



An intertidal fish shows thermal acclimation despite living in a rapidly fluctuating environment

Carmen Rose Burke da Silva¹ · Cynthia Riginos¹ · Robbie Stuart Wilson¹

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Abstract

The co-evolution of acclimation capacity and thermal performance breadth has been a contentious issue for decades, and little is known regarding the extent to which acclimation alters the shape of acute thermal performance curves. Current acclimation theory suggests that when daily variation is large and unpredictable ectotherms should not acclimate but should evolve wide performance breadths, allowing maintenance of performance across a wide thermal range. The subtropical intertidal zone, however, experiences a large amount of daily thermal variation, but daily means and ranges shift in predictable ways with season, where daily and seasonal variation is roughly equal. We predicted that animals in this habitat would maintain their capacity to acclimate and that performance breadth would not be altered by acclimation to maintain function with rapidly fluctuating daily temperatures. We tested our prediction using a subtropical goby, *Bathygobius cocosensis*, which lives in tide pools that vary widely, over days and seasons. We exposed *B. cocosensis* to winter (12–17 °C) and summer (30–35 °C) thermal conditions for six weeks and then measured the thermal dependence of burst swimming speed, routine and maximum metabolic rate, and ventilation rate between 12 and 36 °C. *B. cocosensis* exhibited an acclimation response for burst swimming speed, maximum metabolic rate and metabolic scope, but acclimation did not alter the shape of acute thermal performance curves. These results indicate that thermal acclimation can occur when short-term thermal variability is large and equal to seasonal variation, and wide performance breadths can be maintained with acclimation in heterogeneous environments.

Keywords Acclimation · Performance · Climate change · Plasticity · Thermal variation · Co-evolution

Introduction

Global climate change is increasing environmental thermal means, variability and stochasticity (IPCC 2014). Animals can respond to thermal change within their lifetime by moving to environments with more suitable temperatures (behavioural thermoregulation) (Walther et al. 2002; Sunday et al. 2011; Campbell et al. 2018) or they can acclimate (Wilson and Franklin 2002; Angilletta 2009; Riddell et al. 2018).

Thermal acclimation, also known as reversible plasticity, is the modification of an organism's underlying physiology to allow maintenance of performance in changed environmental conditions (Huey et al. 1999; Wilson and Franklin 2002; Angilletta 2009; Beaman et al. 2016). Acclimation to changed thermal conditions has the potential to result in fitness benefits (Wilson and Franklin 2002; Ghalambor et al. 2007), because performance traits such as metabolism and locomotion affect growth, behaviour and development (Le Galliard et al. 2004; Wilson et al. 2007; Seebacher 2009). Fitness benefits associated with acclimation have the potential to occur when changes in environmental conditions are predictable and there are adequate environmental cues for future thermal conditions (Levins 1968; DeWitt 1998; Kingsolver and Huey 1998; Johnston and Temple 2002; Gabriel 2005). The environmental conditions that promote the evolution of thermal acclimation and thermal performance curve shape, however, have remained a controversial topic over the past 50 years (Janzen 1967; Lynch and Gabriel 1987; Huey and Kingsolver 1989; DeWitt 1998; Wilson and Franklin

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✉ Carmen Rose Burke da Silva
Carmen.dasilva@uq.net.au

¹ School of Biological Sciences, Faculty of Science, The University of Queensland, Saint Lucia, Brisbane 4072, Australia

2000; Gabriel 2005; Deere and Chown 2006; Ghalambor et al. 2007; Tewksbury et al. 2008; Deutsch et al. 2008; Healy and Schulte 2012; Rohr et al. 2018).

Thermal performance curves describe the way temperature affects an animal's performance, with the peak of the curve representing an organism's thermal performance optimum and the breadth of the curve representing the range of temperatures for adequate performance (Huey and Stevenson 1979; Huey and Kingsolver 1989; Gilchrist 1996; Angilletta et al. 2002; Angilletta 2006; Schulte et al. 2011). Thermal variability is believed to play an important role in shaping an organism's capacity to acclimate and the breadth of their thermal performance curve (Levins 1968; Huey and Kingsolver 1989; Wilson and Franklin 2000; Huey et al. 2012; Dillon et al. 2016). Many studies suggest that organisms in variable environments should evolve wide thermal performance breadths and the capacity to acclimate; conversely, animals in stable thermal environments should evolve narrow performance curves and little or no capacity to acclimate (Janzen 1967; Lynch and Gabriel 1987; Huey and Kingsolver 1993; Gilchrist 1995; Stillman 2003; Tewksbury et al. 2008; Deutsch et al. 2008; Rohr et al. 2018). Many exceptions exist, however, where there are examples of animals in stable environments acclimating (e.g. Brown and Feldmeth 1971; Cunningham and Read 2002; Glanville and Seebacher 2006; Franklin et al. 2007; Bilyk and DeVries 2011); organisms in thermally variable conditions with no capacity to acclimate (e.g. Wilson and Franklin 2000; Deere and Chown 2006); and organisms in variable environments having the capacity to acclimate and having wide thermal performance curves (e.g. Johnson and Bennett 1995; Healy and Schulte 2012).

The way “thermal variability” is defined is important as the magnitude of daily and seasonal thermal variability together is likely to affect the co-evolution of thermal performance curve breadth and acclimation capacity, which often leads to different combinations of acclimation capacity and thermal performance curve shape (Wilson and Franklin 2000; Gabriel 2005; Healy and Schulte 2012; Dillon et al. 2016; Pörtner and Gutt 2016). In addition, many combinations of daily and seasonal thermal variability and predictability exist in nature but we still have a limited understanding of how acclimation capacity and thermal performance breadth co-evolve in different environments, and how thermal acclimation might alter the shape of thermal performance curves. Gaining a deeper understanding of the relationships between thermal variability, acclimation capacity and performance curve shape will allow predictions of species responses to changing climates to be improved and for more specific and targeted conservation approaches to be implemented.

Some studies have investigated how both daily and seasonal thermal variability correlates with the shape of species

thermal performance curves and their capacity to acclimate (Johnson and Bennett 1995; Wilson and Franklin 2000; Deere and Chown 2006; Niehaus et al. 2011; Schuler et al. 2011; Healy and Schulte 2012; Pereira et al. 2017; Rohr et al. 2018). Generally, most recent theory suggests that when seasonal thermal variation is predictable and greater than daily thermal fluctuations, animals should evolve the capacity to acclimate and have narrow thermal performance curves (Fig. 1a) (Wilson and Franklin 2002; Gabriel 2005; Gabriel et al. 2005; Sinclair et al. 2006). For example, larval amphibians that inhabit aquatic environments where seasonal thermal variation is greater than daily thermal fluctuations often have capacity to acclimate to seasonal conditions and have narrow thermal performance curves (Wilson and Franklin 1999, 2000). When larval amphibians develop into adult frogs they transition into a predominantly terrestrial habitat where daily thermal fluctuations are greater than in aquatic environments, and these animals often have no capacity to acclimate but have wide thermal performance curves (Fig. 1b) (Wilson and Franklin 2000). Large daily thermal fluctuations are often perceived to mask seasonal thermal change, making seasonal change unpredictable and costly and, therefore, thermal acclimation unlikely to occur (DeWitt 1998; Gabriel 2005; Gabriel et al. 2005). Here, we examine these expectations in the context of the marine intertidal zone where large daily thermal fluctuations occur but predictable seasonal variation is present.

