

Comparative thermal performance of the reef-building coral *Orbicella franksi* at its latitudinal range limits

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Abstract

Temperature drives biological responses that scale from the cellular to ecosystem levels and thermal sensitivity will shape organismal functions and population dynamics as the world warms. Reef-building corals are sensitive to temperature due to their endosymbiotic relationship with single-celled dinoflagellates, with mass mortality events increasing in frequency and magnitude. The purpose of this study was to quantify the thermal sensitivity of important physiological functions of a Caribbean reef-building coral, *Orbicella franksi*, through the measurement of thermal performance curves (TPCs). We compared TPC metrics (thermal optimum, critical maximum, activation energy, deactivation energy, and rate at a standardized temperature) between two populations at the northern and southern extents of the geographic range of *O. franksi*. We further compared essential coral organismal processes (gross photosynthesis, respiration, and calcification) within a site to determine which function is most sensitive to thermal stress using a hierarchical Bayesian-modeling approach. We found evidence for differences in thermal performance, which could be due to thermal adaptation or acclimatization, with higher TPC metrics (thermal optimum and critical maximum) in warmer Panama, compared to cooler Bermuda. We also documented the hierarchy in thermal sensitivity of essential organismal functions within a population: respiration was less sensitive than photosynthesis, which was less sensitive than calcification. Understanding thermal performance of corals is essential for projecting coral reef futures, given that key biological functions necessary to sustain coral reef ecosystems are thermally mediated.

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Introduction

Evidence that anthropogenic climate change is impacting the natural world continues to accumulate (Parmesan and Yohe 2003; Hoegh-Guldberg and Bruno 2010; Poloczanska et al. 2013; Hansen and Stone 2015). This warming is causing widespread impacts on marine populations and communities, as well as direct and indirect effects on humans (Hoegh-Guldberg and Bruno 2010; Doney et al. 2012; Poloczanska et al. 2013; Hughes et al. 2017a). Warming and numerous other environmental changes caused by CO₂ emissions (e.g., acidification, altered upwelling and current patterns, greater stratification, etc.) are also clearly altering ecosystem functioning (Nagelkerken and Connell 2015). For example, the temperature-dependence of individual-level processes (e.g., respiration, photosynthesis, predation, growth rate, and calcification) can cumulatively (across populations and species) lead to striking changes in ecosystem function (e.g., nutrient recycling, net production, and net calcification). This is especially true when foundation species are affected, altering functions such as habitat provisioning (Dove and Sammut

2007; Hettinger et al. 2012; Lemasson et al. 2017). To improve predictions of organismal to ecosystem responses to environmental change, it is necessary to quantify both individual/genotype and population response to warming and also functional sensitivities.

An effective way to empirically characterize the sensitivity of ectotherms across populations and individual-level processes is using a Thermal Performance Curve (TPC), which quantifies the shape of the relationship between biological rates of “performance” (e.g., respiration or growth) and environmental temperature (Fig. 1; Table 1). TPC parameters such as critical minimum (CT_{min}), critical maximum (CT_{max}), and thermal optimum (T_{opt}) describe the limits and optima of a chosen process with changing temperature (Huey and Stevenson 1979; Huey and Kingsolver 1989; Angilletta 2009). The positive and negative slopes on either side of T_{opt} are the rates of activation (E) and deactivation (E_h) energy, respectively, and indicate the sensitivity of the process. Species with high E and E_h (i.e., steeper slopes on either end of the curve) will be most sensitive, because they will quickly move from optimal to suboptimal conditions with only small changes in temperature. The rate at a standardized temperature, $b(T_c)$, is often used to compare rates between organisms or functions at a reference temperature (Padfield et al. 2017). Each of these TPC parameters can be compared among populations and species, locations with different thermal histories (e.g., across latitudes), and over time to predict future community composition and the functional consequences of environmental change.

In the context of climate change, applying a TPC approach to quantify thermal adaptation is essentially a space-for-time substitution (Pickett 1989; Blois et al. 2013; Faber et al. 2018)—a widely used approach when the practical temporal extent of a study cannot match the process of interest. There is extensive evidence of “adaptation” to spatial temperature gradients in a wide range of organisms, from local (e.g., tens of meters) to regional (100 s of km) scales (e.g., Berkelmans and Willis 1999; Berkelmans 2002; Sanford and Kelly 2011; Oliver and Palumbi 2011; Baumann and Conover 2011; Castillo et al. 2012; Thomas et al. 2012). Such phenotypic gradients presumably reflect an underlying selection gradient and can provide clues about numerous aspects of thermal adaptation, such as fitness costs and other trade-offs and the plausible range of survivable temperatures.

Coral reefs are being severely affected by global climate change. Like many other foundation species, the corals that build tropical reefs are being lost in response to anthropogenic warming (Hughes et al. 2017b, 2018a). Coral cover has declined dramatically on reefs worldwide over the last

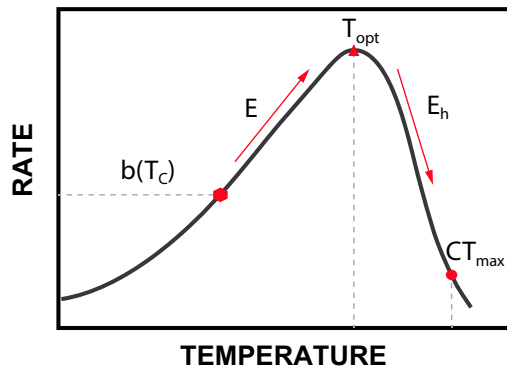


Fig. 1 Thermal performance curve characteristics, with comparative temperature metrics identified by the red symbols. See Table 1 for an explanation of each parameter

Table 1 Equations and parameters used in constructing thermal performance curves and calculating derived quantities

Model/derived quantities	Equation
Modified Sharpe–Schoolfield for high-temperature inactivation	$\log(\text{rate})_i = b(T_c) + E\left(\frac{1}{T_c} - \frac{1}{K \cdot T_i}\right) - \log\left(1 + e^{E_h\left(\frac{1}{K \cdot T_h} - \frac{1}{K \cdot T_i}\right)}\right)$
Thermal optimum	$T_{opt} = \left(\frac{E_h \cdot T_h}{E_h + (K \cdot T_h \cdot \log\left(\frac{E_h}{E} - 1\right))}\right)$
Parameters	Description
$b(T_c)$	Log rate at a constant temperature ($\mu\text{mol cm}^{-2} \text{h}^{-1}$)
E	Activation energy (electron volts, eV)
E_h	Temperature-induced inactivation of enzyme kinetics past T_h for each population (electron volts, eV)
K	Boltzmann constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$)
T_c	T_c is the reference temperature at which no low or high-temperature inactivation is experienced (defined here as 300.15 K or 27 °C)
T_h	Temperature (K) at which half the enzymes are inactivated
T_i	Temperature i in Kelvin (K)

