Upper-mesophotic and shallow reef corals exhibit similar thermal tolerance, sensitivity and optima

Katelyn Gould[1] [iD] · John F. Bruno[1] · Rebecca Ju[2] · Gretchen Goodbody-Gringley[3]

Abstract The physiology of ectotherms living in marine environments is strongly influenced by their local thermal experience. Scleractinian corals living near their thermal optimums are increasingly vulnerable to bleaching and mortality as oceanic heat waves increase globally. Mesophotic coral ecosystems (MCEs) below 30 m depths are characteristically cooler than adjacent shallow water reefs, which according to theory should result in differential metabolic responses to temperature between depths. How local temperatures influence physiological responses in mesophotic corals is poorly understood. We compared thermal sensitivities of four coral species between a shallow (5–10 m) and upper-mesophotic (30−35 m) reef in Bermuda. Thermal performance curves (TPC) were measured in laboratory mesocosms for four common coral species (*Diploria labyrinthiformis, Orbicella franksi, Montastraea cavernosa* and *Porites astreoides*) across a wide range of temperatures (19−36). Our results indicate that the maximum rate of gross photosynthetic (GP) performance (GP-P_{max}) and the mean overall photosynthetic rates (GP-*lnc*) varied significantly among species. In contrast, thermal sensitivity (P_{max}, T_{opt}, *lnc*, *E*, *Eh*, or *Th*) did not vary between depths for conspecifics except for deactivation energy (GP-*Eh*) in *D. labyrinthiformis*. Additionally, gross respiration (*R*) did not differ among species or between depths for any thermal metric. Similar metabolic responses between depths suggest that local adaptation and/or acclimatization to different thermal conditions is likely not occurring. Instead, upper-mesophotic corals in Bermuda do not have lower bleaching thresholds than shallow water conspecifics, but similar thermal sensitivities supporting the potential for MCEs to function as a thermal refuge.

Keywords Refuge · Physiology · Thermal performance curves · Thermal optimum · Bermuda · Climate change

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Introduction

Ectotherms in marine environments are vulnerable to external conditions, predominately increasing seawater temperature. Ocean warming results in decreased rates of biological processes such as enzymatic functioning, whole organism metabolism, reproduction and behavior, which vary across individuals and populations. Measuring biological rates over a range of temperatures enables researchers to compare thermal sensitivities of individuals and populations among locations and across environmentally heterogenous landscapes or seascapes (Angilletta 2009). Differences in thermal ranges and sensitivities among habitats can be caused in part by local adaptation/acclimatization (Angilletta 2009), phenotypic plasticity (Sawall et al. 2015) and/or inherited thermal tolerance through epigenetics (Dixon et al. 2015). Evolutionary thermal biology predicts that individuals in colder

environments should have lower thermal optimum (T_{opt}) and thermal performance maximums (P_{max}) and higher sensitivities (E & Eh) when compared to individuals in warmer environments (Angilletta et al. 2006; Schult et al. 2011). As a notable example, Silbiger et al. (2019) found evidence of local adaptation and/or acclimatization in the coral *Orbicella franksi*, where corals from cooler Bermuda sites had lower performance rates and optimal temperature requirements compared to their warm-water conspecifics in Panama.

Characterization of thermal sensitivities and ranges in organisms can be achieved by constructing thermal performance curves (TPC), which define the relationship between performance rates (in this study, gross photosynthesis and respiration) of an individual/species and temperature. TPC have a characteristic shape (see Fig. 1 and Table 1 in Silbiger et al. 2019), where performance rates (metabolic, behavioral, or physiological) rapidly rise from

zero (thermal minimum, CT_{min}) with increasing temperature (activation energy, E) and peak at the thermal optimum (T_{opt}) and performance maximum (P_{max}). Following the peak is typically a rapid decline in performance (deactivation energy, Eh), culminating where organismal performance is zero (CT_{max}). The temperature at which enzymatic activity halts lies along the Eh slope and is termed the enzyme deactivation temperature (Th) and the overall mean performance rate across all temperatures is defined as *lnc*. Thermal minimum and maximum (CT_{min} & CT_{max}) demarcate an individuals or species thermal range, while performance maximum represents the peak performance rate at their ideal temperature (T_{opt}) (Huey et al. 1989, 1993; Angilletta et al. 2002; Angilletta 2009). TPC with steep E and Eh slopes (higher values) will be more thermally sensitive due to thermal conditions rapidly shifting from optimal to suboptimal. High thermal sensitivity implies that a small change in temperature causes
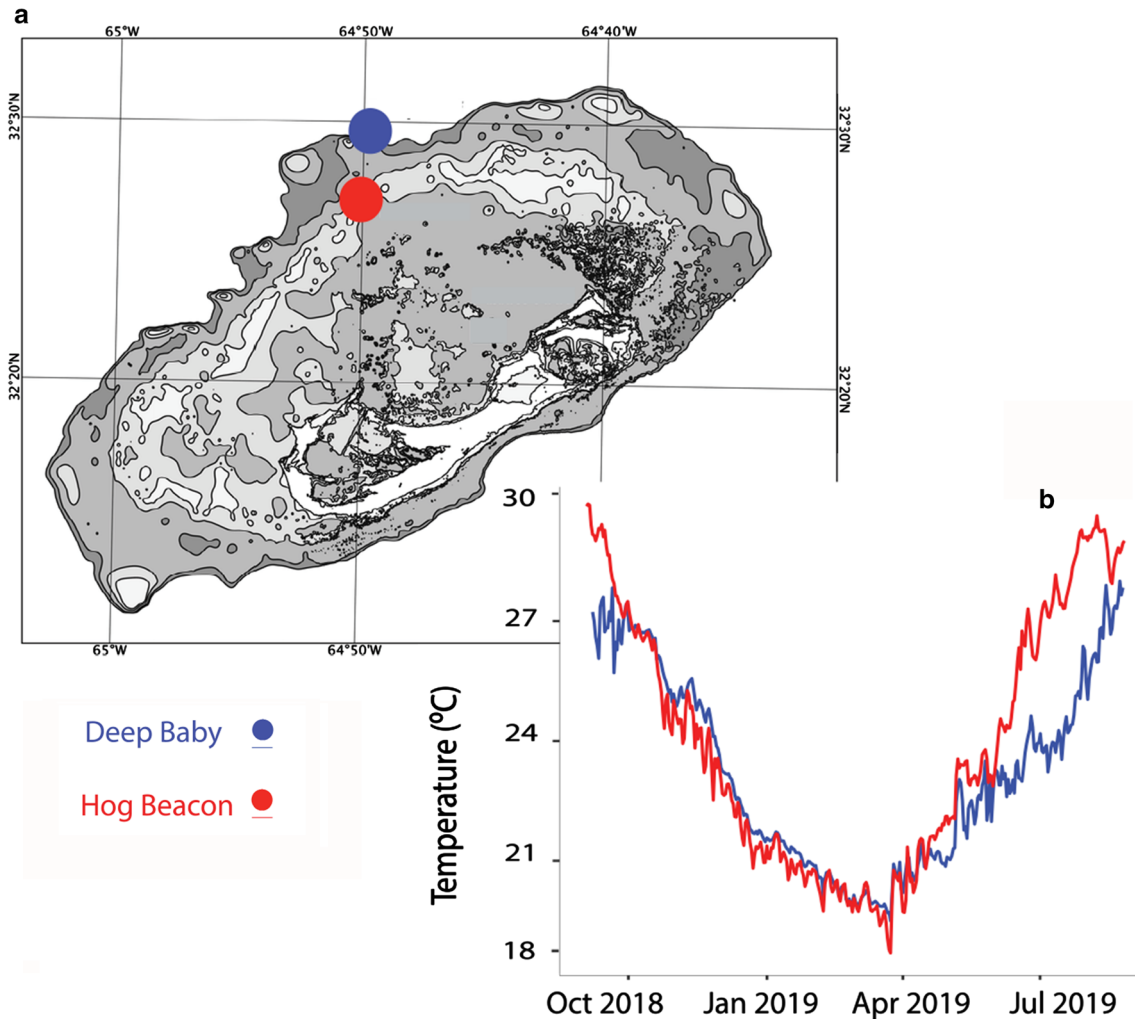

