

Latitudinal variation in thermal performance of the common coral, *Pocillopora* spp

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Summary Statement

We used thermal performance curves to evaluate the sensitivity of the common Pacific coral *Pocillopora* to rising temperature, and we report little variation in these curves over 44° of latitude.

Abstract

Understanding how tropical corals respond to temperatures is important to evaluating their capacity to persist in a warmer future. We studied the common Pacific coral *Pocillopora* over 44° of latitude, and used populations at three islands with different thermal regimes to compare their responses to temperature using thermal performance curves (TPCs) for respiration and gross photosynthesis. Corals were sampled in the

local autumn from Moorea, Guam, and Okinawa where mean ($\pm$ s.d.) annual seawater temperature is $28.0 \pm 0.9^{\circ}\text{C}$, $28.9 \pm 0.7^{\circ}\text{C}$, and $25.1 \pm 3.4^{\circ}\text{C}$, respectively. TPCs for respiration were similar among latitudes, the thermal optimum (T_{opt}) was above the local maximum temperature at all three islands, and maximum respiration was lowest at Okinawa. TPCs for gross photosynthesis were wider, implying greater thermal eurytopy, with a higher T_{opt} in Moorea versus Guam and Okinawa. T_{opt} was above the maximum temperature in Moorea, but was similar to daily temperatures over 13% of the year in Okinawa, and 53% of the year in Guam. There was greater annual variation in daily temperatures in Okinawa than Guam or Moorea, which translated to large variation in the supply of metabolic energy and photosynthetically fixed carbon at higher latitudes. Despite these trends, the differences in TPCs for *Pocillopora* were not profoundly different across latitudes, reducing the likelihood that populations of these corals could better match their phenotypes to future more extreme temperatures through migration. Any such response would place a premium on high metabolic plasticity and tolerance of large seasonal variations in energy budgets.

Introduction

Understanding how organisms respond to rising temperature is one of the greatest challenges facing modern biologists (He and Silliman 2019; Keys et al., 2019). The effect of temperature on organism physiology and ecology (Bruno et al., 2015) mediates the impacts of climate change on the structure and function of ecosystems (Trisos et al., 2020; Parmesan et al., 2022). Warmer temperatures, for example, can accelerate reproductive phenology to create a mismatch of early life stages to environmental conditions affecting fitness (Inouye, 2022), modulate microbial growth and metabolism (Abirami et al., 2021), and kill corals through bleaching (Hughes et al., 2017) and disease (Ruiz-Moreno et al., 2012). The deterministic ways by which temperature affects rates of biological reactions (Bruno et al., 2015; Somero et al., 2017) indicate that a warmer biosphere will have consequences beyond the damage already detected, generally having negative implications (Parmesan and Yohe, 2003; Parmesan, 2006).

These possibilities highlight the need for scientific advances in the study of the biological effects of a warmer planet (Bruno et al., 2015; Smith et al., 2023).

Confronted by rising temperature, organisms exhibit a diversity of responses that differ depending on their reliance on homeothermy versus poikilothermy (Fuller et al., 2012; Wagner et al., 2023). The implications of rising temperature are generally more profound for poikilotherms for which performance depends on the temperature of their surroundings (Wagner et al., 2023). Motile poikilotherms have the option of moving to more favorable thermal conditions, but otherwise must endure the physiological consequences of warmer conditions, unless acclimatization or adaptation can modulate their response (Fuller et al., 2012). Depending on the extent to which these changes are beneficial, performance translates to fitness that determines how populations will change in size in a warmer world. The biological effects of temperature have been studied for over a century (Peebles, 1898), and the theme has had a specialized journal for nearly 50 years (Bowler and Heath, 1975). Yet the thermal biology of many taxa still is being discovered for the first time through climate change research (Sinclair et al., 2016; Herrando-Perez et al., 2023).

Reef corals have become a focus of thermal biology because they live close to their upper thermal limit (Brown and Cossins, 2011), and through bleaching at high temperature, have experienced region-wide mortalities that have profoundly changed coral reefs (Hughes et al., 2017). For scleractinian corals, understanding the mechanisms underlying their susceptibility to high temperature (Brown and Cossins, 2011), and whether they can reduce the population-level risks of exposure to warm conditions (Putnam, 2021), is important. Since region-wide coral bleaching was first recorded in the 1980s (Glynn, 1993), there have been substantial advances in understanding how corals are affected by temperature (Brown and Cossins, 2011) and the complex processes culminating in bleaching (Helgoe et al., 2024). Appreciation of the genetic diversity and flexibility of the microbial symbionts of corals (LaJeunesse et al., 2018), as well as the possibilities for parents to modulate the fitness of their offspring through epigenetic effects (Eirin-Lopez and Putnam, 2019), has unveiled the sophisticated repertoire of tools available to corals to respond to rising temperature

(Putnam et al., 2017; Putnam, 2021). Migration or range extension can offer an alternate means to reduce the exposure of coral populations to warm water (Yamano et al., 2011; Madin et al., 2016).

Formal analyses of thermal performance curves (TPCs) have become popular in studies of the response of corals to temperature, because they provide a means to rigorously compare complex biological responses among taxa, conditions, and locations (Silbiger et al., 2019; Jurriaans and Hoogenboom, 2019). They have, however, been informally applied (e.g., without curve fitting) to corals for more than 40 years (Jokiel and Coles, 1977), and have been used in other systems for decades (Huey and Stevenson, 1979). TPCs can be defined by different types of mathematical functions (Padfield et al., 2021), the choice among which depends on the physiological basis of the thermal response, the experimental purpose of the study, and the scope and quantity of data with which the curves can be prepared. The mathematical parameters of TPCs fit to empirical data can be used to define multiple aspects of organismic thermal biology, including the range of temperatures over which the organism is likely to survive (i.e., the thermal niche breadth) (Sinclair et al. 2016). Of particular value is the notion that variation in the parameters of TPCs (e.g., the temperature at which maximum performance is attained, T_{opt}) across space and time can be used to diagnose acclimatization or adaptation (Silbiger et al., 2019; Jurriaans and Hoogenboom, 2020). TPCs for corals have been estimated for respiration, photosynthesis, and PSII photochemistry (e.g., Anton et al., 2020; Gould et al., 2021; Jurriaans and Hoogenboom, 2019, 2020; Silbiger et al., 2019) and in one case, calcification and symbiont density (Bernardet et al., 2019). While these response variables describe how physiology maps onto temperature, inferring benefits through adaptive value is problematic when the consequences for fitness are unknown.

The response of corals to temperature can be evaluated by comparing TPCs among populations experiencing different temperature regimes (Jurriaans and Hoogenboom, 2019; Banc-Pandi et al., 2022), which can provide insight into the possibility of thermal acclimation or adaptation. Locations where temperatures are upwardly extreme relative to those throughout the geographic range of the coral can provide clues to how the coral

phenotype might respond to higher temperatures (Coles and Riegl, 2013). In American Samoa, analyses of corals in back reef pools with extreme (to 35°C) and variable temperatures (daily range of 5.6°C) have revealed local adaptation through organismic traits and up-regulation of protective genes in *Acropora hyacinthus* and *Porites lobata* (Barshis et al., 2012). Studies of corals across latitudinal gradients are also yielding valuable insights, with *Porites cylindrica* and *Acropora* spp. across 9° of the Great Barrier Reef showing a mismatch of host T_{opt} for respiration and photosynthesis to local conditions, but alignment for symbiont performance (Jurriaans and Hoogenboom, 2019). Over 18° in the Red Sea, six coral species in the north lived below their T_{opt} for respiration and photosynthesis, while in the south, they lived close to, or above their T_{opt} (Banc-Prandi et al., 2022).

The present study focuses on *Pocillopora* spp. corals, which are abundant in multiple reef habitats throughout the Indo-Pacific (Pinzon et al., 2013). TPCs for respiration and gross photosynthesis were compared among corals from Moorea, Guam, and Okinawa, which span 44° of latitude from the southern to the northern hemisphere. By sampling across latitudes, corals were obtained from thermal regimes differing in annual mean and range in seawater temperatures. We tested the hypotheses that: (a) TPCs for respiration and gross photosynthesis differ among locations, (b) TPCs differ between respiration and gross photosynthesis, and (c) curve parameters for TPCs at high latitude are matched to cooler and more variable conditions (i.e., reduced metabolism, lower T_{opt} , and greater breadth of TPCs), when compared to low latitudes. The rationale for the locational effect was provided by latitudinal variation in coral TPCs (Jurriaans and Hoogenboom, 2019; Banc-Pandi et al., 2022) and the benefits for organisms to match TPCs to local conditions (Sinclair et al., 2016). The contrast between respiration and gross photosynthesis was chosen because these response variables characterize mostly host and symbiont processes, respectively (Muscatine, 1990). Our analyses of TPCs focus on highest rate of the response variables as a standardized metric of peak metabolic performance, the temperature at which this is achieved (T_{opt}) as a means to address how metabolic performance maps onto the ambient temperature regime, and an indicator of the width of the curve (alpha in the Gaussian curve, described below) as means to evaluate the thermal niche breadth. In this formulation, T_{opt} does not

necessarily reflect the temperature favoring maximum fitness, and thus has an equivocal relationship to an environmental temperature of high selective value to the coral. We integrate the results to explore the implications of latitudinal variation in TPCs on the potential for *Pocillopora* spp. to respond in beneficial ways to rising seawater temperature throughout the tropical Pacific.

List of symbols and abbreviations

AIC_c – Akaike Information Criterion adjusted for small sample sizes

GTR – generalised time-reversible

LED – light emitting diode

PAR – photosynthetically active radiation

PCR – polymerase chain reaction

PFD – photon flux density

PSII – photosystem II

RFLP – restriction fragment length polymorphism

T_{opt} – temperature at which performance is highest on the TPC, often construed as the overall thermal optimum, or sometimes as the temperature at which fitness is maximized

TPC – thermal performance curve

TSM – thermal safety margin

Materials and methods

Overview

The study contrasted the thermal biology of corals from Moorea (-17.5°, -149.8°), Guam (13.5°, 144.7°), and Okinawa (26.6°, 127.9°), crossing 44° of latitude and different thermal environments. *Pocillopora* is a common genus of scleractinian corals found

throughout the Indo-Pacific, and it was used to evaluate plasticity in the phenotypic response to differing temperatures that can provide insight into the capacity of corals to tolerate warming seas. Most corals in this genus (excluding the brooders *P. acuta* and *P. damicornis*) are considered “competitive” (Darling et al., 2012) because they are efficient at resource use, they reproduce by broadcast spawning, and can dominate fore reef habitats (Darling et al., 2012; Johnston et al. 2017, 2022).

Thermal performance curves (TPCs (Sinclair et al. 2016)) were used to quantify the effects of temperature using dark respiration and gross photosynthesis as response variables (Fig. S1). The thermal context of each location was characterized through the mean daily seawater temperatures over the 5 years preceding the present analyses, as calculated with daily resolution through ongoing monitoring programs in each location. Temperature was recorded with finer temporal resolution in Moorea and Guam (described below), but these values were averaged by day for the present analysis. These programs were maintained in different ways in each location, and while they broadly indicate the extent to which the environments vary among locations, the different methodologies indicate that absolute contrasts among locations should be completed with caution. In most cases, the mean daily seawater temperature was calculated using 5 years of daily records, but sample sizes were < 5 for the days of the year in which 5 replicate days were not sampled every year due to logistical constraints.