30 years (from ~60 to <20% on some reefs), in large part due to ocean warming (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012; Hughes et al. 2018b) causing mass bleaching (i.e., the loss of the corals' symbiotic dinoflagellates and their nutritional benefits to the host, e.g., Oakley and Davy 2018). While there are numerous local causes of coral loss (e.g., pollution, destructive fishing practices, tourism, etc.), the single most detrimental stressor to date is thermal stress from anomalous heating events (i.e., heat-waves) and its associated complications (i.e., bleaching, disease, reduced calcification, etc.; Harvell et al. 2002; DeCarlo et al. 2017; Hughes et al. 2017b). Reef-building corals and their dinoflagellate symbionts live close to their physiological thermal maximum, and as a result, warming of 1 °C or more above local mean monthly maxima can reduce fitness and cause tissue loss or whole-colony mortality (Hoegh-Guldberg 1999; Baker et al. 2008), with significant negative implications for reef structure and function (Couch et al. 2017; Hughes et al. 2018a; Stuart-Smith et al. 2018). In the case of corals, there are numerous mechanisms that could enable local thermal adaptation, including genetic adaptation and physiological acclimatization of the host, changes in endosymbiont composition, and the bacterial microbiome (Putnam et al. 2017).

Hermatypic corals have several key physiological traits that scale up to influence ecosystem function. These traits include photosynthesis, respiration, and calcification, which generate much of the carbon on a coral dominated reef, power coral metabolic processes, and build the three-dimensional structure of the reef, respectively. Importantly, these traits are likely to have different responses to temperature, because they are controlled by different enzymatic machineries. For example, coral holobiont photosynthesis is dependent on single-celled dinoflagellates (in the family Symbiodiniaceae, LaJeunesse et al. 2018). These endosymbionts act as light and temperature sensors for the coral host and typically initiate the cascade of dysbiosis and bleaching through the generation of reactive oxygen species production, due to excess excitation energy in the photosystems under increasing temperatures (Oakley and Davy 2018). Because hermatypic corals are able to survive, at least temporarily, post-bleaching (Tchernov et al. 2011), holobiont respiration is likely to be less sensitive to temperature than photosynthesis, especially if food is available (Hughes and Grottoli 2013). Furthermore, because light-enhanced calcification is hypothesized to be dependent on energy supplied by Symbiodiniaceae (Allemand et al. 2011), corals may substantially reduce calcification when production is low (e.g., during bleaching events; Castillo et al. 2014; Barkley et al. 2018). Finally, the ratios between these different processes can change with temperature and have implications for survival and the long-term persistence of certain coral functions

(Coles and Jokiel 1977; Castillo and Helmuth 2005; Bahr et al. 2018).

The purpose of this study was to quantify the thermal sensitivity of important physiological functions of a reef-building coral with the goals of (1) comparing responses among colonies (putative clones) of the Caribbean coral *Orbicella franksi* between two populations at the northern (cool, Bermuda) and near the southern (warm, Panama) extent of the geographic range of this species and (2) comparing essential coral physiological processes (gross photosynthesis, respiration, and calcification) within a site (Bermuda) to determine which function is most sensitive to thermal stress. We hypothesized that corals in Panama would have higher thermal optima than Bermuda based on thermal history and that respiration rates would be more thermally tolerant than photosynthesis and calcification based on symbiont sensitivity to light and temperature and evidence for their contributions to dysbiosis (Venn et al. 2008; Lesser 2011; Oakley and Davy 2018). To test these hypotheses, we quantified thermal performance curves using a set of hierarchical Bayesian models.

Materials and methods

Study sites (Panama and Bermuda)

The Bocas del Toro Archipelago is located on the Caribbean coast of Panama at 9°N, 82°W, on the border of Costa Rica (Fig. 2b). It is composed of a complex network of islands and mainland peninsulas fringed by mangroves with well-developed seagrass beds and coral reefs (Collin 2005). The region hosts a high diversity of scleractinian corals, with 61 species documented, and mean coral coverage of 26.9% (Guzman et al. 2005). Long-term temperature records from shallow fringing reef systems within the Bocas del Toro Archipelago monitored from 1999 to 2004 document an annual mean seawater temperature of 28.5 °C, ranging from a mean of 25.9 °C in Jan–Feb to 29.7 °C in Sept–Oct (Kaufmann and Thompson 2005).

Located at approximately 32°N, 64°W, 1049 km south-east of Cape Hatteras (US central east coast), Bermuda's sub-tropical coral reefs represent the northernmost shallow-water reef system in the Atlantic Ocean (Fig. 2c). Annual reefal temperatures across the shallow reef platform (3–18 m depth) range from 15 to 30 °C (Coates et al. 2013; Locke et al. 2013a), which allows a variety of tropical marine organisms to live in this region, including 38 hermatypic and ahermatypic scleractinian coral species (Locke et al. 2013b). Bermuda is markedly cooler, however, than typical Caribbean reefs. For example, during the wintertime, on average, inshore SST is 8 °C cooler in Bermuda than Panama (Fig. 2d). Maximum temperature in the summer is