The intertidal zone is known to experience extensive daily thermal fluctuations with changing tides, solar radiation and wind (Johnson 1975; Helmuth 1999; Helmuth et al. 2006), but the mean, maximum and minimum daily temperatures gradually shift with season, allowing seasonal changes to be predictable despite large daily fluctuations. Previous studies have found that temperate intertidal fish species, such as killifish (*Fundulus heteroclitus*) and sculpins (*Oligocottus maculosus* and *Myoxocephalus scorpius*), that experience large fluctuations in daily and seasonal temperature have the capacity to thermally acclimate to seasonal temperatures and have wide thermal performance curves (Johnson and Bennett 1995; Temple and Johnston 1998; Fangue et al. 2006, 2008, 2011; Healy and Schulte 2012). In these conditions, thermal acclimation has little effect on the performance breadth of aerobic scope in killifish, where wide performance breadths are hypothesised to be required to maintain physiological function with rapid short-term thermal fluctuations (Healy and Schulte 2012). These temperate intertidal species, however, experience greater seasonal thermal variation (approx. 15–20 °C) (Fangue et al. 2008) than daily thermal fluctuations (approx. 5–10 °C) (Sidell et al. 1983; Fangue et al. 2008). Few studies have assessed the extent to which acclimation alters the shape of the acute thermal performance curves in organisms that experience roughly

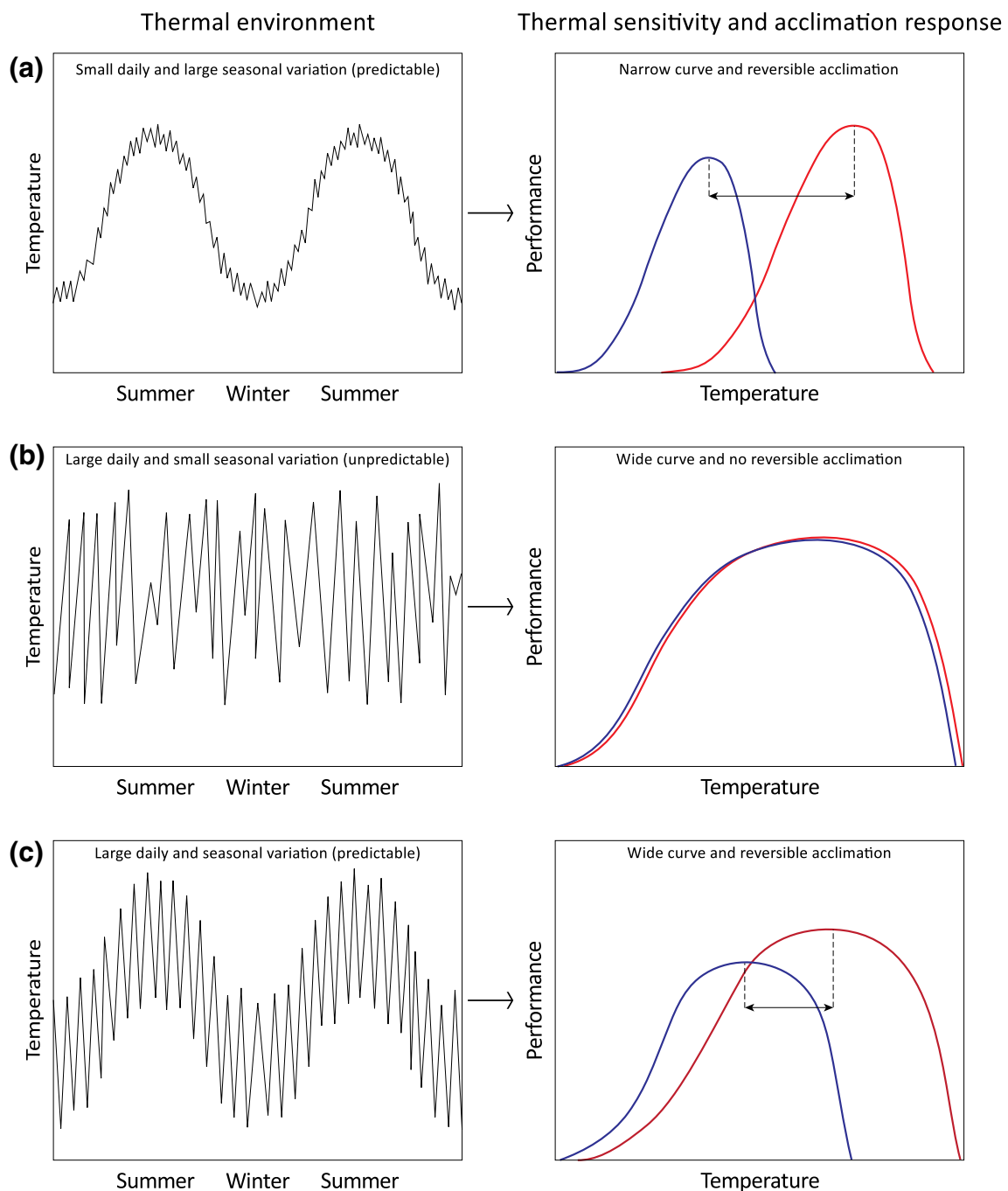


Fig. 1 Conceptual illustration on how magnitude of daily thermal fluctuations and seasonal thermal variations affects thermal performance breadth and capacity for reversible acclimation. **a** Illustrates environments with small daily and large seasonal thermal variations: animals in those environments are predicted to have narrow thermal breadths and the capacity to acclimate. **b** Illustrates an environment with large daily thermal fluctuations and little seasonal variation: ani-

mals in those environments are expected to have wide thermal performance curves and no capacity to acclimate. **c** Illustrates an environment where magnitude of daily thermal fluctuations and mean seasonal thermal variation is equal but there is predictable seasonal change, animals in these environments are expected to have wide thermal performance curves and the capacity to acclimate

equal daily and seasonal thermal variation, such as subtropical ectotherms. We expect that acclimation capacity and performance breadth will be maintained in organisms that experience equal daily and seasonal thermal variation

when seasonal variation remains predictable (Fig. 1c) and that acclimation will have little effect on altering the shape of thermal performance curves.

