed the basis of a global thermal stress monitoring system led by the National Oceanographic and Atmospheric Administration's Coral Reef Watch Program (NOAA

CRW; Liu et al. 2003, 2014). The magnitude and duration of remotely sensed SSTs above a fixed, locally defined Maximum Monthly Mean (MMM) temperature predicts the level of thermal stress on a coral reef region, called Degree Heating Weeks (DHW). The NOAA CRW daily satellite coral bleaching product defines the amount of DHWs associated with coral bleaching stress and mortality (Heron et al. 2016) and has guided targeted observations and management responses at reef locations worldwide. Despite these advances, the spatiotemporal resolution of remotely sensed data (5 km resolution) prevents precise thermal stress quantification at smaller scales, as it misses bleaching heterogeneity present within many reef regions and within individual reefs (Oliver and Palumbi 2011; Schoepf et al. 2015; Hughes et al. 2018; Safaie et al. 2018; Genevier et al. 2019).

Differential bleaching responses at smaller scales have been attributed to small-scale (< 5 km) variation in the magnitude and duration of thermal stress and can be poorly reflected by DHW predictions (Langlais et al. 2017; Safaie et al. 2018; McClanahan et al. 2019). Climatic and local environmental parameters not included in NOAA CRW's predictive toolbox but possibly as important for understanding coral responses to heat stress are small-scale interannual and diurnal temperature variability (Donner 2011; Oliver and Palumbi 2011), stress exposure duration (Berkelmans 2002; Middlebrook et al. 2008), heating rate (Middlebrook et al. 2010), water flow and internal waves (McClanahan et al. 2005; Wyatt et al. 2020), and light stress (Skirving et al. 2018; Mason et al. 2020).

Another aspect of the NOAA CRW monitoring program is the assumption that coral reef thresholds remain constant over time (Van Hooidonk et al. 2013). Sully et al. (2019) revealed coral bleaching temperatures from the past decade are ∼ 0.5 °C warmer than the previous decade, suggesting a recent adjustment in thermal thresholds of surviving coral populations. Moreover, many studies have demonstrated the capacity of coral communities to acclimatize to repeated heat stress exposures (Bellantuono et al. 2012; Howells et al. 2013; Palumbi et al. 2014; Bay and Palumbi 2015), and that recent exposure to temperature variation can beneficially influence coral physiological tolerance (McClanahan et al. 2005; Oliver and Palumbi 2011; Barshis et al. 2013; Palumbi et al. 2014; Morikawa and Palumbi 2019). It is suggested that reef areas with large environmental fluctuations contain corals with higher heat tolerance in comparison with corals from more thermally stable environments (Oliver and Palumbi 2011; Kenkel et al. 2013; Palumbi et al. 2014; Kenkel et al. 2015; Camp et al. 2017; Barshis et al. 2018; Safaie et al. 2018; Sully et al. 2019). These variable environmental regimes across small-scale heterogeneous reef habitats provide opportunities for coral populations to modify and increase their thermal thresholds through mechanisms of acclimatization

and adaptation (Boyd et al. 2016). A better understanding of thermal stress exposures and individual coral responses over various temporal and spatial scales will play a crucial role in determining coral thermal thresholds and ultimately reef-scale bleaching susceptibilities.

Previously, we examined whether two massive coral species from the naturally variable backreef pools of Ofu Island, American Sāmoa, could modify their stress tolerance via acclimatization to the highly variable (HV) pool. These backreef pools are < 5 km apart and nearly identical in species diversity and percent live coral cover yet have distinct differences in small-scale environmental variability driven by tidal cycle and pool size (Craig et al. 2001; Smith et al. 2007; Oliver and Palumbi 2011). The HV pool (4400 m^3 at low tide) experiences summer temperatures as high as 35 °C, with up to 6 °C daily fluctuations (Craig et al. 2001, Klepac and Barshis 2020), whereas the moderately variable pool (MV; 51,300 m^3 at low tide) ranges daily from 28 to 33 °C, and the less variable (LV; size unknown) pool ranges daily from 28 to 32.5 °C (Klepac and Barshis 2020). The HV pool is recognized to contain more thermally tolerant corals than nearby coral populations (Oliver and Palumbi 2011; Barshis et al. 2013; Palumbi et al. 2014; Morikawa and Palumbi 2019) and elicit increases in thermal tolerance in corals transplanted into the HV pool (Palumbi et al. 2014). However, in contrast to corals from the genus *Acropora*, we recently demonstrated that *Porites lobata* and *Goniastrea retiformis* corals did not increase thermal tolerance following transplantation into the HV pool, and more importantly, native HV *P. lobata* had a reduced tolerance under acute heat stress (Klepac and Barshis 2020). We did not observe enhanced physiological performance as typically expected, despite greater environmental variation in the HV pool, and hypothesized that a finer spatiotemporal scale of increased heat duration and magnitude, coupled with recent bleaching stress, could contribute to our contrasting results. Previous studies reported distinct temperature parameters for each pool but did not calculate how different metrics of *in situ* heat loading above local bleaching thresholds may influence coral stress responses. To improve our understanding of backreef climatologies, derived thermal thresholds, and *in situ* heat loading, we compare various scales of *in situ* temperature data to the remotely sensed NOAA CRW DHW 5 km product to explore how high resolution *in situ* climatology compares to remotely sensed data and relates to the physiological differences we observed previously in *P. lobata*. Moreover, we sampled additional colonies, tracked natural bleaching responses, and conducted a reciprocal transplant experiment between the HV and the moderately variable (MV) pool to elucidate (a) whether thermal tolerance changed following transplantation in the HV pool, (b) whether natural bleaching responses varied across the pools,

and (c) whether HV corals exhibited reduced thermal tolerance regardless of transplant environment.