Common approaches used in all three locations

In Moorea, seawater temperature was recorded at 10-m depth on the fore reef of the north shore (using a Sea-Bird SBE39, accuracy $\pm 0.002^{\circ}\text{C}$, resolution 0.0001°C , Sea-Bird Electronics, Bellevue, WA) with the sensor < 0.1 km from the site of coral collection; values were augmented with data from a Hobo logger (U22-001, accuracy $\pm 0.2^{\circ}\text{C}$, resolution 0.02°C , Onset Computer Corp., Bourne, MA) for 136 days from 18 August 2019 (accessed 12 December 2019 and summarized in Edmunds 2021). The Hobo logger was utilized with the manufacturer’s calibration. Temperature was recorded at 0.0083 Hz and averaged by day before calculating the daily mean $\pm$ s.e.m. over five years (2015–2019). In Guam, seawater temperature was recorded at 0.5-m depth by

the Ritidian wave rider buoy Station 52202 (<https://www.ndbc.noaa.gov/>, accessed 2 June 2023), which is ~ 14 km from the site of coral collection. Temperature was recorded at 0.0006 Hz and averaged by day before calculating the daily mean $\pm$ s.e.m. over five years (2018-2022). In Sesoko, daily seawater temperature was recorded manually using a 5 L bucket deployed from the lab jetty, which was ~ 1 km from the site of coral collection. Temperature records (recorded with a thermometer $\pm$ 0.1°C, 1-NM-11, Ando Keiki Co., Ltd., Japan) were obtained from Singh et al. (2022) and were used to calculate the daily mean $\pm$ SE over five years (2016–2020).

The study was completed during October (Guam) and November (Okinawa) 2022, and May (Moorea) 2023. These periods sampled during the local autumn in the northern and southern hemispheres, so that the corals experienced similar relative changes in their recent thermal histories when they were collected. The experiments were completed in near-identical ways in each location, with the same equipment, and by the same investigator (Edmunds). Some aspects of the experiments differed among locations through the constraints of local logistic, and these differences are described below.

Coral collections sampled *Pocillopora* spp. from a fore reef habitat (~ 4–5 m depth), and targeted colonies that morphologically resembled '*Pocillopora verrucosa*' (after Veron et al. 2000). Recent work has highlighted the extent to which in situ gross morphology is unreliable for resolving species in this genus (Pinzon et al., 2013; Burgess et al., 2021; Johnston et al., 2022; Voolstra et al., 2023), so all samples were genetically identified to species. The study corals are referred to as *Pocillopora* spp. Five colonies were collected in each location to each supply > 9 branches (i.e., clone mates) that were prepared as nubbins (Birkeland, 1976). Following collection, colonies were fragmented into pieces < 60-mm tall to fit in the respiration chamber, and were attached upright onto PVC bases using Coral Glue (Ecotech, Bethlehem, PA). Nine replicates were prepared from each colony for the measurement of metabolism using independent replicates at eight temperatures, with one replicate of each host genotype tested at each temperature and one replicate preserved for genetic identification of the coral host. This design supported a test of temperature effects without being confounded by donor colony-level genetic variation. Prepared corals were maintained in a shallow tank

supplied with flowing seawater at a temperature and photon flux density (PFD, from sunlight) close to that expected at the collection depth, and metabolism was measured over 4–9 days beginning ~ 4 days after collection.

The experiment exposed corals to each one of the treatment temperatures for 60–120 minutes before measuring respiration and photosynthesis. Exposure durations were standardized to prevent confounding effects of varying incubation times at each temperature. The eight temperature treatments employed were chosen to span the annual range of temperatures at the three locations, and they were tested in a random sequence, usually with one temperature each day, and independent replicates of each host genotype for each temperature. The five corals tested in any one group were staged into the treatment tank (~ 20 L) to keep exposure durations close to 60–120 minutes. The treatment tank was darkened and regulated through heating (200W Jager Heaters, Eheim AEH3617090) and cooling (with water pumped through a closed loop submerged in an ice bath) that was controlled using a digital controller (Neptune A3 Apex, Morgan Hill, CA). The water jacket surrounding the respiration chamber was connected in series with the seawater in the temperature tank, thus ensuring the metabolism was recorded at the same temperature as the treatment. Treatment temperatures were periodically monitored by hand using a certified digital thermometer ($\pm 0.001^{\circ}\text{C}$, model 15-077, Fisher Scientific, Pittsburgh, PA, USA).

Preceding each measurement day, the corals were kept in darkness overnight, with darkness maintained the following morning until the corals were transferred to the treatment tank. Each day, one coral from each of the five genotypes was transferred to a darkened tank that was maintained at the temperature selected for that day. On some days, two treatments were completed sequentially in the same manner. Respiration and photosynthesis were measured in a respirometer made from a cylindrical acrylic chamber (238 mL) that was jacketed with a water bath to maintain temperature. Corals were supported on a perforated disk within the chamber, beneath which a 30-mm spin bar circulated seawater. The lid was sealed to the chamber, and oxygen (O_2) saturation in the seawater was measured with an optode (FOSPOR-R with silicon overcoat, Ocean Insight, Orlando, FL). The manufacturers specifications indicate 0.05% accuracy and 0.1% resolution at 90% O_2 saturation, with 0.0003%/hr drift. The effects of drift and

accuracy were mitigated through daily two point calibrations under controlled conditions (described below).

The optode was connected to a NeoFox (Ocean Insight, Orlando, FL) spectrometer, that was temperature compensated using the manufacturer's thermister inserted into the chamber, and operated using NeoFox Viewer 2.9 software (Ocean Insight, Orlando, FL) in a Windows environment. The probe was calibrated daily in a chemical zero (sodium sulphite and 0.01M sodium tetraborate) and air-saturated seawater (100% saturation) at the treatment temperature, and O₂ solubility in seawater was determined using gas tables (N. Ramsing and J. Gundersen, Unisense, Aarhus, Denmark). The chamber was surrounded by a darkened shroud during measurements of respiration, and photosynthesis was recorded beneath the same shroud augmented with an LED lamp (Aqua Illumination, Hydra 64) suspended above the chamber. The lamp was operated at 75% power across all wavelengths of light to provide a PFD of 890–1,058 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ within the range of photosynthetically active radiation (PAR). PFD was measured with a cosine-corrected sensor (Li-Cor LI 192) attached to a meter (Li-Cor LI 250A).

The chamber was filled with unfiltered seawater from the seawater system used to maintain the corals in the lab, and after the coral was placed in the chamber, it was sealed and the optode inserted. Unfiltered seawater was used as the effects of coral metabolism on the O₂ saturation of the seawater in the chambers was large relative to fluxes in control trials that were attributed, in part, to the microbial flora of unfiltered seawater. Dark respiration was measured within ~ 5–10 minutes of sealing the chamber, or until a stable decline in O₂ was recorded, and was recorded at $\geq 80\%$ O₂ saturation to avoid saturation-dependency of respiration (Edmunds and Davies, 1986). Following the measurement of respiration, the LED lamp was switched on at 75% power and net photosynthesis recorded for ~ 5–20 minutes or until a stable increase in O₂ was recorded to $< 110\%$ O₂ saturation. Gross photosynthesis was calculated by subtracting dark respiration from net photosynthesis with adherence to the sign convention that O₂ uptake is negative and evolution is positive. Each set of experiments included two dark controls and two light controls that were run in identical way to the trials with corals, except the chamber contained only seawater. The displacement volume of the corals

was recorded to calculate the volume of seawater in the chamber, and the area of the coral tissue was measured using aluminum foil (Marsh 1970). Respiration and gross photosynthesis were normalized to coral area and time in units of $\text{nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$ and both were expressed on a positive scale for clarity of presentation.

A separate experiment was completed with two nubbins from each site to quantify the relationship between photosynthesis and PFD within the PAR range, and to ensure that photosynthesis in the TPC trials was measured under saturating light conditions. Trials were completed at the conclusion of the thermal experiments using the same respiration chamber and optode described above. O_2 flux was measured in darkness and eight sequentially increasing PFDs created by operating the LED lamp at power outputs ranging from 10–100%. The corals were maintained at each PFD for 2–10 minutes, or until a steady rate of change in O_2 saturation was achieved, with trials constrained to 80–110% O_2 saturation. O_2 fluxes were corrected for controls, and standardized to coral area (measured as described above) and time in units of $\text{nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$. Line plots of net photosynthesis versus PFD were used to evaluate the PFD at which photosynthesis reached an approximate plateau (i.e., it saturated with respect to light).

Thermal performance of Pocillopora spp. in Moorea

Measurement of coral thermal performance were completed in May 2023, and the corals ($n = 5$ colonies) were collected from the north shore on 26 April (-17.476° , -149.838°). Corals were prepared as nubbins and placed into a tank at $28.1 \pm 0.1^\circ\text{C}$ that was illuminated at $1,060 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (recorded with Li-Cor LI 193 sensor) using LED lamps, and supplied with a constant flow of seawater; the corals remained in this tank until trials commenced on 1 May. Two randomly selected temperatures were tested each day, and the analysis contrasted $22.1 \pm < 0.1^\circ\text{C}$, $25.4 \pm < 0.1^\circ\text{C}$, $27.1 \pm < 0.1^\circ\text{C}$, $28.3 \pm < 0.1^\circ\text{C}$, $30.1 \pm 0.1^\circ\text{C}$, $31.9 \pm 0.1^\circ\text{C}$, $32.6 \pm < 0.1^\circ\text{C}$, and $33.9 \pm 0.1^\circ\text{C}$ (mean $\pm$ s.e.m., $N = 4\text{--}7$), and photosynthesis was measured at $995 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (recorded with a Li-Cor LI 192 sensor).

Thermal performance of Pocillopora spp. in Guam

Measurements of coral thermal performance were completed in October 2022, and the corals ($n = 5$ colonies) were collected in front of the closed Tanguisson Power Plant on 20 October (13.543° , 144.807°). Corals were prepared as nubbins and placed in a tank at $30.1 \pm 0.2^\circ\text{C}$ that was illuminated by natural sunlight screened to a maximum of $825 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (recorded with a Li-Cor LI 192 sensor), and supplied with a constant flow of seawater; the corals remained in this tank until trials commenced on 24 October. One randomly selected temperature was tested daily, and the analysis contrasted $22.9 \pm 0.1^\circ\text{C}$, $26.1 \pm 0.1^\circ\text{C}$, $28.1 \pm < 0.1^\circ\text{C}$, $29.0 \pm < 0.1^\circ\text{C}$, $30.9 \pm 0.1^\circ\text{C}$, $32.7 \pm < 0.1^\circ\text{C}$, $33.9 \pm 0.1^\circ\text{C}$, and $35.5 \pm 0.1^\circ\text{C}$ (mean $\pm$ s.e.m., $N = 6\text{--}15$), and photosynthesis was measured at $890 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (recorded with a Li-Cor LI 192 sensor).