Fig. 1 **a** Bermuda reef platform designating location of reef sites: Hog Beacon (red circle) and Deep Baby (blue circle), **b** Annual in situ temperature (°C) data recorded with two HOBO ProV2 loggers from Sept. 2018 − Aug. 2019. Daily temperatures were averaged (48 measurements/day) across 2 loggers per site and graphed as values

Table 1 Summary statistics for linear regression models with interacting terms ($\sim$ species*depth) for all gross photosynthesis and respiration thermal performance parameters. E = activation energy, Eh = deactivation energy, Th = temperature enzymatic inactivity, T_{opt} = thermal optimum, lnc = mean performance rate, P_{max} = maximum rate of performance

Performance parameter	Performance metric	df	P statistic	p-value
P_{max}	GP	3	0.372	0.774
lnc	GP	3	0.967	0.434
T_{opt}	GP	3	0.568	0.645
E	GP	3	2.106	0.145
Eh	GP	3	1.379	0.080
Th	GP	3	0.768	0.530
P_{max}	R	3	0.033	0.992
lnc	R	3	1.170	0.352
T_{opt}	R	3	0.125	0.944
E	R	3	1.143	0.362
Eh	R	3	1.262	0.323
$\log Th$	R	3	0.787	0.520

dramatic physiological responses, while low thermal sensitivity indicates a large change in temperature is required to cause a similar response. Among-population variations in TPC shape (i.e., shifts in the height of the curve, position of T_{opt}, or the breadth of the curve) can be indicative of localized phenotypic plasticity and/or adaptation (Huey et al. 1989; Knies et al. 2009).

Shallow water corals live at or close to their thermal maximum and an increase in seawater temperature of 1 °C can result in large-scale bleaching and mortality (Sheppard et al. 2020). Globally, approximately 30% of coral reefs are categorized as severely damaged, while 50−75% of live coral cover has declined in the last 30−40 yrs (Schutte et al. 2010; De'ath et al. 2012; Jackson et al. 2014; Precht et al. 2020). In the Caribbean, shallow coral reef systems have been disproportionately impacted by anthropogenic stressors, leading to substantial decline in living coral cover, e.g., from $\sim$ 50% to $\sim$ 10% from 1977 to 2001 (Gardner et al. 2003; Precht et al. 2020) and from $\sim$ 33% prior to 1984 to $\sim$ 16% in 2006 (Bruno et al. 2007; Bruno et al. 2009; Schutte et al. 2010). Impacts to corals are expected to escalate as exposure to thermal stress continues to increase annually (Muñiz-Castillo et al. 2019).

Mesophotic Coral Ecosystems (MCEs), generally found between depths of 30−100 m, may be buffered from anthropogenic and natural stressors compared to shallower reefs in some regions (Lesser et al. 2009; Bongaerts et al. 2010; Kahng et al. 2014; Holstein et al. 2016; Prasetia et al. 2017; Kahng et al. 2016; Frade et al. 2018; Pinheiro et al. 2019). MCEs are characterized as light-dependent communities in subtropical and tropical waters beginning at 30 m and can extend to the depth at which photosynthesis can no longer be sustained ($\sim$ 150 m) (Hinderstein et al. 2010; Lesser et al. 2009; Loya et al. 2016). Laverick et al. (2020) define the upper-mesophotic zone as lying between $\sim$ 36 and 62 m based on preferred light conditions of shallow and mesophotic corals. Many species of

scleractinian corals have a broad depth distribution ranging from shallow to mesophotic depths. For example, Carpenter et al. (2008) found that out of the 845 species of corals globally, 704 were assigned conservation status and 40% of those threatened are found within the first 20 m, while the remaining 60% survive at depths greater than 20 m. Kramer et al. (2020) found corals across 14 families and 45 genera were more abundant in mesophotic (55.6%) compared to shallow depths (44.4%), in the Gulf of Eilat/Aqaba.

Due to relative proximity to the surface and the coastline, it has been suggested that thermal anomalies, bleaching, disease, pollution and storms may have greater impacts to shallow reefs compared to MCEs (West and Salm 2003; Lesser et al. 2009; Kahng et al. 2012, 2016). For example, shallow reef temperatures are driven by atmospheric thermal dynamics and wind and due to their depth can experience aggressive heat accumulation leading to water stratification. Once stratified, mixing of thermal layers can occur via internal waves, upwelling, or high winds; however this depends on the stratification depth, tidal forcing and reef-slope angle (Wyatt et al. 2019). Heat accumulation with a high residence time (average time reef is exposed to heat) can trigger extreme thermal anomalies leading to coral bleaching (Wyatt et al. 2019; Baird et al. 2009). However, as depth increases, heat accumulation decreases leading to generally cooler and more stable temperatures on MCEs (Turner et al. 2019).

Rocha et al. (2018) observed coral bleaching at mesophotic depths in the Pacific and Caribbean as well as sediment coverage and physical damage in both shallow and mesophotic (135 m) reefs in the Bahamas following Hurricane Matthew in 2016. Likewise, Smith et al. (2016) documented multiple occurrences of bleaching and disease on MCEs in the US Virgin Islands. In addition, MCEs may disproportionately suffer from upwelling and low temperature stress events leading to cold water bleaching due to

their position at greater depths (Kobluk et al. 1994; Bak et al. 2005; Menza et al. 2007; Studivan 2018). Thus, MCEs are not immune to the impacts of environmental stress. Rather, stable and cooler temperatures in MCEs are suggested to result in lower thermal thresholds for coral bleaching (Smith et al. 2016), which affect the resilience of MCEs and their capacity to serve as a coral refuge under future climate scenarios. However, whether MCEs are measurably more protected from environmental and anthropogenic stressors than shallow reefs and if locational biases play a role in this variation, remains unclear (Rocha et al. 2018; Turner et al. 2018).