Materials and methods

Coral collection & transplantation

Ten colonies of *P. lobata* were sampled from the LV, MV, and HV backreef pools between July 1 and 3, 2016 ($n = 30$). Colonies were chosen based on visual appearance (non-bleached), size (1.5–3 m diameter), and at a distance of ~5 m from other colonies to minimize clonality (sensu Baums et al. 2006). From each colony, 24 cores (i.e., ramets) were collected and affixed to nylon bolts with marine epoxy and secured to a rack using wingnuts. Two to three ramets from three to four colonies from each site were randomly assigned to site-specific transplant racks, yielding 24–36 ramets per grid with eight grids each at HV and MV, and four grids at LV (Fig. 1A). Half of the MV and LV samples (12 ramets/colony, $n = 120$ per site) were transplanted into the HV pool and the other half remained at the respective native reef site as control groups. In addition, half of the samples from the HV pool were randomly mixed with MV ramets and transplanted into the MV site. Transplantation of HV samples into the MV pool occurred on July 13th, and MV and LV samples were transplanted into the HV pool July 15th, 2016. This resulted in six transplant groups: HV_HV, HV_MV, MV_HV, MV_MV, LV_HV, and LV_LV (origin_destination).

Ofu backreef temperature profiling

To investigate the specific temperature profiles of the three backreef pools that are within the 5 km pixel produced by NOAA CRW's product, we obtained the National Park of American Sāmoa's (NPSA) Ofu Island temperature records spanning 2000–2017 (Barker 2018). We also received the 5 km satellite pixel NOAA CRW product containing Ofu Island (−14.177949, −169.654364) via a custom request to NOAA CRW staff to calculate pool-specific NOAA CRW DHW. The NOAA CRW dataset's calculated month with the highest maximum temperature (MMM) across years 1985–2012 was April (28.9 °C) and was applied to the NPSA dataset for each pool to then calculate NOAA CRW Hot spots and Degree Heating Weeks for the backreef pools of Ofu following NOAA's CRW SST climatology product methodology (Liu et al. 2006). In addition to these datasets, HOBO® Pendant temperature loggers (Onset Computer Corporation, Bourne, MA) were attached to each transplant rack and collected *in situ* temperatures every 10 min for the experimental duration. For each pool, temperature data were averaged across racks and binned
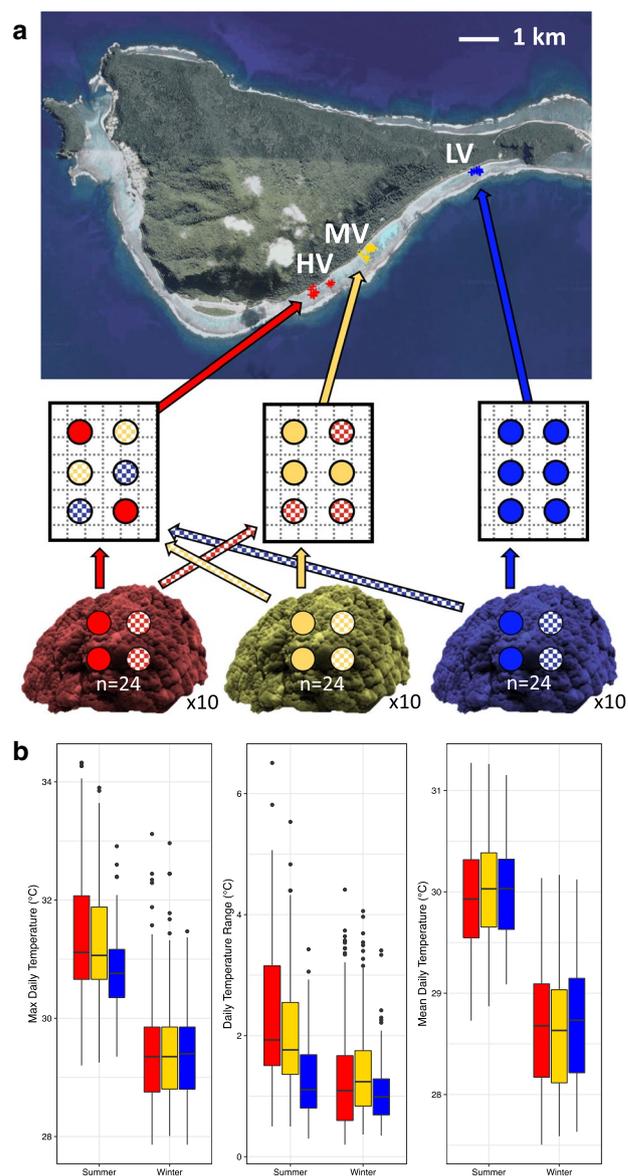
Fig. 1 Transplant experiment and *in situ* temperature metrics of backreef sites on Ofu Island, American Sāmoa. **A** Ten *P. lobata* colonies (cross symbols) were sampled from three backreef pools—HV (red), MV (yellow), LV (blue). Twenty-four ramets from each colony were sampled from each site ($N = 720$), and half were transplanted into either the HV or MV (excluding LV ramets) common garden (checkered arrows and circles) and the other half were returned to the native site (solid arrows and circles). After 1 (August 2016) and 6 months (February 2017), two ramets per colony per site were collected for acute heat stress experiments. **B** Seasonal *in situ* daily max temperatures, daily temperature range, and daily mean temperatures of the backreef pools from July 2016–February 2017. Winter includes July–October, and summer includes October–February. Boxplots display the median (horizontal line), first and third quartile (hinges), and largest/smallest value no further than 1.5*IQR (whiskers)

into either austral winter (April 16th–October 15th) or austral summer (October 16th–April 15th).