Thermal performance of Pocillopora spp. in Okinawa

Measurements of coral thermal performance were completed in November 2022, and the corals ($n = 5$ colonies) were collected off Sesoko Island on 24 November (26.629° , 127.858°). Corals were prepared as nubbins and placed in a tank at $23.8 \pm 1.6^\circ\text{C}$ that was illuminated by natural sunlight screened to a maximum of $326 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (recorded with a Li-Cor LI 192 sensor), and supplied with a constant flow of seawater; the corals remained in this tank until trials commenced on 27 November. One randomly selected temperature was tested daily, and the analysis contrasted $21.0 \pm 0.1^\circ\text{C}$, $26.8 \pm < 0.1^\circ\text{C}$, $28.3 \pm 0.1^\circ\text{C}$, $29.9 \pm 0.1^\circ\text{C}$, $31.9 \pm 0.1^\circ\text{C}$, $32.4 \pm < 0.1^\circ\text{C}$, $33.2 \pm < 0.1^\circ\text{C}$, and $35.0 \pm < 0.1^\circ\text{C}$ (mean $\pm$ s.e.m., $N = 7\text{--}11$), and photosynthesis was measured at $1,058 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (recorded with a Li-Cor LI 192 sensor).

Thermal Performance Curves (TPC)

TPCs were estimated for respiration and photosynthesis with best-fit relationships (Fig. S1) selected from: (i) a symmetrical Gaussian (Angilletta, 2006), and (ii) a Gaussian-Gompertz (Martin and Huey, 2008). These relationships were selected because of their

common use in preparing TPCs (Comeau et al., 2016; Jurrians and Hoogenboom, 2019), the principles of parsimony and the utility of simpler models, and our objective of comparing the temperature at which the dependent variable was maximized (T_{opt}) and curve widths among locations using eight temperature treatments. Relationships were fit using least squares non-linear regressions, with model selection using AIC_c. The constants mathematically defining the TPCs (see equations 1 and 2 below) were obtained from the parameter values selected by the curve fitting routines for the best-fit relationships. Since the objective was to compare TPCs among corals from different latitudes, a single functional relationship was selected as the best compromise for corals from the three locations. Curves were independently fit to the five coral genotypes from each site, and to the data pooled among coral genotypes by site. The two approaches contrasted the value of less robust fits for each individual coral (with eight data points) versus more robust fits by pooling results among corals within each location (with ~ 40 data points).

(i) Symmetrical Gaussian

$$Rate = Max \times e^{(-0.5 \times (\frac{Temp - T_{opt}}{\alpha})^2)} \quad \text{equation 1}$$

where Rate = dependent variable (dark respiration or gross photosynthesis, nmol O₂ cm⁻² min⁻¹), Max = maximum fitted value of respiration or photosynthesis, Temp = independent variable (temperature, °C), T_{opt} = optimum temperature on fitted relationship for dark respiration or gross photosynthesis, and alpha (α) = measures half the width of the thermal performance curve (°C). In the best-fit relationships, T_{opt} represents the temperature at which the dependent variable is highest, and the terminology reflects historic precedence rather than the inference that the maximum rate is optimal with respect to fitness.

(ii) Guassian-Gompertz

$$Rate = Max \times e^{(-e^{\beta(Temp - T_{opt})} - \alpha(Temp - T_{opt})^2)} \quad \text{equation 2}$$

where Rate = dependent variable (respiration or photosynthesis, $\text{nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$), Max = maximum fitted value of respiration or photosynthesis, Temp = independent variable (temperature, $^{\circ}\text{C}$), T_{opt} = optimum temperature on fitted relationship for dark respiration or gross photosynthesis, alpha (α) = slope of ascending portion of the relationship ($\text{nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1} ^{\circ}\text{C}^{-1}$), and beta (β) = slope of descending portion of the relationship ($\text{nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1} ^{\circ}\text{C}^{-1}$).

Genetic analysis and identification of genetic lineages

Laboratory protocols for genetically identifying the *Pocillopora* samples slightly differed among islands as outlined in Supplementary Information. Briefly, genomic DNA was extracted from preserved samples and the mtORF barcoding region was amplified using PCR. Moorea samples were amplified using the FATP6.1 and RORF primers and protocol as in Flot et al. (2008) and sequenced in the forward direction with the FATP6.1 primer at Florida State University on an Applied Biosystems 3730 Genetic Analyzer with Capillary Electrophoresis. Guam samples were amplified using newly designed primers (Poc_MT_ORFf1: 5'-TGCAAAATTTAAGTAATGTGGGTTT-3' and Poc_MT_ORFr1 5'-CACCTGGAGGTGTTTCTACCTT-3') and sequenced at Epoch Life Sciences (Missouri City, TX) in both directions with diluted PCR primers on an ABI3730XL sequencer as in Combosch et al. (2024). Okinawan samples were amplified with the primer pair FATP6.1/RORF (Flot et al., 2008) and by MacroGen Japan (<http://www.macrogen-japan.co.jp/>) using the same primer pairs as for the PCR (as in Sinniger et al., 2017). Forward and reverse sequences from Guam and Okinawa were aligned using MAFFT v7.49 (Katoh and Standley, 2013) in GENEIOUS v.9.1.8 (Biomatters). Forward sequences from Moorea were aligned using Clustal Omega in GENEIOUS PRIME 2023.2.1. Individual consensus sequences were generated and aligned with forward sequences from Moorea and previously published mtORF haplotypes (Gélin et al., 2017; Johnston et al., 2022). Alignments were manually trimmed to 927bp and then quality-trimmed using G-Blocks online (<http://phylogeny.lirmm.fr>; Castresana, 2000) with default settings but allowing gap positions in final blocks, reducing the alignment length

to 817 bp. Alignments were re-imported into GENEIOUS and phylogenetic analyses were conducted using Bayesian and Maximum Likelihood algorithms.

Maximum likelihood analyses were conducted using RAxML 8.2.8 (Stamatakis, 2014) as implemented in Geneious. A unique GTR model of sequence evolution was used with corrections for a discrete gamma distribution (G) for site-rate heterogeneity (GTRGAMMA) with a proportion of invariable sites and 1000 bootstraps.

In addition, Bayesian inference analyses were carried out with MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001). Analyses were conducted with the default GTR model of sequence evolution and a gamma-shaped rate variation with a proportion of invariable sites. MrBayes analyses started with random trees, default priors and two runs, each with 4 Markov chains. Convergence diagnostics were assessed in Geneious, and the runs were allowed to proceed until the average deviation of split frequencies reached < 0.01 (~ 2 M generations).

The naming conventions in Forsman et al. (2013), Pinzón et al. (2013), and Johnston et al. (2017) were used to associate haplotypes with nominal species names. Since both *P. meandrina* and *P. grandis* share the mtORF haplotype 1 sequence, we differentiated samples identified as haplotype 1 using a PCR-based restriction fragment length polymorphism (RFLP) gel assay of the histone 3 marker using PocHistone primers, Xho1 restriction enzyme, and protocols detailed in Johnston et al. (2018). The mtORF and Histone markers have previously been validated as suitable species-level markers to delineate *Pocillopora* species, based on whole mitochondrial genomes and genome-wide sequencing (Johnston et al., 2022; Oury et al., 2023; Voolstra et al., 2023). The nuclear genomes of mtORF haplotypes 1 (*P. meandrina*) and 8 are indistinguishable, despite being distinct mitochondrial lineages (Johnston et al., 2022). Therefore, colonies identified as haplotype 8 were included with colonies identified as haplotype 1 in *P. meandrina*, which was also justified based on their similar within-reef distribution patterns and responses to heat waves (Burgess et al., 2021; Johnston et al., 2022).

Statistical approaches. TPCs were fitted using least squares linear regression conducted with XLSTAT statistical software (version 2023.1.3, Lumivera, Denver, CO) that operates within an Excel environment (version 16.72, Microsoft, Redmond, WA).

Since non-linear least squares regressions are sensitive to the choice of starting values for parameters, we thoroughly checked the sensitivity of the final parameter estimates to different starting values. As an additional check, we also compared our parameter estimates to those generated by the `nls.multstart` package in R (Padfield et al. 2021), and got similar results. For models that converged, the best-fit options were selected by AIC_c. Temperature was the independent variable, and respiration and gross photosynthesis were dependent variables. Curve parameters (described above) were compared among latitudes using one way ANOVA using coral host genotypes as replicates.

Results

Thermal environment

Mean ambient seawater temperature in each location was assessed over 5 years using records of opportunity that originate from different sources, notably with respect the accuracy of measurements and the depth at which the measurements were made. While it is reasonable to expect the temperature measured at the surface from a dock (Okinawa) to slightly differ from that recorded at 10 m depth (Moorea), the records so obtained revealed very large differences in excess of those that might be expected from methodological artifacts (Fig. 1). The grand mean ($\pm$ s.e.m.) in Moorea was $28.0 \pm 0.1^\circ\text{C}$, and daily temperature ranged from 26.5°C to 29.4°C throughout the year; in Guam, it was $28.9 \pm 0.1^\circ\text{C}$, and ranged from 27.7°C to 30.1°C ; and in Okinawa, it was $25.1 \pm 0.2^\circ\text{C}$, and ranged from 19.2°C to 30.8°C . When the corals were collected, the long-term average temperature was declining in all three locations: in Moorea, temperature was declining from a high in April of 29.4°C to 28.7°C when the experiment began (a decline of $0.033^\circ\text{C d}^{-1}$ over ~ 20 days); in Guam, it was declining from a high in early October of 30.1°C to 29.6°C when the experiment began (a decline of $0.031^\circ\text{C d}^{-1}$ over ~ 18 days); and in Okinawa, it was declining from a high in mid-August of 30.6°C to 24.3°C when the experiment began (a decline of $0.061^\circ\text{C d}^{-1}$ over ~ 105 days).

Evaluation of maximum photosynthesis

To facilitate the interpretation of gross photosynthesis, net photosynthesis versus PFD plots were prepared. Photosynthesis was saturated with respect to light at $\sim 1,000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at all three locations (Fig. S2), demonstrating that photosynthesis employed in the TPC analysis was measured under saturating light conditions.

Thermal performance of Pocillopora spp. in Moorea

Corals were exposed to the eight temperatures treatments for 94 ± 4 minutes (mean $\pm$ s.e.m., range 60–140 minutes, $N = 40$) before measuring metabolism. Respiration ranged from $5.249 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$ (at 22.1°C) to $13.199 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$ (at 32.6°C) and gross photosynthesis from $10.597 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$ (at 32.6°C) to $23.223 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$ (at 30.1°C).