The purpose of this study was to measure thermal sensitivities among four Western Atlantic coral species to (1) compare performance responses between depth-zones (shallow vs. upper-mesophotic) and (2) among species (*Diploria labyrinthiformis, Montastraea cavernosa, Orbicella franksi* and *Porites astreoides*) to determine whether coral populations exhibit depth-specific thermal sensitivities relative to their unique temperature exposures. Specifically, we compared TPC metrics during both gross photosynthesis and respiration responses in corals from a shallow (5–10 m) and upper-mesophotic (30–35 m) reef site in Bermuda. If upper-mesophotic corals are locally adapted to cooler, stable temperature ranges, we expected to see lower thermal optimums compared to shallow reef corals adapted to warmer, highly variable temperatures. As such, we hypothesized that upper-mesophotic corals would be less heat-tolerant than shallow corals resulting in lower thermal optimum (T_{opt}) and increased thermal sensitivities (high E and Eh values) and shallow corals would exhibit a higher T_{opt} with reduced thermal sensitivity.

Methods

Site selection

This study was performed on the North Atlantic Bermuda platform across two reef sites which vary by depth and environmental conditions (Fig. 1): a shallow rim reef (Hog Beacon; 8−10 m depth; 32°27′26′N, 64°50′05′W) and an upper-mesophotic reef (Deep Baby; 30−35 m depth; 32°29′18′N, 64°51′18′W). On November 26th, 2018, three colonies (∼ 40 cm diameter) from each of the following four coral species: *D. labyrinthiformis, M. cavernosa, O. franksi* and *P. astreoides*, were collected by hammer and chisel with a minimum of 5 m distance between colonies to ensure collection of distinct genotypes. The four coral species were chosen due to their abundance across depth and their varied thermal sensitivities and ecological strategies (Darling et al. 2012). Immediately upon returning to the Bermuda Institute of Ocean Sciences (BIOS)

mesocosm facility, coral colonies were fragmented into 8 individual ramet nubbins using a wet table saw. Ramets were on average 20.7 cm² (SD = 4.2 cm²) and all metabolic rates were standardized to individual's surface area and volume. Ramets were maintained in common garden conditions with depth-specific light (upper-mesophotic coral's light reduced by 37%) and ambient seawater temperature (measured in situ on collection day, 22 °C) in one 380-gallon flow-through filtered seawater (FSW) system for 24hrs to acclimate. A short acclimation period was selected in order to minimize confounding effects of the common garden environment to experimental responses while minimizing measuring a stress response due to removal and fragmenting. However, potential impacts of the recovery time as well as the low sample size (n = 3 genotype per species) should be considered when interpreting our results.

Maximum PAR measurements reflected values taken at daily peak irradiance on the day of collection (283.90 μmol photons m⁻² s⁻¹ on the shallow reef and 97.32 μmol photons m⁻² s⁻¹ on the upper-mesophotic site). Mesocosm tank mimicked average seasonal in situ light readings collected with paired HOBO pendant temperature loggers from September−October 2018. Temperature and salinity were quantified in the wet lab holding totes to mimic the ambient temperature of the BIOS mesocosm facility to 22 °C, controlled by an Apex Aquacontroller (Neptune Systems to ± 0.1 °C). Filtered seawater (5 μm filter) was replenished daily and stored in three large 20-gallon Rubbermaid (BRUTE tote storage) containers, two holding totes and one experimental tote. Water was recirculated and controlled for temperature in each individual tote with a chiller (AquaEuroUSA Max Chill-1/13 HP Chiller) and heaters (AccuTherm Heater 300 W) controlled to ± 0.1 °C by the Apex Aquacontroller.

In situ temperature data was collected from September 3rd, 2018−August 13th, 2019 at Hog Beacon and September 7th, 2018−August 21st, 2019 at Deep Baby with paired ProV2 temperature loggers and HOBO pendant temperature and light loggers (lux converted to photosynthetically active radiation; PAR). Loggers sampled at 30-min intervals and data values were averaged across paired loggers (Fig. 1). Similarly, an additional temperature data deployment occurred with two HOBO pendant temperature and light loggers (lux) from September 3rd, 2018−October 15th, 2018 at Hog Beacon and at Deep Baby from September 7th−November 18th, 2018 to provide supplementary temperature and irradiance. These pendant loggers were removed from the sites and used to convert lux light levels to PAR in the mesocosm. Used in combination with an underwater cosine corrected sensor (MQ-510 quantum meter Apogee Instruments, spectral range of 389−692 nm ± 5 nm) corresponding lux values

were converted to PAR. We achieved this by taking simultaneous measurements every hour for a week to identify the PAR values from equivalent lux measurements. This allowed us to use the PAR sensor during the experimental procedure (real-time measurements) while still accounting for the lux measurements taken in situ. Common garden irradiance exposure was modified for upper-mesophotic corals by placing shade cloths over the flow-through system, reducing ambient light levels by 37% thus mimicking in situ PAR measurements (283.90 µmol photons m^{-2} s^{-1} on the shallow reef; 97.32 µmol photons m^{-2} s^{-1} on upper-mesophotic).

Metabolic responses

One of 8 ramets from each genet and species (n = 3 ramets/species/site) was randomly assigned to one of eight temperature treatments (19, 21, 23, 26, 29, 32, 34, or 36 °C). Assay temperatures were randomized by day and each temperature trial consisted of 3 forty-minute incubation's (continuous 20-min dark and light trial). Each temperature incubation measured 8 individual ramets and one empty control chamber (FSW only). Individuals were randomized into a trial and incubation chamber. The control chamber accounted for oxygen consumption and production of microorganisms and bacteria within seawater. The metabolic rate from each incubation's control chamber was subtracted from each corresponding experimental chamber to correct for background metabolic activity.

The eight assay temperatures were chosen to capture Bermudian corals natural thermal range of 17−30 °C (yearly sea surface average of 23 °C, Locarnini et al. 2006, & yearly maximum of 29 °C, Coates et al. 2013) and above (31−36 °C), to quantify TPC parameters. Due to collection restrictions on coral size and number of individuals, each genotype produced 9−10 nubbins after fragmentation. Therefore, we chose eight assay temperatures to reflect cooler minimum temperatures found in the upper-mesophotic zone based on the missing lower end of the thermal range used in Silbiger et al. (2019) (24, 26, 27, 29, 31, 32, 34, 36 °C). Assay temperatures were concentrated around the lower and upper limits (2 °C gap compared to 3 °C gap around thermal maximum) of the performance ranges estimated in Silbiger et al. (2019) to refine performance metrics (thermal sensitivities, E & Eh) at the boundaries of their thermal range and to ensure upper-mesophotic thermal optima was represented (shallow *O. franksi* predicted to be < 31 °C, see Fig. 3 in Silbiger et al. 2019).