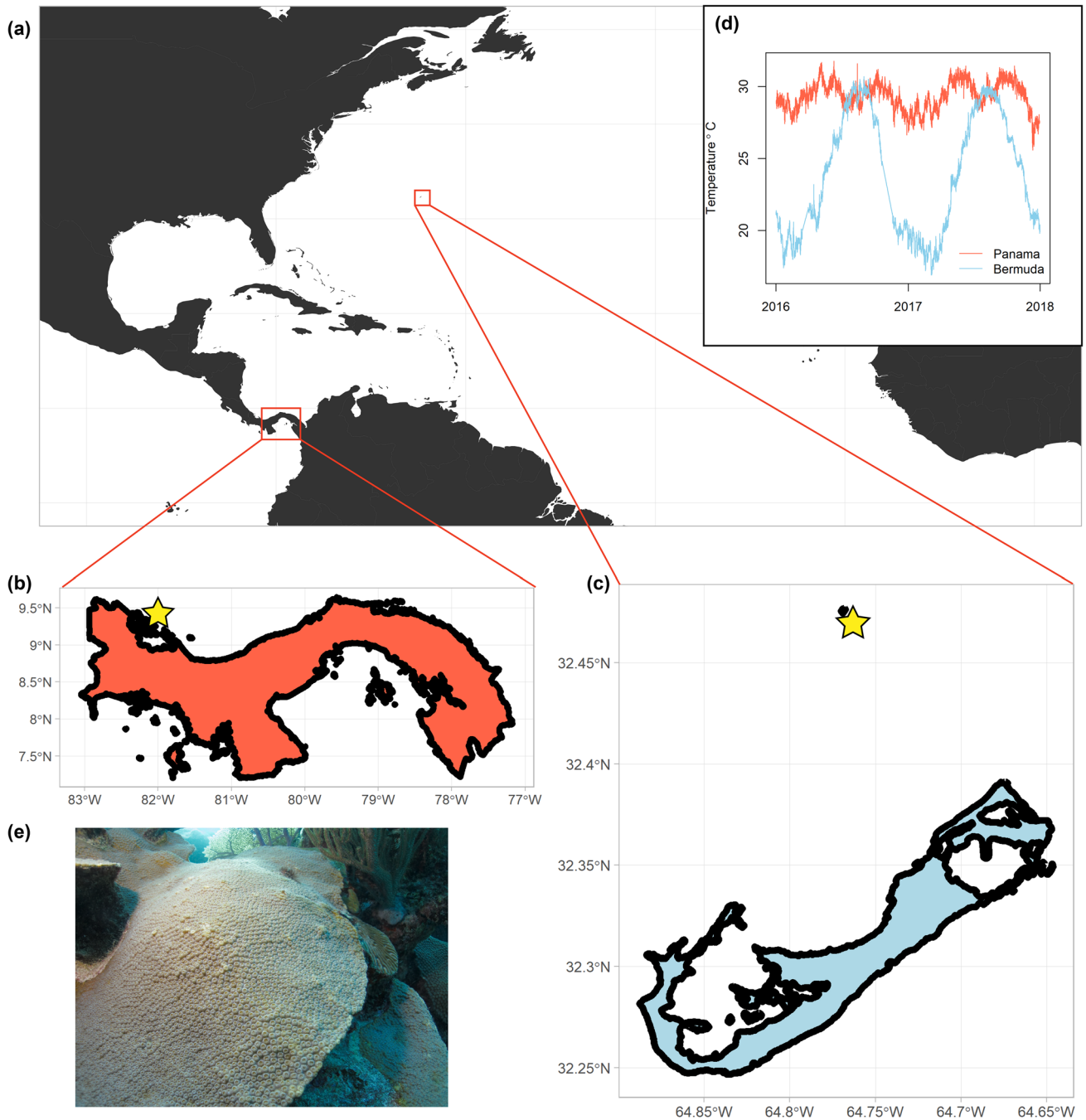


Fig. 2 a–c Map of study sites, d thermal histories, and e image of *Orbicella franksi*. Yellow stars in b Panama (orange) and c Bermuda (blue) maps indicate collection sites. Inset in the top right d shows the thermal histories for each location (data sets provided by the Physical

Monitoring Program of the Smithsonian Tropical Research Institute; NOAA National Data Buoy Center) and inset on the bottom left e is an image of *O. franksi* from the collection site in Bermuda (PC: N. Silbiger)

also $> 1\text{ }^{\circ}\text{C}$ lower in Bermuda than in Panama. Importantly, this has led to minimal impacts of coral bleaching in Bermuda (Cook et al. 1990; Smith et al. 2013).

Study species

The *Orbicella* spp. complex, containing the sibling species *O. annularis*, *O. faveolata*, and *O. franksi*, has been a dominant group of reef-building corals in the Caribbean, since at least the late Pleistocene (for ~ 1.2 million years) (Aronson

and Precht 2001) has the broadest geographic distribution across the western Atlantic, ranging from Brazil in the south to Bermuda in the north (Budd et al. 2012), and is a vital component of Caribbean reefs. The Caribbean has warmed at a rate of 0.27 °C per decade between 1985 and 2009 (Chollett et al. 2012), causing mass mortality of *Orbicella* via bleaching and infectious disease outbreaks (e.g., Weil 2004; Bruckner and Hill 2009). *O. franksi* is, therefore, an ideal coral for our study given its abundance in both Panama and Bermuda, its reef-building role, and its recent listing as threatened under the U.S. Endangered Species Act.

Sample collection

In Bermuda, specimens of *O. franksi* ($N=4$ colonies) were collected from the reefs at Hog Breaker, which is located on the rim reef of the northern lagoon (32° 27'26.38"N, 64° 50'5.1"W; Fig. 2c), at a depth of 8–12 m on Sept. 30, 2017. Bottom seawater temperature at the time of collection was recorded on a Shearwater Petrel dive computer as 26.1 °C. In Panama, specimens of *O. franksi* ($N=4$ colonies) were collected from the reefs at Crawl Cay on Nov. 25, 2017, which sits on the ocean facing side of the archipelago between Isla Bastimentos and Isla Popa (9° 14'37.8"N; 82° 08'25"W; Fig. 2b), at a depth of 5–10 m. This site was selected based on its distance from the mainland and the town of Bocas del Toro, to minimize the impacts of terrestrial runoff and nearshore anthropogenic impacts and to more closely reflect the conditions of the rim reef collection site in Bermuda. Bottom seawater temperature at the time of collection was recorded on a Shearwater Petrel dive computer as 27.8 °C. All samples were collected with a hammer and chisel. Sampled colonies in both locations were separated by a minimum of 5 m to reduce the probability of selecting clones.