The best-fit TPCs for respiration converged using the Gaussian function, but not the Gaussian-Gompertz function. Both models converged for gross photosynthesis, and the best fits (lowest AIC_c) were obtained with the Gaussian function. TPCs for respiration revealed an increase with temperature, a T_{opt} of 35°C , a maximum of $10.3 \pm 0.4 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$, and an alpha of $10.8 \pm 0.9^\circ\text{C}$; the data did not support a rigorous description of the declining portions of the relationships beyond T_{opt} . For gross photosynthesis, TPCs revealed an increase with temperatures, a T_{opt} of $31.9 \pm 1.6^\circ\text{C}$, a maximum gross photosynthesis of $19.1 \pm 0.6 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$, and an alpha of $10.0 \pm 2.2^\circ\text{C}$. For respiration and gross photosynthesis, T_{opt} was above ($> \sim 1.9^\circ\text{C}$) the greatest daily temperature experienced each year, and the annual range of daily temperatures occupied a small portion of the ascending segment of the TPCs for respiration and gross photosynthesis (Fig. 2C, F).

Thermal performance of Pocillopora spp. in Guam

Corals were exposed to the eight temperatures for 77 ± 3 minutes (mean $\pm$ s.e.m., range 53–132 minutes, $N = 40$) prior to measuring metabolism. Respiration ranged from $3.605 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$ (at 26.1°C) to $15.520 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$ (at 30.9°C) and gross

photosynthesis from 11.401 nmol O₂ cm⁻² min⁻¹ (at 29.0°C) to 31.918 nmol O₂ cm⁻² min⁻¹ (at 32.7°C).

The best-fit TPCs for respiration converged using the Gaussian function, but not the Gaussian-Gompertz function, and while both models converged for gross photosynthesis, the best fits (lowest AIC_c) were obtained with the Gaussian function. TPCs for respiration revealed an increase with temperatures, a T_{opt} of 33.8 ± 3.5°C, a maximum respiration of 9.8 ± 0.7 nmol O₂ cm⁻² min⁻¹, and an alpha of 9.2 ± 3.7°C; the data did not support a rigorous description of the declining portion of relationships beyond T_{opt}. For gross photosynthesis, TPCs revealed a relationship centered on the current thermal regime. T_{opt} was 29.7 ± 0.6°C, maximum gross photosynthesis was 21.7 ± 1.2 nmol O₂ cm⁻² min⁻¹, and alpha was 6.8 ± 1.1°C. For respiration, T_{opt} was ~ 2.8°C above the greatest daily temperature each year, but for gross photosynthesis, T_{opt} corresponded to the most common daily temperature. The annual range of daily temperatures occupied a small portion of the TPCs, corresponding to the ascending portion for respiration, and the apogee for gross photosynthesis (Fig. 2B, E).

Thermal performance of Pocillopora spp. in Okinawa

Corals were exposed to the eight temperatures for 86 ± 3 minutes (mean ± s.e.m., range 59–145 minutes, N = 40) prior to measuring metabolism. Respiration ranged from 2.688 nmol O₂ cm⁻² min⁻¹ (at 21.0 °C) to 11.554 nmol O₂ cm⁻² min⁻¹ (at 32.4 °C) and gross photosynthesis from 5.140 nmol O₂ cm⁻² min⁻¹ (at 35.0 °C) to 26.110 nmol O₂ cm⁻² min⁻¹ (at 32.4 °C).

TPCs for respiration converged to solutions using the Gaussian function, but not the Gaussian-Gompertz function, and while both models converged for gross photosynthesis, the best fits were obtained with the Gaussian function. The Gaussian function for respiration revealed an increase over temperature, a T_{opt} of 34.5 ± 3.2°C, a maximum respiration of 6.1 ± 0.5 nmol O₂ cm⁻² min⁻¹, and an alpha of 10.9 ± 3.1°C; the data did not support a rigorous description of the declining portions of relationship at temperatures > T_{opt}. For gross photosynthesis, the Gaussian function revealed a relationship centered on the upper range of the current thermal regime. T_{opt} was 29.7 ±

0.6°C, maximum gross photosynthesis was $19.6 \pm 0.8 \text{ nmol O}_2 \text{ cm}^{-2} \text{ min}^{-1}$, and alpha was $7.3 \pm 0.9^\circ\text{C}$. For respiration, T_{opt} was $\sim 3.5^\circ\text{C}$ above the greatest daily temperature experienced each year, but for gross photosynthesis, T_{opt} corresponded to the warmest 33% of the days each year. The annual range of daily seawater temperatures operated over the majority of the TPCs for respiration and gross photosynthesis (Fig. 2A, D).

Contrasting TPCs among locations

TPC parameters were extracted from the respiration versus temperature and gross photosynthesis versus temperature relationships (Fig. 3, Table S1). There were only 6 measures of Respiration- T_{opt} (and none from Moorea) because this parameter did not fall within the temperature range tested in many cases (Fig. 2, Table S1). Respiration-Max differed among locations and was reduced in Okinawa versus Guam and Moorea; Respiration- T_{opt} did not differ between Okinawa and Guam; and Respiration-Alpha did not differ among locations (Table 2). Photosynthesis-Max did not differ among locations; Photosynthesis- T_{opt} differed among locations, and was elevated in Moorea compared to Guam and Okinawa; and Photosynthesis-Alpha differed among locations and was greater in Moorea compared to Guam (Table 2). Based on mean values, Respiration-Max in Okinawa was 27% lower than in Guam and 29% lower than in Moorea, Photosynthesis- T_{opt} in Moorea was 9% higher than in Okinawa and 10% higher than in Guam, and Photosynthesis-Alpha in Moorea was 48% higher than in Guam.

Genetic identity of corals

Phylogenetic analyses of the mitochondrial Open Reading Frame (ORF) with both RAxML (Fig. S3a) and MrBayes (Fig. S3b) identified the same four haplotypes for the 15 samples: the five corals from Moorea contained mtORF haplotypes 1 (4 colonies) and haplotype 8 (1 colony). RFLP-analyses following Johnston et al. (2018) indicate that all four haplotype 1 colonies were *P. meandrina* and, therefore, all five colonies from Moorea were *P. meandrina*. All five corals from Guam had haplotype 5 and belonged to *P. acuta*. Corals from Okinawa were split between haplotype 3 (3 colonies, i.e., *P.*

verrucosa), and one colony each with haplotype 1 and haplotype 8. Subsequent RFLP-analyses indicated that the haplotype 1 colony belonged to *P. meandrina* (Table S1; Figs. S3a & b).

While the haplotype and species identities were identical with both approaches (i.e., RAxML and MrBayes), the phylogenetic relationships among the haplotypes resolved differently with the two approaches. In the RAxML tree (Fig. S3a), *P. acuta* and *P. verrucosa* are more closely related to each other than to *P. meandrina*. In contrast, the MrBayes tree (Fig. S3b) indicates that *P. acuta* and *P. meandrina* are more closely related to each other than to *P. verrucosa*.

Discussion

Overview

Our results reveal similarities among TPCs for *Pocillopora* spp. from different latitudes where thermal regimes are different (Fig. 1), and these regimes differ in the degree to which they span the breadth of the TPCs (Fig. 2). TPCs for respiration were similar in shape among locations, although maximum respiration was reduced by 27–30% in Okinawa versus Guam and Moorea. Varying temperatures translate into similar changes in respiration in all locations, but the actual seawater temperatures in each location create different implications of the TPCs for metabolic performance. With respiration maximized at ~ 31°C in Okinawa and Guam (but at a higher temperature in Moorea), and a larger thermal range in Okinawa versus the other locations, *Pocillopora* spp. in Okinawa must tolerate a near-halving of the supply of metabolic energy in winter versus the summer. This may leave corals depleted of metabolic energy to support chemical and mechanical work, but through a reduced demand for respiratory substrates, it might allow rapid accumulation of food reserves during the winter (Thornhill et al., 2011). Larger food reserves could alleviate the negative implications of depressed photosynthesis in the summer (Fig. 2D), and provide insurance against

greater depression of photosynthesis under extreme high temperatures (i.e., beyond T_{opt}).

TPCs for gross photosynthesis, which are a function of the symbiotic algae within the corals, varied among locations. In Moorea, T_{opt} for gross photosynthesis was higher than in Guam or Okinawa, and corals were exposed to the narrowest range of temperatures (Fig. 1). This effect is intriguing, for in Moorea our genetic identification of the coral host revealed that our analyses were completed with *Pocillopora meandrina* (Table 1. Fig. S3), which was resistant to the most recent thermal bleaching in 2019 which killed 71% of the colonies of *P. cf. effusa* (Burgess et al., 2021). In Moorea, the discrepancy between T_{opt} for gross photosynthesis and the current mean seawater temperature suggest there may be a thermal safety margin (TSM [Pinsky et al., 2019]) of $\sim 3^{\circ}\text{C}$ for this trait in *P. meandrina*, which may have been important in reducing mortality following the 2019 bleaching. In this case, the TPCs for gross photosynthesis might be a closer approximation of a fitness-based TPC. TPCs for gross photosynthesis were also more convex in Okinawa and Guam versus Moorea (i.e., their alphas were smaller in Okinawa and Guam) (Fig. 3), indicating an erosion of TSMs, and perhaps indicating that higher temperatures would cause large declines in gross photosynthesis. In Okinawa, *Pocillopora* spp. must tolerate a near-halving in supply of photosynthetically fixed carbon in the winter versus the summer, and should temperatures as high as 33.5°C occur, will experience large reductions in photosynthesis. A critical outcome of these trends is the need for further research to resolve coral TPCs across latitudes with species resolution.

The regularity with which corals are now being exposed to high temperatures (Hughes et al., 2018a; Smith et al., 2023) has resulted in vast numbers of corals dying through thermal stress. Most have been directly killed through bleaching (Hughes et al., 2018a,b), while others have succumbed to the indirect effects of warming, for example, increased severity of diseases (Maynard et al., 2015; Howells et al., 2020; Burke et al., 2023). These trends have been ongoing since the 1980s (Hoegh-Guldberg, 1999), but even after 40 years of research, there remains a pressing need to understand the physiological basis of the susceptibility of corals to high temperature (van Woesik et al., 2022). An important aspect of the thermal stress response of corals is regional variation

in thermal tolerance. For *Pocillopora* spp. sampled over ~ 67% of the latitudinal range of corals in the tropical Pacific (Muir et al., 2022), TPCs showed only small variation over 44° of latitude, but greater differences in sensitivity to high temperature for photosynthesis than respiration. These results suggest that *Pocillopora* spp. may not have the metabolic capacity to tolerate high temperatures “hidden” within its biogeographic range. In this regard, our results are similar to those of Álvarez-Noriega et al. (2023), who found that growth TPCs for *Pocillopora* spp. were conserved over the Great Barrier Reef.

As our TPCs were measured before genotyping the coral host samples, genetic identification of the hosts occurred after the fact, revealing multiple species present in the study (Table 1, Fig. S3). Therefore, we cannot determine whether our contrasts of TPCs among locations describe separate populations within a taxon, multiple host or algal species, or a combination of effects. Nonetheless, our sampling targeted highly abundant morphotypes of *Pocillopora* spp., and their TPCs indicate that temperature increases of 2–4°C (relative to the current local maximum) could not be tolerated by *Pocillopora* spp. without substantial depression of respiration and gross photosynthesis. At the highest latitude, *Pocillopora* spp. in Okinawa live in a variable annual thermal regime, which causes large changes in respiration and photosynthesis between winter and summer. In order for poleward range expansion to be a viable option for corals to “escape” hot equatorial seawater (Yamano et al., 2011; Price et al., 2019; Yuan et al., 2023), it is likely that migrating corals will need to tolerate highly dynamic annual energy budgets.

