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Global warming may disproportionately affect larger adults in a predatory coral reef fish

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Abstract

Global warming is expected to reduce body sizes of ectothermic animals. Although the underlying mechanisms of size reductions remain poorly understood, effects appear stronger at latitudinal extremes (poles and tropics) and in aquatic rather than terrestrial systems. To shed light on this phenomenon, we examined the size dependence of critical thermal maxima (CTmax) and aerobic metabolism in a commercially important tropical reef fish, the leopard coral grouper (*Plectropomus leopardus*) following acclimation to current-day (28.5 °C) vs. projected end-of-century (33 °C) summer temperatures for the northern Great Barrier Reef (GBR). CTmax declined from 38.3 to 37.5 °C with increasing body mass in adult fish (0.45–2.82 kg), indicating that larger individuals are more thermally sensitive than smaller conspecifics. This may be explained by a restricted capacity for large fish to increase mass-specific maximum metabolic rate (MMR) at 33 °C compared with 28.5 °C. Indeed, temperature influenced the relationship between metabolism and body mass (0.02–2.38 kg), whereby the scaling exponent for MMR increased from 0.74 ± 0.02 at 28.5 °C to 0.79 ± 0.01 at 33 °C, and the corresponding exponents for standard metabolic rate (SMR) were 0.75 ± 0.04 and 0.80 ± 0.03. The increase in metabolic scaling exponents at higher temperatures suggests that energy budgets may be disproportionately impacted in larger fish and contribute to reduced maximum adult size. Such climate-induced reductions in body size would have important ramifications for fisheries productivity, but are also likely to have knock-on effects for trophodynamics and functioning of ecosystems.

Keywords: body size, climate change, critical thermal maximum, Great Barrier Reef, metabolic rate, *Plectropomus leopardus*, thermal tolerance

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Introduction

Sustained and ongoing increases in atmospheric and ocean temperatures due to anthropogenic climate warming (IPCC, 2013) are having significant biological impacts on individuals, species and ecosystems (e.g. Walther *et al*., 2002; Parmesan & Yohe, 2003; Perry *et al*., 2005; Hofmann & Todgham, 2010). Temperature plays a vital role in the ecology of organisms as it influences rates of biochemical and physiological processes. This is especially pertinent for ectotherms because their body temperature is primarily governed by environmental temperature rather than through physiological thermoregulation (Dawson, 1975; Brett & Groves, 1979). Sensitivity to the thermal environment varies both between species (e.g. Farrell, 2009) and within species. Within-species differences in thermal tolerance can result from adaptation to specific local thermal regimes (e.g. Eliason *et al*., 2011), but tolerance can also vary among individuals with size and ontogeny (e.g. Coulson *et al*., 2001; Peck *et al*., 2013).

The best-documented effects of changing thermal regimes on species and ecosystems have been shifts in species' distributions to higher altitudes and latitudes (Walther *et al*., 2002; Parmesan & Yohe, 2003; Root *et al*., 2003; Feary *et al*., 2014). Also, phenological changes are increasingly apparent (Stenseth *et al*., 2002; Walther *et al*., 2002; Visser & Both, 2005; Taylor, 2008), sometimes with dramatic consequences for predator–prey interactions (Durant *et al*., 2007; Yang & Rudolf, 2010). More recently, a reduction in the body size of species has been proposed as a third universal response to global warming (Daufresne *et al*., 2009; Gardner

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et al., 2011; Ohlberger, 2013), with likely consequences for population dynamics, ecosystem function and productivity (Millien *et al.*, 2006; Arendt, 2007; Cheung *et al.*, 2013; Vindenes *et al.*, 2014).