Samples were brought back to the respective marine laboratory [Bermuda Institute of Ocean Sciences (BIOS) or Smithsonian Tropical Research Institute (STRI)] submerged in seawater in insulated coolers. Once at the lab, the colonies were immediately fragmented with a hammer and chisel into 11 replicate ramets and maintained in seawater flow through systems outside under ambient light and ambient temperature conditions (~27 °C and ~28 °C in Bermuda and Panama, respectively), where they were allowed to recover for 24–72 h before experimentation. The relatively short recovery time, due to logistical constraints, could lead to potential sampling effects. Therefore, our results should be interpreted with this caveat in mind. In Bermuda, samples were moved after the recovery period to a holding tank inside the laboratory in ambient seawater temperature (~27 °C) under greenhouse lights (Sun Blaze T5 High Output Fluorescent Light Fixtures) at 130 ± 6 (mean \pm SE, $n=9$) $\mu\text{mol m}^{-2} \text{s}^{-1}$ (which was above saturating light conditions; Fig. S1) prior to TPC measurements, while in Panama, the samples were

continuously maintained in the outdoor ambient conditions (~28 °C) until TPC measurements.

Photosynthesis–irradiance curves

Prior to experimental exposures, coral fragments from two genotypes ($N=2$) were used to generate photosynthesis–irradiance (PI) curves for each location to determine saturating irradiance for assessing rates of photosynthesis. Fragments were placed in individual acrylic respiration chambers (620 mL) with a magnetic stir bar and 5 μm filtered seawater in Bermuda and 50 μm filtered in Panama, with individual temperature (Pt1000) and fiber-optic oxygen probes [Presens dipping probes (DP-PS7-10-L2.5-ST10-YOP)]. PI curves were run at ambient temperatures in each location (27 °C in Bermuda and 28 °C in Panama). Oxygen was measured every second in the coral chambers ($N=2$) and blank chambers ($N=2$). Fragments were exposed to nine light levels generated by LED lights hung above the chambers (Arctic-T247 Aquarium LED, OceanRevive): 0, 31, 63, 104, 164, 288, 453, 610, and 747 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in Bermuda and 0, 22, 65, 99, 210, 313, 476, 613, and 754 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in Panama. Light levels were determined by an underwater cosine corrected sensor (MQ-510 quantum meter Apogee Instruments, spectral range of 389–692 nm \pm 5 nm).

Rates of oxygen flux were extracted using repeated local linear regressions with the package *LoLinR* (Olito et al. 2017) in R (R Core Team 2013), corrected for chamber volume, blank rates, and normalized to coral surface area calculated by tracing of planar area of the flat *O. franksi* samples using ImageJ (Schneider et al. 2012). *LoLinR* was run with the parameters of L_{pc} for linearity metric (L_{pc} = the sum of the percentile ranks of the Zmin scores for each component metric) and $\alpha=0.2$ (minimum window size for fitting the local regressions, which is the proportion of the total observations in the data set) for observations, and thinning of the data from every second to every 20 s for both locations. A non-linear least squares fit (NLLS; Marshall and Biscoe 1980) for a non-rectangular hyperbola was used to identify PI curve characteristics of each species. This model is as follows:

$$P_{\text{net}} = \frac{\phi\text{PAR} + \sqrt{(\phi\text{PPFD} + P_{\text{max}})^2 - 4\Theta\phi\text{PAR} P_{\text{max}}}}{2\Theta} - R_d, \quad (1)$$

where the parameters are P_{net} and P_{max} (area-based net and maximum gross photosynthetic rates, respectively), R_d (dark respiration, started at min rate in the dark), AQY (ϕ , apparent quantum yield), PAR (photosynthetically active radiation), and Theta (Θ , curvature parameter, dimensionless).

These PI curves identified saturating irradiance (I_k) of 110 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for Bermuda and 184 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for Panama, with no indication of photoinhibition (Fig.

S1). Subsequent measurements of photosynthetic rates were completed at $553 \pm 22 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Bermuda and $623 \pm 21 \mu\text{mol m}^{-2} \text{s}^{-1}$ in Panama to ensure that the corals were at saturating light conditions.

Characterizing metabolic thermal response

For TPC measurements, fragments were placed in individual respiration chambers to measure photosynthesis and dark respiration rate, as light-enhanced dark respiration rates (Edmunds and Davies 1988) (hereafter, respiration or R_d), after ~60 min of light exposure. The respirometry setup consisted of six 620 ml chambers with magnetic stir bars. Samples were measured in a series of runs that consisted of replicate fragments ($N=4$) and blank chambers ($N=2$), and included 60 min under saturating irradiance, followed by 60 min of dark. New fragments from the same colonies ($N=4$ colonies/genotypes) were used for each temperature run, resulting in acute TPC curves. Each colony/genotype was divided into $N=8$ (Bermuda) or $N=11$ (Panama) fragments, such that there was one fragment from each genotype per temperature (a total of $N=32$ in Bermuda and $N=44$ in Panama). Importantly, while these acute and non-ramping TPCs provide good comparative (relative) metrics of thermal responsiveness, they overestimate the metrics relative to samples acclimatized to each temperature, or ramped through all the temperatures (Schulte et al. 2011; Sinclair et al. 2016). We measured net photosynthesis and dark respiration at 8 temperatures in Bermuda (24, 26, 27, 29, 31, 32, 34, 36 °C) and 11 temperatures in Panama (26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 37 °C). Temperature was controlled to ± 0.1 °C by a thermostat system (Apex Aquacontroller, Neptune Systems) using a chiller (AquaEuroUSA Max Chill-1/13 HP Chiller) and heaters (AccuTherm Heater 300 W). Respirometry chambers containing both corals and blanks were placed into the pre-heated/chilled coolers once the temperature was stable and measurements started immediately. Rates of oxygen flux were extracted following the methods described above and gross photosynthesis (GP) was calculated as the absolute values of net photosynthesis plus dark respiration.

In Bermuda only, we also measured light and dark calcification across the seven temperatures. Calcification rates were calculated using the total alkalinity (A_T) anomaly technique (Chisholm and Gattuso 1991). Water samples ($N=3$ replicates) for A_T were collected in thrice rinsed, acid washed 250 mL Nalgene bottles from the temperature-controlled seawater prior to incubation and then again from each chamber (both corals and blanks) after the 60 min incubation. A_T samples were immediately preserved with 100 μL of 50% saturated HgCl_2 . A_T was analyzed using open cell potentiometric titrations (Dickson et al. 2007) on a Mettler T5 autotitrator. A certified reference material (CRM,

Reference Material for Oceanic CO_2 Measurements, A. Dickson, Scripps Institution of Oceanography) was run at the beginning of each sample set. The accuracy of the titrator was always less than 0.8% off from the standard and the precision was $< 5 \mu\text{mol kg}^{-1}$ between sample replicates.

