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Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures

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Abstract

Equatorial populations of marine species are predicted to be most impacted by global warming because they could be adapted to a narrow range of temperatures in their local environment. We investigated the thermal range at which aerobic metabolic performance is optimum in equatorial populations of coral reef fish in northern Papua New Guinea. Four species of damselfishes and two species of cardinal fishes were held for 14 days at 29, 31, 33, and 34 °C, which incorporated their existing thermal range (29–31 °C) as well as projected increases in ocean surface temperatures of up to 3 °C by the end of this century. Resting and maximum oxygen consumption rates were measured for each species at each temperature and used to calculate the thermal reaction norm of aerobic scope. Our results indicate that one of the six species, *Chromis atripectoralis*, is already living above its thermal optimum of 29 °C. The other five species appeared to be living close to their thermal optima (ca. 31 °C). Aerobic scope was significantly reduced in all species, and approached zero for two species at 3 °C above current-day temperatures. One species was unable to survive even short-term exposure to 34 °C. Our results indicate that low-latitude reef fish populations are living close to their thermal optima and may be more sensitive to ocean warming than higher-latitude populations. Even relatively small temperature increases (2–3 °C) could result in population declines and potentially redistribution of equatorial species to higher latitudes if adaptation cannot keep pace.

Keywords: Apagonidae, coral reef fish, global warming, latitudinal gradient, oxygen consumption, Pomacentridae

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Introduction

Species living at extreme latitudes (equator and poles) may be particularly sensitive to global warming because they evolved in a relatively stable thermal environment and are expected to exhibit narrow thermal tolerance ranges (Tewksbury *et al*., 2008). The thermal range for optimum aerobic performance (thermal optima; T_{opt}) in such species may only span a few degrees, whereas temperate species need to perform over a much wider range of temperatures(Deutsch *et al*., 2008; Somero, 2010; Nguyen *et al*., 2011; Sunday *et al*., 2011). Furthermore, theory suggests that populations living at thermally stable latitudes (e.g., near the equator or poles) have less capacity for thermal acclimatization (i.e. physiological, anatomical, or biochemical modifications that occur within a lifetime to cope with natural changes in temperature) than populations living in more thermally variable, high-latitude locations (Pörtner, 2002; Stillman, 2003; Somero, 2010; Neuheimer *et al*., 2011; Nguyen *et al*., 2011). This latitudinal pattern is predicted because the physiological costs to acclimatize to a wide temperature range may outweigh any potential benefits if those temperatures are rarely experienced (Angilletta, 2009). Moreover, there may be no selection pressure to tolerate temperatures outside of what the populations are regularly experiencing. Equatorial populations of marine species are predicted to be especially sensitive to rising temperature because they experience an even narrower temperature range than equatorial populations of terrestrial species (due to the large heat storage capacity of water). In addition, their geographical ranges more closely conform to organismal thermal tolerance limits than the geographical ranges of terrestrial species, especially near equatorial boundaries (Sunday *et al*., 2011, 2012). Consequently, the 2–3 °C warming of tropical oceans

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projected to occur by the end of this century due to climate change (IPCC, 2007; Poloczanska *et al.*, 2007; Ganachaud *et al.*, 2011) could have serious impacts on equatorial populations of many marine organisms.

Coral reef ecosystems are already facing a biodiversity crisis that is exacerbated by global climate change (Hughes *et al.*, 2003; Bellwood *et al.*, 2004). For coral reef fishes, rising ocean temperatures may not be immediately lethal (Mora & Ospína, 2001), but could have significant impacts on individual performance that will ultimately affect population demography and biogeographic distributions (Munday *et al.*, 2008b; Nilsson *et al.*, 2009). For example, an increase in average temperature of 2–3 °C significantly compromises growth and reproduction of some species (Munday *et al.*, 2008a; Donelson *et al.*, 2010; Pankhurst & Munday, 2011; Rushworth *et al.*, 2011; Zarco-Perelló *et al.*, 2012). The mechanistic explanation for the effects on individual performance may be related to how temperature influences O_2 uptake, transport, and delivery, also known as oxygen- and capacity-limited thermal tolerance (OCLTT) (Pörtner, 2001; Pörtner & Knust, 2007; Pörtner & Farrell, 2008; Eliason *et al.*, 2011). The physiological scope for aerobic performance (aerobic scope), calculated as the difference in O_2 consumption between resting and maximal performance (Fry & Hart, 1948; Priede, 1977), represents the oxygen available – in excess of that required for basic maintenance of the organism – for activities essential to support biological fitness (e.g., activity, feeding, and reproduction). In principle, a species may perform optimally at a particular temperature (T_{opt}); above or below T_{opt}, the aerobic scope narrows and therefore performance falls (Pörtner & Farrell, 2008). The temperature range of optimal performance spans T_{opt} and is delimited by upper and lower pejus temperatures (Frederich & Pörtner, 2000).The pattern has been demonstrated for several temperate species, such as Atlantic cod, Sockeye salmon, pink salmon, and banded morwong (Sylvestre *et al.*, 2007; Farrell *et al.*, 2008; Clark *et al.*, 2011; Eliason *et al.*, 2011; Neuheimer *et al.*, 2011) and for an increasing number of tropical species. For example, aerobic scope may be reduced by as much as 65% in tropical reef fishes acclimated to temperatures only 2 °C above their T_{opt} (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010; Johansen & Jones, 2011). Temperature-induced reductions in aerobic scope have ecological consequences because less energy is available for vital life history processes that shape population dynamics and community structure (Pörtner & Peck, 2010).