The observation that warmer environments are associated with smaller body size was first described for endotherms across latitudes ('Bergmann's rule', Bergmann, 1847). This latitudinal cline in maximum body size also applies to a range of ectotherms (Ray, 1960; Angilletta & Dunham, 2003; Kingsolver & Huey, 2008; Daufresne *et al.*, 2009). Overall, reductions in maximum body size of ectotherms in response to climate warming appear to be strongest in tropical and polar environments, as these species have often evolved in more stable thermal conditions (Tewksbury *et al.*, 2008; Somero, 2010; Ohlberger, 2013). Moreover, increasing evidence suggests that thermal effects on body size are stronger in aquatic systems (Forster *et al.*, 2012; Verberk & Atkinson, 2013; Horne *et al.*, 2015) and in larger species (Daufresne *et al.*, 2009; Forster *et al.*, 2012), which is of particular relevance to fisheries productivity due to the correlation between body size and fecundity (Blueweiss *et al.*, 1978). Some models predict sustained declines in the maximum size of marine fishes from 2000 to 2050 as ocean temperatures warm (Cheung *et al.*, 2013), yet the underlying mechanisms responsible for the observed 'temperature–size rule' (Atkinson, 1994) remain poorly understood (Angilletta *et al.*, 2004; Gardner *et al.*, 2011; Clark *et al.*, 2012; Ohlberger, 2013).

For ectothermic organisms, particularly aquatic ectotherms, the supply of oxygen to fuel metabolic demands has been proposed as an important driver of the temperature–size rule (Atkinson *et al.*, 2006; Forster *et al.*, 2012), where oxygen supply may limit maximum attainable body size (Czarnoleski *et al.*, 2015). In nearly all ectotherms, standard (aerobic) metabolic rate (SMR) is positively related to temperature (Gillooly *et al.*, 2001), such that any increase in temperature causes an increase in basal energy and oxygen requirements. As a result, growth rate and size at age may be negatively impacted at higher temperatures unless organisms can compensate through greater food intake or a reallocation of energy resources (e.g. maintaining growth at the expense of reproductive output) (Sheridan & Bickford, 2011).

Metabolic rate often scales allometrically with body size (Clarke & Johnston, 1999; Darveau *et al.*, 2002), with smaller-bodied individuals and species having higher energy demands per unit of body mass. Accordingly, juveniles typically have higher mass-specific metabolic rates than adults, which may be associated with their higher growth rates and often elevated activity levels (Hou *et al.*, 2008). The relationship between body size and metabolic rate in ectotherms may be complicated by the fact that temperature can influence the scaling exponent (slope) within a species (Killen *et al.*, 2010; Glazier *et al.*, 2011; Ohlberger *et al.*, 2012). Furthermore, thermal sensitivity can change throughout ontogeny. Very early life-history stages (gametes and developing larvae) and larger reproductively mature individuals are thought to be most vulnerable to temperature change, whereas juveniles and young adults appear to be more resilient to thermal extremes (Peck *et al.*, 2009, 2013; Righton *et al.*, 2010; Clark *et al.*, 2013a). This has been linked to the oxygen limitation paradigm, where a higher aerobic scope [the difference between SMR and maximum metabolic rate (MMR)] in juveniles is thought to augment thermal tolerance in comparison with earlier life stages or older, more sedentary animals (Peck *et al.*, 2004, 2013). While these ideas remain the topic of much debate (Clark *et al.*, 2013b,c), it is clear that understanding size-dependent responses of species to increasing temperatures is critical in identifying the most vulnerable life stages and the likely consequences of climate warming.

Here, we investigate size-based variation in the thermal sensitivity of a large-bodied reef fish, the leopard coral grouper (*Plectropomus leopardus*), which is among the most ecologically and economically important species on coral reefs in the Indo-Pacific. We hypothesize that acclimation to +3 °C above current summer maxima will have a stronger metabolic impact on large rather than small individuals, such that small individuals will have a higher critical thermal maximum (CTmax). As body size is often correlated with reproductive output, where smaller individuals produce fewer or smaller offspring (Green, 2008), a warming-induced population-level trend towards smaller adult body size is likely to affect ecosystem function and have important implications for maintaining sustainable fisheries.