We had two key aims. Firstly, we aimed to assess if an organism that experiences large but roughly equal daily and seasonal variation with predictable seasonal fluctuations had the capacity to acclimate to seasonal conditions; and finally, we aimed to assess the extent to which acclimation to seasonal conditions altered the shape of thermal performance curves. We used *Bathygobius cocosensis* (Bleeker 1854) (Fig. 2), an intertidal fish commonly known as Cocos Frillgoby as our study organism. They are the most common intertidal fish on the east coast of Australia (Griffiths 2000) and have a widespread geographic distribution. Our study site in south-east Queensland, Point Lookout North Stradbroke Island, experiences 6 °C of thermal variation between seasonal high tide means (Supplementary Figs. 1 and 2; and seasonal high tide (sea surface temperature) data collected by the navy meteorological and oceanography (METOC) harvester). Specifically, high tide rock pool temperatures are 26 °C in the summer (January) and 20 °C in the winter (July). On a daily basis, rock pools fluctuate with diurnal tides, solar radiation and wind, where they have been observed to fluctuate by about 6 °C daily (Supplementary Figs. 1 and 2). Therefore, both daily fluctuations and seasonal means vary by about 6 °C. As *B. cocosensis* experiences large daily thermal fluctuations and predictable seasonal changes, we hypothesised that *B. cocosensis* would possess the capacity to acclimate and have wide thermal performance breadths, and that thermal acclimation would have little effect on the shape of their thermal performance curve.

Methods

Bathygobius cocosensis were collected from rock pools at Point Lookout, North Stradbroke Island in southeast Queensland, Australia (GPS coordinates 27.4347°S, 153.5305°E).



Fig. 2 *Bathygobius cocosensis* in a rock-pool in south-east Queensland. Photographed by CRB da Silva

Fish were collected using a battery-operated bilge-pump and hand nets at low tide in April 2016. Fish were transported to the University of Queensland by vehicle in oxygen-saturated bags within insulated containers. Fish were anaesthetised (0.3×10^{-3} mg L⁻¹ of Aqui-S®) (Griffiths 2000; Malard et al. 2016) and tagged with Visible Implant Elastomer (VIE) fluorescent subdermal tags (Northwest Marine Technologies®, Inc.). Individual tags allowed unique recognition during experiments. VIE tags do not impact mortality or growth rates (FitzGerald et al. 2004). The sample sizes reported below were determined prior to field collection using a power analysis for consideration of pre-specified effect sizes. Animal ethics was approved by The University of Queensland's Animal Ethics committee: Permit: SBS/425/2015. Collection in Moreton Bay was approved by the Fisheries Permit: QS2015/MAN340, and National Parks Permit: 18241.

We assessed if *B. cocosensis* had the capacity to acclimate to seasonal conditions by exposing them to extreme winter and summer thermal conditions that they experience at their thermal range limits. Cold treatment conditions mimicked winter (July) sea surface temperatures in (temperate) southern New South Wales (southern species range limit) and warm treatment conditions mimicked summer (January) sea surface temperatures in the (tropical) Northern Territory (northern Australian range limit) (Royal Australian Navy—Sea Surface Temperature Data Base 2017). Fish were eased into thermal exposure conditions at a rate of 5 °C/day from a starting temperature of 25 °C. Warm fish ($n = 32$) were separated into six tanks (about five fish per tank) in a controlled temperature room set at 30 °C; during the day aquarium heaters increased tank temperature to 35 °C (heating started at 6 a.m. and stopped at 6 p.m.). This daily variation in temperature mimicked changes in tide pools with solar radiation, where the upper thermal experimental temperature was around 3 °C above average summer rock-pool temperatures at Point Lookout QLD. Cold fish ($n = 33$) were separated into six tanks (about 5 fish per tank) in a controlled temperature room set at 12 °C. Timed heaters increased tank temperature to 17 °C between 6 a.m. and 6 p.m. Fish were exposed to the warm and cold thermal treatments for 6 weeks prior to testing. Both warm and cold treatment temperatures varied by 5 °C on a daily basis so that magnitude of temperature fluctuation between treatments was identical. Both warm and cold treatments were set on a 12:12 h light–dark cycle, where 6 a.m.–6 p.m. was light. Individuals were tested at random between the warm and cold treatments to account for any changes in metabolic rate based on circadian rhythm.

Fish were brought to acute testing temperatures at a rate of 3 °C/h [an appropriate rate to test the acute thermal performance of an intertidal fish (Schulte et al. 2011)]. Only one performance trait (except maximum ventilation rate which

was tested with maximum metabolic rate) was tested at one acute test temperature per day across all individuals. Test temperature and individual fish order were randomised for each performance measure.

Performance testing

Burst swimming speed was assessed at the test temperatures of 15 °C, 22 °C, 28 °C and 33 °C in a randomised order. Burst swimming responses were assessed in a 35 × 24 × 4 cm aquarium with a 20 cm measuring tape placed in the field of view for calibration. The aquarium was secured inside an arena made of plywood and a mirror angled at 45°. A Panasonic Lumix DMC-TZ40 camera recorded the image at 100 frames per second off the mirror. Burst swimming responses were elicited by gently tapping the fish's tail using a metal rod when fish were motionless on the bottom of the tank. Instantaneous swimming speed was extracted from videos using KINOVEA© [experimental version 0.8.25-x64 (<http://www.kinovea.org>)]. Only swimming responses where the fish exhibited a C-start escape response were analysed. The point between the eyes of each fish was digitised to ensure a consistent point was tracked. A minimum of three burst responses was recorded for each fish and the maximum instantaneous speed for each escape response was determined. The maximum instantaneous speeds for each fish were averaged at each test temperature and used in statistical analysis.