We also used the NPSA pool-specific *in situ* temperature time series dataset spanning the years 2000–2017 to generate local climatologies and calculate Degree Heating metrics for each pool: NOAA CRW DHW, *in situ* DHW, and *in situ* "Degree Heating Half Hours" (DHHH). Following the NOAA CRW Ofu methodology, but excluding the bleaching years 2002–03 and 2015–17, MMMs for each pool were calculated as the average nightly temperature for a given month across years from the years 2000–2001 and 2004–2014. A separate, adjusted 5 km Ofu MMM of 29.5 °C was calculated from the same range and non-bleaching years (2000–2001, 2004–2014) subset from the NOAA CRW 5 km Ofu-specific time series dataset to specifically match the temporal range and compare with our *in situ* calculations. The NPSA *in situ* temperature records were measured continuously (every 30 min) so we also used daily averaged values to compute more precise climatologies for each backreef pool. April was the site-specific MMM to calculate hot spots and *in situ*, bleaching year excluded, DHWs. We investigated a finer-scale metric of heat loading, DHHH, by summing hot spot values over the number of rows (30 min increments) totaling a 12-week rolling window ($n = 4032$), and then dividing by 336 (7 days of half hour increments).

Coral growth and acute heat stress assays

At 1 month (August 5–8, 2016) and 6 months (February 9–11, 2017) following transplantation, two ramets were collected per colony per transplant group (2 ramets*10 colonies*6 transplant groups, $n = 120$ ramets/timepoint) from the grids in the three backreef pools, scrubbed to remove fouling organisms, and buoyant weighed prior to controlled thermal stress experiments. Ramets were placed in a modified version of the Coral Bleaching Automated Stress System (CBASS; Voolstra et al. 2020; Evensen et al. 2021), constructed from Coleman 24L Party Stacker Coolers™ as head and sump tanks. A pump provided a flow of 88.9 mL s^{-1} to the head tank, fitted with six LED bulbs (Phillips PAR38) with a light level of ~500 ± 20 μM quanta m^{-2} s^{-1} (Li-Cor LI 193 spherical quantum sensor) and a 12 h light/dark photoperiod. A flow-through drip system provided 2.5 mL s^{-1} of local seawater throughout the duration of the experiment.

Controlled temperature ramp exposures occurred similar to Klepac & Barshis (2020). Briefly, samples were randomly assigned within two control and two heat tanks. In the heat tank, temperature increased over 3 h from 28 to 36.5 °C, followed by a 3 h hold at 36.5 °C, then a ramp down to and hold at 28 °C for 16 h. The control tank was set to remain stable at 28 °C for 22 h (Fig. S1). Samples were immediately wrapped in foil and stored at -20 °C until transportation back to Old Dominion University and subsequent storage at -20 °C.

A final timepoint for growth only occurred at 24 months (June 2018). All remaining transplanted ramets (~ 4 ramets/colony/transplant group) were removed from the pools, cleaned of encrusting growth, and buoyant weighed. Growth rates were calculated as follows: ((final weight-initial weight)/initial weight)/number of weeks on the raw buoyant weights of ramets (assuming constant epoxy and bolt weight), then averaged for each transplant colony to avoid pseudoreplication.

Symbiodiniaceae physiology under heat stress

Dark-adapted maximum quantum yield (F_v/F_m) of photosystem II (PSII) was measured to quantify heat stress responses of *Symbiodiniaceae* during the acute assays (Warner et al. 1996). Following 30 min of dark-adaptation, ramets were repeatedly measured on top in triplicate at 0 and 21 h of the experiment using a pulse amplitude modulation (PAM) fluorometer (Junior-PAM, Walz, Germany). Instrument settings were as follows: Measuring Light Intensity = 6; Saturation Intensity = 12; Saturation Pulse Width = 0.6 s; Gain = 2.

Preserved coral tissue was airbrushed from the skeleton using 35ppt unfiltered, artificial seawater. The resulting slurry was homogenized, centrifuged, and resuspended in 5 mL of unfiltered seawater before aliquoting out 3 mL and further centrifugation to separate the algal pellet from seawater for chlorophyll measurements. To determine chlorophyll concentrations, 5 mL of cold 90% acetone was added to the pelleted material, which was then homogenized using a glass tissue homogenizer and a 25 mm GF/F filter for cellular disruption and then stored at 4 °C for 24 h. Absorbance spectra were measured using an Ocean Optics UV–Vis Miniature Spectrometer (Key Largo, FL), and cellular chlorophyll *a* and c_2 values were calculated following the Ritchie (2006) equation for dinophytes. Total chlorophyll ($a + c_2$) absorbance was normalized to acetone volume (5 mL), aliquot (3 mL), and total slurry volume (5 mL) and then scaled to the surface area of each ramet, measured using the paraffin wax method (Veal et al. 2010).

Natural bleaching of donor colonies

During the 6-month timepoint, the Sāmoan archipelago had begun experiencing a mass bleaching event (American Samoa Coral Reef Advisory Group 2017), where bleaching affected many corals in Ofu's backreef pools. We sampled small cores (2 cm^2) of both affected (i.e., lightest visible area) and healthy (i.e., darkest visible area) regions of donor colonies at all sites. In addition, we recorded the percent area bleached for each colony. Chlorophyll concentration and surface area were processed and measured as aforementioned. Healthy and affected chlorophyll values were averaged to

produce a mean chlorophyll value of each colony to account for potential intra-colony physiological differences.

Statistical analyses

The interactive effects between season and backreef pool on mean daily temperature range, min, max, and mean temperatures were tested using the 'aov' function (*stats*; Chambers et al. 2017) with season and backreef pool as fixed factors in Rv3.6.3 (R Core Team 2018). Post hoc pairwise comparisons were conducted using 'emmeans' contrasts (*emmeans*; Lenth et al. 2020). *In situ* DHWs were compared across pools using a sliding window analysis followed by a Wilcox rank-sum test (*stats*) for 2-week windows (sliding by 1 week) where DHWs were greater than 0 °C week^{-1} (sensu Sale et al. 2019). Multiple tests were sequentially Bonferroni adjusted.