While experimental studies show that reef fish populations can be sensitive to small increases in water temperature (Nilsson *et al.*, 2009; Johansen & Jones, 2011), many species also have large geographical ranges that span temperature ranges that are greater than the projected increase in ocean temperature due to global warming (Munday *et al.*, 2008b). This suggests that populations are acclimatized or adapted to their local thermal environment along a latitudinal gradient. Adaptation to the very narrow equatorial temperature range may cause equatorial populations of reef fishes to be far more sensitive to global warming than populations of the same species from higher latitudes. The aim of this study was twofold: (i) to determine if the temperature increases projected for the end of the century due to global warming have significant effects on the aerobic performance of equatorial reef fish populations and (ii) to determine whether their optimal temperature range for performance differs from that of higher latitude populations, suggesting local adaptation to higher average and maximum summer temperatures. Many reef fish species are numerically abundant across wide latitudes (Randall *et al.*, 1997), and so we chose populations that may be experiencing the highest and narrowest range of environmental temperatures when compared with higher latitude counterparts. We also chose species for which data were already available from higher latitude populations (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010; Johansen & Jones, 2011). Specifically, we selected four widely distributed species of damselfishes (family Pomacentridae), an abundant and diverse guild of coral reef fishes (Allen, 1991), and two species of cardinal fishes (family Apogonidae) that have been found to exhibit marked temperature sensitivity in previous studies (Gardiner *et al.*, 2010). Species were also chosen based on their similar habitat preferences, all being strongly coral associated. The damselfishes are all planktivorous, whereas the cardinal fishes are nocturnal predators, feeding on small invertebrates. Despite dietary differences, we expected all species to exhibit similar metabolic requirements, given that they all utilize the median paired fin locomotory mode – predominantly using their pectoral fins for swimming and manoeuvring on the reef (Fulton, 2007). We predicted that: (i) the thermal range where aerobic scope is optimum would be closely associated with the temperature range equatorial populations presently experience (28–31 °C); (ii) aerobic scope would decline sharply at elevated temperatures consistent with global warming scenarios (2–3 °C above present day); and (iii) the optimal thermal range of each species would be narrower for equatorial populations compared with populations of the same species, or sister species, from higher latitudes.

Materials and methods

Study site and species

This study was conducted at Nago Island, New Ireland Province, Papua New Guinea (2°35.765′S; 150°46.193′E; PNG). Nago Island is the closest near-equatorial location that is both readily accessible and at approximately the same longitude to previous studies on the thermal sensitivity of reef fishes conducted on the Great Barrier Reef (GBR) (Nilsson *et al*., 2009; Gardiner *et al*., 2010), thereby enabling comparisons with studies conducted at higher latitudes. Four damselfish species (mean mass ± SD; mean standard length ± SD), *Dascyllus melanurus* (3.02 ± 0.87 g; 39.5 ± 3.8 mm), *Chromis atripectoralis* (2.62 ± 0.65 g; 43.7 ± 5.1 mm), *Pomacentrus moluccensis* (2.94 ± 0.97 g; 40.4 ± 3.8 mm), and *Acanthochromis polyacanthus* (4.43 ± 1.31 g; 47.8 ± 5.5 mm) were selected to compare with previously investigated species (Nilsson *et al*., 2009; Gardiner *et al*., 2010). The exception was *D. melanurus*, which has a distribution centered at the equator and might be expected to have higher thermal optima than its congener from higher latitudes (*D. aruanus*) investigated in previous studies. Two cardinal fish species (mean mass ± SD; mean standard length ± SD), *Zoramia leptacantha* (1.02 ± 0.16 g; standard lengths unavailable) and *Cheilodipterus quinquelineatus* (3.31 ± 0.83 g; 54.4 ± 5.1 mm) were also selected, the former specifically for its equatorial distribution and the latter as a more broadly distributed species (Randall, 2005).

Fish were collected from shallow reefs near Nago Island using a barrier net or hand nets and clove oil anaesthetic (Munday & Wilson, 1997). Fish were maintained at the National Fisheries Authority's Nago Island Mariculture and Research Facility in aquaria supplied with flow-through seawater at ambient summer temperatures (30 °C) for 3–4 days. When normal feeding behavior had resumed, fish were separated into four temperature treatment groups. Fish were fed to satiation twice daily with aquaculture pellets (damselfishes) (NRD pellets, INVE Aquaculture, Salt Lake City, UT, USA) or hatched *Artemia* spp. (cardinal fishes). Food was withheld 24 h prior to experimentation to ensure a postabsorptive state (Niimi & Beamish, 1974), a time we determined sufficient for damselfish and cardinal fish of this size (J. L. Rummer, unpublished data). Furthermore, holding tanks were maintained free from algae to ensure feeding only occurred during prescribed times (e.g., grazing on tank algae could not substantially contribute to metabolic demand). All animal care and experimental protocols complied with James Cook University ethics regulations (permit: A1722).

In August of 2011, a submersible temperature logger (Odyssey™ Dataflow Systems PTY Limited, Christchurch, New Zealand) was deployed (2°39.904′S; 150°44.006′E) at a depth of 1 m near the areas where fish were collected for this study and set to record water temperatures every 30 min until the logger was retrieved in March 2012. This timeframe spans the coolest and warmest seasonal temperatures in the region. Data from that temperature logger were used to estimate the maximum, minimum, and average temperatures these particular populations experience in their natural habitat.

Temperature treatments

Four temperature treatments were selected (29, 31, 33, and 34 °C) that represented the range of summer ocean temperatures experienced at the study location (ca. 29–31 °C) and a possible 2–3 °C increase in temperature due to global change (33 and 34 °C). Six aquaria were assigned to each temperature treatment and 10–12 fish per species were distributed evenly among aquaria. Aquaria were supplied with a constant flow of seawater, aerated by means of an electric air pump, and heated using 300-watt submersible heaters (EHEIM GmbH & Co. KG, Deizisau, Germany). Because ambient outside air temperature was on average 30 °C, additional aquaria were set up in an air-conditioned room (adjusting lights for a 12 : 12 photoperiod) to maintain water temperatures at the lowest temperature treatment (29 °C). All other aquaria were maintained under shelter outside the laboratory. Temperature in treatment aquaria was increased or decreased at a rate of 0.5 °C per day until the desired temperature was reached. Fish were then maintained at treatment temperatures for 12–14 days prior to experimentation, which is thought to be sufficient time for metabolic acclimation to warmer temperatures (Barrionuevo & Fernandes, 1998; Nilsson *et al*., 2010). Temperatures in each aquarium were measured four times daily and maintained within ±0.2 °C of the desired temperature. All fish survived and continued feeding at all temperatures investigated (29, 31, 33, and 34 °C) with the exception of *A. polyacanthus*. After 2 days at 34 °C, *A. polyacanthus* individuals stopped eating, and we recorded 100% mortality within 7 days. All other species continued eating throughout the 34 °C exposure period, although we observed feeding to noticeably decrease at 34 °C when compared with the lower holding temperatures.