Materials and methods

Animal collection and acclimation conditions

A total of 31 adult and 16 juvenile *P. leopardus* were collected during March–April 2012 on reefs within 15 km of Lizard Island (14°41′S, 145°27′E) in the northern Great Barrier Reef (GBR), Australia. Adult fish ranging in size from 360 to 570 mm (total length) and 0.475 to 2.375 kg were caught using hand lines. Juvenile fish, 130–210 mm and 0.021–0.105 kg, were collected on SCUBA using barrier nets and an anaesthetic spray of diluted clove oil. To keep track of each individual, adult fish were tagged dorsally with a T-bar anchor tag (Hallprint, Hindmarsh Valley, SA, Australia), while juvenile fish were subcutaneously injected in the mid-dorsal and mid-ventral region with a unique combination of coloured visible implant elastomer tags (Northwest Marine Technology Inc, Shaw Island, WA, USA).

Adult fish were allocated to four plastic tanks (two 1000-L and two 2000-L tanks), and juveniles were divided into four 60-L plastic tanks (stocking densities were kept consistent). All holding tanks were aerated and received continuous flow-through water at an average temperature of 28.5 °C (average daily range 27.3–29.3 °C across the study). Fish were given 3–5 days to settle into captivity before respirometry experiments were conducted at 28.5 °C on all adult fish and half of the juvenile fish. Data from these initial respirometry experiments are considered herein to be from '28.5 °C short-term acclimated' fish. Following approximately 14 days in captivity, the temperature in one of the 2000-L tanks containing 12 adult fish and two of the 60-L tanks containing a total of eight juvenile fish was increased at a rate of 0.5 °C day^{-1} until 33 °C was reached. The remaining 19 adults and eight juveniles were maintained at 28.5 °C. The high temperature was chosen to represent an end-of-century summer forecast for the northern GBR under a high emission scenario (IPCC, 2013). The thermal conditions were maintained for an additional 4–5 weeks, with respirometry trials conducted at two different points during this time. A total of 12 adult fish and eight juveniles were measured within 3–5 days of reaching 33 °C (data considered herein to be from '33 °C short-term acclimated' animals), and the adults were measured again at 4–5 weeks of reaching 33 °C (termed '33 °C long-term acclimated') alongside nine adults and eight juveniles from the 28.5 °C group (termed '28.5 °C long-term acclimated'). For conservation and logistical reasons, we were not able to hold juvenile fish in captivity at 33 °C for longer than 1 week. Fish were fed sardines (*Sardinops sagax*) every second day to satiation, but fasted for 48 h before respirometry trials to remove the influence of digestive processes on the measurements. All protocols were conducted in accordance with the James Cook University Animal Ethics Committee (A1723).

Respirometry

Respirometry was conducted in static flow-through respirometers using best practices in aquatic respirometry (see Clark *et al.*, 2013b). Respirometers were custom-built from cylindrical PVC pipes to suit the size of the fish, and each respirometer contained a transparent window (15 × 8 cm) to ensure light could enter. Large respirometers were 23.5 cm in diameter and 68 cm long with a total volume of 30 L. Small respirometers for juvenile fish had a diameter of 11 cm, were 26 cm long and had a volume of 2.5 L. All respirometers were equipped with a closed-circuit recirculation loop with an inline pump, which ensured that the respirometer water remained well mixed. A contactless oxygen sensor (Firesting O_2; PyroScience, Aachen, Germany) was positioned in the recirculation loop of each respirometer to record oxygen concentration continuously at 0.5 Hz. An automated flush pump on each respirometer replaced the respirometer water with aerated seawater for 3–7 min every 10–15 min (depending on temperature and fish size), and oxygen consumption rate ($\dot{M}O_2$) was calculated from the rate of decline in oxygen concentration of the water inside the respirometers between flush cycles.

To commence respirometry trials, randomly selected fish were individually hand-netted from their holding tanks and placed into a 500-L circular 'exercise tank' at the treatment temperature (28.5 or 33 °C) where they were subsequently coaxed to burst swim by an experimenter for 3 min. This is considered to be the most appropriate exercise protocol for inducing maximal metabolic rates (MMR) in fish species that do not naturally swim for prolonged periods (e.g. Reidy *et al.*, 1995; Kieffer, 2000; Clark *et al.*, 2013b; Roche *et al.*, 2013). After the 3-min exercise protocol, each fish was hand-netted and exposed to air for 1 min, during which time the body mass and length were measured. The fish was then placed into a respirometer at the treatment temperature, which was sealed within 15 s to commence $\dot{M}O_2$ measurements. Fish remained in respirometers for 20–24 h to monitor postexercise metabolic recovery and measure resting levels of $\dot{M}O_2$ (i.e. SMR). All respirometers were routinely wiped down and cleaned to ensure that background respiration remained negligible throughout the study.