We quantified the maximum ventilation and metabolic rate of each individual fish at 15 °C, 22 °C, 28 °C, 33 °C, and 36 °C (and 12 °C for ventilation rate only) in a randomised order. We tested maximum ventilation rate by chasing a fish (with a hand net) for a minute to elicit a sustained escape response. Fish were then immediately placed into a transparent petri dish and filmed ventrally for 60 s using a Panasonic Lumix DMC-TZ40 camera at a rate of 100 frames per second. Ventilation rate was then determined by visually counting the number of operculum ventilations over 60 s. Immediately after ventilation rate was filmed, fish were placed in a 133 mL respirometer with a magnetic stirrer that produced a current within the respirometer for the fish to swim against (the current was turned up until fish could just maintain forward movement within the water column) to assess maximum metabolic rate. A PreSens Fibox 4 (POF-L2.5-1) with a polymer optical fiber and oxygen minisensor spots (batch ID—140117-001) was used to measure percentage air saturation (% a.s.) (one measurement/second) within the respirometer over 5 min of testing. After individual fish were tested, they were then placed in an oxygen-saturated recovery bucket where the water temperature changed at a rate of 3 °C/h to bring the fish back to their treatment conditions. Three control (no fish) water samples were taken at

each test temperature over 5 min to assess for any oxygen consumption or production within the bottle during testing. Metabolic rate (VO_2) was calculated using the following formula:

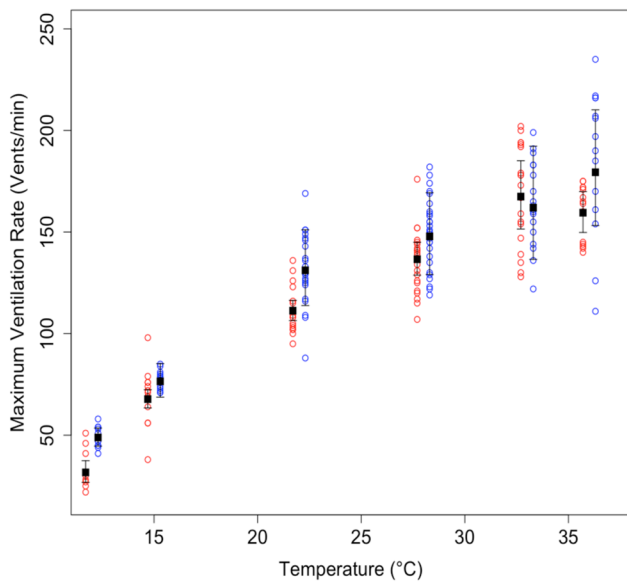
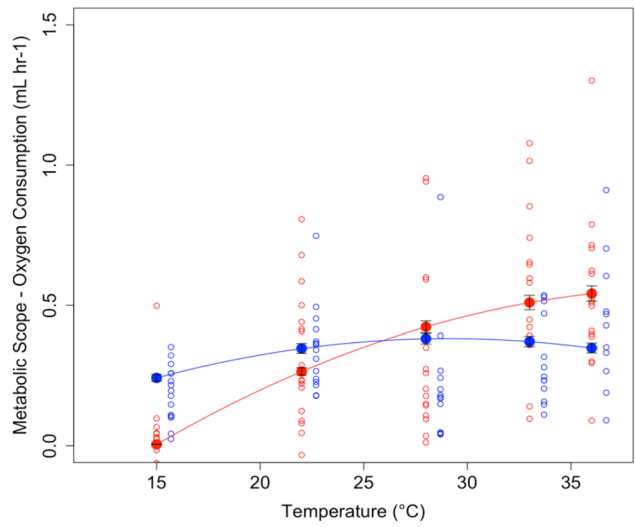
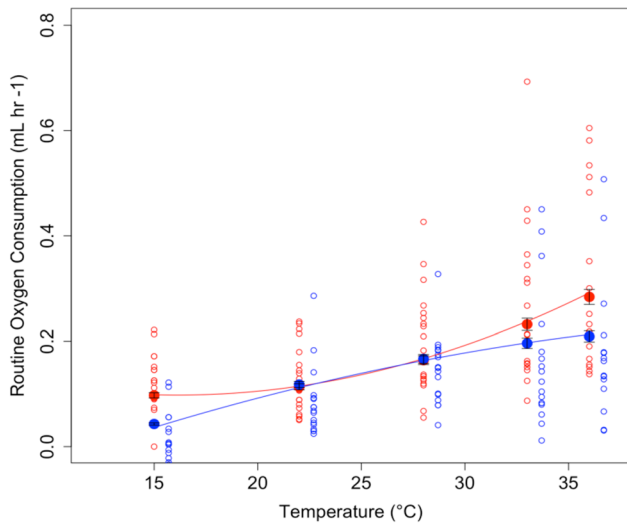
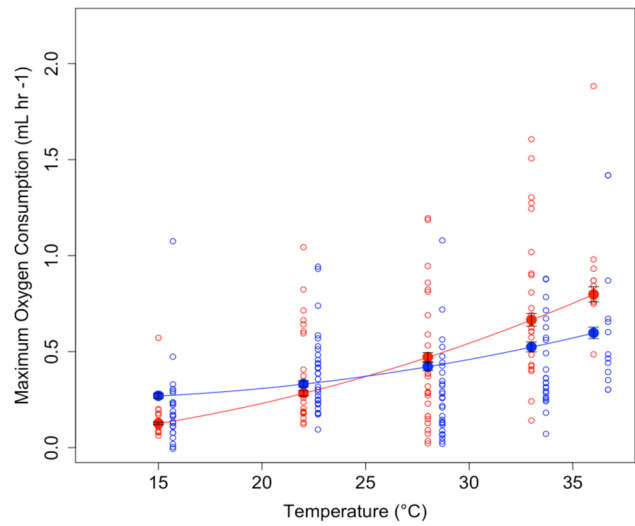
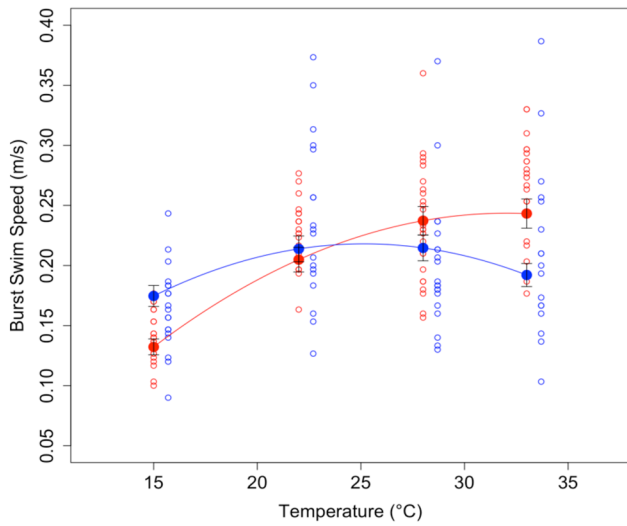
$$VO_2 = -1 \times ((m_f - m_c) \div 100) \times V \times BO_2,$$

where m_f was the slope of the percent air saturation consumed over time by *B. cocosensis* and m_c was the slope of the percent air saturation consumed over time within the control respirometer (no fish). V was the volume of water within the respirometer and BO_2 represented the oxygen solubility of seawater at 35 ppt at each test temperature.