Resting and maximum oxygen consumption

The use of resting respirometry chambers has been found to provide a reliable estimate of standard or resting metabolic rates (Clark *et al*., 2013; Roche *et al*., 2013). Therefore, intermittent-flow respirometry was used to determine resting O_2 consumption rates ($\dot{M}O_{2\mathrm{Rest}}$) for eight individuals of each species at their respective temperature treatments. Respirometry was only performed during daylight hours (on average three trials per day), and species and temperature treatments were randomized. Fish were placed individually into 285-ml darkened respirometry chambers submerged in a temperature-controlled aquarium at the same temperature as their experimental treatments and allowed 90 min to habituate to the chamber. In preliminary experiments, we could see (but the fish could not see us or their neighbors) that these small, warm water fishes calmed inside the covered resting chambers very quickly, and that 90 min was ample time to ensure O_2 consumption rates had reached the lowest possible values, beyond which O_2 consumption rates did not significantly vary. After 90 min, the O_2 consumption rates no longer deviated or continued to decrease for at least 8 h (Data S1; Fig. S1). Submersible pumps supplied a constant water flow

(150 l h^{-1}) from the aquaria into and through the chambers while a peristaltic pump (MINIPULS® 3; Gilson, Inc., Middleton, WI, USA) maintained flow within each chamber (maximum, 5340 ml h^{-1}). Then, water flow into each chamber was stopped for 15 min every 30 min over a period of at least 90 min. The time the water flow was interrupted was short enough to ensure O_2 did not fall below 80% saturation (see best practices in Clark *et al.*, 2013). Temperature-compensated O_2 concentration (mg l^{-1}) vs. time (s) of the water within each chamber was continuously recorded (1 s^{-1}) using oxygen-sensitive REDFLASH dye on contactless spots (2 mm) adhered to the inside of each chamber and linked to a Firesting Optical Oxygen Meter (Pyro Science e. K., Aachen, Germany) via fiber-optic cables. Data were analyzed using Lab Chart version 6.1.3, (AD Instruments, Colorado Springs, CO, USA). The first and last minute of each slope were excluded from analysis to maintain consistency. Then, $\dot{M}O_{2\text{Rest}}$ (mg kg^{-1} h^{-1}) was calculated from the average of the last three slopes of O_2 consumed per second ($R^2 \geq 0.90$), minus the background O_2 consumption. Background O_2 consumption was determined for each chamber at the start of each trial prior to introducing a fish into a chamber, and again at the end of each trial after removing the fish. Initial background O_2 consumption as well as a proportion of the additional background O_2 consumption that had (assumed linearly) accumulated during the trial was subtracted from each slope. Whenever background O_2 consumption rates exceeded 5% of the $\dot{M}O_{2\text{Rest}}$ of the fish, we rinsed the chambers with a 10% bleach solution and then soaked them in clean water. Temperature quotients (Q_{10}) were calculated using mean $\dot{M}O_{2\text{Rest}}$ values (R_1 and R_2) for each species at low (T_1 = 29 °C) and high (T_2 = 34 °C) temperature using the following equation: $Q_{10} = (R_2/R_1)^{(10/(T_2 - T_1))}$.

Following $\dot{M}O_{2\text{Rest}}$ fish were held in individual mesh baskets for up to 1 h prior to determining maximum O_2 consumption rates ($\dot{M}O_{2\text{Max}}$). Fish were then placed individually into a 770-ml sealed cylinder submerged in a temperature-controlled aquarium at the same temperature as their experimental treatment. A water current within the cylinder was created using a magnetic stirring bar and plate (below the cylinder), and the water speed was increased over a period of ca. 1 min. to the maximum speed at which the fish could sustain a steady position (defined as maximum sustained swimming speed; see (Nilsson *et al.*, 2007) for further details). If the fish could no longer hold position in the chamber, the speed was decreased slightly until steady swimming resumed. The decrease in O_2 concentration in the cylinder was monitored with an oxygen probe (WTW OXI 340i, WTW Wissenschaftlich-Technische Werkstätten GmbH, Weilheim, Germany) while the fish was swimming for a period of 6 min., which was enough time to obtain a maximum rate of O_2 consumption but short enough such that the water O_2 in the chamber did not fall below 80% saturation. The $\dot{M}O_{2\text{Max}}$ was calculated as the decrease in oxygen concentration over that period of time when the fish was swimming maximally, but otherwise as described above for $\dot{M}O_{2\text{Rest}}$. Absolute ($\dot{M}O_{2\text{Max}} - \dot{M}O_{2\text{Rest}}$) aerobic scope was calculated for each fish.

Latitudinal temperature variations and aerobic scope comparisons

Historical temperature data were obtained from the Integrated Global Ocean Services System (IGOSS) satellite sea surface temperatures taken in 1° latitude/longitude grids near Kavieng (2.5°S; 150.5°E) monthly from November 1982 until April 2012. Temperature data were also compiled from near two other research stations within approximately the same longitude for a total latitudinal range of ca. 2321 km (courtesy of J. Lough, Australian Institute of Marine Science). Specifically, Lizard Island (14.5°S; 145.5°E) and Heron Island (23.5°S; 152°E) GBR, Australia, were chosen because data exist for aerobic scope T_{opt} for several of the same fish species examined in the current study (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010). The summer maximum, average, and minimum as well as the annual average and winter minimum sea surface temperatures were plotted for each location for comparison.

Local temperatures and the thermal range where aerobic scope was greatest were compiled for five species of damsel-fishes represented by three populations. In addition to the present results from PNG, data for *C. atripectoralis*, *P. moluccensis*, and *A. polyacanthus* were also investigated at Lizard Island (experimental temperatures ranging 29–33 °C) and Heron Island (27–33 °C) during two previous studies (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010). However, *D. melanurus* was only investigated at the equatorial site (PNG). The sister species, *D. aruanus*, was investigated at Lizard (29–33 °C) and Heron (27–32 °C) Islands and was therefore used for those locations. Data from the two previous studies (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010) were collected in an almost identical manner as in this study with the exception of respirometry chamber size. Raw data for $\dot{M}O_{2\text{Rest}}$ and $\dot{M}O_{2\text{Max}}$ from both of these previous studies in addition to further data collected to increase sample sizes and add temperature groups (N. Gardiner, unpublished data) were used to compare with data collected in the current study (Fig. S2). To do this, all aerobic scope values were recalculated and ranked from highest to lowest within each species from each location. In addition to the 32 measurements for each species (24 for *A. polyacanthas*) we derived from the present study, we used 40, 34, 34, and 16 measurements from Heron Island data and 38, 33, 31, and 32 measurements from Lizard Island data for *P. moluccensis*, *A. polyacanthus*, *C. atripectoralis*, and *D. aruanus* respectively. The top 25% of those values were selected and the corresponding acclimation temperatures at which those fish performed were reported as mean ± SD. This represented the temperature range for optimal aerobic performance for each species at each location. Optimal performance range data were superimposed onto the historical temperature data for each location. The data from the past experiments (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010) are directly comparable to the findings of the present study as nearly the same experimental protocol and comparable equipment were used to assess the different fish populations representing different latitudes and climatologies.