Generalized linear mixed models ('lmer' function) were used to examine the interactive effects of time (1- and 6-month), transplant group (HV_HV, HV_MV, MV_HV, MV_MV, LV_HV, LV_LV), and treatment (control and heat) on weekly growth (sans treatment), photochemical efficiency (F_v/F_m), and total chlorophyll. Transplant group was considered a fixed variable since the nature of the transplantation effort was unbalanced (i.e., not all origins were in all destinations [no HV in LV, or LV in MV]). Models were run with coral colony nested within tank as a random effect. Residual normality and homogeneity of variance was tested using Shapiro–Wilk (*stats*) and Levene's HOV tests (*car*; Fox & Weisberg 2019), respectively. Post hoc multiple comparisons with multivariate adjustments were used to assess time*transplant group*treatment, time*transplant group, or time*treatment interactions using the *emmeans* package.

The natural bleaching event provided an opportunity to examine the relationship between donor colony and transplanted ramet bleaching. First, a linear mixed model incorporating fixed effects of site (HV, MV, LV), sample (donor, heated ramet, control ramet), and colony as a random effect

was tested against total chlorophyll values, with post hoc comparisons of significant factors. Then, a Pearson's correlation was run against donor and control ramet total chlorophyll, as well as a correlation matrix comparing days spent over the nighttime NPSA bleaching threshold (*in situ* MMM + 1°C = 30.2/3 °C) and total chlorophyll of each sample type.

To investigate how coral holobiont physiological variables (weekly growth, control F_v/F_m, control total chlorophyll) related to temperature metrics averaged over 1 month prior to each timepoint (monthly mean and minimum temperatures, MMM, daily temperature range [DTR], 90th quartile daily range, CRW DHW, night DHW, *in situ* DHW, and *in situ* DHHH), we conducted a Pearson's correlation matrix test (*stats*) between each physiological variable and each temperature metric. In addition, a principal component analysis (PCA) was used to visualize log-transformed variables in a multivariate space. Log-transformed values were first centered and scaled prior to conducting the PCA and subsequent PERMANOVA using the 'adonis' function in the *vegan* package (Oksanen et al. 2018) with the dissimilarity index method set to 'Euclidian.' Analytical scripts and data files are available on GitHub (https://github.com/courtneyklepac/Remotely-sensedVSinsitutemps_coralbleaching).

Results

Ofu backreef temperature profiling

From July 2016–January 2017, the HV and MV pools had greater daily temperature range (DTR), maximum, and minimum daily temperatures during summer (October–January) and winter months (July–October; DTR and minimum only) than the LV pool (aov site*season; DTR $p < 0.01$, max $p < 0.01$, min $p = 0.01$; Fig. 1B). Summer maximum temperatures were 33.4 ± 0.4 °C (mean $\pm$ SD) in the HV pool and 33.8 ± 0.6 °C in the MV pool in contrast to 32.1 ± 0.6 °C

Table 1 Comparison of calculated MMMs from NOAA CRW Ofu 5 km remotely sensed nighttime Sea Surface Temperatures (full dataset spanning 1985–2017 and reduced dataset spanning 2000–2017

excluding bleaching years 2002 and 2015–2017) and NPSA *in situ* temperature dataset spanning 2000–2017 (nighttime and daily; bleaching years 2002 and 2015–2017 excluded)

	NOAA CRW 5 km 1985–2017 (°C)	NOAA CRW 5 km 2000–2017 (bleaching years excluded) (°C)
Mean monthly maximum		
Ofu	28.9	29.5
	Nighttime, non-bleaching *in situ* NPSA temperature time series (°C)	24-h, non-bleaching *in situ* NPSA temperature time series (°C)
Mean monthly maximum		
HV	29.2	29.4
MV	29.3	29.5
LV	29.3	29.5