Routine metabolic rate of each fish was assessed at 15 °C, 22 °C, 28 °C, 33 °C and 36 °C (in a randomised order) in darkened (black plastic covered) respirometers in a darkened laboratory. Fish were placed in 350 mL respirometers with open tops (covered with mesh to avoid fish escape) for 1 h within a water bath prior to testing to allow oxygenated water flow to circulate the respirometers while the fish adjusted to test conditions and allowed metabolic rates to stabilize. Respirometer chambers were then sealed and placed on the magnetic stirrer at 100 rpm to create a weak current to ensure homogeneous oxygen saturation within the respirometer. Stirrers were necessary because bottom dwelling fish-like gobies often sit still at the bottom of the respirometer and oxygen concentrations can become inconsistent throughout the respirometer. Oxygen consumption was measured every 15 min over 1 h of testing using the PreSens Fibox 4. Aerobic scope was calculated by subtracting routine metabolic rate from maximum metabolic rate for each fish at each test temperature. The standard length and mass of each fish was measured and recorded once all thermal performance tests were complete.

Statistics

We fitted linear mixed effect models using the *nlme* library (Pinheiro et al. 2018) in the R statistical package (R Core Team 2013) to assess if long-term warm or cold exposure had an effect on performance across a range of test temperatures. The acute effect of test temperature was modelled as a second-degree polynomial and set as a continuous variable (except for ventilation rate where it was set as a fixed factor due to the large amount of variance in the data set). The effect of acclimation was tested by assessing the interaction between test temperature and treatment. Fish length (burst swim speed only) or mass was set as covariates. Individual fish number was nested within tank number and these were set as random factors. Global model parameters were estimated according to Grueber et al. (2011). The library *MuMIn* (Barton and Barton 2015) was used to create a set of models from the global model using the dredge function. Akaike information criterion and the Akaike weight



Legend: Blue points illustrate cold exposed fish performance and red points display warm exposed fish performance. Small outline points indicate raw performance values for each individual at each acute test temperature.

Larger filled circles represent model mean performance values at acute test temperature. Second degree polynomial linear mixed effect model curves are displayed for warm and cool exposed fish.

Standard error bars are shown for all performance traits at each test temperature except maximum ventilation where 95% confidence intervals are shown. No curve is shown for maximum ventilation due to temperature being treated as a categorical factor instead of continuous in model.

Fig. 3 Thermal dependence of warm and cold-exposed *Bathygobius cocosensis*. **a** Thermal dependence of burst swimming speed (warm-exposed fish $n=25$, cold-exposed fish $n=20$). **b** Thermal dependence of maximum metabolic rate (warm-exposed fish $n=27$, cold-exposed fish $n=29$). **c** Thermal dependence of routine metabolic rate (warm-exposed fish $n=20$, cold-exposed fish $n=17$). **d** Thermal dependence of metabolic scope (maximum - routine metabolic rate) (warm-exposed fish $n=16$, cold-exposed fish $n=13$). **e** Thermal dependence of maximum ventilation rate (warm-exposed fish $n=23$, cold-exposed fish $n=28$). Standard error bars are shown in black for each performance trait graph

of each model were estimated to assess model fit probability. Multimodel averaging (Burnham and Anderson 2002) was used to calculate parameter averages from all models with Akaike weights above zero. Parameter values from the averaged models were used to calculate the most likely performance means for each treatment group across all test temperatures. We assessed that the effect treatment (warm or cold-exposure) had across test temperatures on performance.

Individual thermal performance curve breadths were calculated using Gilchrist (1996) formula:

$$B = \sqrt{\sum_{i=1}^N \left[\frac{P_i(T_i - T_{opt})}{P_{max}} \right]^2},$$

where N is the number of test temperatures, T_i is the temperature i , P_i is the performance at a certain test temperature, T_{opt} is the temperature at which performance is optimal, and P_{max} is the maximum performance rate. We compared average performance curve breadths between treatments for each performance measure using independent t tests.

Results

Burst swimming speed

We found that long-term exposure to cold or warm thermal environments (treatment) affected the thermal sensitivity of burst swimming speed (Fig. 3a; Tables 1, 2) (test temperature \times treatment (slope): estimate = $-0.448 \pm SE = 0.069$, $Z = 6.428$, $P < 0.001$). The shape of the warm- and cold-exposed fish thermal performance curves, however, was not altered by thermal acclimation (test temperature \times treatment (quadratic curvature): estimate = $-0.018 \pm SE = 0.073$, $Z = 0.236$, $P = 0.814$). The cold-exposed fish swam 15% faster than warm-exposed fish when tested at 15 °C on average, and warm-exposed fish swam 24% faster than cold-exposed fish when tested at 33 °C on average. Differences in burst swimming speed were not apparent at test temperatures 22 °C or 28 °C (Fig. 3a). Warm-exposed fish had thermal performance breadths of 11.63 ± 0.55 °C and the

cold-exposed fish had a mean thermal performance breadth of 12.43 ± 0.76 °C; differences in thermal performance breadth were not statistically significant ($t_{40} = -0.870$, $P = 0.389$). These results suggest that *B. cocosensis* have the capacity to acclimate burst swimming speed to extreme seasonal thermal conditions; however, the shape of their thermal performance curves is not altered by thermal acclimation.

Maximum metabolic rate

Long-term exposure to cold or warm thermal conditions affected the thermal sensitivity of maximum metabolic rate (Fig. 3b; Tables 3, 4) (test temperature \times treatment (slope): estimate = $-1.64 \pm SE = 0.429$, $Z = 3.804$, $P < 0.001$). Like burst swimming speed, the shape of the acute thermal performance curves for the warm- and cold-exposed fish was not altered by thermal acclimation (test temperature \times treatment (quadratic curvature): estimate = $-0.396 \pm SE = 0.394$, $Z = 0.997$, $P = 0.319$). At the test temperature 15 °C cold-exposed fish had average maximum metabolic rates that were 33% greater than the average maximum metabolic rate of warm-exposed fish. At the test temperatures 33 °C and 36 °C, the warm-exposed fish had average maximum metabolic rates that were 67% and 27% greater than the average cold-exposed fish maximum metabolic rates, respectively. There were no observable differences in maximum metabolic rates between warm or cold exposed fish at 22 °C or 28 °C (Fig. 3b). Cold-exposed fish had predicted (as we did not sample full performance curve) thermal performance breadths of 11.72 ± 1.65 , which was greater than the predicted thermal performance breadths of warm-exposed fish which was 6.95 ± 0.8 °C ($t_{38} = -2.6$, $P = 0.013$).