To avoid synergistic effects of temperature treatments over time (i.e., thermal stress loading), we tested one individual at each temperature to measure instantaneous thermal stress, allowing relative parameter estimate comparisons at each temperature level (n = 192). Individual coral fragments were transferred to the experimental indoor wet laboratory at approximately 8:00 AM daily, kept in complete darkness to dark acclimate for at least 30 min and then tested for 20-min in the dark followed by a 20-min light incubation (583.5 ± 3 µmol photon m^{-2} s^{-1}). After each temperature trial corals were immediately frozen and maintained in a − 80 °C freezer at BIOS for subsequent analyses.

To determine thermal sensitivities, discrete measurements of temperature dependent metabolism, net photosynthetic (*NP*) and respiration (*R*) rates, were collected via respirometry. Nine, 650-mL closed acrylic incubation chambers with a fiber-optic oxygen probe sensor (Presens dipping probes [DP-PSt-7–10-L2.5-ST10-YP]) measured oxygen evolution in both dark *R* and light *NP* trials sequentially. All chambers were equipped with a magnetic stir bar and locked into a custom-built motor powered magnetic stirring table as in Silbiger et al. (2019). This setup ensured continuous water circulation in each chamber to prevent oxygen super-saturation. Respirometry chambers were submerged in temperature controlled FSW in the experimental tote and covered with a tarp to ensure complete darkness for the first twenty-minute trial to estimate dark respiration rates.

To estimate photosynthetic rates, a full spectrum aquarium light (MARS AQUA 300 W LED) was suspended above the chambers and set at an average of 583.5 µmol m^{-2} s^{-1}. The irradiance value used for the light incubations was derived from photosynthesis-irradiance (PI) curves and based on saturating irradiances (I_k) and the point of photoinhibition for all species (Fig. S1). Prior to experimental trials, we tested eight corals, two from each species and across depth (n = 1 per genotype) in respirometry chambers held at ambient temperature (22 °C). We ran 20-min incubations under eleven light intensities averaging: 0, 105, 218, 272, 408, 506, 538, 710, 802, 902 and 1003 µmol photon m^{-2} s^{-1}. Due to differences in irradiance experienced at depth ($\sim$ 37% reduction) we expected upper-mesophotic corals to be photoinhibited at lower light levels (Kahng et al. 2019); however we found no evidence of photoinhibition at either depth (Fig. S1). We selected 580 µmol photon m^{-2} s^{-1} (583.5 ± 3 µmol photon m^{-2} s^{-1}, mean ± SE, n = 10) as the experimental light level to reflect a value below the point of photoinhibition and above the saturating irradiances found at both depths, I_k of 141.5 µmol photon m^{-2} s^{-1} for shallow and 94.6 µmol photon m^{-2} s^{-1} for the upper-mesophotic (Fig. S1).

PAR measurements for each chamber were quantified before each experimental light trial with an underwater cosine corrected sensor. Metabolic rates were extracted from oxygen concentrations recorded by the Pre-Sens

Measurement Studio 2 software (v. 2.1.0.443) from the raw change in oxygen over the dark and light trials in base R v. 3.5.2 (R Core Team, 2018) using repeated local linear regressions in the package *LoLinR* (Olito et al. 2017). Following protocols outlined in Silbiger et al. (2019), raw metabolic rates were normalized to chamber volume and surface area using a planar tracing approach as outlined in Naumann et al. (2009). Surface area was quantified (in cm^2) from pictures (n = 3) taken immediately before each trial and estimated with image analysis software ImageJ v1.

Statistical analysis

Oxygen rates used in the PI curve were extracted and fit to a nonlinear least squares regression of a non-rectangular hyperbola (Marshall et al. 1980) and analyzed using the methods described by Silbiger et al. (2019) to extract curve parameters: area-based net and maximum gross photosynthetic (GP) rates, NP and R. Thermal sensitivities were characterized by constructing TPC following the Sharpe–Schoolfield model (Sharpe et al. 1977; Schoolfield et al. 1981).

Metabolic rates were calculated from absolute values of NP plus dark R to obtain gross photosynthesis (GP) (Hoogenboom et al. 2006; Lyndby et al. 2018). Log-transformed oxygen concentrations (GP & R) were averaged for each coral species and site, fit to a nonlinear least squares regression using the statistical program base R and run through *nls.multstart* (Padfield et al. 2016). Uncertainty around each curve was accounted for with bootstrapping calculating ± 95% confidence bands around predictions. Metabolic processes were separated into gross photosynthesis and respiration and thermal performance parameters E, Eh, Th, lnc, T_{opt} and P_{max} were estimated for each genotype. Parameter outliers were identified and removed using Cook's distance (values 4 times greater than the mean were considered outliers). ANOVA assumptions were tested with the Levene's test for homogeneity of variance and the Shapiro–Wilk's test for normality of residuals. Variables that violated ANOVA assumptions (Th parameter during respiration; Shapiro-Wilk's test: $p = 0.0104$) were log-transformed prior to subsequent analyses.

Linear regression models were run for each performance metric using the *lm* function in R statistical software including interactions between the fixed effects, depth and species. This was followed by a one-way ANOVA testing the effect of depth within each species. We performed a mixed model with genotype as a random effect; however, it was found to show collinearity to both depth and species and subsequently removed from the model. Post hoc Tukey's HSD tests were performed to reveal significant effects between variables. Similarly, gross photosynthesis

measurements for each species at each temperature tested were divided by the corresponding R values and used to construct and compare photosynthesis and respiration ratios (P:R). A linear model was run using the *lm* function in R to assess the interaction between fixed effects depth and species.

Temperature data collected during September 2018–August 2019 was compared using a paired *t* test in *ggpubr*. Subsequently, we tested the average daily temperature with a linear *lm* model and 0.05 alpha between sites to determine significant effects. To identify seasonal differences, we tested summer and winter months using the same methodology.

Results

The in situ temperature data show patterns consistent with previous thermal descriptions in Bermuda (Goodbody-Gringley et al. 2015). The shallow rim reef (Hog Beacon) experienced a yearly mean temperature of 23.3 °C ± 3.05 (mean ± SD) fluctuating between 18.5 and 30.2 °C (Δ 11.7 °C). The upper-mesophotic reef (Deep Baby) had a mean temperature of 23.4 °C ± 2.4 (mean ± SD) varying from 19 to 28.7 °C (Δ 9.7 °C) during an annual cycle (Fig. 1). Temperatures across depth fluctuated differentially seasonally, showing an overlap in mean temperatures, while highlighting broader fluctuations in shallow maximum and minimums throughout the year. Comparison of average daily temperature between sites further confirmed different thermal environments (*t* test*; p = 8.1e-08* & linear model; $p = 3.058e-07$, df = 35.810, F = 26.22). During the winter months (November − April) sites experienced equivalent average temperatures (deep = 21.6 °C, shallow = 21.3 °C; *t* test*; p = 0.4825* & linear model; $p = 0.4824$, df = 58, F = 0.4999), while during summer months (May − October) there was a significant difference in temperatures where Hog Beacon was 1.6 °C warmer than Deep Baby (deep = 24.7 °C, shallow = 26.3 °C; *t* test; $p = 0.0047$ & linear model; $p = 0.0046$, df = 54, F = 8.719).