Fig. 2 Comparison of *in situ* versus satellite temperature measurements for Ofu Island from 2000 to 2017. **A** Mean daily temperatures from the NOAA CRW Ofu 5 km satellite product (gray line) and NPSA *in situ* pool datasets (HV: red, MV: yellow, and LV: blue lines). **B** DHW derived from the NOAA CRW Ofu 5 km satellite product using the MMM of 28.9 °C. Pool-specific DHWs were calculated using the same MMM. **C** *in situ* DHW using the NPSA *in situ* temperature data to calculate pool-specific MMMs. DHWs were derived from each pool's MMM value (HV = 29.4 °C, MV & LV = 29.5 °C), excluding bleaching years. The gray line in this panel represents the Ofu 5 km DHW calculated for the same years as the *in situ* DHWs (see Table 1). **D** *in situ* DHHH calculated from pool-specific MMMs. Gaps signify missing temperature data
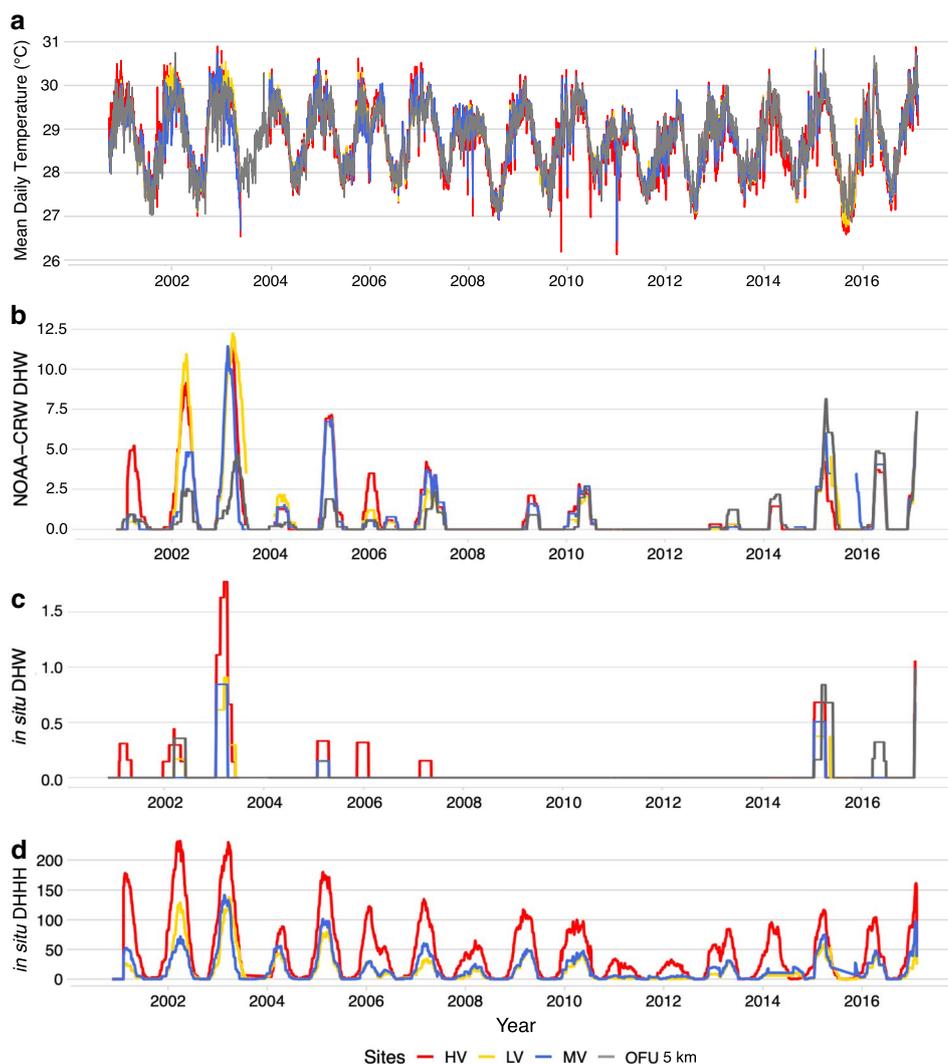
in the LV pool (Table S1). Summer DTRs for HV and MV pools were 1.6- to 1.8-fold greater than summer DTR in the LV pool (Table S1). All temperature metrics were greater in the summer compared to winter months. In addition, the HV, MV, and LV pools experienced 122, 128, and 106 d over the nighttime NPSA bleaching threshold of 30.2/3 °C (i.e., HV/MV/LV *in situ* MMM + 1 °C; Table 1, S1), respectively, of which 75% of these days were during the summer months. Moreover, the HV pool had 56, 28, and 9 d over MMM + 2, + 3, + 4 °C, whereas the MV pool had 57, 23, and 5 d, and the LV pool had only 29, 4, and 0 d over these thresholds (Table S1).

Daily *in situ* climatologies derived from the NPSA 2000–2017 temperature dataset of each backreef pool used to calculate *in situ* nighttime only MMMs (per NOAA CRW methods) resulted in similar but slightly higher MMM values for each pool (Table 1). An adjusted Ofu 5 km MMM of 29.5 °C resulted after incorporating the exact timespan for which we had corresponding *in situ* data (2000–2001,

2004–2014). Daily *in situ* MMMs for each pool were greater than nighttime *in situ* MMMs and the satellite-derived MMM of 28.9 °C but similar to the adjusted Ofu 5 km MMM (Table 1).

The NOAA CRW Ofu 5 km product's MMM of 28.9 °C was derived from 1985 to 2012 satellite nighttime sea surface temperatures (Table 1; Liu et al. 2014) and was used to calculate NOAA CRW DHW for each pool (Fig. 2B). From 2002 to 2007, pool-specific DHWs were two- to fourfold greater than Ofu 5 km DHWs ($p < 0.01$), where sliding window analysis revealed pool-specific DHWs had approximately 20–30 2-week sliding windows of significantly greater DHWs per year than the Ofu 5 km time series. From 2009–2010, pool-specific DHWs had 12 2-week sliding windows that were twofold greater than Ofu 5 km DHWs ($p < 0.01$). However, from 2014 to 2016, this trend switched to Ofu 5 km DHWs having significantly greater DHWs in comparison with pool-specific DHWs (Fig. 2A). Utilizing daily *in situ* pool-specific MMMs instead of the
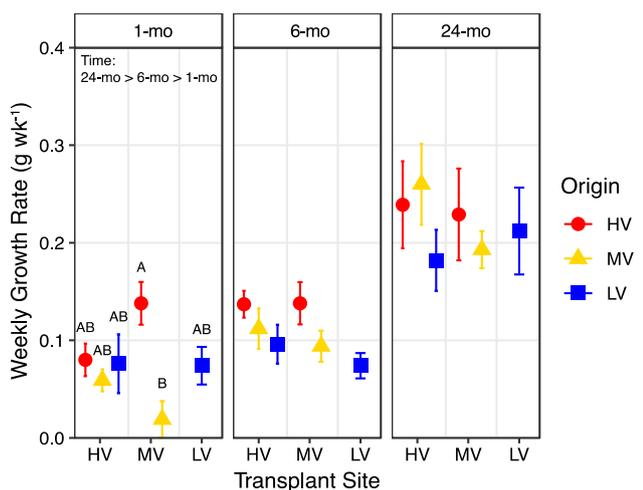
Fig. 3 Mean weekly growth rates (g wk^{-1}) of *P. lobata* with respect to transplant destination and time. Tukey's pairwise comparisons for significant overall effects are displayed, within timepoint significant comparisons are denoted with letters, and error bars are 95% confidence intervals

satellite-derived Ofu 5 km MMM (28.9 °C) resulted in a 0.05–0.1-fold decrease in DHWs (Fig. 2C vs. B), as the higher MMM values resulted in fewer calculated DHWs. For daily *in situ* DHWs, the HV pool had a greater number of DHWs than both the MV and LV pool during the years 2001–2003, 2005–2007, 2015, and 2017 ($p < 0.01$, Fig. 2C). The MV pool had greater numbers of DHWs than the LV pool during 2002 and 2015 ($p < 0.01$). For DHHH, the HV pool had more DHHH than the MV and LV pools across the entire time series (Fig. 2D) and a greater amount of overall heat loading regardless of bleaching years ($p < 0.01$). Moreover, the LV and MV pools did not differ in DHHH heat loading over time, except for during 2002.