Statistical analyses

Data are presented as mean ± SEM or SD as specified. One-way ANOVAs and Holm–Sidak post-hoc tests (as necessary) were used to compare aerobic scope between treatment temperatures for each species post-exercise. For the latitudinal comparison between species and locations, a one-way ANOVA was used to compare the mean of the optimal performance temperature range and Brown-Forsythe and Bartlett's tests used to compare SD. Statistical analyses were conducted using SigmaPlot for Windows 11.0.0.77 (Systat Software, Inc., Chicago, IL, USA) and Prism 6 (GraphPad Software, Inc., La Jolla, CA, USA).

Results

Resting and maximum oxygen consumption

Of the six coral reef fish species investigated, three exhibited a significant increase in $\dot{M}O_{2\mathrm{Rest}}$ between 33 and 34 °C (Fig. 1). In one species, *C. atripectoralis*, $\dot{M}O_{2\mathrm{Rest}}$ was significantly elevated between 29 and 31 °C and then further elevated between 33 and 34 °C (Fig. 1e). Two species exhibited no significant change in $\dot{M}O_{2\mathrm{Rest}}$ with elevated temperatures (Fig. 1a and f). Temperature quotients (Q_{10}) were calculated to characterize the influence of temperature on metabolic rate, which typically doubles or triples (i.e. $Q_{10} = 2–3$) with each 10 °C increase in ambient temperature. For *D. melanurus*, the Q_{10} calculated for $\dot{M}O_{2\mathrm{Rest}}$ between 29 and 34 °C was 2.1, whereas the response to temperature was greater in *P. moluccensis* and *C. atripectoralis* ($Q_{10} = 4.8$ and 7.2, respectively). All remaining calculated Q_{10} values were <2.0 (Table 1).

For four of the six species $\dot{M}O_{2\mathrm{Max}}$was highest at 29 or 31 °C, and above 31 °C, $\dot{M}O_{2\mathrm{Max}}$ was reduced significantly (Fig. 1). The exceptions were *Z. leptacantha* and *P. moluccensis*. The $\dot{M}O_{2\mathrm{Max}}$ of *Z. leptacantha* remained unchanged between 29 and 33 °C, but fell at 34 °C; whereas, the $\dot{M}O_{2\mathrm{Max}}$ of *P. moluccensis* increased between 31 and 33 °C and remained elevated at 34 °C (Fig. 1b and f). $\dot{M}O_{2\mathrm{Max}}$ ranged from ca. 700 to 1100 mg O_2 kg^{-1} h^{-1} for all species except for *C. atripectoralis*, which had a $\dot{M}O_{2\mathrm{Max}}$ ranging from ca. 1000 to 1600 mg O_2 kg^{-1} h^{-1} (Fig. 1e).

Collectively, the changes in $\dot{M}O_{2\mathrm{Rest}}$ and $\dot{M}O_{2\mathrm{Max}}$ resulted in significant peaks (T_{opt}) or plateaus in absolute aerobic scope at a maximum temperature of 31 °C for *A. polyacanthus*, *D. melanurus*, and *C. quinquelineatus* and 33 °C for *Z. leptacantha*. The highest aerobic scope value for *C. atripectoralis* was calculated at 29 °C, but because we did not test fish at lower temperatures, we do not know if this is a peak or plateau (Fig. 2e). The other five species, on average, increased aerobic scope from 29 °C by at least 20%, and by as much as 140%, at their optimal temperatures for aerobic scope. Beyond 31 °C, scope decreased significantly by 49% in *A. polyacanthus* and *D. melanurus* (Fig. 2a,b), and by 53% in *C. quinquelineatus* (Fig. 2c), whereas a significant reduction in scope did not occur until 33–34 °C in *P. moluccensis* (39%; Fig. 2d) and *Z. leptacantha* (72%; Fig. 2f). In contrast, aerobic scope significantly declined by 45% between 29 and 31 °C in *C. atripectoralis* (Fig. 2e).

Absolute aerobic scope was plotted for each of the six species in conjunction with the minimum (27.9 °C), average (29.6 °C), and maximum (31.3 °C) temperatures logged between August 2011 and March 2012 near where fish were collected (Fig. 2). For *A. polyacanthus*, *D. melanurus*, *C. quinquelineatus*, and *C. atripectoralis*, aerobic scope was found to be numerically highest (T_{opt}) at temperatures immediately within the 3.4 °C range recorded during the 8 month temperature logging period. By comparison, the T_{opt} for aerobic scope of *P. moluccensis* and *Z. leptacantha* fell above the maximum temperature. The numerically highest aerobic scope for *P. moluccensis* and *Z. leptacantha* was 33 °C, but *Z. leptacantha* also maintained an elevated aerobic scope (no significant differences from 33 °C) at 29 and 31 °C (Fig. 2f).

Latitudinal temperature variations and aerobic scope

The optimal performance range for the four damselfish species was plotted in conjunction with data compiled from previous studies for the same species investigated at sites near Lizard Island (experimental temperatures ranging 29–33 °C) and Heron Island (27–33 °C), GBR, Australia (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010) (Fig. S2) and the IGOSS satellite sea surface temperatures taken near all three locations between November 1982 and April 2012 (Fig. 3). The only exception was that *D. melanurus* was investigated in the current study, whereas the congener, *D. aruanus*, was studied at both Lizard and Heron Islands. There were no statistical differences in the mean of the optimal performance range (one-way ANOVA) or SD (Brown–Forsythe test and Bartlett's test) among populations in any of the species investigated. Consequently, when optimal performance range (i.e. mean ± sd) was plotted in conjunction with the historical temperature data, distinct differences were apparent between populations. For the equatorial populations, the optimal performance range mean was below the average summer temperature for only one of the species examined (*C. atripectoralis*), and the range of optimal performance overlapped with the span of the minimum and maximum summer temperatures for all species examined. By contrast, at the highest latitude, Heron Island, not only the mean, but the optimal