Thermal performance curves for each species show overlap between shallow and upper-mesophotic corals in both gross photosynthesis and respiration rates (Fig. 2). No significant interactive effects between depth and species were found for any gross photosynthesis or respiration thermal performance parameters (Table 1.)

Gross photosynthetic performance parameters E, Eh, Th, T_{opt}, lnc and P_{max} did not differ significantly by depth when assessing across all species (see Fig. 3 and S2; $p = 0.170$, $p = 0.0799$, $p = 0.152$, $p = 0.106$, $p = 0.4339$ and $p = 0.774$ respectively). Photosynthesis metric Eh (deactivation energy) was significantly different between depths
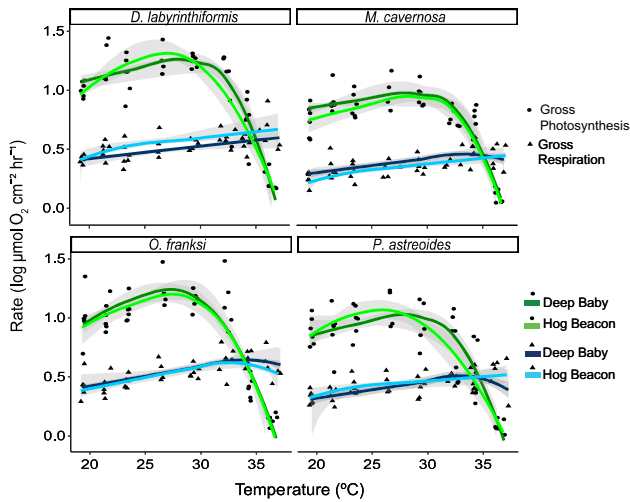
Fig. 2 Gross photosynthesis (circles) and respiration (triangles) measured in μmol O_2 cm^{-2} hr^{-1} across four coral species (n = 192). Fitted lines represent medians from three genotypes per species ± gray 95% bootstrap confidence bands. Upper-mesophotic corals from Deep Baby are dark green (photosynthesis) and dark blue (respiration). Hog Beacon curves are light green (photosynthesis) and light blue (respiration) and depict shallow water coral
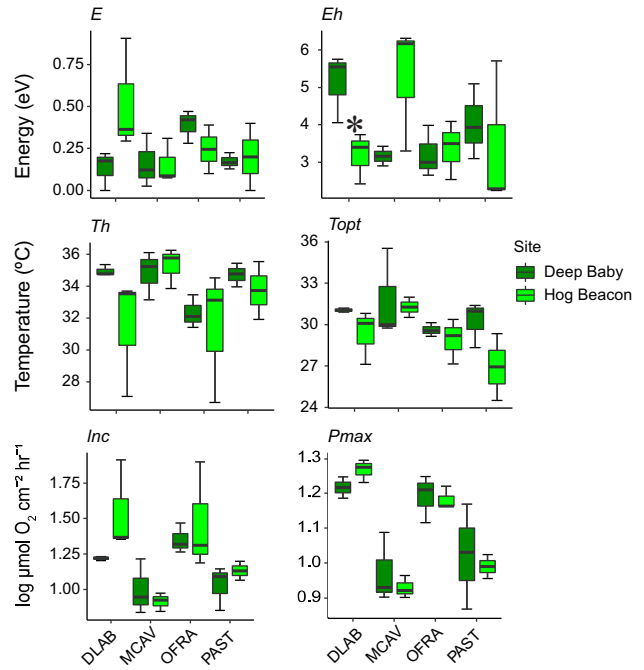

Fig. 3 Box and whisker plots of thermal performance parameters for gross photosynthesis compared between depths and species (n = 187, 5 unique outliers). The centerlines of boxes are median values and whiskers represent upper and lower 1.58*IQR (inter-quantile range). DLAB = *Diploria labyrinthiformis*; MCAV = *Montastraea cavernosa*; OFRA = *Orbicella franksi*; and PAST = *Porites astreoides*. Upper-mesophotic corals from Deep Baby are represented by dark green and shallow corals from Hog Beacon are light green. The black asterisk over DLAB for (Eh) denotes a significant one-way ANOVA result ($p = 0.0435$ between depths within *Diploria labyrinthiformis*). E = activation energy, Eh = deactivation energy, Th = temperature enzymatic inactivity, T_{opt} = thermal optimum, lnc = mean performance rate, P_{max} = maximum rate of performance

for *D. labyrinthiformis* only (see Fig. S3; one-way ANOVA; $p = 0.0435$). Gross respiration performance parameters did not differ significantly by depth for any species (see Fig. 4 and S4; E: $p = 0.22$, Eh: $p = 0.785$, log Th: $p = 0.666$, T_{opt}: $p = 0.762$, lnc: $p = 0.088$, & P_{max}: $p = 0.449$).

Overall, gross photosynthetic parameters E, Eh, Th and T_{opt}, did not differ significantly by species (Fig. S5; $p = 0.362$, $p = 0.504$, $p = 0.133$ and $p = 0.159$ respectively); however, P_{max} and lnc did differ ($p = 4.02e^{-06}$, df = 18, F = 21.11 and $p = 0.0031$, df = 19, F = 6.592). Subsequent Tukey's HSD tests were performed to identify pairwise differences between species, significant p-values are listed in Table 2. Further, comparisons among species for thermal performance parameters for gross respiration performance rates were not significant (Fig. S6; E: $p = 0.228$, Eh: $p = 0.48$, log Th: $p = 0.293$, T_{opt}: $p = 0.438$, lnc: $p = 0.231$ and P_{max}: $p = 0.0511$).

Photosynthesis to respiration (P:R) ratios remained constant from 19 to 30 °C but declined rapidly from 31 to 36 °C (Fig. 5 & Fig. S7). Upper-mesophotic and shallow reef corals showed similar P:R curves with a non-significant linear regression for the interaction of species and depth (species; $p = 0.066$, df = 3, F = 2.44, depth; $p = 0.796$, df = 1, F = 0.0673 and interaction; $p = 0.75$, df = 3, F = 0.403).

Similar to P:R curves, GP thermal optimums (temperature at peak performance) did not differ between depths. In fact, when comparing between depths all upper-mesophotic corals had larger T_{opt} values than shallow; *D.*

labyrinthiformis (31.05 °C ± 0.204 & 29.34 °C ± 1.96), *M. cavernosa* (31.76 °C ± 3.28 & 31.27 °C ± 0.732), *O. franksi* (29.61 °C ± 0.488 & 28.91 °C ± 1.62) and *P. astreoides* (30.24 °C ± 1.656 & 26.92 °C ± 3.41) respectively.