Interpreting variation in TPCs for corals

TPCs quantify thermal performance, and in their most stringent form, evaluate fitness as a function of temperature (Sinclair et al., 2016). TPCs based on fitness can reveal the temperature at which evolutionary success is maximized, and they can be used to project fitness under future warmer conditions (Sinclair et al., 2016). For reef corals, TPCs previously have been applied in ways similar to the present application (e.g., Silbiger et al., 2019; Jurriaans and Hoogenboom, 2019), and they have advanced

understanding of the temperatures under which traits like respiration and photosynthesis are maximized. Extending such conclusions to evolutionary success is problematic however, since the relationships between physiological traits and fitness are poorly known in corals. For respiration and gross photosynthesis, their functional implications lie in the provision of metabolic energy for work (Edmunds and Davies, 1986), and photosynthetically fixed carbon to fuel respiration and synthesis (Muscatine, 1990; Grottoli et al., 2006), respectively. Elevated respiration can reflect a beneficial capacity to support work, or the detrimental consequence of rapid consumption of energy reserves (Porter et al., 1989; Anthony et al., 2009). Depressed respiration can reveal an inability to supply metabolic demands, or the benefits of conserving food reserves (Jacobson et al., 2016). For photosynthesis, interpreting empirical rates requires knowledge of the requirements for photosynthetically fixed carbon in respiration and synthesis (Muscatine et al., 1981), the role of heterotrophy (Grottoli et al., 2006), and the capacity for nutritional plasticity (Wall et al., 2021). Against this backdrop, it is not possible to interpret the present results in terms of a preferred optimum temperature in different locations, or holistic tolerance of extreme conditions.

There are still few examples of TPCs for corals with which the present results can be compared. Working with the Caribbean coral *Orbicella franksi* in Panama and Bermuda, for which TPCs for respiration, gross photosynthesis and net calcification (Bermuda only) were prepared, Silbiger et al. (2019) reported differences in TPCs between locations. T_{opt} for gross photosynthesis was 2.2°C higher for corals from Panama versus Bermuda, and the curve parameters differed among traits, with respiration having a higher T_{opt} than either gross photosynthesis or net calcification. Working with four Caribbean corals and testing for variation in TPCs for respiration and photosynthesis among taxa and depths (8–10 m versus 30–35 m) in Bermuda, Gould et al. (2021) described differences in curve parameters among taxa for photosynthesis (but not respiration), and little evidence of differing thermal sensitivities between depths. On the Great Barrier Reef, Jurriaans and Hoogenboom (2019) examined TPCs for net photosynthesis and respiration in *Acropora intermedia*, *A. valenciennesi* and *Porites cylindrica*, and found T_{opt} to vary over 9° of latitude, although the values did not correspond to the mean temperature in each location. Finally, Banc-Prandi et al. (2022)

compared TPCs for respiration and gross photosynthesis for five corals across 18° of latitude in the Red Sea, and found latitudinal differences in T_{opt} for *Stylophora pistillata*. Their study included nominally the same pocilloporid as studied herein (*P. verrucosa* identified morphologically), and T_{opt} for gross photosynthesis in this species did not vary between latitudes (~28.4°C), while T_{opt} for respiration was only resolved in the north (32.5°C).

Of greater utility in providing values with which the present study can be compared, are TPCs for *Pocillopora acuta* and *Pocillopora* spp. (corresponding to *P. meandrina* morphology, Veron and Pichon, 1976; Veron, 2000) from Moorea (Becker and Silbiger, 2021; Becker et al., 2021). Respiration, gross photosynthesis, and net calcification (*P. acuta* only) were used to estimate TPCs, with results that are similar to those reported herein. For *P. acuta*, TPC parameters differed among sites, with T_{opt} for gross photosynthesis varying from 29.6° to 31.2°C, for dark respiration from 32.9°C to 36.1°C, and for net calcification from 28.5°C to 30.7°C (Becker and Silbiger, 2021). For *Pocillopora* spp. exposed to ambient and enriched nutrients, T_{opt} for gross photosynthesis and respiration was unaffected by nutrients, although maximum rates (at T_{opt}) of both traits were elevated by nutrients (Becker et al., 2021).

Thus, previous work with TPCs for corals has shown equivocal results with respect to spatial and latitudinal variation for multiple traits. TPC parameters differ among colonies < 1 km (Becker and Silbiger, 2021), or 1000s of kilometers (Silbiger et al., 2019; Jurrians and Hoogenboom, 2019) apart, but in other cases, they are consistent within species over both small and large spatial scales (Gould et al., 2020; Banc-Prandi et al., 2022). The present results reveal modest differences in TPC parameters for two traits sampled in several *Pocillopora* spp. over a regional scale, and the results are most consistent with the hypothesis of limited local thermal adaptations in a broadly distributed coral taxon. Given the equivocal conclusions that are emerging regarding spatial variation in coral TPCs, and the limitations of the present (and other) studies (described below), it would be beneficial to quantify TPCs for multiple traits in multiple species at numerous locations using standardized approaches.

Limitations of the study

While studies of organism physiology across large spatial scales are integral to attaining the goals of macrophysiology (*sensu* Chown, 2022), in part to improve the capacity to forecast the implications of global climate change (Osovitz and Hofmann, 2007; Chown and Gaston, 2015), the completion of studies at appropriate scales of space and time pose technical and biological challenges. These emerged in the present study to place constraints on the inferences that could be supported. While the technical challenges were reduced by using identical equipment in all locations, and by having a single investigator complete the experiments, the biological limitations are more acute.

First, we standardized our experiments by working with a ubiquitous coral from a common habitat and depth, with collections targeting the morpho-species *Pocillopora verrucosa* (Veron and Pichon, 1976; Veron, 2000). Recently, Burgess et al. (2021) and Johnston et al. (2022) have described host genetic variation within *Pocillopora* spp. in Moorea, as well as phenotypic variation among species and haplotypes, and this work influenced how the present corals were selected. By sampling corals from a narrow depth range, we sought to minimize the collection of multiple species (see Fig. 3 in Johnston et al., 2022), and while this previous work indicated that *P. verrucosa* was not common in Moorea, and is rare at 5-m depth, the morphology of the colonies we collected led us to believe they were *P. verrucosa* (Veron and Pichon, 1976; Veron, 2000). With respect to colony identity we were incorrect (Table 1).

Genetic analyses of our corals revealed three species that were unequally represented among locations (Table 1). It is not possible, therefore, to reject the hypothesis that the differences in TPCs among latitudes reflect the species sampled, or a combination of effects attributed to the genotypes of the hosts and their symbionts (Armstrong et al., 2023; Kemp et al., 2023). In Moorea, *P. meandrina* contains mostly *Cladocopium latusorum*, *P. verrucosa* contains *C. pacificum* (Johnston et al., 2022b), and *P. acuta* contains *Durusdinium* and occasionally *Breviolum*, *Symbiodinium*, or *Cladocopium* (Rouzé et al., 2019). In Guam, *P. verrucosa* and *P. damicornis* contain *Cladocopium* and *Durusdinium* (Rowan, 2004; Torrado and Combosch, unpublished data); and in Sesoko (Okinawa), *P. damicornis* contains *Cladocopium* (Lien et al., 2013). Together,

the different hosts (Table 1) and their potentially different algal symbionts, create uncertainty in interpreting the underlying causes of regional contrasts of TPCs. It is reasonable to expect phenotypes to differ among *Pocillopora* species (Burgess et al., 2021), and the response to thermal stress to differ among conspecific hosts harboring different algae, as occurs in *P. grandis* containing *D. glynnii* versus *C. latusorum* in the eastern Pacific (Turnham et al., 2023). Nonetheless, our conclusions for the genus *Pocillopora* remain valid, although the causes of the latitudinal effects are more complex than can be explained by regional variation among populations of one coral species. In this context, it is interesting that our TPC parameters are similar in *P. verrucosa* and *P. meandrina* in Okinawa (Table S1), which is inconsistent with (but does not refute) the hypothesis that our conclusions are confounded by latitudinal differences in the host or symbiont genotypes.

Second, corals were sampled at each island in the same local season, after the maximum annual seawater temperatures had been reached. Nevertheless, thermal histories differed among locations. When the corals were sampled in Okinawa, the long-term records of seawater temperature indicated they had experienced ~ 100 days of cooling from ~ 30.6°C, whereas corals in Guam had experienced ~ 18 days of cooling from ~ 30.1°C. Sampling corals at similar times relative to local seasons in three locations over 5,000 km is a formidable logistical challenge, but the importance of thermal legacies in determining future performance in corals (Ainsworth et al., 2016; Wall et al., 2021) indicates that addressing these challenges would be worthwhile. One consequence of these effects that would be interesting to explore is the juxtaposition of the TPC relative to the range of temperatures characteristic of each latitude (Fig. 2). In Okinawa relative to Guam and Moorea, the majority of the ascending portion of the TPC is sampled by the annual range of temperatures (but only a narrow portion in Guam and Moorea) and for gross photosynthesis, therefore, the corals spend very little of the year (~ 13% based on number of days) operating at maximum performance for this trait. Two implications of these patterns that would benefit from explicit experimental testing, are (1) fitness TPCs are more divergent from metabolic TPCs at high latitudes, and (2) strong metabolic plasticity is likely to be positively associated with fitness at high latitude (Sawall et al., 2014).

Summary

The objective of this study was to test for differences in thermal sensitivity of a ubiquitous coral genus over its latitudinal range. As a rationale, we sought insight into the possibility that migration could shift thermally tolerant phenotypes into locations where they could sustain high fitness under future conditions. This concept includes latitudinal range extensions, which have been posited as a means to “escape” high temperatures in equatorial waters (Abrego et al., 2021). While evidence of poleward range extensions of corals has been recorded (Price et al. 2019), including in Japan (Yamano et al., 2011), and Florida (Precht and Aronson, 2004), the environmental conditions facilitating these trends are not well known (Abrego et al., 2021). Tolerance of cooler and more seasonally extreme temperatures is thought to be important in corals migrating poleward (Madin et al., 2016; Abrego et al., 2021).

We found limited evidence of regional variation in TPCs for respiration and gross photosynthesis in *Pocillopora* spp. This result is inconsistent with the notion of local adaptation of reef corals (Sanford and Kelly, 2011; Howells et al., 2012), here for respiration and gross photosynthesis in populations of *Pocillopora* spp., and it provides little hope that migrations of *Pocillopora* spp. in the Pacific could modulate their regional response to increasing temperature. By highlighting the large extent to which respiration and gross photosynthesis varies through a year at high latitudes, we detected an emergent physiological property that may influence whether corals can persist in such locations. Tolerance of thermal regimes at high latitudes requires accommodation of dynamic energy budgets supplying seasonally variable amounts of metabolic energy, and the photosynthetically fixed carbon necessary to support this delivery.