Because calcification from the alkalinity anomaly is the sum of all calcification and dissolution processes in the coral, all exposed skeleton on the corals was covered with parafilm immediately prior to measurements to minimize dissolution of the carbonate framework. Light and dark calcification rates ($\mu\text{mol CaCO}_3 \text{ cm}^{-2} \text{ h}^{-1}$) were calculated using the following equation:

$$\text{Calcification} = \frac{\Delta A_T \cdot V \cdot \rho}{2 \cdot t \cdot \text{SA}}, \quad (2)$$

where ΔA_T ($\mu\text{mol kg}^{-1}$) is the difference in A_T between the initial and post-incubation samples (note: ΔA_T in the blanks was subtracted from the ΔA_T in the coral samples to account for any calcification due to other calcifiers in the seawater), V (cm^3) is the volume of water in the chamber accounting for the volume of the coral, ρ is the density of seawater (average density = 1.023 g cm^{-3}), t (h) is the incubation time (~1 h), and SA (cm^2) is the surface area of the corals determined by tracing of planar area of the flat *O. franksi* samples using ImageJ (Schneider et al. 2012). ΔA_T was divided by 2, because 1 mol of CaCO_3 is produced for every 2 mols of A_T . Values were divided by 1000 to yield $\mu\text{mol CaCO}_3 \text{ cm}^{-2} \text{ h}^{-1}$. Changes in dissolved inorganic nutrients were assumed to be minor in an hour incubation, making it unnecessary to account for nutrient concentrations in the alkalinity anomaly. Salinity was also measured in the pre- and post-incubation water samples (~37), but no evaporation was noted, as the chambers were airtight. We present our results as net calcification ($\text{NC} = \text{light calcification} + \text{dark calcification}$).

Model construction

We used Bayesian hierarchical models with Markov Chain Monte Carlo (MCMC) simulations to estimate coral thermal tolerance metrics for GP, R_d , and NC. One outlier in the NC data (temperature = 26 °C) was removed due to contamination of an alkalinity sample. $\text{Log}(x+1)$ GP, R_d , and NC rates were fit to modified Sharpe–Schoolfield models for high-temperature inactivation (Sharpe and DeMichele 1977; Schoolfield et al. 1981) (Table 1; Fig. 1). We ran three separate models to explicitly test the hypotheses that TPC parameters for GP (model 1) and R_d (model 2) differ between the Bermuda and Panama populations and that TPC parameters differ among the three organismal functions in Bermuda only (model 3). To get reliable estimates of all TPC parameters, the maximum experimental temperature needs to be high enough to bring the measured rate to near zero. We did not achieve near-zero R_d

rates in Panama (highest temperature measured was 37 °C), thus making the Panama versus Bermuda comparison for R_d unreliable. Therefore, for comparisons between populations (Panama versus Bermuda), we only present the GP model in the main text and we included the R_d model results in the Supplement (see Figs. S2–4). T_{opt} and CT_{max} were both estimated within the MCMC chain. CT_{max} was calculated as the temperature at which there was a 90% loss of maximum rate (i.e., rate at T_{opt}). For detailed model description, please see Supplemental Materials.

Model fitting and analysis

We ran our model using MCMC algorithms in JAGS (just another Gibbs sampler) (Plummer 2003) called from R (R Core Team 2013) using the R packages, *rjags* (Plummer 2011) and *dclone* (Sólymos 2010). We ran three parallel chains of length 2.5 M, with a burn-in of 2 M, and a thinning parameter of 1/2000 to account for high autocorrelation in the chains, leaving a total of 13,500 samples for inference.

We assessed convergence by checking all trace plots, ensuring that all chains were well-mixed, and calculating Gelman–Rubin statistics (Gelman and Rubin 1992) for all parameters (all of which were < 1.05). To assess model fit, we used posterior predictive checks by adding a step in each MCMC iteration to simulate data based on our model’s posterior predictive distribution and then comparing it to our observed dataset. Goodness of fit was evaluated using Bayesian p values, which are based on comparing the discrepancies between observed and simulated data. Bayesian p values for the mean, standard deviation, and coefficient of variance for all models were between 0.49 and 0.53 (close to 0.5), indicating that differences between observed and simulated data are likely due to chance. Finally, we plotted our observed versus predicted data from the model simulations and they were in close agreement (Figs. S5–6).

For our numerically generated posterior samples, we report median values with two-tailed 95% Bayesian credible intervals (BCI) for each parameter (essentially, Bayesian confidence intervals). We used the *compare_levels* function in the *Tidy-Bayes* package (Kay 2018) to make pairwise comparisons of each parameter among populations and organismal functions. Pairwise comparisons with credible intervals that do not overlap zero are considered to be statistically different from each other. All R and JAGS code are available on github (https://github.com/njsilbiger/Comparative_thermal_tolerance_of_Ofranski) and citable at Zenodo (<https://doi.org/10.5281/zenodo.3333002>) (Silbiger 2019).

Results

Differences in TPC parameters between populations

The Panama and Bermuda coral populations had markedly different functional responses to temperature (Fig. 3). Specifically, for GP, the corals from Panama were more thermally tolerant than those from Bermuda, with a 2.17 °C higher T_{opt} (0.95–3.65 °C [95% BCI]) and a 1.59 °C higher CT_{max} (0.93–2.61 °C [95% BCI]; Figs. 4, S7). The Panama population also had higher GP rates overall. At the reference temperature (27 °C), the $\log(x+1)$ GP rate was 0.24 $\mu\text{mol cm}^{-2} \text{h}^{-1}$ higher (0.13–0.32 $\mu\text{mol cm}^{-2} \text{h}^{-1}$ [95% BCI]) in Panama than Bermuda (Figs. 4, S7). Panama corals also had a marginally steeper deactivation energy (E_h) than Bermuda corals, meaning that GP drops out more quickly in Panama once it reaches its thermal optimum, but the activation energy (E) was the same between the two populations (Fig. 4). For dark respiration comparisons between Panama and Bermuda, see Supplemental Material (Figs. S2–4).