Coral growth

Weekly growth rates for *P. lobata* differed by the interaction between time and transplant group. After 1 month of transplantation, HV corals transplanted into the MV pool had seven times greater weekly growth rates than MV native corals (HV_MV 0.138 ± 0.05 g week^{-1} vs. MV_MV 0.019 ± 0.04; $p = 0.05$; Fig. 3). Weekly growth rates were higher overall in 6-month versus 1-month ramets ($p = 0.02$), but there was no difference among individual ramets from 1 to 6 months nor in paired ramets at the 6-month timepoint. Ramets that remained in their transplant site for 2 yr (June 2018) had coral weekly growth rates that were 2–3 times higher than the 6- and 1-month samples, respectively, for HV_HV, MV_HV, LV_LV, and MV_MV transplant groups (Fig. 3). In June 2018, there were no differences in weekly growth rates among paired native and transplant ramets.
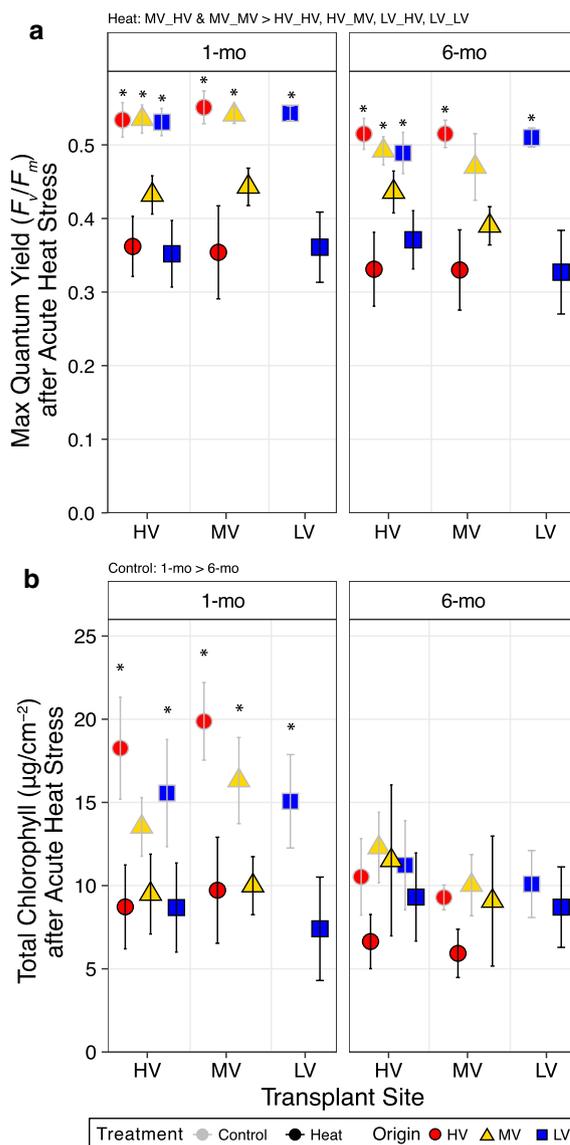
Fig. 4 **A** Mean maximum quantum yield (F_v/F_m) and **B** total chlorophyll (μg cm^{-2}) of control (gray outline) and heated (black outline) Symbiodiniaceae following acute heat stress with respect to transplant destination and time. Error bars represent 95% confidence intervals, Tukey's pairwise comparisons for significant effects are displayed above panels, and asterisks within each panel signify an effect of treatment for each timepoint

Symbiodiniaceae photophysiology under experimental and natural stress

Overall, there was a significant effect of transplant group ($p < 0.01$), treatment ($p < 0.01$), and the interaction of the two ($p < 0.01$) on F_v/F_m values after 21 h of heat stress. Heated MV_MV and MV_HV corals had ~ 1.2-fold higher F_v/F_m values in comparison with all other transplant groups (Fig. 4A). There was an effect of treatment during both time-points, except at 6 months where MV_MV corals were the

only transplant group that did not have significantly reduced F_v/F_m under acute heat stress. During this timepoint, heated MV_MV corals had higher F_v/F_m values than both HV_HV ($p = 0.01$) and HV_MV corals ($p < 0.01$), and MV_HV corals had greater F_v/F_m values than HV_HV corals ($p = 0.02$).

There was an overall treatment by time interaction for total chlorophyll per surface area, where acute heat stress reduced total chlorophyll in 1-month (except MV_HV) but not in 6-month transplants (Fig. 4B). In addition, control total chlorophyll values decreased almost 0.45–0.65-fold by the 6-month timepoint, which was at the beginning of the 2017 mass bleaching event.

During the onset of the local bleaching event in 2017, donor colony total chlorophyll values did not differ across backreef sites, where average percent bleaching was 21.5 ± 19.2%, 19.7 ± 13.8%, and 31.3 ± 27.0% for HV, MV, and LV corals, respectively (Fig. S3). Donor colony total chlorophyll values were not correlated with control ramet total chlorophyll (Pearson's R = − 0.26, $p = 0.20$; Fig. S4) but were greater than both control and heated values (*emmeans* $p < 0.01$ for both; Fig. S5). Moreover, donor and control ramet total chlorophyll values did not correlate with number of days spent over 31 and 32 °C nor with *in situ* DHW.