Discussion

Contemporary views on depth-dependent coral thermal sensitivity is that deeper, cooler, more thermally stable environments should result in lower bleaching thresholds for corals (Howells et al. 2012; Smith et al. 2016). Given the statistically cooler temperatures documented on MCEs in Bermuda (Goodbody-Gringley et al. 2015), we predicted that upper-mesophotic corals would have lower thermal optima and higher thermal sensitivities compared to shallow water populations. Instead, we found similar thermal optima and sensitivities between depths for all species examined, suggesting that local adaptation and/
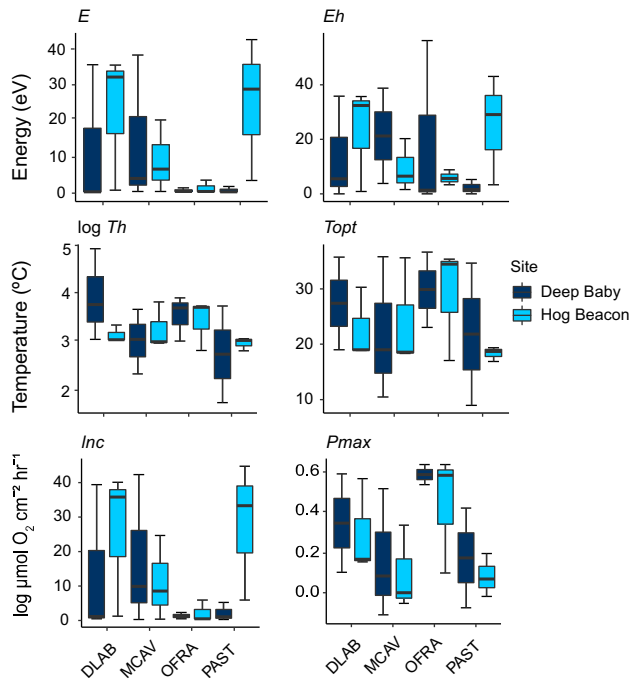
Fig. 4 Box and whisker plots of thermal performance parameters for respiration compared between depths and species (n = 188, 4 unique outliers). The centerlines of boxes are median values and whiskers represent upper and lower 1.58*IQR (inter-quantile range). DLAB = *Diploria labyrinthiformis*; MCAV = *Montastraea cavernosa*; OFRA = *Orbicella franksi*; and PAST = *Porites astreoides*. Upper-mesophotic corals from Deep Baby are represented by dark blue and shallow corals from Hog Beacon are light blue. E = activation energy, Eh = deactivation energy, Th = temperature enzymatic inactivity, T_{opt} = thermal optimum, lnc = mean performance rate, P_{max} = maximum rate of performance

or acclimatization to temperature has not occurred in these populations. Our findings show nearly identical gross photosynthesis and respiration TPC between depths and notably all but one upper-mesophotic coral species (*O. franksi*) had *GP* thermal optimums above the mean shallow water yearly maximum (30.2 °C). These results illustrate the potential role of upper-mesophotic reefs in Bermuda as
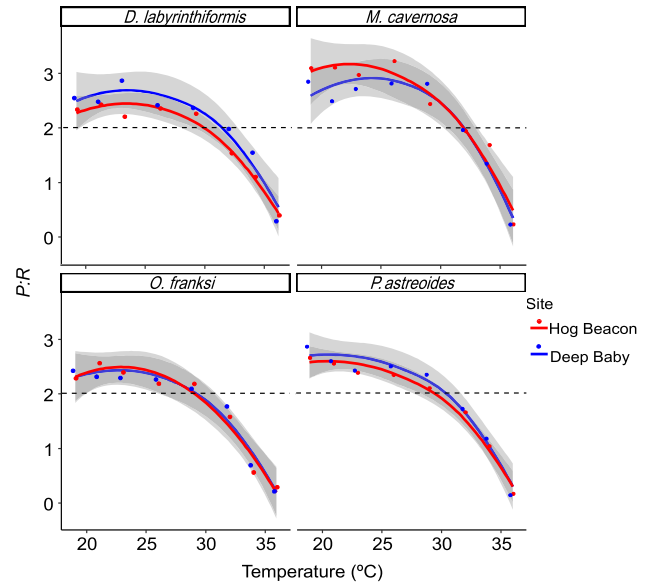

Fig. 5 Photosynthesis respiration ratios for upper-mesophotic (blue) and shallow reef (red) by temperature for each species (n = 192). Solid lines represent the average fitted values and the gray bands are 95% confidence intervals. The black dashed horizontal line is where $P{:}R = 2$ (i.e., the upper threshold for long-term survival)

thermal refuge for these four species under future climate change scenarios and warrants further investigation.

Differences in annual reef temperature between the shallow and upper-mesophotic sites documented in this study conform with previous studies, showing cooler more stable thermal environments in MCEs due to thermoclines, upwelling and decreased heat attenuation at depth (Leichter et al. 2006, 2012; Smith et al. 2008, 2016; Lesser et al. 2009; Brandt et al. 2013; Smith et al. 2013a, b, c; Goodbody-Gringley et al. 2015; Bongaerts et al. 2015; Kahng et al. 2019). While thermal variation between our reef sites was significantly different over a 1-yr period, concordant with findings in previous studies at similar depths (Goodbody-Gringley et al. 2015, 2018), the latitudinal position of

Table 2 Summary statistics for significantly different post hoc Tukey-HSD pairwise species comparisons for gross photosynthesis metrics, P_{max} and lnc. Significant differences are denoted with an asterisk (*p*-values < 0.05). DLAB = *Diploria labyrinthiformis*;

MCAV = *Montastraea cavernosa*; OFRA = *Orbicella franksi*; and PAST = *Porites astreoides*. P_{max} = performance maximum & lnc = mean performance rate

Performance parameter	Species	Mean ± SD(μmol O_2 cm^{-2} h^{-1})	Pairwise comparison	Difference	*p*-values
lnc	*O. franksi*	1.4 ± 0.258	OFRA − MCAV	0.4511	0.008*
lnc	*D. labyrinthiformis*	1.38 ± 0.014	DLAB − MCAV	0.4245	0.013*
lnc	*M. cavernosa*	0.95 ± 0.056	NA	NA	NA
P_{max}	*O. franksi*	1.17 ± 0.053	OFRA − PAST	0.1944	0.0036*
P_{max}	*D. labyrinthiformis*	1.24 ± 0.046	DLAB − MCAV	0.324	1.3e^{-5}*
P_{max}	*M. cavernosa*	0.92 ± 0.078	MCAV − OFRA	−0.2582	1.2e^{-5}*
P_{max}	*P. astreoides*	0.98 ± 0.121	PAST − DLAB	−0.26001	3.1e^{-5}*