Routine metabolic rate

Long-term exposure to cold and warm thermal conditions did not affect the thermal sensitivity of routine metabolic rate (test temperature \times treatment (slope): estimate = -0.082 ± 0.133 , $Z = 0.608$, $P = 0.543$) (Fig. 3c; Tables 5, 6). Thermal acclimation did not alter the shape of the acute thermal performance curve (test temperature \times treatment (quadratic curvature): estimate = -0.338 ± 0.193 , $Z = 1.742$, $P = 0.081$). At the test temperatures 15 °C and 36 °C, the warm-exposed fish had routine metabolic rates that were 704% and 65% greater than the average cold-exposed fish routine metabolic rates, respectively. Routine metabolic rate did not differ between warm and cold-exposed fish at 22 °C, 28 °C, or 33 °C. Warm-exposed fish had predicted thermal performance breadths of 11.35 ± 1.0 °C, which was greater than the predicted breadths of cold-exposed fish which was 7.39 ± 0.53 °C ($t_{40} = 3.363$, $P = 0.002$).

Table 1 Top models of *B. cocosensis* burst swimming speed with fish length, treatment (thermal exposure) and test temperature

Terms in the model	df	LogLik	AIC _c	ΔAIC _c	w _i
1. Fish length + poly(test temperature, 2) + treatment + poly(test temperature, 2) · (treatment)	14	298.289	-565.8	0.00	0.923
2. Poly(test temperature, 2) + treatment + poly(test temperature, 2) · (treatment)	13	294.616	-560.9	4.96	0.077

All models include fish number nested within tank number as random factors. Models are ranked according to AIC_c, and only models with w_i values greater than 0 are presented

Aerobic scope

Exposure to warm or cold thermal conditions affected the thermal sensitivity of aerobic scope (Fig. 3d; Tables 7, 8) (test temperature × treatment (slope): estimate = -1.84 ± SE = 0.347, Z = 5.228, P < 0.001). Again,

thermal acclimation did not alter the shape of the acute thermal performance curve (test temperature × treatment (quadratic curvature): estimate = 0.065 ± 0.314, Z = 0.205, P = 0.837). On average, at 15 °C the cold-exposed fish had aerobic scopes that were 416% greater than the warm-exposed fish, and at 33 °C and 36 °C the warm-exposed fish had aerobic scopes that were 90% and 39% greater than the cold-exposed fish, respectively. At 28 °C, there was no difference in aerobic scope between warm and cold-exposed fish. Cold-exposed fish had predicted thermal performance breadths of 9.83 ± 1.46 °C, which was greater than the predicted breadth of warm-exposed fish (6.26 ± 0.9 °C) (t₂₅ = -2.119, P = 0.268).

Maximum ventilation rate

Exposure to warm or cold thermal conditions did not affect the thermal sensitivity of maximum ventilation rate (Fig. 3e) (Tables 9, 10). Warm and cold-exposed fish had maximum ventilation rates that were significantly different

Table 2 Averaged linear mixed effect model summary of the response of burst swimming speed to fish length, treatment and test temperature

Coefficients	Estimate ± SE	Z	P
Intercept	0.138 ± 0.036	3.837	<0.001
Fish length	0.002 ± 0.0008	2.158	0.031
Poly(test temperature, 2) 1 (slope)	0.544 ± 0.055	9.872	<0.001
Poly(test temperature, 2) 2 (quadratic curvature)	-0.176 ± 0.056	0.0568	0.0019
Treatment 2	-0.006 ± 0.017	0.290	0.772
Poly(test temperature, 2)1 · treatment (slope)	-0.448 ± 0.069	6.428	<0.001
Poly(test temperature, 2)2 · treatment (quadratic curvature)	-0.018 ± 0.073	0.236	0.814

Table 3 Top models of *B. cocosensis* maximum metabolic rate (VO₂) with fish mass, treatment (thermal exposure) and test temperature

Terms in the model	df	LogLik	AIC _c	ΔAIC _c	w _i
1. Mass + treatment + test temperature + poly(test temperature, 2) · (treatment)	15	47.167	-62.1	0.00	0.996
2. Mass + poly(test temperature, 2)	13	39.28	-50.9	11.22	0.004
3. Mass + treatment + poly(test temperature, 2)	12	36.69	-47.9	14.15	0.001

All models include fish number nested within tank number as random factors. Models are ranked according to AIC_c, and only models with w_i values greater than 0 are presented

Table 4 Averaged linear mixed effect model summary of the response of maximum metabolic rate (VO₂) to fish mass, treatment and test temperature

Coefficients	Estimate ± SE	Z	P
Intercept	0.168 ± 0.030	5.524	<0.001
Mass	0.316 ± 0.026	11.686	<0.001
Treatment 2	-0.026 ± 0.027	0.974	0.330
Poly(test temperature, 2)1 (slope)	2.75 ± 0.320	8.512	<0.001
Poly(test temperature, 2)2 (quadratic curvature)	0.572 ± 0.299	1.961	0.049
Treatment · poly(test temperature, 2)1 (slope)	-1.64 ± 0.429	3.804	<0.001
Treatment · poly(test temperature, 2)2 (quadratic curvature)	-0.396 ± 0.394	0.997	0.319

Table 5 Top models of *B. cocosensis* routine metabolic rate (VO_2) with fish mass, treatment (thermal exposure) and test temperature

Terms in the model	df	LogLik	AIC _c	ΔAIC _c	w _i
1. Mass + treatment + temperature + poly(test temperature, 2) · treatment	10	216.602	−411.9	0.00	0.846
2. Mass + treatment + poly(test temperature, 2)	8	212.218	−407.6	4.29	0.099
3. Mass + poly(test temperature, 2)	7	210.537	−406.4	5.46	0.055

All models include fish number nested within tank number as random factors. Models are ranked according to AIC_c and only models with w_i values greater than 0 are presented

Table 6 Averaged linear mixed effect model summary of the response of routine metabolic rate (VO_2) to fish mass, treatment and test temperature

Coefficients	Estimate ± SE	Z	P
Intercept	0.056 ± 0.016	3.542	0.0004
Mass	0.125 ± 0.0104	11.919	<0.001
Treatment 2	−0.029 ± 0.015	1.697	0.089
Poly(test temperature, 2)1 (slope)	0.87 ± 0.093	9.226	<0.001
Poly(test temperature, 2)2 (quadratic curvature)	−0.252 ± 0.114	2.19	0.028
Treatment · poly(test temperature, 2)1 (slope)	−0.082 ± 0.133	0.608	0.543
Treatment · poly(test temperature, 2)2 (quadratic curvature)	−0.338 ± 0.193	1.742	0.081

Table 7 Top model of *B. cocosensis* metabolic scope (VO_2) with fish mass, treatment (thermal exposure) and test temperature

Terms in the model	df	LogLik	AIC _c	ΔAIC _c	w _i
1. Mass + treatment + poly(test temperature, 2) + poly(test temperature, 2) · (treatment)	14	52.339	−73.4	0.00	1