Coral physiology in relation to temperature metrics

Coral holobiont physiological variables (growth rate, control F_v/F_m, control total chlorophyll) and their relationship to environmental metrics such as monthly minimum and maximum temperatures, MMM, maximum DTR, 90th quartile range, NOAA CRW DHW, nighttime *in situ* DHW, daily *in situ* DHW, and DHHH were examined using a Pearson's correlation matrix (Fig. 5). Weekly growth was positively correlated with all temperature metrics, in contrast to control F_v/F_m and total chlorophyll that were negatively associated with all temperature metrics except 90th quartile daily range (and nighttime *in situ* DHW for F_v/F_m; Fig. 5), with a stronger correlation for total chlorophyll values compared to F_v/F_m. A PCA of control ramet variables further demonstrated the relationship among coral physiology and environment (Fig. 6), where PC1 explains 45.3% of the variance, and PC2 explains 32.9% of the variance. Individual points differ by time, where temperature metrics correlate with PC1 and physiological trait values are different between 1 month (PC1 > 0) and 6 months (PC1 < 0; $p < 0.01$; Fig. 6) especially for total chlorophyll.

Discussion

The complex relationship between thermal variability and bleaching sensitivity

Increased thermal variability is generally beneficial for coral growth and bleaching resistance at exposures up to the local thermal optimum (Buddemeier et al. 2008; Lough 2008; Rivest et al. 2017; Safaie et al. 2018), especially in the Ofu backreef (Oliver and Palumbi 2011; Thomas et al. 2018). Here, backreef coral growth was positively correlated with multiple temperature metrics, and other *P. lobata* research on Ofu Island also demonstrated greater coral growth in the backreef compared to forereef environments, attributed to differences in thermal variability between the two habitats (Smith et al. 2007; Barshis et al. 2018). Although increased thermal variability was positively correlated with backreef coral growth, it appears growth is decoupled from thermal tolerance (see Edmunds 2017), as HV_MV corals grew the most initially but did not exhibit increased thermal tolerance 6 months following transplantation. In contrast to growth, thermal variability metrics had a strong negative relationship with *P. lobata* chlorophyll levels in native pool control ramets (Fig. 5). Seasonality is recognized as a driver of coral pigment cycles (Fitt et al. 2000), with greater concentrations in winter, and here, coral ramets also had reduced pigment concentrations during the austral summer, which could be attributed to natural seasonal patterns and/or initial bleaching stress.

Coral bleaching in Ofu's backreef typically begins March–April and bleaching severity has been shown to vary across species and pool of origin (Morikawa and Palumbi 2019; Thomas et al. 2019). During the bleaching events of 2015 and 2017, greater bleaching was observed in corals originating from the MV pool compared with the HV pool in a common garden (Morikawa and Palumbi 2019). Here, the early onset of natural bleaching stress observed in February 2017 did not result in site-specific differences in percent bleaching and total chlorophyll among wild donor *P. lobata* colonies. It is possible that donor corals may not have accrued enough heat stress to demonstrate measurable site-specific bleaching responses at the time they were measured. Moreover, there was no correlation between field donor and control ramet chlorophyll levels (Fig. S4), contrary to the findings of Morikawa and Palumbi (2019). In this instance, it appears unlikely that the bleaching responses of experimental ramets could serve as a proxy for bleaching susceptibility in natural coral populations, but could instead represent size-specific bleaching responses (Hughes and Jackson 1985; but see Edmunds 2017) between the larger donor colonies (> 1–2 m diameter) and small ramets (2–3 cm cores).

In contrast to relatively mild bleaching responses observed in donor colonies during the hottest month of

Fig. 5 Pearson correlation heatmap based on scaled average for 120 ramets (all sites, both timepoints) of control *P. lobata* physiology and Ofu temperature metrics. Colors and values within the squares represent the magnitude and direction of the Pearson correlation according to the key. Non-significant ($p > 0.05$) Pearson pairwise correlations are indicated with an "X."

	F_v/F_m	chlorophyll	mean temp	min temp	MMM	DTR	dr90	CRW DHW	night insitu DHW	insitu DHW	insitu DHHH
growth	−0.01	−0.13	0.3	0.27	0.29	0.31	0.12	0.3	0.22	0.28	0.27
F_v/F_m		0.25	−0.24	−0.23	−0.21	−0.18	−0.04	−0.24	−0.16	−0.2	−0.19
chlorophyll			−0.59	−0.58	−0.52	−0.48	−0.1	−0.59	−0.42	−0.51	−0.49
mean temp				0.96	0.94	0.88	0.24	1	0.79	0.92	0.9
min temp					0.8	0.76	−0.06	0.96	0.7	0.84	0.81
MMM						0.94	0.55	0.93	0.85	0.94	0.93
DTR							0.51	0.89	0.91	0.96	0.96
dr90								0.24	0.44	0.4	0.42
CRW DHW									0.81	0.93	0.91
night insitu DHW										0.97	0.98
insitu DHW											1

this study (February 2017), experimentally heated ramets revealed site-specific variation in bleaching. Previous studies examining thermal tolerances of Ofu backreef *P. lobata* demonstrated a strong effect of origin, where HV and MV corals had higher tolerance limits than nearby forereef corals (Barshis et al. 2018). Similar to Barshis et al. (2018), there was an effect of native reef environment on chlorophyll fluorescence under experimental acute heat stress, however, it was native MV corals that had greater F_v/F_m values than HV native and transplanted ramets. Also, native MV coral F_v/F_m values were not affected by acute heat stress in February (6-mo), and total chlorophyll of MV ramets transplanted into the HV pool did not respond to acute heat stress in August (1-mo), suggesting that MV corals had greater tolerance limits than other backreef *P. lobata* examined herein. Sustained growth and bleaching resistance demonstrated by MV corals during this study and in Klepac & Barshis (2020) suggests that moderately variable environments with conditions just below an organism's thermal optimum could maximize fitness (Tr$_{max}$; Martin and Huey 2008) as climate warms. These results also indicate *P. lobata* in this system behaves differently than previously examined species

from Ofu's backreef pools. While most thermal tolerance studies of branching corals on Ofu have shown greater heat tolerance in HV native coral populations or corals transplanted into the HV pool (Thomas et al. 2018), we consistently found no effect of the HV common garden increasing bleaching tolerance *and* increased tolerance limits in MV *P. lobata* over two bleaching years (Klepac & Barshis 2020; this study). These reproducible results indicate reduced thermotolerance in massive corals from the highly variable backreef environment of Ofu Island relative to corals from the MV pool, likely due to chronic environmental variability that has become too physiologically costly under times of thermal stress.