Bermuda makes these reefs unique. Being the northernmost subtropical reef in the Atlantic, Bermuda's juxtaposition of the warm Gulf Stream current and cool temperatures found at high latitudes leads to temperature fluctuations. The temperature variation in Bermuda is generally cooler than typical Caribbean reefs but is strikingly variable and skewed towards the low end of the average range in tropical reef ecosystems. For instance, Bermudian corals can experience yearly minimums of 15 °C while corals at lower latitudinal reef locations experience minimum temperatures of roughly 25 °C in Panama (2016−2018) (Silbiger et al. 2019), 21 °C in the Florida Keys National Marine Sanctuary (FKNMS) and 20 °C in the Flower Garden Banks National Marine Sanctuary (FGBNMS) (both 2005−2009) (Haslun et al. 2011). Similarly, average summer maximums of 31 °C in Panama (Randall et al. 2020), 30.5−31 °C in FKNMS (Haslun et al. 2011; Manzello 2015) and 30−30.5 °C in FGBNMS (Precht et al 2008; Haslun et al. 2011) are common. Yet, the average maximum summer temperature in Bermuda is 30.2 °C in shallow reefs and 28.7 °C in the mesophotic, which is 0.2−1.2 °C lower than the former.

Our results indicate that when temperatures are separated by season (summer and winter), there is no difference in daily winter temperatures between depth, suggesting both shallow and upper-mesophotic reefs are exposed to the same extreme minimum temperatures (shallow; 18.5 °C and upper-mesophotic; 19 °C). Extreme thermal exposure (cold or warm) is known to contribute to similarities in thermal tolerances, despite differences in daily mean temperatures (Buckley & Huey 2016). Therefore, the similar extreme minimum temperatures experienced at both sites may be more significant in determining thermal sensitivities than the differences in mean daily temperatures during the summer months (shallow; 26.3 °C and upper-mesophotic; 24.7 °C), despite the shallow being on average 1.6 °C higher than upper-mesophotic.

Past research on corals has shown temperature fluctuations can substantially contribute to thermal tolerance (Oliver et al. 2011; Guest et al. 2012; Kenkel et al. 2015; Schoepf et al. 1819; Cziesielski et al. 2019); however, the effect of "thermal stability" found in upper-mesophotic reefs may be eclipsed by the overall latitudinal position and broad temperature exposure typical of this subtropical system. While dramatic temperature fluctuations are not uncommon in tropical reefs (Ofu, American Samoa; 24.5−35 °C and 25−32 °C and 14.7−32.4 °C in Tung Ping Chau, China), Bermuda's propensity toward a lower yet tapered thermal range compared to Ofu & Tung Ping Chau may explain the unique thermal stability and persistence between depths in Bermuda (Thomas et al. 2018; McIlroy et al. 2019). Specifically, McIlroy et al. (2019) found that corals in Tung Ping Chau persisted during low

temperature exposure while seasonal variation negatively impacted coral productivity and metabolism. The low temperatures experienced at both depths in Bermuda may outweigh the impacts of localized thermal fluctuation on thermal sensitivities.

Our results provide evidence that upper-mesophotic habitats in Bermuda may serve as thermal refuge for some coral species, addressing a larger theory regarding roles of MCEs in the survival of shallow reefs. Evidence for this theory has been mixed, however (Bongaerts et al. 2010; Goodbody-Gringley et al. 2015; Holstein et al. 2016; Loya et al. 2016; Semmler et al. 2017; Smith et al. 2016; Bongaerts et al. 2017; Goodbody-Gringley et al. 2018; Kim et al. 2019; Pinheiro et al. 2019). A thermal refuge is defined as a reef that is thermally buffered, with the potential to provide viable offspring for adjacent damaged reef following a disturbance (Bongaerts et al. 2010). Smith et al. (2016) argued that to be a thermal refuge mesophotic corals cannot have a lower bleaching threshold than their shallow water conspecifics. Despite the cooler buffered environment of MCEs, an increase in temperature above the mean summer maximum of local conditions can cause thermal stress and bleaching, negating the main premise of the hypothesis (Smith et al. 2016). Thus, for the refuge to function mesophotic corals must have similar thermal sensitivities as their shallow water counterparts. As demonstrated in our results, we show that the upper-mesophotic reef in Bermuda has significantly different yearly temperatures, yet no difference in associated coral thermal optima, or thermal sensitivities compared to shallow corals. The physiological metrics captured for four common coral species by our study, combined with temperature observation through time (this study, Goodbody-Gringley et al. 2015, 2018), suggest that Bermudian MCEs meet these criteria to serve as thermal refuge.

Generally, physiological and metabolic stress induced by temperature extremes increase with magnitude and frequency of exposure and sensitivities can vary throughout ontogeny, among species and across seasons (Buckley et al. 2016). Consequently, the interpretation of our results needs to address three caveats: 1) we measured metabolic responses in 4 species of adult Bermudian corals 2) in December via 3) heat-shock methodology. These three experimental limitations have important implications in our overall understanding of thermal sensitivities in shallow and upper-mesophotic corals in Bermuda. To characterize upper-mesophotic reefs as a refuge, thermal sensitivities between depths should be measured at multiple life stages, specifically larval and coral recruits. Previous research by Goodbody-Gringley et al. (2018) has found similarities in fecundity of adult *P. astreoides* from the same reef sites used in our study. Additionally, they found shallow reef larvae were similar in size and Symbiodinaceae densities

compared to upper-mesophotic larvae; however, shallow corals had lower growth, survival and settlement rates. These results suggest heightened recruitment potential and coral resilience in upper-mesophotic reefs and if applied in concert with thermal performance curves for larvae may bring us closer to determining the role of upper-mesophotic reefs in future climate scenarios.

Furthermore, our study was performed in December of 2018 and coral resistance to heat stress is known to differ across seasons. Thermal sensitivities are not fixed but can be modified throughout an organism's life in response to acute heat shocks resulting in heat hardening or acclimatizing to seasonal conditions (Buckley et al. 2016). For example, photosynthesis rates are often higher in the summer, whereas during the winter, corals are more susceptible to photodamage and pigment loss (Scheufen et al. 2017). This winter vulnerability can negatively impact coral responses and lead to cold-water bleaching (Lirman et al. 2011). Although there have not been any reports or evidence of cold-water bleaching in Bermuda since 1902 (Schopmeyer et al. 2012), Hog Beacon did experience a lower average minimum temperature (18.5 °C) than Deep Baby (19 °C), which could have negatively affected shallow coral metabolic rates. While winter temperatures were statistically similar between shallow and mesophotic depth zones during our study, summer temperatures were on average 1.6 °C higher in shallow versus mesophotic depths.