All models include fish number nested within tank number as random factors. Models are ranked according to AIC_c, and only models with w_i values greater than 0 are presented

Table 8 Linear mixed effect model summary of the response of metabolic scope (VO_2) to fish mass, treatment and test temperature

Coefficients	Estimate ± SE	Z	P
Intercept	0.162 ± 0.037	4.33	<0.001
Mass	0.186 ± 0.022	8.346	<0.001
Treatment 2	−0.006 ± 0.039	0.145	0.885
Poly(test temperature, 2)1 (slope)	2.28 ± 0.237	9.523	<0.001
Poly(test temperature, 2)2 (quadratic curvature)	−0.45 ± 0.215	2.07	0.0385
Treatment · poly(test temperature, 2)1 (slope)	−1.84 ± 0.347	5.228	<0.001
Treatment · poly(test temperature, 2)2 (quadratic curvature)	0.065 ± 0.314	0.205	0.837

from each other at 12 °C ($F_{1,6} = 8.105$, $P = 0.0293$), 22 °C ($F_{1,9} = 8.44$, $P = 0.0174$), 28 °C ($F_{1,8} = 8.824$, $P = 0.0179$) and 36 °C ($F_{1,9} = 5.3703$, $P = 0.0457$); however, there was no effect on the thermal sensitivity of performance as both warm- and cold-exposed fish ventilations rates increased linearly at similar rates as temperature increased. There was no difference in maximum ventilation rate between warm and cold-exposed fish at 15 °C ($F_{1,5} = 3.507$, $P = 0.12$) and 33 °C ($F_{1,6} = 0.3476$, $P = 0.577$). There was no difference in the predicted thermal performance breadth

for maximum ventilation rate between warm-exposed fish (10.62 ± 0.5 °C) and cold-exposed fish (11.49 ± 0.56 °C) ($t_{27} = -1.132$, $P = 0.268$).

Discussion

Theory predicts that acclimation should not occur when daily thermal fluctuations are large or unpredictable and when animals have wide thermal performance curves

Table 9 Top models of *B. cocosensis* maximum ventilation rate (vents/min) with fish mass, treatment (thermal exposure) and test temperature

Terms in the model	df	LogLik	AIC _c	ΔAIC _c	w _i
1. Mass + test temperature + treatment + poly(test temperature, 2) · treatment	8	22	−206.7	0	0.743
2. Test temperature + treatment + poly(test temperature, 2) · treatment	7	21	−204.6	2.13	0.257

All models include fish number nested within tank number as random factors. Models are ranked according to AIC_c, and only models with w_i values greater than 0 are presented

Table 10 Averaged linear mixed effect model summary of the response of metabolic scope (VO₂) to fish mass, treatment and test temperature

Coefficients	Estimate ± SE	Z	P
Intercept	3.485 ± 3.486	36.913	<0.001
Mass	−0.046 ± 0.017	2.640	0.008
Test temperature 15 °C	0.763 ± 0.010	7.513	<0.001
Test temperature 22 °C	1.257 ± 0.095	13.06	<0.001
Test temperature 28 °C	1.462 ± 0.092	15.801	<0.001
Test temperature 33 °C	1.667 ± 0.094	17.564	<0.001
Test temperature 36 °C	1.616 ± 0.103	15.575	<0.001
Treatment	0.437 ± 0.096	3.962	<0.001
Test temperature 15 °C · treatment	−0.314 ± 0.110	2.827	0.005
Test temperature 22 °C · treatment	−0.269 ± 0.103	2.585	0.0097
Test temperature 28 °C · treatment	−0.354 ± 0.099	3.549	<0.001
Test temperature 33 °C · treatment	−0.469 ± 0.105	4.427	<0.001
Test temperature 36 °C · treatment	−0.314 ± 0.116	2.685	0.00758

(Tomanek and Somero 1999; Wilson and Franklin 2000; Gabriel 2005; Gabriel et al. 2005). Wide thermal performance curves, however, are likely to evolve when short-term thermal variability is large (Lynch and Gabriel 1987; Gabriel 2005; Wilson and Franklin 2000). Therefore, if long-term thermal variability remains predictable and short-term thermal fluctuations remain large, thermal performance curve shape should not be altered with thermal acclimation to seasonal change (see Healy and Schulte 2012). Thus, we predicted that *B. cocosensis* would possess the ability to thermally acclimate with seasonal change, despite inhabiting the thermally variable intertidal

zone, and would have wide thermal breadths that would not be altered by thermal acclimation.

We found that *B. cocosensis* had the capacity to acclimate burst swimming speed, maximum metabolic rate and aerobic scope to seasonal thermal conditions and had wide thermal performance breadths for all performance traits, supporting our hypotheses. In addition, thermal acclimation did not alter the shape of thermal performance curves for any performance traits. These findings support the idea that animals are likely to evolve the capacity to acclimate when long-term (seasonal) variation is large but predictable, and maintain wide thermal breadths when short-term (daily) variation exists. Similar patterns have been observed in temperate intertidal fish such as killifish and sculpins, where they have the capacity to acclimate and possess wide thermal performance curves in variable daily and seasonal thermal conditions (Johnson and Bennett 1995; Temple and Johnston 1998; Fanguie et al. 2006, 2008, 2011; Healy and Schulte 2012). Here, we discuss that the capacity *B. cocosensis* has to acclimate despite living in a rapidly fluctuating subtropical environment, and how thermal acclimation had little effect on altering the shape of thermal performance curves.

Bathygobius cocosensis possessed the ability to acclimate their burst swimming response to cold and warm thermal environments and had thermal breadths over a range of 11 °C (exceeding the magnitude of average daily thermal variation they experience in nature). Maintenance of burst swimming speed with changing temperature is important for survival, as slower escape speeds can decrease the probability of escape from predators (Husak 2006a, b; Walker et al. 2005). Maintenance of broad thermal performance curves across acclimation treatments indicates that when organisms from variable thermal environments acclimate, their thermal optima and breadth may shift with temperature along the x-axis of the thermal performance curve, but the curve itself is likely to retain its shape (also observed by Healy and Schulte (2012) in killifish aerobic scope). Again, these results are similar to those on other intertidal fish such as killifish and sculpins (Johnson and Bennett 1995; Temple and Johnston 1998), where they have the capacity to acclimate burst swimming speed and have relatively wide thermal performance curves. Our results support the idea that in *B. cocosensis* acclimation will occur even if both daily and seasonal thermal variations are large.