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Competing interests

The authors declare they have no competing interests of relevance to publication of this paper.

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Data availability

All data reported in this manuscript are available at <https://www.bco-dmo.org/> and can be accessed through the following DOIs: xxx, xxx, and xxx.

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Figures and Tables

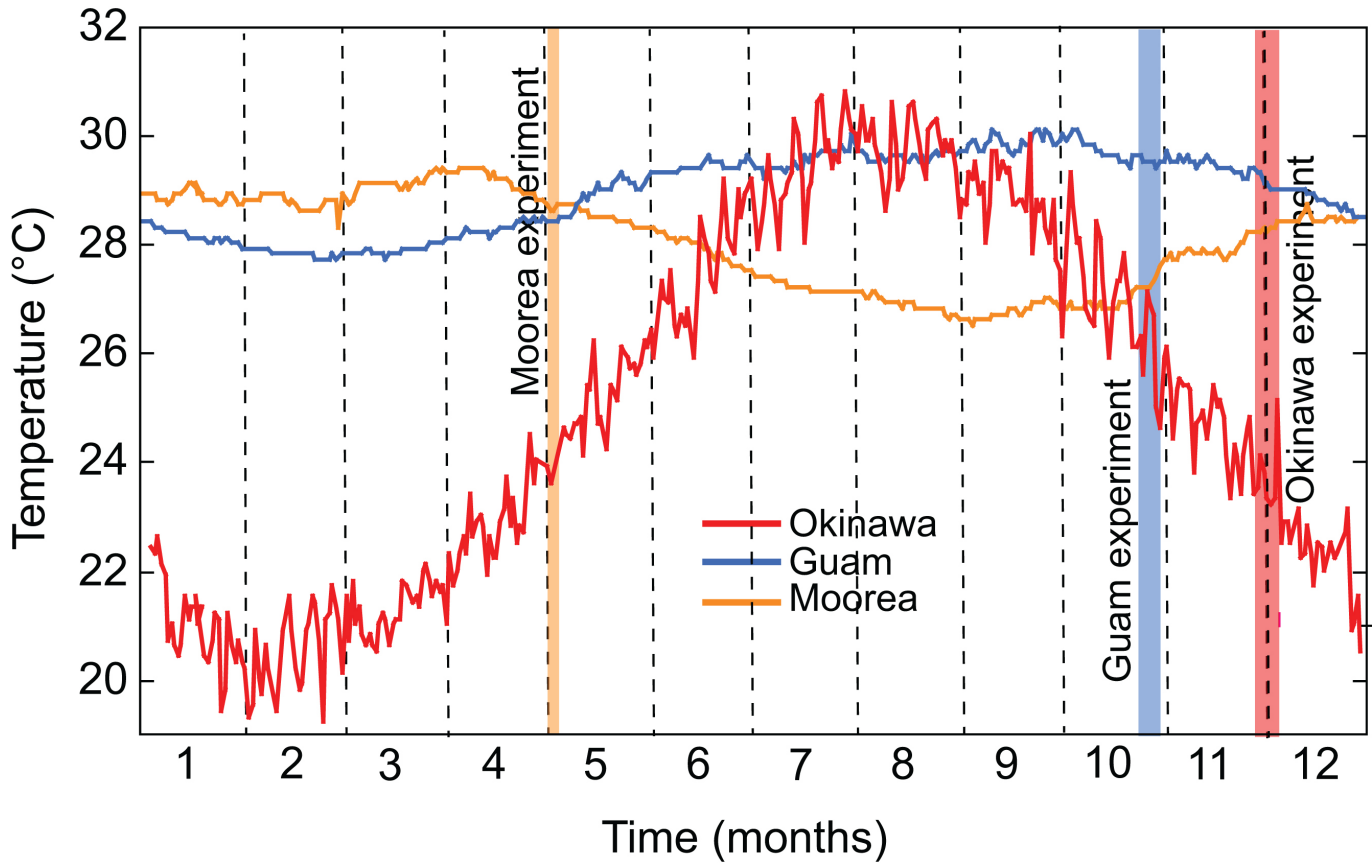


Fig. 1. Mean daily seawater temperature at the three sites. Values plotted along a continuous axis with day resolution but with dashed vertical lines showing days separated by months (1 = January, 2 = February, etc.). Vertical bars (color matched by site) showing when the metabolism experiments were conducted.

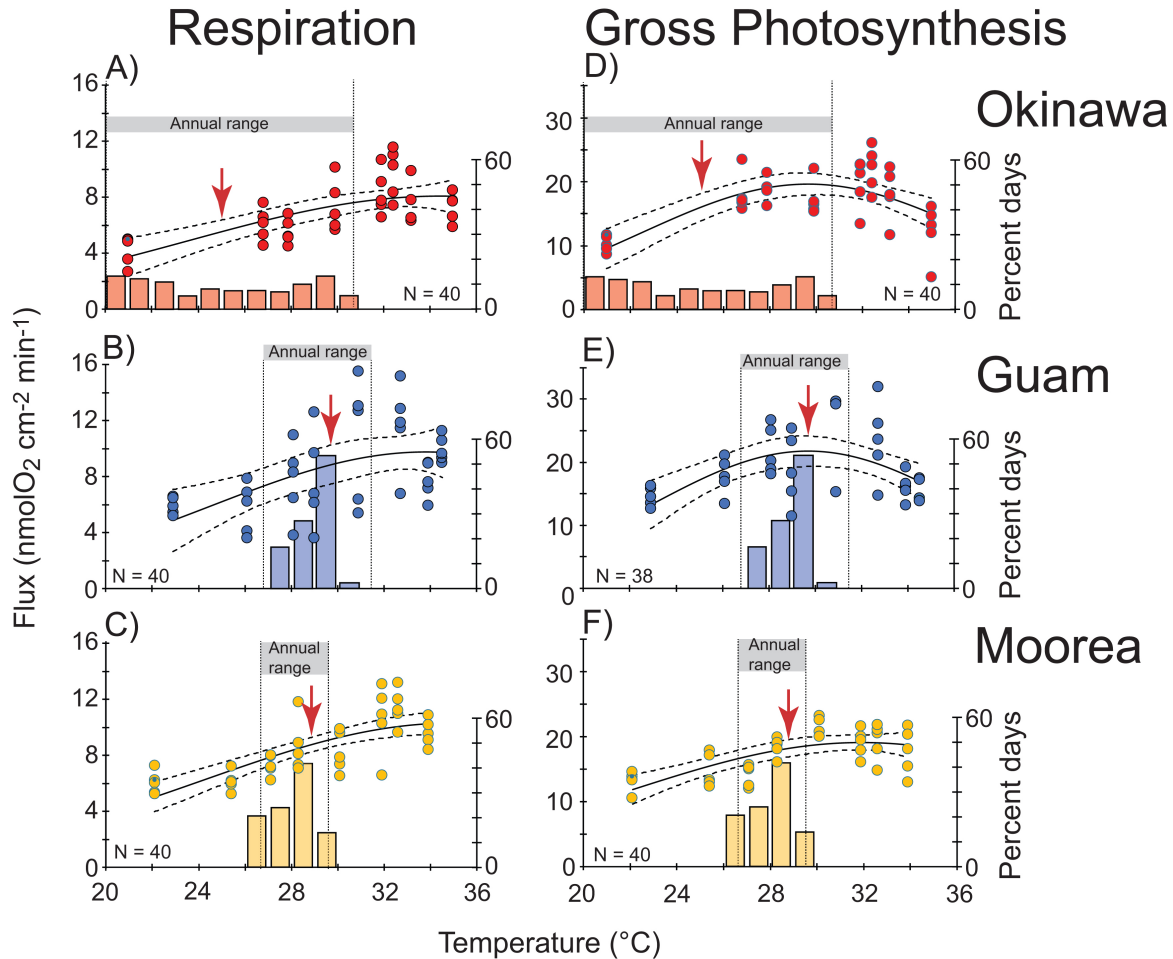


Fig. 2. Dark respiration and gross photosynthesis of *Pocillopora* spp. (left Y-axis) as a function of temperature in Okinawa (A,D), Guam (B,E), and Moorea (C,F).

Each symbol represents a coral (sample sizes, *N*), solid lines are best-fit Gaussian relationships, and dashed lines show 95% confidence intervals. Gray bar and vertical dash lines show annual range in temperature (Fig. 1), and red arrows show mean temperature when the experiments were conducted. Histograms show frequency distributions of one year of mean (*N* = up to 5 years) daily temperatures (right Y-axis) for each site with a class interval of 1.9°C (20.1–22.0°C, etc.).