Just as metabolic responses can differ depending on season of testing, the methodological approach can also elicit different responses. In our study, we measured coral responses to heat-shock (short-term instantaneous stress) under acute incubation periods (40 min), which inherently has negative effects on performance due to the lack of an acclimation period. As this methodology is not representative of natural conditions (save marine heat waves), the heat-shock method provides instantaneous stress responses that can be used to identify relative thermal sensitivities, ranges and limits. The heat-shock method has been demonstrated to estimate thermal responsiveness, but it may overestimate metrics relative to individuals that are acclimatized to (heat-stress experiment) or ramped through all temperatures (Schulte et al. 2011; Sinclair et al. 2016). Further research is needed to delineate the effect of temperature ramping rates and long-term thermal exposure on performance between depths. Supplementary heat-stress experiments analyzing TPC and P:R curves can refine our understanding of coral capacity to sustain long-term survival and persistence.

Generally, P:R curves are used to identify differences between coral reliance on autotrophic products from Symbiodinaceae and the maintenance needs (respiration) of the coral-algae symbiosis (Coles et al. 1977; Castillo

et al. 2005). Consistent with our results, P:R curves commonly decline when temperatures surpass the thermal optimum (Castillo et al. 2005; Coles et al. 1977). However, for corals to maintain long-term survival, P:R values of 2 or higher are necessary (Coles et al. 1977). In our study, the temperature at which all species P:R fell below 2 was ∼ 30 °C (Fig. 5), but the capacity to sustain this ratio over time remains unknown, reinforcing the need for long-term heat-stress studies. It appears that shallow reef corals in Bermuda are currently living at or near their thermal maxima, with annual peak temperatures exceeding 30 °C. Thus, while bleaching events are historically rare for the island, global temperature increases may cause substantial changes to coral survivability in Bermuda in the near future.

Long-term survival and stability of coral communities have been typical of Bermudian reefs (MEP 2007, Smith et al. 2013a, b, c; Courtney et al. 2017, 2020); however, predicted temperature increases (0.01 °C per year down to 400 m depth) still pose a threat if temperatures exceed species thermal optimums and P:R survival thresholds. To date, Bermuda has experienced one major bleaching event documented in 1988 (Cook et al. 1990) followed by several minor bleaching events recurring annually after 1999 (Smith et al. 2013a, b, c; Courtney et al. 2017, 2020). Characterized by pale, blotchy, or white tissue, these bleaching events did not exceed 30% of total coral population in the four species in our study, nor was there any significant mortality (up to 25 m).The lack of mortality has been attributed to temporal heat attenuation during July − September caused by the prevailing climatological conditions associated with Bermuda's high latitudinal position (Smith et al. 2013a, b, c).

Moreover, it has been shown that corals exposed to prior thermal stress events can acclimatize and resist bleaching during future temperature exposures (Brown et al. 2002), including trans-generational acclimatization in offspring of corals exposed to high temperatures (Putnam et al. 2015). This is consistent with the 1988 bleaching event having the highest impact on corals while subsequent events were less severe (Smith et al. 2013a, b, c). Yet neither Cook et al. (1990) or Courtney et al. (2017) observed or collected corals on upper-mesophotic reefs leaving speculation as to whether impacts were more or less substantial at depth. Due to their depths and inherent oceanic features (cold water upwelling and thermocline depth) lowering heat stress, upper-mesophotic reefs may have additional protection from thermal anomalies up to 1 °C (Bridge et al. 2014) negating seasonal bleaching impacts. For example, Frade et al. (2018) found significantly less bleaching and mortality in mesophotic corals (40% bleached, 6% death at 40 m) compared to shallow (60−69% bleached, 8−12% death at 5−25 m) during the 2016 mass bleaching event in

the Great Barrier Reef. Further research analyzing upper-mesophotic coral cores and temperature variation may help disentangle whether long-term acclimation or abiotic factors have influenced the similarities in thermal sensitivities.

The only difference in observed thermal sensitivities between depths occurred in *D. labyrinthiformis* conspecifics (Fig. 3 & Fig. S3) for the *GP* deactivation rate (*Eh*). Upper-mesophotic *D. labyrinthiformis* had a steeper slope (5.122 ± 0.926 eV; mean $\pm$ SD) compared to shallow *D. labyrinthiformis* (3.188 ± 0.681 eV; mean $\pm$ SD), indicating higher sensitivity in corals from Deep Baby. The sharp decline in *Eh* suggests photosynthesis drops out more rapidly after surpassing the thermal optimum, indicating coral/algae metabolic costs outweigh the photosynthetic input. This may have implications for bleaching severity and recovery rates post stress events and may indicate sensitivity in enzymatic machinery (RuBISCo during photosynthesis) in upper-mesophotic Symbiodinaceae for this species (Hill et al. 2014).

Although we did not characterize algal symbiont assemblages in this study, previous research in Bermuda (Savage et al. 2002; Yost et al. 2012; Serrano et al. 2014, 2016; Reich et al. 2017) found Symbiodiniaceae assemblages and densities did not differ across depth (4−24 m) within the four species used in our study (Lajeunesse et al. 2018; Yost et al. 2012). Thus, we do not anticipate Symbiodiniaceae variation across our study sites. The uniformity of coral Symbiodiniaceae assemblages found between depths is attributed to Bermuda's isolated high-latitudinal location and vertical mixing (Reich et al. 2017), which may also explain the high levels of coral genetic connectivity. Genomic analyses performed across depths (≤ 10 m, 15−20 m and ≥ 25 m) for *P. astreoides* and *M. cavernosa* showed no genetic differentiation (Serrano et al. 2014, 2016). While it is unclear how *D. labyrinthiformis* and *O. franksi* populations differ across depth in Bermuda, we expect similar patterns of connectivity due to Bermuda's geographical isolation, identical Symbiodiniaceae assemblages found between depths (Yost et al. 2012) and the life-history traits of theses corals (Darling et al. 2012). Therefore, the similarities in thermal sensitivities found between depths may be a consequence of genetic and symbiont similarities.

While bleaching in response to thermal anomalies has been reported for reefs across variable depth gradients (Rocha et al. 2018; Smith et al. 2013a, b, c; Turner et al. 2018) there is a striking gap in physiological response data (specifically, TPC) for assessing thermal sensitivities in corals. Understanding thermal performance is essential for predicting future responses to changing thermal conditions. Here we advance our understanding of coral thermal sensitivities and tolerance thresholds and show that, in Bermuda, corals on shallow and upper-mesophotic reefs respond similarly to a wide range of temperatures (19−36 °C). Our findings therefore suggest that upper-mesophotic reefs in Bermuda may serve as a thermal refuge for coral survival under future climate change scenarios. Although these results may ultimately be unique to Bermuda, identification of reef systems beyond Bermuda with similar refuge potential is critical to the effective management and conservation of these critically threatened ecosystems in the face of global coral reef decline.

Data availability All R code and data are available on github (https://github.com/GouldKate/TPC_mesophoticvsshallow_Bermuda).

Declaration

Ethical statement All research completed during this project was done under the official permit from the Department of Environment and Natural Resources in Bermuda License NO. 201807100.

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