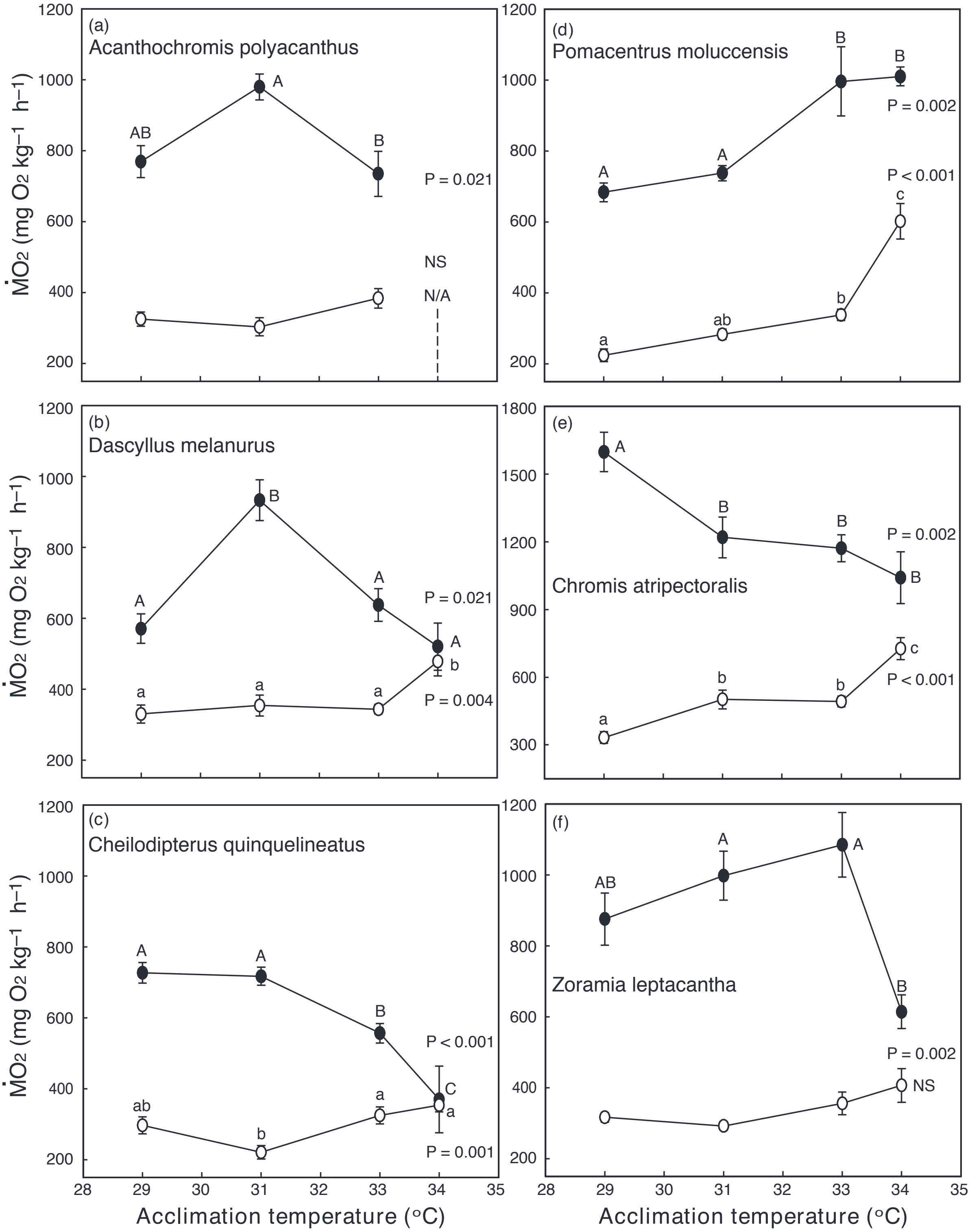

Fig. 1 Resting (open circles; $\dot{M}O_{2Rest}$) and maximum (filled circles; $\dot{M}O_{2Max}$) O_2 consumption rates for six coral reef fishes investigated upon acclimation to 29, 31, 33, and 34 °C. Measurements were not possible for *A. polyacanthus* at 34 °C (indicated by N/A). All graphs are scaled identically with the exception of *C. atripectoralis*. All data are means ± SEM $n = 8$ for each species and each temperature. Within a species, significant differences between resting values are demarcated by lower-case letters; whereas, significant differences between maximum values are demarcated by upper-case letters. Statistical significance (one-way ANOVA) is indicated by the *P*-value. NS indicates a nonsignificant relationship.

Table 1 Temperature quotients (Q_{10}) calculated for the changes in $\dot{M}O_{2\mathrm{Rest}}$ between acclimation temperatures

	Q_{10} values		
Species	29–31 °C	29–33 °C	29–34 °C
A. polyacanthus	0.7	1.5	n/a
D. melanurus	1.4	1.1	2.1
C. quinquelineatus	0.2	1.3	1.4
P. moluccensis	3.2	2.8	7.2
C. atripectoralis	7.8	2.7	4.8
Z. leptacantha	0.7	1.3	1.7

A. polyacanthus did not survive when held at 34 °C. Therefore, no $\dot{M}O_{2\mathrm{Rest}}$ values are available for calculating the 29–34 °C Q_{10} for that species.

performance range exceeded the maximum summer temperature in all but one species (*D. aruanus*). The pattern at Lizard Island was intermediate to PNG and Heron Island. None of the means of the optimal performance range were below the average or maximum summer temperatures, but the optimal performance range for three of the four species overlapped the maximum summer temperatures.

Discussion

Equatorial populations of four of the six species investigated in this study appear to be living at or above their optimal temperatures for aerobic performance. One of these species (*C. atripectoralis*) exhibited a decrease in aerobic scope by 45% between 29 and 31 °C, temperatures that encompass the current-day annual range for the study site. Interestingly, the other two species (*P. moluccensis* and *Z. leptacantha*) maintained aerobic scope when held at temperatures ca. 2 °C above summer maxima. However, for all species held at 3 °C above current-day temperatures, aerobic scope declined and even approached zero in two species, *D. melanurus* and *C. quinquelineatus*. One species, *A. polyacanthus*, was unable to survive short-term exposure to 34 °C. This species is a direct developer, which is not the norm among reef fishes, and is known to exhibit strong genetic structure among populations (Bay *et al.*, 2008). Consequently, *A. polyacanthus* populations may exhibit stronger local adaptation of their critical thermal limits than other species, leading to a very steep decline in performance at the higher temperatures. Aerobic scope has been classically referred to as a proxy for individual performance (Fry, 1971); although, potential limitations with this idea have been outlined in a recent review (Clark *et al.*, 2013). Still, the significant temperature-induced reductions in aerobic scope observed here in all species at 3 °C above current-day temperatures may be expected to have ecological consequences because less energy may be available for vital life history processes such as growth, reproduction, and predator-prey interactions (Pörtner & Peck, 2010). Our results are consistent with the hypothesis that equatorial populations of marine organisms that experience a narrow range of seasonal temperatures may be especially vulnerable to elevated temperatures due to global warming.