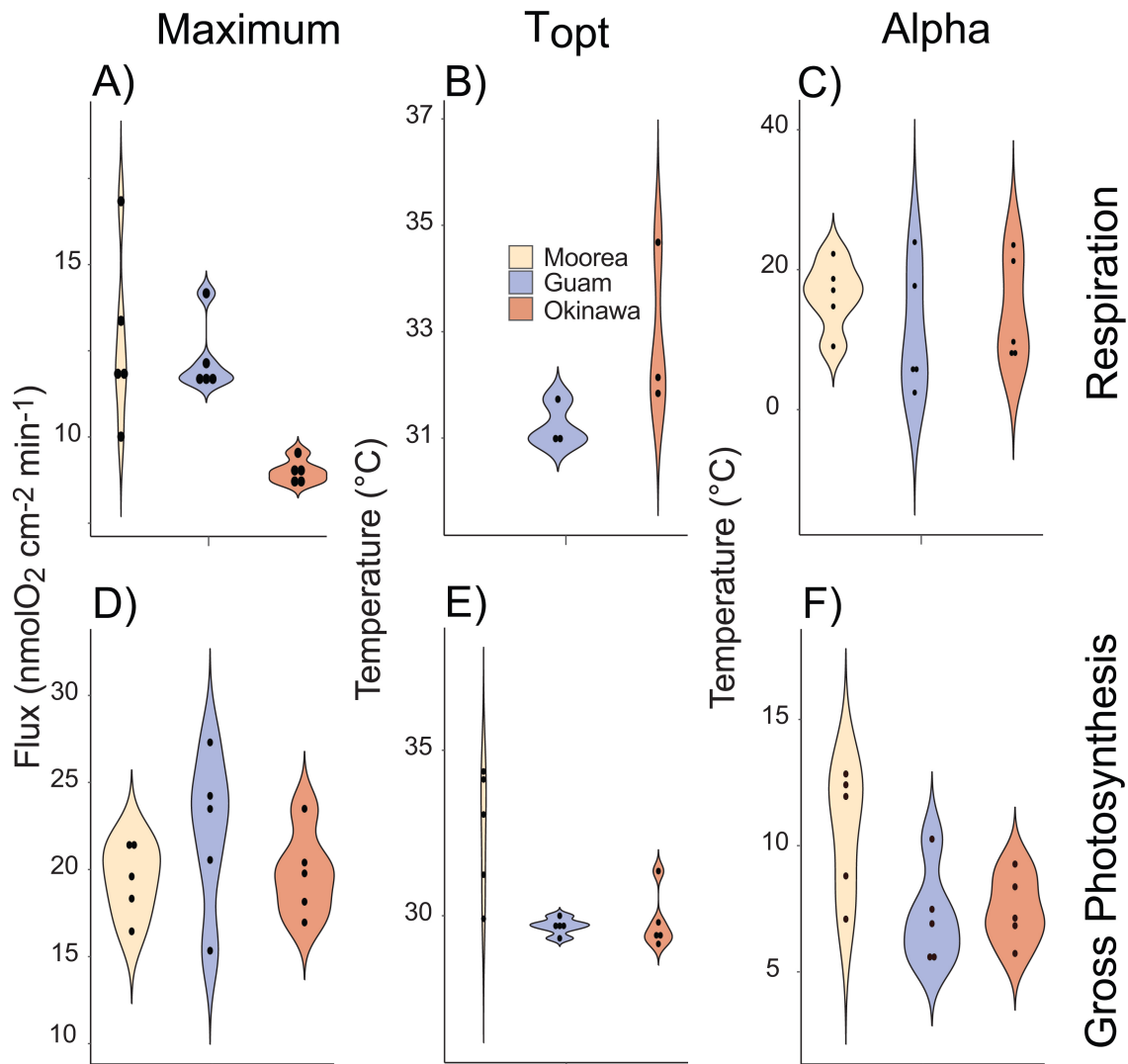


Fig. 3. Violin plots showing curve parameters (Maximum, T_{opt} , and Alpha, Fig. 1) from Gaussian relationships (Table 2) describing the response of respiration (A-C) and gross photosynthesis (D-F) to temperature for *Pocillopora* spp. in Moorea, Guam, and Okinawa. $N = 38-40$ corals (5 genotypes, each dot shows one genotype by site) for each location. T_{opt} values are not displayed where data were insufficient to resolve this parameter; all values for Moorea were $> 33.9^{\circ}\text{C}$.

Table 1. Summary of genetic contrasts of *Pocillopora* spp. among locations.

Colony	Genetic identity		
	Moorea	Guam	Okinawa
A	Haplotype 1a, <i>P. meandrina</i>	Haplotype 5, <i>P. acuta</i>	Haplotype 3f, <i>P. verrucosa</i>
B	Haplotype 1a, <i>P. meandrina</i>	Haplotype 5, <i>P. acuta</i>	Haplotype 1a, <i>P. meandrina</i>
C	Haplotype 1a, <i>P. meandrina</i>	Haplotype 5, <i>P. acuta</i>	Haplotype 3f, <i>P. verrucosa</i>
D	Haplotype 8a, <i>P. meandrina</i>	Haplotype 5, <i>P. acuta</i>	Haplotype 3f, <i>P. verrucosa</i>
E	Haplotype 1a, <i>P. meandrina</i>	Haplotype 5, <i>P. acuta</i>	Haplotype 8a, <i>P. meandrina</i>

Table 2. Statistical contrasts of TPC parameters (Figs. 2, 3) using ANOVA with Model III sum of squares. F = statistic, df = degrees of freedom, P = probability (bold for significance). Post-hoc contrasts completed through Tukey procedures contrasting Moorea (M), Guam (G), and Okinawa (O).

DV	Parameter	Contrast	Post-hoc
Respiration	Maximum	F = 8.026, df = 2, 12, P = 0.006	G = M; O < G, M
	T _{opt}	F = 3.121, df = 1, 4, P = 0.152	O = G
	Alpha	F = 0.621, df = 2, 12, P = 0.554	O = G = M
Gross photosynthesis	Maximum	F = 1.085, df = 2, 12, P = 0.369	O = G = M
	T _{opt}	F = 8.590, df = 2, 12, P = 0.005	M > G, O; O = G
	Alpha	F = 4.572, df = 2, 12, P = 0.033	M > G; M = O; G = O

Supplementary Materials and Methods

Genetic analyses of corals

Moorea

Genomic DNA was extracted using Chelex 100 (Bio-Rad, USA). Samples were incubated in 150 μ L of 10% Chelex 100 for 60 mins at 55°C followed by 15 mins at 95°C. After centrifuging, the supernatant was used for PCR amplification of the mitochondrial Open Reading Frame (mtORF) using the FATP6.1 and RORF primers and protocol in Flot et al. (2008). 5 μ L of PCR product was cleaned with 2 μ L of Exo-CIP Rapid (New England BioLabs, Ipswich, MA), and placed in a thermocycler for 4 mins at 37°C and 1 min at 80°C. Cleaned PCR products were sequenced in the forward direction with the FATP6.1 primer at Florida State University on an Applied Biosystems 3730 Genetic Analyzer with Capillary Electrophoresis.

Guam

Guam samples were preserved in DESS (Seutin et al., 1991; Voolstra et al., 2022) and stored at -20°C. Genomic DNA was extracted using GenCatch Genomic DNA extraction kits (Epoch, Sugar Land, TX) following a slightly modified manufacturer's protocol. Extracted DNA was used as a template for PCR amplifications of the same mtORF marker, using newly designed primers (Poc_MT_ORFf1: 5'-TGCAAATTTAAGTAATGTGGGTTT-3' and Poc_MT_ORFr1 5'-CACCTGGAGGTGTTTCTACCTT-3'). The PCR amplification protocol involved an initial denaturation step at 94°C for 120s, followed by 34 cycles of denaturation at 94°C for 30s, annealing at 53°C for 30s, extension at 75°C for 75s, and a final extension step at 72°C for 600s. PCR products were verified using agarose gel electrophoresis and

successful amplifications were sent to Epoch Life Sciences (Missouri City, TX) for sequencing in both directions with diluted PCR primers on an ABI3730XL sequencer, as in Combosch et al. (2024).

Okinawa

Okinawan specimens were preserved in guanidine solution and DNA extraction as well. Amplification of the putative mitochondrial open reading frame (mtORF) was conducted using the primer pair FATP6.1/RORF (Flot et al., 2008). Amplified PCR products were purified using ExoSAP-IT (USB Corp., USA) and Sanger sequencing was performed by MacroGen Japan (<http://www.macrogen-japan.co.jp/>) using the same primer pairs as for the PCR followed Sinniger et al. (2017). In addition, to distinguish between *P. meandrina* and *P. grandis*, RFLP assay of the histone 3 marker was performed following the same methods as detailed above for the Moorea specimens.

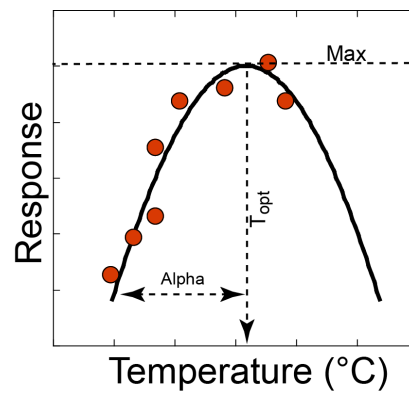


Fig. S1. Schematic showing the Gaussian function fitted to hypothetical data (dots) showing the relationship between a physiological response (Y axis) and temperature (X axis) and the parameters of the curve (Max, T_{opt} , and alpha). The distribution of the points to the left of the curve illustrates the scope of the present sampling that did not include responses to the right of the curve because of their lack of ecological relevance (Fig. 1) and the high likelihood that they would negatively affect the corals.

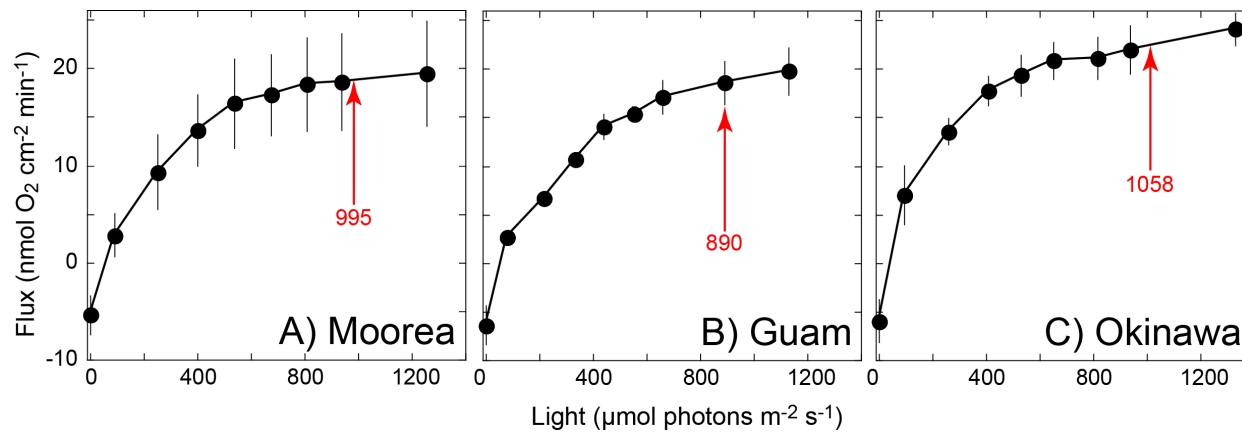


Fig. S2. Mean net photosynthesis ($\pm$ SD, $n = 2$ nubbins from separate colonies) versus light (photon flux density [PFD] of photosynthetically active radiation [PAR], $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) curves for *Pocillopora* spp. from fore reef habitats (5-m depth) in Moorea, Guam, and Okinawa. Relationships show that photosynthetic saturation was reached at $\sim 1000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and that the PFD at which photosynthesis was measured (red lines and numbers) to prepare the TPC responses supports the interpretation of these values as maximum rates.