Differences in TPC parameters among organismal functions within a population

The TPCs among the three organismal functions tested (GP, R_d , and NC) were also substantially different from one another (Fig. 5a). In Bermuda, the general pattern in thermal tolerance was $R_d > GP > NC$ (Figs. 6, S8). Specifically, R_d had the highest T_{opt} (Fig. S8) and was 0.67 °C (-0.4 – 1.72 °C

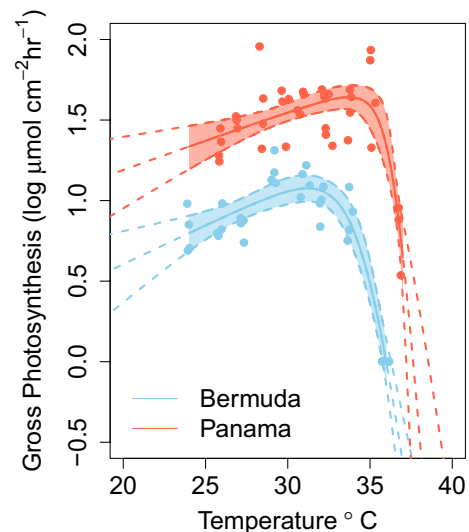


Fig. 3 Thermal performance curves of $\log(x+1)$ gross photosynthesis rates ($\mu\text{mol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$) from Panama (orange) and Bermuda (blue). Each dot represents an individual fragment ($n=32$ in Bermuda; $n=44$ in Panama) of *Orbicella franski* from 4 putative clones. Lines are medians \pm 95% BCI drawn from the posterior distribution. The shaded regions are the temperatures, where data were collected

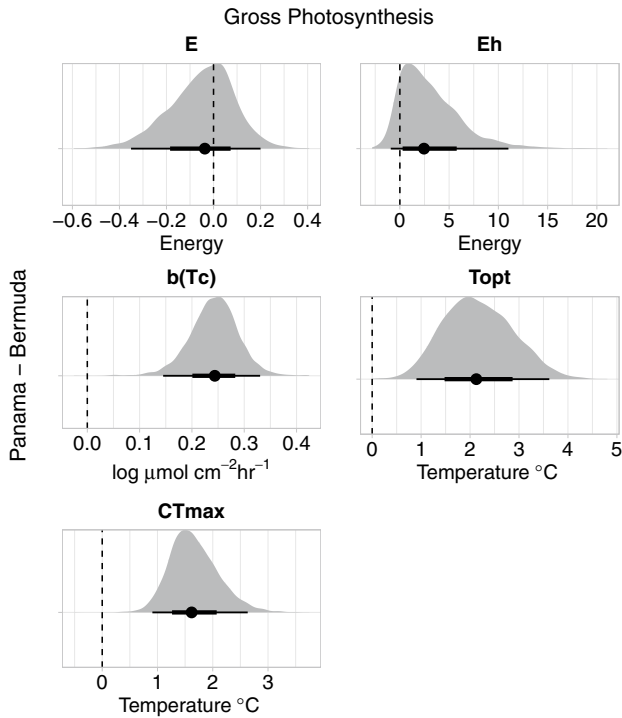


Fig. 4 Pairwise comparisons of thermal performance metrics from Panama and Bermuda for gross photosynthesis. Dot and whiskers below each distribution are the median and 50% (thick whiskers) and 95% (thin whiskers) BCI for each parameter. If the whiskers do not cross the dashed vertical line at 0, then the populations are considered to be statistically different from one another. Positive differences indicate the metric is higher in Panama than Bermuda corals

[95% BCI] higher than GP and 1.69 °C (0.72–3.02 °C [95% BCI] higher than NC (Fig. 6). While none of the CT_{max} values were statistically different from one another, on average, R_d still had the highest CT_{max} (Fig. S8). GP had the steepest deactivation energy (E_h) and was 3.15 (1.36–5.27 [95% BCI]) and 2.92 (0.89–5.07 [95% BCI]) higher than NC and R_d , respectively (Fig. 6). None of the activation energies (E) were significantly different from one another.

The hourly GP: R_d and NC:GP ratios also varied by temperature (Fig. 5b). GP: R_d generally declined with temperature, although it leveled off between approximately 27 and 30 °C. The GP: R_d ratio reached 1, where gross photosynthesis and respiration were equal, at 34.9 °C. NC:GP followed a unimodal curve, where the highest ratio (i.e., the most efficient calcification per unit production rate) was at 27.9 °C.

Variance components in thermal performance metrics

Clone-level variation in TPC metrics was generally low (Fig. S9). Variance in $b(T_c)$ due to differences between populations was 3.6× higher than variance due to differences

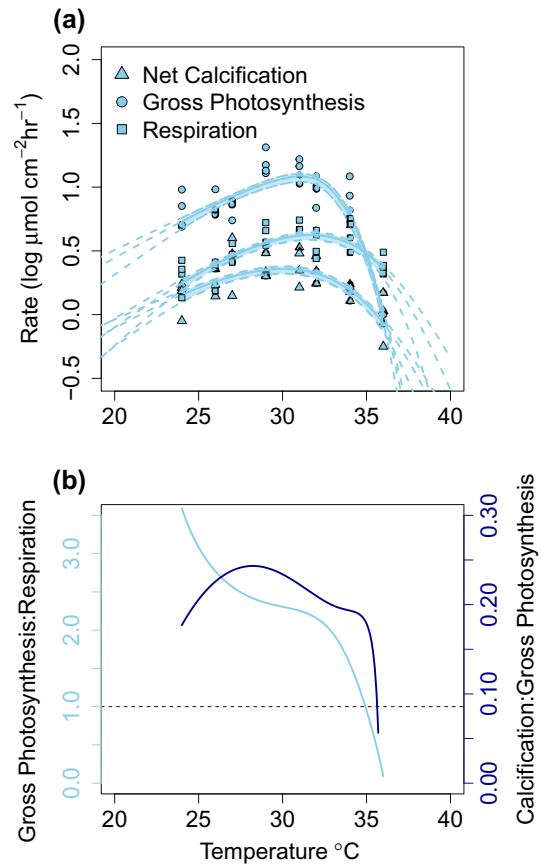


Fig. 5 a Thermal performance curves of $\log(x+1)$ gross photosynthesis (circles), dark respiration (squares), and net calcification (triangles) rates ($\mu\text{mol O}_2$ or $\text{CaCO}_3 \text{ cm}^{-2} \text{ h}^{-1}$) for Bermuda corals. Each dot represents an individual fragment ($n=32$) of *Orbicella franksi* from 4 putative clones across 8 temperatures. Lines are medians \pm 95% BCI drawn from the posterior distribution. The shaded regions are the temperatures, where data were collected. **b** Hourly GP: R_d (light blue) and NC:GP (dark blue) lines by temperature. Lines are from the best fit (median) from the model and the rates were back transformed before taking the ratio. Dashed horizontal line is at a GP: $R_d=1$. Any value < 1 indicates that the dark respiration rate is higher than the gross photosynthesis rate

among clones within a site. Similarly, variance in $b(T_c)$ among the three organismal functions was 2.7× higher than variance among clones.