Resting and maximum oxygen consumption

A decreased capacity to perform aerobically (reduced aerobic scope) is predicted by some to be key in determining the response of marine fish to increased ocean temperature (Pörtner, 2001; Pörtner & Knust, 2007). Our results suggest that equatorial populations may have optimized the rate functions that sustain metabolism to within or below the narrow temperature range they experience annually (27.9–31.3 °C). Within this range, resting O_2 consumption rates (a proxy for basal metabolic needs) remain low, while maximum O_2 consumption rates remain high. Beyond this temperature range, however, an increase in $\dot{M}O_{2\mathrm{Rest}}$, a decrease in $\dot{M}O_{2\mathrm{Max}}$, or both contribute to decreasing aerobic scope by 39–72% for four of the species we investigated. Our results highlight the need to understand how temperature influences $\dot{M}O_{2\mathrm{Rest}}$ and $\dot{M}O_{2\mathrm{Max}}$ individually, as well as combined ($\dot{M}O_{2\mathrm{Max}}$□$\dot{M}O_{2\mathrm{Rest}}$) as aerobic scope.

Resting metabolic rate, like many biological rate functions, exhibits a predictable response to temperature (an approximate doubling or tripling for every 10 °C increase, Q_{10} □ 2–3) (Schmidt-Nielsen, 1990; Clarke & Johnston, 1999). When $\dot{M}O_{2\mathrm{Rest}}$ increases with temperature, the minimum energy required for basal maintenance of the organism is increased. In two of the damselfish species investigated here, the increase in $\dot{M}O_{2\mathrm{Rest}}$ between 29 and 34 °C was dramatic (Q_{10} = 7.2, 4.8, Table 1).In other words, at 34 °C, over twice as much energy is required for these species to maintain routine metabolic processes than at 29 or 31 °C. Interestingly, this occurred in these two species with little change in $\dot{M}O_{2\mathrm{Max}}$. We hypothesize that the high Q_{10} values could be a product of the stable, narrow thermal range experienced by these small tropical fishes. If tropical fishes are locally adapted to their thermal environment, do not regularly experience temperature fluctuations, and do not move far from these microhabitats, there would be no drive to possess such metabolic compensation. Therefore, the surprise might actually be the species exhibiting a Q_{10} of ca. 2. For example, *D. melanurus* held at 34 °C exhibited a moderate 45% increase in resting metabolic rates (Q_{10} = 2.1, Table 1); however, $\dot{M}O_{2\mathrm{Max}}$ decreased such that no differences could be

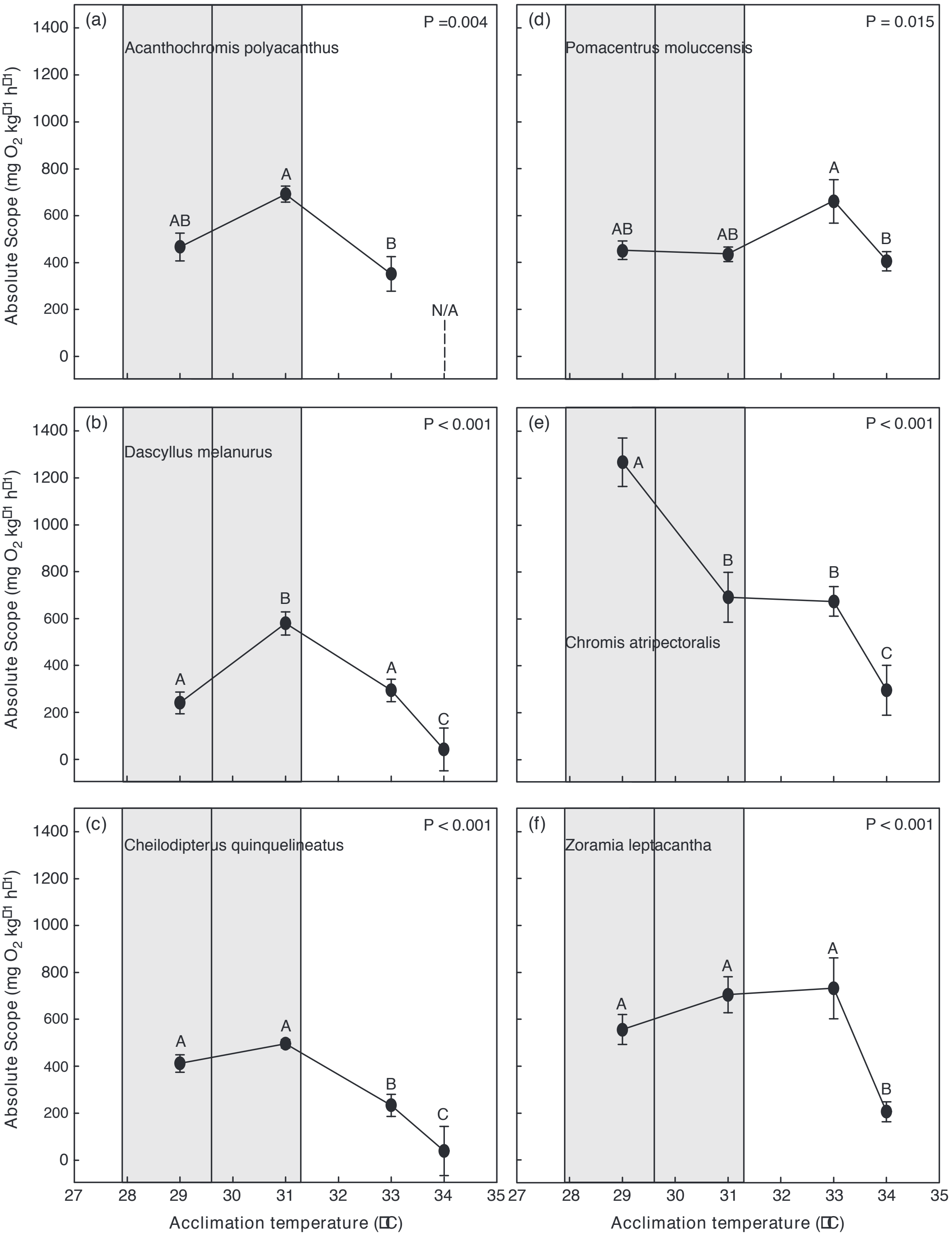

Fig. 2 Absolute aerobic scope ($\dot{M}O_{2\mathrm{Max}} - \dot{M}O_{2\mathrm{Rest}}$) for six coral reef fishes investigated upon acclimation to 29, 31, 33, and 34 °C and the range of temperatures recorded for the site near where fish were collected. Measurements were not possible for *A. polyacanthus* at 34 °C (indicated by N/A). All data are means ± SEM, $n = 8$ for each species and each temperature. Within a species, significant differences between values are demarcated by lower-case letters; whereas, significant differences between maximum values are demarcated by upper-case letters. Statistical significance is indicated by the *P*-value. The shaded gray area demarcates the minimum, average, and maximum temperatures recorded between August 2011 and March 2012 by data loggers deployed at a depth of 1 m near where fish were collected.