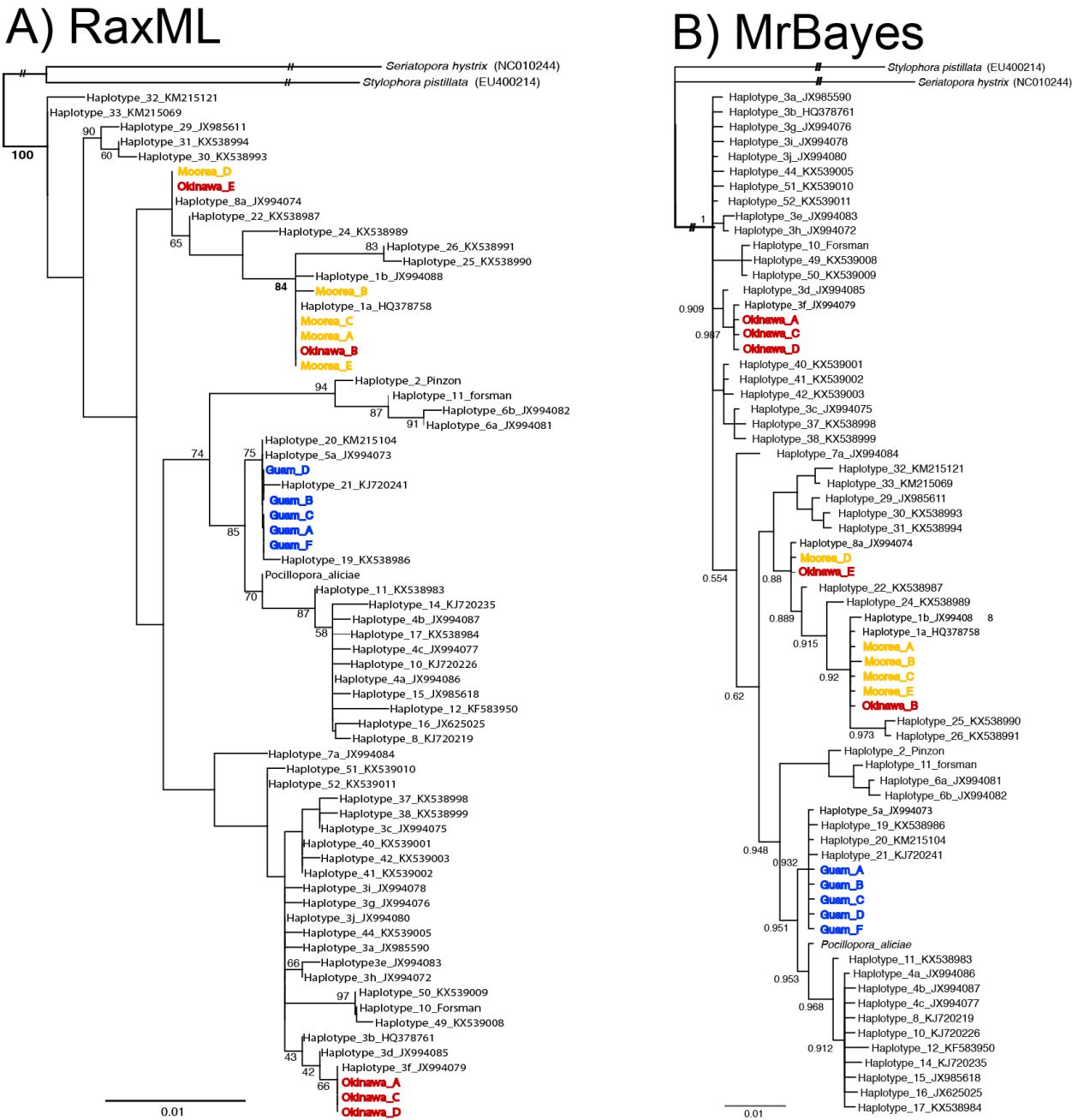


Fig. S3. Phylogenetic analyses of the 15 samples used in experiments (color-coded by island: yellow = Moorea, red = Okinawa, blue = Guam) within a broad phylogenetic context of *Pocillopora* haplotypes from published studies (Gélin et al., 2017; Johnston et al., 2022), based on a) Maximum Likelihood analyses with RAXML 8.2.8 (Stamatakis, 2014) and b) Bayesian inference analyses with MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001). Although the phylogenetic relationships among ORF sequences differ between methods, the same haplotype identities were identified with both approaches, as indicated in bold, and species identity (Table 1) was assigned to each sample following Forsman et al. (2013), Pizon et al. (2013) and Gélin et al. (2017).

Table S1. Summary of model fits for TPC for respiration and gross photosynthesis (dependent variables, DV) by coral colony (A-E, genetically identified to species, Table 1) for Guam, Okinawa, and Moorea. Results present for Gaussian (Curve = G) and Gaussian-Gompertz (Curve = G-G) fits where models converged based on 7–8 replicates (N). MSE = mean square error, AIC_c = Akaike information criterion adjusted for small samples sizes, Max = maximum predicted value of the DV using the best-fit model, T_{opt} = temperature (°C) at which DV is maximized († = temperature beyond the range of thermal treatments applied), Alpha = for Gaussian curves, half the width of the TPC (°C, ± SE), and for Gaussian-Gompertz curves, the slope (± SE) of the ascending portion of the best-fit curve (nmol O₂ cm⁻² min⁻¹ °C⁻¹), and Beta = for the Gaussian-Gompertz curve, the slope (± SE) of the descending portion of the curve (nmol O₂ cm⁻² min⁻¹ °C⁻¹). n/a = not applicable.

Site	DV	Curve	Coral	N	MSE	AIC _c	Max	T _{opt}	Alpha	Beta
Guam	Respiration	G	A, <i>P. acuta</i>	8	13.828	25.711	11.73 ± 2.40	50†	23.94 ± 6.88	n/a
		G	B, <i>P. acuta</i>	8	2.950	31.827	12.14 ± 1.35	30.98 ± 1.08	5.70 ± 1.64	n/a
		G	C, <i>P. acuta</i>	8	4.789	30.104	11.70 ± 4.27	50†	17.69 ± 5.34	n/a
		G	D, <i>P. acuta</i>	8	3.802	28.257	11.64 ± 1.07	31.00 ± 0.95	5.85 ± 1.44	n/a
		G	E, <i>P. acuta</i>	8	12.661	37.881	14.17 ± 2.90	31.73 ± 0.50	2.44 ± 0.62	n/a
	Gross Photosynthesis	G-G	A, <i>P. acuta</i>	7	33.772	88.696	23.91 ± 7.11	50†	<0.001 ± 0.001	n/a
		G	A, <i>P. acuta</i>	7	13.489	42.296	23.48 ± 2.31	30.0 ± 1.00	6.91 ± 1.92	n/a
		G-G	B, <i>P. acuta</i>	7	75.117	94.302	24.53 ± 10.07	50†	<0.001 ± 0.001	n/a
		G	B, <i>P. acuta</i>	7	27.19	47.203	27.30 ± 3.41	29.72 ± 0.86	5.66 ± 1.45	n/a
		G-G	C, <i>P. acuta</i>	8	28.868	61.357	60†	20.00 ± 20.31	<0.001 ± 0.017	n/a
		G	C, <i>P. acuta</i>	8	8.411	34.609	15.34 ± 1.57	29.32 ± 2.14	10.26 ± 6.05	n/a
		G-G	D, <i>P. acuta</i>	8	48.135	65.447	22.51 ± 7.94	50†	<0.001 ± 0.001	n/a
		G	D, <i>P. acuta</i>	8	16.773	40.131	24.23 ± 2.32	29.78 ± 0.73	5.52 ± 1.15	n/a
		G-G	E, <i>P. acuta</i>	8	41.864	64.330	19.55 ± 6.99	50†	<0.001 ± 0.001	n/a
		G	E, <i>P. acuta</i>	8	27.070	43.961	20.55 ± 2.84	29.61 ± 1.71	7.48 ± 3.49	n/a
Okinawa	Respiration	G	A, <i>P. verrucosa</i>	8	3.291	27.104	8.72 ± 1.38	34.68 ± 5.51	8.42 ± 4.67	n/a
		G	B, <i>P. meandrina</i>	8	1.885	22.645	9.02 ± 0.59	32.14 ± 2.79	9.70 ± 3.57	n/a
		G	C, <i>P. verrucosa</i>	8	0.409	10.426	9.54 ± 9.31	49.88†	21.24 ± 21.91	n/a
		G	D, <i>P. verrucosa</i>	8	5.098	30.605	8.70 ± 1.02	31.84 ± 3.00	7.76 ± 3.76	n/a
		G	E, <i>P. meandrina</i>	8	1.203	19.050	9.04 ± 14.81	50†	23.53 ± 48.52	n/a
	Gross Photosynthesis	G-G	A, <i>P. verrucosa</i>	8	16.701	56.978	26.66 ± 6.04	50†	0.001 ± 0.001	n/a
		G	A, <i>P. verrucosa</i>	8	7.095	33.248	20.4 ± 1.20	31.35 ± 1.55	8.37 ± 2.11	n/a

		G-G	B, <i>P. meandrina</i>	8	24.150	59.929	60†	31.80 ± 2.26	0.011 ± 0.005	n/a
		G	B, <i>P. meandrina</i>	8	11.952	37.421	23.49 ± 1.87	29.15 ± 0.89	6.83 ± 1.33	n/a
		G-G	C, <i>P. verrucosa</i>	8	27.925	61.091	19.24†	50†	<0.001 ± 0.001	n/a
		G	C, <i>P. verrucosa</i>	8	11.138	36.857	18.15 ± 1.72	29.80 ± 1.26	7.13 ± 1.90	n/a
		G-G	D, <i>P. verrucosa</i>	8	60.965	67.337	18.47†	50†	<0.001 ± 0.001	n/a
		G	D, <i>P. verrucosa</i>	8	26.108	43.671	19.78 ± 2.80	29.46 ± 1.27	5.73 ± 1.76	n/a
		G-G	E, <i>P. meandrina</i>	8	15.710	56.489	41.36†	20.46†	< 0.001 ± 0.100	n/a
		G	E, <i>P. meandrina</i>	8	7.012	33.154	16.96 ± 1.38	29.36 ± 1.55	9.27 ± 2.91	n/a
Moorea	Respiration	G	A, <i>P. meandrina</i>	8	1.620	21.431	13.37 ± 25.90	50†	22.27 ± 48.19	n/a
		G	B, <i>P. meandrina</i>	8	2.041	23.280	16.84 ± 2.87	50†	18.70 ± 2.67	n/a
		G	C, <i>P. meandrina</i>	8	5.067	30.555	10.01 ± 5.48	37†	14.75 ± 25.5	n/a
		G	D, <i>P. meandrina</i>	8	4.158	28.974	11.78 ± 3.16	36†	9.04 ± 6.057	n/a
		G	E, <i>P. meandrina</i>	8	2.309	24.268	11.89 ± 16.32	44†	17.07 ± 29.29	n/a
	Gross Photosynthesis	G-G	A, <i>P. meandrina</i>	8	10.282	53.098	24.42 ± 4.49	50†	0.001 ± <0.001	n/a
		G	A, <i>P. meandrina</i>	8	6.011	31.923	19.60 ± 1.15	31.24 ± 2.00	8.80 ± 2.93	n/a
		G-G	B, <i>P. meandrina</i>	8	6.812	49.804	26.42 ± 3.66	50†	0.001 ± <0.001	n/a
		G	B, <i>P. meandrina</i>	8	4.734	30.012	21.26 ± 1.83	34.12 ± 6.30	12.84 ± 7.10	n/a
		G-G	C, <i>P. meandrina</i>	8	14.361	55.771	22.41 ± 5.11	50†	0.001 ± 0.001	n/a
		G	C, <i>P. meandrina</i>	8	11.238	36.928	18.33 ± 1.98	33.06 ± 8.61	12.41 ± 11.21	n/a
		G-G	D, <i>P. meandrina</i>	8	4.838	47.067	27.93 ± 3.30	50†	0.001 ± <0.001	n/a
		G	D, <i>P. meandrina</i>	8	3.314	27.159	21.56 ± 1.70	34.36 ± 4.86	11.95 ± 4.98	n/a
		G-G	E, <i>P. meandrina</i>	8	11.410	53.930	18.67 ± 4.39	50†	0.001 ± 0.001	n/a
		G	E, <i>P. meandrina</i>	8	5.156	30.694	16.45 ± 1.18	29.91 ± 1.10	7.09 ± 1.77	n/a

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