Discussion

Our results indicate that two populations with different thermal histories respond differently to acute warming. Specifically, corals in Bermuda were less heat tolerant than those in Panama. Both T_{opt} and CT_{max} were greater for photosynthesis and T_{opt} was also greater for respiration (note the statistical significance of this difference was marginal). These differences in TPC metrics between populations, despite

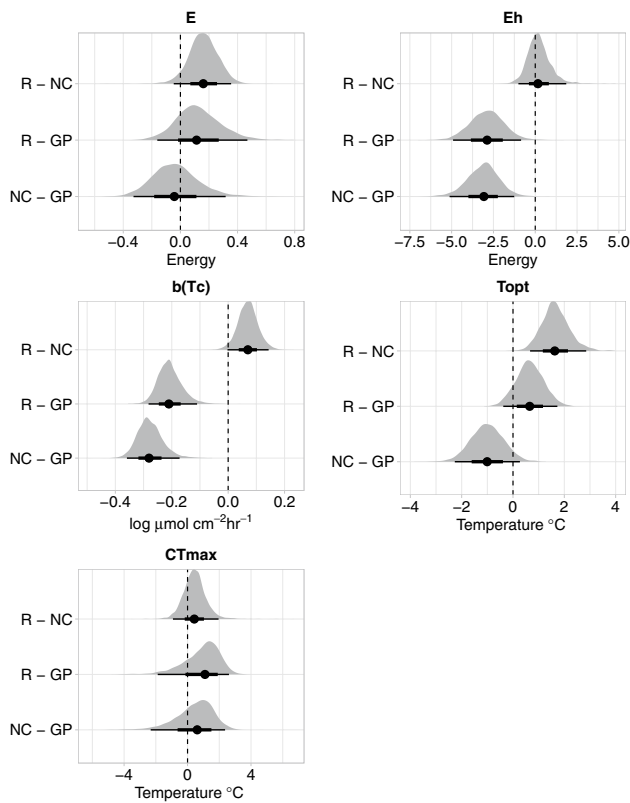


Fig. 6 Pairwise comparisons of thermal performance metrics from Bermuda comparing the three organismal functions measured. R is light-enhanced dark respiration, GP is gross photosynthesis, and NC is net calcification. Dot and whiskers below each distribution are the median and 50% (thick whiskers) and 95% (thin whiskers) BCI. If the whiskers do not cross the dashed vertical line at 0 then the organismal functions are considered to be statistically different from one another

minimal recovery and acclimation time, highlight that *O. franski* can adapt to local thermal regimes. Aichelman et al. (2019) found comparable adaptive capacity to thermal history across a latitudinal gradient (Rhode Island and Virginia, USA) in the temperate coral *Astrangia poculata* using similar methodology. Notably, the observed differences in thermal tolerance in the current experiment roughly match the difference in the average maximum summertime high at the two experimental locations (Panama average yearly maximum temperature between 2016 and 2018 is ~ 1.2 °C higher than Bermuda; Fig. 2d). Importantly, there are several differences in the thermal regimes between Panama and Bermuda, and both the mean and variance in environmental temperature can affect coral metabolism (e.g., Putnam and Edmunds 2011) and thermal sensitivity (e.g., Safaie et al. 2018). While there are several other environmental differences between Bermuda and Panama, a likely explanation for the observed thermal sensitivities is the fairly large (for a tropical and sub-tropical system) differences in maximum temperature (Fig. 2d). However, the comparison of phenotypic traits

between populations in this, or any other latitudinal study, should be interpreted with caution, as the results cannot be clearly attributed to temperature alone.

Assuming that the local temperature regime is a dominant cause of the observed among-population differences, numerous evolutionary and ecological processes could underlie this environmental matching. First, natural selection for thermally tolerant host genotypes in Panama could lead to adaptation to the local thermal regime and genetic population differentiation (Torda et al. 2017). Genetic analyses indicate that populations of the sibling species *O. faveolata* are generally well-mixed across the Caribbean basin (Rippe et al. 2017), with the confamilial species *Montastraea cavernosa* exhibiting high rates of genetic connectivity between Bermuda and the Bocas del Toro region of Panama (Goodbody-Gringley et al. 2012). *O. franski* is, therefore, expected to also have well-mixed populations with genetic exchange occurring between the two sample locations. Second, both the coral host and endosymbiont could be physiologically acclimatized to local temperatures (Brown and Cossins 2011). For example, epigenetic mechanisms could enable the Panama corals to be more tolerant of extreme high temperatures (Eirin-Lopez and Putnam 2019). Third, the dominant symbionts could be genetically differentiated (Baker et al. 2004), resulting in differential thermal tolerance. This appears to be possible, as historically Bermuda is dominated by *Brevolium* (clade or phylotype B) (Savage et al. 2002a, b; Venn et al. 2006), whereas Panama appears to be dominated by *Symbiodinium* (clade or phylotype A), and also hosts *Cladocopium* and *Durusdinium* (Toller et al. 2001; Garren et al. 2006), previously clades C and D, respectively (LaJeunesse et al. 2018). Numerous studies have found substitutions of thermally sensitive endosymbionts by more tolerant ones in both space and time (e.g., Baker et al. 2004; Boulotte et al. 2016), but genetic analyses of Symbiodiniaceae were not completed in our study. Fourth, it is also possible that differences in the coral-associated microbial community affect responses of host and symbiont to the temperature treatments (Webster and Reusch 2017). While our study was not designed to tease apart the relative contributions of these or other potential mechanisms leading to less thermally sensitive genotypes at the warmer site, several studies have found evidence supportive of thermal acclimation across spatial gradients (Sunday et al. 2011; Howells et al. 2012; Aichelman et al. 2019).