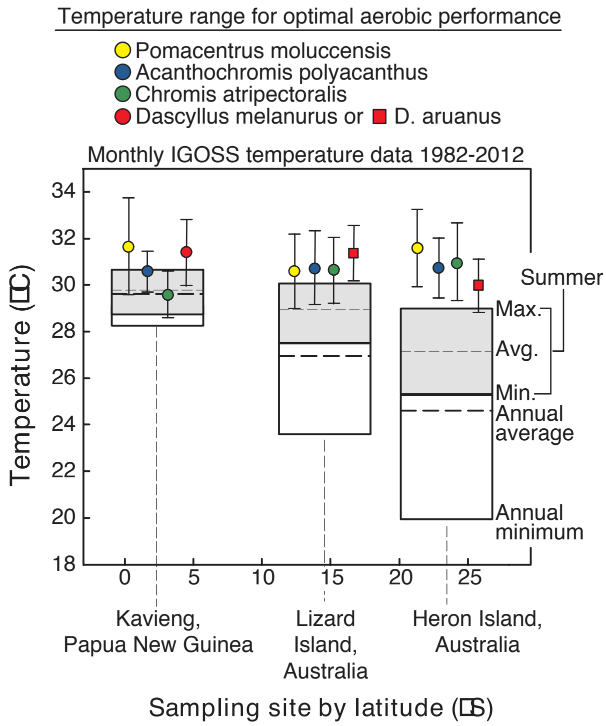

Fig. 3 Local temperatures and the temperature range for optimal aerobic performance for five species of damselfishes represented by three populations spanning 2321 km from the southern Great Barrier Reef (GBR) to Papua New Guinea. Sampling sites are represented by their latitudinal position (°S). Each species is represented by a unique color. Note: *D. melanurus* was only investigated at the equatorial site; whereas, *D. aruanus* was investigated only at Lizard and Heron Islands. All individuals tested within each species and population were ranked by maximal aerobic scope. The top performers (the top 25% of aerobic scope values) within each species and population were selected, and the corresponding temperatures were plotted on this graph as mean □ SD to represent the range of optimal performance. Gray rectangles represent the summer maximum, average, and minimum sea surface temperatures for each site. A thin, hashed line and a thick, hashed line represent each site's annual summer average and overall average respectively. The temperature blocks extend to include each location's annual minimum sea surface temperatures as well. Sea surface temperatures are from monthly IGOSS data collections between 1982 and 2012 (see Materials and methods for further details).

detected between $\dot{M}O_{2\mathrm{Rest}}$ and $\dot{M}O_{2\mathrm{Max}}$ and aerobic scope neared zero (Fig. 1b, 2b). Thus, in *D. melanurus*, the sharp decrease in $\dot{M}O_{2\mathrm{Max}}$ contributed more to the diminished aerobic scope at 34 °C than the increase in $\dot{M}O_{2\mathrm{Rest}}$ (Data S1). Along with *D. melanurus*, three other reef fishes we investigated exhibited Q_{10} values less than 2 for $\dot{M}O_{2\mathrm{Rest}}$ (Table 1) and thus, in theory, the capacity to largely offset the temperature-induced increase in resting metabolic rates within the temperature range tested. The cost for these species, however, may be at the level of maximal performance, as $\dot{M}O_{2\mathrm{Max}}$ was largely temperature-dependent. The behavior and functional role of each species on the reef will dictate at which level saving energy will be most important. For example, the trade-off for some species may a loss of maximum aerobic performance to save energy at rest, whereas others may survive increased costs at rest as long as they can maintain maximum aerobic performance. It is therefore important to investigate both the trends in resting and maximum metabolic rates and each species' behavior and functional role within its ecosystem when interpreting what is driving declines in their aerobic scope.

Thermal specialization in equatorial species/populations

We observed variations in thermal sensitivity and potentially metabolic efficiency among closely related species. Our findings reflect a mix of equatorial specialists and geographically widespread species (thermal generalists) at our study site in northern PNG. Near the equator, *D. aruanus* is largely replaced with its congener *D. melanurus* (Allen, 1991). With a high Q_{10} and the most bell-shaped aerobic scope thermal reaction norm (Fig. 2b), *D. melanurus* may be an equatorial specialist, predominating more thermally stable, low latitude habitats, without the extensive latitudinal range of congener, *D. aruanus*. The geographically widespread *C. atripectoralis*, a species that occurs all the way to the most southerly coral reefs in Australia, exhibited a decrease in aerobic scope across all temperatures, the lowest T_{opt} and optimal performance range of the six species investigated and a high Q_{10}, suggesting some level of temperature sensitivity in equatorial populations of this species. In contrast, we observed that the notably thermally tolerant sister species damselfish, *C. viridis* (Nilsson *et al.*, 2009), was largely absent from our study site. The lemon damsel, *P. moluccensis*, is also geographically widespread and exhibited an optimal performance range ranging from just under 30 to almost 34 °C, which extends beyond current day maximum temperatures at all latitudes (Nilsson *et al.*, 2009; Gardiner *et al.*, 2010). Compared to damselfishes, cardinal fishes were expected to exhibit marked temperature sensitivity (Gardiner *et al.*, 2010). However, both species investigated exhibited relatively wide thermal optima, centered around 31 °C for the widely distributed *C. quinquelineatus* but ranging 29–33 °C for the tropical specialist, *Z. leptacantha*. Whole organism performance clearly declined, if not diminished at 34 °C in at least five of the species we examined; notably, we were not able to hold *A. polyacanthus* at 34 °C, even for a short period of time. There have been other instances in the literature where a species' aerobic scope optimal temperature is very close to lethal temperatures (Clark *et al.*, 2013), and this warrants further investigation. It may be that *A. polyacanthus*, especially equatorial populations, will be especially vulnerable to ocean temperatures projected to occur by the end of this century. Our result show that the T_{opt} for aerobic performance may closely resemble local temperature ranges for equatorial populations, but may also indicate that the area is not comprised strictly of equatorial specialists.