Bathygobius cocosensis also possessed the capacity to acclimate maximum metabolic rate to seasonal thermal conditions, where thermal performance curve shape remained wide and was not affected by seasonal acclimation. Acclimation of maximum metabolic rate allows physiological traits that are oxygen demanding (like sustained swimming and aerobic and anaerobic recovery) to be maintained under variable thermal conditions (Brett 1964). Although we found an acclimation response for maximum metabolic rate, routine

metabolic rate did not show complete acclimation; the warm-exposed fish had higher metabolic rates on average than the cold-exposed fish at both warm and cold test temperatures. Aerobic scope, however, showed a similar acclimation response to maximum metabolic rate; this was not surprising because routine metabolic rate values were proportionally small compared to maximum metabolic rate values across all test temperatures. Like burst swimming speed and maximum metabolic rate, acclimation of aerobic scope also did not affect the shape of the thermal performance curve, similarly to intertidal temperate killifish (Healy and Schulte 2012). The large aerobic scope observed shows that *B. cocosensis* have a large capacity to raise their metabolic rate for ecologically important activities (such as growth, maintaining body condition, escaping from predators and catching prey) aiding survival and reproduction. In addition, low aerobic scope at species thermal limits are known to constrict their geographical ranges (Wang and Overgaard 2007; Farrell 2009); hence, the maintenance of high aerobic scope across wide thermal breadths may facilitate the large geographic distribution observed in *B. cocosensis*. In contrast, we found no evidence of seasonal acclimation for maximum ventilation rate. Potentially maximum metabolic rate and ventilation rate are not linked as tightly as one would expect with acclimation in *B. cocosensis*.

It was interesting that *B. cocosensis* had the capacity to acclimate to seasonal thermal conditions at the maximum and minimum of their thermal range (northern Northern Territory and southern New South Wales), which are likely to be outside of the usual thermal conditions that the Point Lookout population experiences in nature. As their thermal performance breadths were wide enough to encompass most of the seasonal thermal variation they experience in the subtropics, and curve shape did not change with long-term extreme thermal exposure; perhaps the Point Lookout population does not require acclimation to function and survive at Point Lookout. They may have retained their capacity to acclimate to seasonal species thermal range extremes as an ancestral artefact, or perhaps it is a survival strategy for organisms with pelagic larval dispersal stages. *B. cocosensis* have a pelagic planktonic larval phase and have the potential to travel great distances from where they were hatched (Thia et al. 2018; da Silva et al. *in review*). Potentially organisms with dispersing larval phases are likely to maintain high levels of plasticity as their settlement location and, therefore, their juvenile and adult life stage thermal environment is unpredictable prior to settlement. The capacity to acclimate has also been observed in *B. fuscus*, a close relative of *B. cocosensis* in the tropical location of Sulawesi Indonesia, which would likely experience less daily and seasonal thermal variability than subtropical *B. cocosensis* populations (Eme and Bennett 2009). The ability *B. fuscus* had to acclimate was both surprising and intuitive, as small

tropical species often have a limited capacity to acclimate (Rohr et al. 2018), but *B. fuscus* inhabit the tidal flat region which experiences thermal variability despite being close to the equator. In addition, *B. fuscus* have species ranges that extend into the subtropics and have a planktonic pelagic larval phase. It would be interesting to compare the acclimation capacity between organisms with larval dispersal phases and organisms with limited dispersal in future studies.

The existing controversy on how thermal variability affects the co-evolution of thermal performance breadth and acclimation capacity has led us to ponder if thermal acclimation alters thermal performance curve shape; if thermal performance curve shape alters capacity to acclimate; or if once plasticity evolves it is retained (despite thermal performance curve shape). Our findings show that acclimation did not affect shape of thermal performance curve across many performance traits in a subtropical intertidal fish. Indeed, other studies have also shown evidence for thermal acclimation having little or no effect on altering the shape of thermal performance curves (i.e. Deere and Chown 2006; Healy and Schulte 2012; Pereira et al. 2017). In addition, further studies have assessed if degree of thermal variability or stochasticity alters the shape of thermal performance curves in aquatic vertebrates or terrestrial isopods; however, thermal performance curve shape was not altered by increased thermal variability or stochasticity (Niehaus et al. 2011; Schuler et al. 2011). Perhaps thermal performance curve breadth determines the degree at which thermal optima can be shifted with thermal acclimation, rather than thermal acclimation shaping the acute thermal performance curve. Or maybe once thermal acclimation evolves (despite performance breadth), it is maintained (as an environmental change insurance policy) over many generations even if it is not required in a stable environment (see Brown and Feldmeth 1971). Sinclair et al. (2006) suggest an interesting alternative perspective that organisms in highly variable thermal environments are unlikely to favour a particular strategy of wide or narrow thermal breadths depending on thermal variability, but are more likely to evolve increased plasticity to allow efficient physiological responses to changes in environmental temperature.

The ability *B. cocosensis* has to acclimate may buffer them from increased temperatures associated with climate change and some studies suggest that plasticity is already protecting some species from climate warming (Rohr et al. 2018; Riddell et al. 2018). Extreme heat events, however, are predicted to result in local population extinctions (Helmuth et al. 2006), as rate of thermal change is likely to be faster than rates of physiological change/acclimation (Peck et al. 2009). A meta-analysis that investigated the correlation between plasticity of upper thermal limits and latitude in terrestrial, aquatic and marine species, however, suggests that plasticity is unlikely to protect species from climate

change as thermal plasticity in upper thermal limits is not correlated with latitude or seasonal variation across taxa (Gunderson and Stillman 2015). While upper thermal limits are important, many of the effects of climate change will occur through reductions in performance at sub-critical temperatures (Kingsolver et al. 2015). Interactions between acclimation capacity and thermal performance breadth will also be important in animal responses to climate change. For example, species that experience great thermal variation may not consistently have great acclimation capacities, but they might have wide thermal performance breadths (Wilson and Franklin 2000; Deere and Chown 2006) and, thus, may be buffered from climate warming through wide breadths rather than capacity to acclimate. Future climate change scenarios predict environments to become more thermally variable and stochastic (IPCC 2014; Vasseur et al. 2014), but predictions of species responses remain limited due to under sampling of physiological capabilities across taxa (Seebacher et al. 2015). The lack of understanding regarding the relationships between climatic variability and performance breadth and acclimation capacity will prove problematic when attempting to predict how different species and populations will respond with climatic change. Gaining a more comprehensive understanding of the interactions between fine-scale environmental variation, thermal breadths and acclimation capacities will help improve predictability of species responses to climate change. In addition, this knowledge will aid conservation biologists to determine which animals are likely to acclimate or adapt in a changing environment and which species should be the focus of conservation effort. Future studies should empirically test and model how the magnitude of thermal variability and predictability directly affects the co-evolution of thermal breadth, acclimation capacity, and fitness in changing environments through time.

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Compliance with ethical standards

Conflict of interest The authors declare that there were no competing interests in this manuscript.

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