In addition to differing thermal sensitivity among populations, we also found that there are differences in thermal sensitivity among metabolic processes within populations. Specifically, GP, R_d, and NC all had different thermal optima (T_{opt}), rates of deactivation (E_d), and rates at a reference temperature [$b(T_c)$] (Fig. 6). Different enzymatic machinery is utilized for each of these traits (e.g., citrate synthase in respiration, RuBISCO in photosynthesis, and Ca-ATPase in

calcification), with some being specific to host or symbiont function. Therefore, in comparison, we hypothesized a priori that holobiont respiration was likely to be less sensitive to temperature than photosynthesis, which was supported by our data. Calcification was the least tolerant trait with the lowest thermal optimum. Other coral studies have also demonstrated that calcification is more sensitive to temperature than photosynthesis and respiration (though not using an explicit TPC approach; e.g., Reynaud et al. 2003; Al-Horani 2005). For example, at high temperatures, *Galaxea fascicularis* in the Red Sea produced less O₂ than it consumed (i.e., higher respiration than photosynthesis rate) and began to decalcify (Al-Horani 2005). Together, these results indicate that corals may be able to survive slight increases in warming (e.g., ~1–2 °C). However, they would still experience declines or even ecological loss of important functions related to fitness, or that are necessary for coral reef ecosystem functioning, such as net ecosystem production and net ecosystem calcification.

Notably, there is extensive literature that show differences in coral metabolic rates in response to temperature, especially using an ANOVA-style design, i.e., with two or three temperature treatment levels. In these types of experiments, patterns in metabolic responses are highly dependent on the temperatures chosen in blocked designs. For example, GP, R_d , and NC will all increase if the high-temperature treatment is below T_{opt} or decrease if the treatment is past its thermal optimum—under normal seawater conditions—leading to highly variable responses across studies (e.g., Edmunds et al. 2001; Reynaud et al. 2003; Edmunds 2008; Comeau et al. 2014; Hoadley et al. 2015; Krueger et al. 2017; Bahr et al. 2018). Coral metabolic responses to temperature are also species-specific (e.g., Edmunds 2008; Hoadley et al. 2015; Camp et al. 2016; Bahr et al. 2018), size-dependent (Edmunds and Burgess 2016), and dependent on other background environmental conditions, such as pH (e.g., Camp et al. 2016; Bahr et al. 2018), nutrient conditions (Nordemar et al. 2003), and food availability (Borell et al. 2008; Ferrier-Pagès et al. 2010). The variability in these responses further highlights the utility of using a TPC approach for comparative analyses.

The ratios of hourly GP: R_d and NC:GP both varied with temperature (Fig. 5). These ratios and how they change with temperature have implications for survival and the long-term persistence of certain functions. For example, corals need a GP: R_d ratio of greater than 2 to maintain long-term autotrophy (Coles and Jokiel 1977). Here, we saw GP: R_d generally declined with temperature, a pattern that has been shown in other coral studies (Coles and Jokiel 1977; Castillo and Helmuth 2005; Bahr et al. 2018), and that the GP: R_d dropped below 2 at 32.7 °C. Therefore, as ocean temperatures continue to warm, *O. franski* may need to shift to more heterotrophic food sources to survive

(Hughes and Grottoli 2013). The NC:GP ratio had a unimodal response to temperature, with the optimal calcification per unit production rate at 27.9 °C. Calcification and photosynthesis are highly coupled in corals and calcifying macroalgae (Goreau 1959; Barnes and Chalker 1990; Gattuso et al. 1999; Schneider and Erez 2006), although the mechanisms linking them continue to be debated (Gattuso et al. 1999, 2000; Cohen et al. 2016). Assessing NC:GP ratios can uncover the amount of CO₂ that can potentially be supplied from calcification to photosynthesis (Gattuso et al. 1999) and how this relationship may change with temperature.

We measured acute TPCs, which can be thought of as an instantaneous thermal “stress test”. While short acclimation times such as ours would underestimate absolute acclimation potential of the tested organisms, as they do not have time to fully acclimate, acute TPCs are used widely for comparative analyses (Schulte et al. 2011). For example, a relatively recent database compilation of studies examining thermal performance contains thousands of entries for > 200 traits across taxa ranging from microbes to animals, spanning ~16 orders of magnitude in body size extracted from ~300 studies (Dell et al. 2013). These TPC studies have helped uncover constraints on thermal acclimation (Rohr et al. 2018) and develop critical advancements in theory (e.g., Metabolic Theory of Ecology; Brown et al. 2004). Such TPC approaches, when conscious of important assumptions and applying appropriate experimental frameworks (Schulte et al. 2011; Sinclair et al. 2016), can provide useful metrics of comparison between organisms, populations, and species.

While there is a massive body of the literature on thermal tolerance of terrestrial and marine organisms (Dell et al. 2011), there is surprisingly less on the thermal performance characteristics of coral reef organisms in an explicit TPC context (but see, Jokiel and Coles 1977, 1990; Rodolfo-Metalpa et al. 2014; Aichelman et al. 2019; Jurriaans and Hoogenboom 2019). Understanding thermal performance of corals is essential for projecting coral reef futures, given that key biological functions necessary to sustain coral reef ecosystems (e.g., photosynthesis, respiration, and calcification) are thermally mediated. Here, we advance this area of research by applying the TPC approach to a variety of fitness related parameters in a reef-building coral across its geographic range, in a robust statistical framework. We suggest that future studies should incorporate multiple species and representatives from other functional groups to better predict ecosystem-level responses to temperature. Understanding how patterns of response differ among genotypes will improve our understanding of the inherent variability in thermal tolerance that exists within and among species and, therefore, potential cascading effects of biodiversity and genetic diversity loss. Taken together, these approaches will provide information critical to informing evidence-based

management and conservation of these threatened ecosystems in the face of a warming ocean.

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Author contributions NJS, JB, GGG, and HP designed the experiment, collected data in Bermuda, provided materials, and edited the manuscript; JB and GGG collected data in Panama; NJS and HP processed the data; NJS statistically analyzed the data.

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Data availability All R and JAGS code and data are available on github (https://github.com/njsilbiger/Comparative_thermal_tolerance_of_Ofranski) and citable at Zenodo (<https://doi.org/10.5281/zenodo.3333002>).

Compliance with ethical standards

Conflict of interest The authors have no conflict of interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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