Latitudinal temperature variations and aerobic scope

We compared the thermal range for which the aerobic scope was the greatest between the three latitudinally distinct populations of damselfishes to determine whether each population's temperature range for optimal performance matched its local thermal environment. Two important patterns emerged from this comparison. First, all three populations seem to have approximately the same mean temperature range for optimal performance despite 21° of latitudinal separation (Fig. 3). Second, the optimal performance range only closely matched the range of summer temperatures experienced for the equatorial populations; whereas, the optimal performance range extended beyond local temperature maxima for higher latitude populations. At Heron Island, the site at the highest latitude, optimal performance ranges exceeded the maximum summer temperature experienced in all but one species. Similar patterns have been described for terrestrial ectotherms, and suggest that, indeed, low latitude species are already living close to their thermal optima and will be most vulnerable to a changing climate (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Nguyen *et al.*, 2011) if adaptation cannot keep pace with increasing temperatures. In contrast, higher latitude species are living in climates currently cooler than their aerobic scope thermal optima and may therefore possess a wider thermal safety margin; climate change increases in sea surface temperatures may even enhance fitness in high latitude populations.

The similar optimal performance range among populations may suggest a lack of local adaptation in aerobic scope; however, our latitudinal comparisons did come with several assumptions, and there are alternative conclusions (Data S1). For example, because aerobic scope declined at temperatures lower than the highest experimental temperature used in the current study (34 °C), we assume we captured the upper limits to aerobic performance for the species we investigated. For some of the Lizard and Heron Island populations, however, the variation around the mean of the optimal performance range extended to the maximum experimental temperature (33 °C), suggesting that the upper thermal limit for aerobic performance could be even higher and therefore the optimal performance range broader in some of the high latitude populations. Furthermore, high latitude populations might be adapted to a greater range of seasonal temperatures that they would normally experience compared with low latitude populations, leading to improved capacity to perform at a range of temperatures, including higher temperatures outside the normal range experienced. This could produce an apparent mismatch between the average temperatures experienced in high latitude populations and the temperatures where aerobic scope is greatest. Consequently, our results could indicate that reef fish populations are more closely adapted to seasonal temperature variations than they are to the average temperatures they experience.

Due to less thermal variability and thus, narrower thermal safety margins, the impact of global warming on coral reef fishes could be the greatest at low latitudes. If adaptation cannot keep pace with climate change, even relatively minor ocean warming (2–3 °C) could result in population declines and potentially the redistribution of equatorial populations to higher latitudes (Nilsson *et al.*, 2009; Nguyen *et al.*, 2011; Sunday *et al.*, 2012). Thermal acclimation (plasticity) may assist some species and populations in coping with future temperature increases; however, thermal performance ranges of stenothermal (e.g., tropical, low latitude, polar) species are expected to be less plastic than eurythermal (often temperate) species (Nguyen *et al.*, 2011). Previous data exist to support minimal short-term capacity for acclimation in adults of two of the species we investigated, *A. polyacanthus* and *P. moluccensis* (Nilsson *et al.*, 2010; Donelson *et al.*, 2011). However, there could be an ontogenetic or trans-generational component, which may be more relevant to keeping pace with the rate of change occurring due to climate change. Indeed, new research has demonstrated developmental acclimation of resting O_2 consumption rates and other life history metrics in *A. polyacanthus* reared for their entire life cycle at current and 3 °C above current temperatures (Donelson *et al.*, 2011). Exposure to elevated temperatures during the early stages of development may condition enzymatic processes to operate more efficiently later as adults (Nilsson *et al.*, 2010), but there may be a cost at the level of diminished growth rates (Munday *et al.*, 2008a; Donelson *et al.*, 2011). *A. polyacanthus* has also been found to exhibit pronounced trans-generational thermal acclimation (Donelson *et al.*, 2012), suggesting that the parental environment plays a role in the offspring's response. Whether equatorial populations of reef fish, including *A. polyacanthus*, have the capacity for developmental and/or trans generational acclimation, however, is unknown and will be a topic of future studies.

Implications and conclusions

In an era of rapid climate change, understanding the link between organisms and environment will be increasingly important in developing management strategies for the conservation of marine biodiversity and the sustainable use of marine fisheries, particularly in the context of food security for dependent human communities. We have demonstrated here that equatorial populations of coral reef species are already living at temperatures close to their thermal optimum for aerobic scope and that even a small amount of ocean warming could cause a significant decline in aerobic scope in these populations. This is a significant advancement to our understanding of global change ecology for marine species. If aerobic scope is closely linked to individual performance (Pörtner & Farrell, 2008; reviewed in Clark *et al*., 2013), then declines in this trait could have implications for long-term sustainability of equatorial fish populations and could drive a range shift of species away from their equatorial boundary (Munday *et al*., 2008b; Nguyen *et al*., 2011; Sunday *et al*., 2012). In addition to the implications for marine diversity, population declines and range shifts would also have significant consequences for human societies in the equatorial zone. There is a concentration of developing countries in the equatorial zone where fish are crucial to the livelihoods and survival of millions of people (FAO, 2012). Climate change may lead to redistribution of global catch potential, with the most significant declines likely to occur near the equator (Cheung *et al*., 2010). Thus, understanding the effect of global warming on reef fishes across their geographical ranges is critical for predicting likely changes in fisheries productivity. This will also be important in determining the most ecologically and economically susceptible geographic locations and countries, and ultimately, tailoring mitigation, management, and conservation strategies to effectively conserve the biodiversity of tropical marine environments and the ecosystems services they provide.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Additional information regarding respirometry methods, latitudinal comparisons, the reanalysis of data, and local adaptation as well as three additional references are provided.

Figure S1. Representative traces from three individual *C. atripectoralis* chased to exhaustion and then immediately placed into respirometry chambers where $\dot{M}O_2$ could be monitored until recovery, which was sooner than 2 h (J. L. Rummer, unpublished data).

Figure S2. Absolute aerobic scope ($\dot{M}O_{2\mathrm{Max}} - \dot{M}O_{2\mathrm{Rest}}$) for five coral reef fish species from three populations (see legend for symbols) investigated upon acclimation to 27, 29, 31, 32, 33, and/or 34 °C.