High-resolution temperature metrics coupled with physiological diagnostics reveal differential bleaching responses

DHW have long been recognized as an effective predictor and monitoring metric for coral bleaching stress (SST; Liu et al. 2006). This study, however, highlights that DHW metrics are quite sensitive to different sources and scales

Fig. 6 A Principal component analysis biplot of physiological trait data for 120 control (i.e., field) ramets of *P. lobata*. Data points are colored by transplant group. Solid black vectors are the loadings for traits, and dashed blue vectors are temperature metric predictors cor-
related with the principal components. **B** The same data but points are colored by time with 95% confidence interval ellipses. PERMANOVA results are displayed for significant effects

of temperature measurements. Alternate but related coral bleaching metrics have been proposed, such as Degree Heating Days (Garde et al. 2014; Wyatt et al. 2020), Light Stress Damage (LSD; Skirving et al. 2018; Mason et al. 2020), and hydrodynamic modelling (Skirving et al. 2006). Here, the magnitude of thermal anomalies at a reef locale depends on whether accumulated heat stress is modeled using NOAA's CRW or *in situ* temperature, and which data and timespan are used to establish the historical climatology. NOAA's CRW products are all calculated from nighttime satellite 5 km SST data (Liu et al. 2003) and can over- or underestimate *in situ* temperature regimes at smaller reef-scales (Liu et al. 2013). When we applied the NOAA CRW 5 km MMM of 28.9 °C for Ofu Island to our *in situ* temperatures, the number of pool-specific *in situ* DHWs was much greater than DHWs from the NOAA CRW remotely sensed data from 2002 to 2007, but then are roughly similar from 2008 to 2017 (Fig. 2A). However, these NOAA CRW-derived DHWs are 2–3 times greater than the *in situ* DHWs derived from each pool's calculated MMM (i.e., Fig. 2A vs. B). The first discrepancy between these two climatologies is the use

of nighttime (NOAA CRW) versus 24 h (*in situ*) temperature data, where nighttime temperature-based climatologies result in lower daily and monthly temperature means and subsequently lower MMMs. Second, NOAA CRW products are based on a 5 km scale compared to our *in situ* temperature loggers (~ 1 km between pools), which result in averaged SST that also contributes to lower MMMs and greater number of DHWs. One additional consideration is the different range of years used to calculate the historical climatologies—our temperature records date back to 2000 versus 1985 for the NOAA CRW 50 km product (Liu et al. 2006). When the same years (2000–2017) were applied to the NOAA CRW dataset, the MMM was 1 °C higher. Given the steady increase in sea surface temperatures over the past decades (Lough et al. 2018), it is very likely a location's MMM would be greater if calculated from a more recent dataset instead of longer historical records dating back multiple decades.

Then which temperature metrics are best for predicting or understanding coral bleaching events? Metrics of thermal stress accumulation—daily variability, acute and cumulative

thermal stress, heating rate, and thermal trajectory—impose different amounts of stress exposure (Safaie et al. 2018; Sully et al. 2019) that could explain bleaching variation. McClanahan et al. (2019) demonstrated that a combination of multiple SST metrics (i.e., peak hot, duration of cool, and temperature bimodality) explained ~ 50% of the variance in coral bleaching prevalence during the global 2016 coral bleaching event as opposed to only 9% explained by DHW. The intensity, frequency, and rate of heat loading also influence coral bleaching outcomes in mass bleaching events (Skirving et al. 2019). High-frequency temperature variability can have a mitigating effect, reducing the odds of severe bleaching outcomes (Safaie et al. 2018; Sully et al. 2019).

Here, we found site-level differences in temperature variability, days over extreme temperatures, and DHW/DHHH, however, we did not observe clear differences in bleaching responses among pools in both our control ramets and donor colonies at the early onset of bleaching. Relatively low bleaching responses despite high variability and Degree Heating metrics could be a result of the timing of our sampling or other non-thermal factors, such as sunlight, turbidity, and water flow and quality differences among the backreef pools. Yet, the most consistent pattern (though subtle) observed among the various thermal metrics was the higher-resolution DHHH revealed greater heat loading in HV, which aligns with increased bleaching sensitivity of HV corals (Klepac and Barshis 2020; this study). Here, high-resolution heat loading metrics (DHHH) align with physiological diagnostics (CBASS and F_v/F_m) to reveal potential sublethal or subbleaching stress in the HV pool. Acute spikes in thermal variation are recognized as beneficial for coral stress responses (Safaie et al. 2018), yet thermal performance theory (Huey and Stevenson 1979) suggests an upper limit, with spikes too far above a thermal optimum likely shifting from protective to stress inducing. Indeed, the combination of thermal spikes with chronic heat loading, as experienced in the HV pool over two consecutive bleaching years (2015 & 2016) and historically in the number of DHHH, may overwhelm coral thermal performance, shifting native corals from the HV pool toward a chronic state of thermal stress susceptibility. Consequently, high-resolution *in situ*-derived metrics may be the most sensitive tools at reef-scales < 5 km to detect small-scale bleaching patterns and to assess thermal limits and, when coupled with bleaching monitoring and/or experimental heat stress, may improve our predictions and understanding of variation in thermal stress-induced coral bleaching.

Declarations

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