Critical thermal maximum

A further 16 adult *P. leopardus* spanning most of the adult size range (350–600 mm; 0.45–2.82 kg) were collected around Lizard Island in November 2012 to test the effects of body mass on the critical thermal maximum (CTmax). While CTmax tests are not typically representative of ecologically relevant heating rates (except, perhaps, in habitats such as tidal pools), they represent a widely used and rapid screening technique to provide an assessment of relative thermal tolerance across species and individuals (Becker & Genoway, 1979; Beitinger *et al.*, 2000; Recsetar *et al.*, 2012). Moreover, CTmax has been shown to correlate well with the thermal distributions of many species (Sunday *et al.*, 2012). Fish were held and fasted in 2000-L flow-through tanks for at least 48 h after capture before being moved to a 400-L tank fitted with a 4.4-kW heating system and vigorous aeration. Fish were allowed to settle in the new tank for 15 min before testing began. The tank was initially kept at ambient local reef temperature with constant water flow, which was subject to daily temperature fluctuations between 26.5 °C (morning) and 29 °C (afternoon). Trials for half of the fish ($n = 8$) commenced in the morning, while the other half commenced in the early afternoon. Starting temperature was included as a variable in the statistical analyses. After the settling period, temperature was raised by 0.1 °C min^{-1} (= 6 °C h^{-1}, see Beitinger *et al.*, 2000; Mora & Maya, 2006) and the temperature at which fish lost equilibrium for 30 s (i.e. CTmax) was recorded. Individual fish were removed from the tank as they reached their CTmax and placed immediately into a 400-L recovery tank at ambient temperature until they regained equilibrium (always within 5 min), after which they were returned to their holding tanks. Dissolved oxygen in the experimental tank was always maintained above 70% air saturation.

Data analysis and statistics

LABCHART software (ADInstruments Pty Ltd, Sydney, Australia) was used to analyse raw oxygen concentration data

Table 1 Log-linear relationships between body mass and absolute standard metabolic rate (SMR), maximum metabolic rate (MMR), aerobic scope (AS) and factorial aerobic scope (FAS) for juvenile and adult *P. leopardus* at 28.5 °C (ambient temperature) and 33 °C following 3–5 days of exposure (Fig. 1)

Metabolic variable (y)	a (SE)	b (SE)	R^2	df	F	P
SMR (28.5 °C)	0.167 ± 0.048	0.747 ± 0.035	0.926	1, 37	460.1	<0.001
SMR (33 °C)	0.650 ± 0.049	0.799 ± 0.025	0.982	1, 18	992.8	<0.001
MMR (28.5 °C)	1.488 ± 0.022	0.740 ± 0.016	0.984	1, 37	2211	<0.001
MMR (33 °C)	1.634 ± 0.027	0.789 ± 0.014	0.995	1, 18	3256	<0.001
AS (28.5 °C)	1.163 ± 0.027	0.738 ± 0.020	0.975	1, 37	1412	<0.001
AS (33 °C)	1.155 ± 0.040	0.782 ± 0.021	0.861	1, 18	111.2	<0.001
FAS (28.5 °C)	1.321 ± 0.043	−0.007 ± 0.030	0.001	1, 37	0.051	0.823
FAS (33 °C)	0.984 ± 0.043	−0.010 ± 0.022	0.010	1, 18	0.191	0.668

Equations are solved as $y = \exp(a) \times \text{mass}^b$. ANCOVAs were used to test for common slopes and elevations between temperatures within a metabolic variable. For SMR, slopes were not significantly different ($F_{1,55} = 1.182$, $P = 0.282$), but elevations were ($F_{1,56} = 37.31$, $P < 0.001$). Slopes were significantly different for MMR ($F_{1,55} = 4.788$, $P = 0.033$), and therefore, elevations were not examined. Slopes and elevations were not significantly different for AS ($F_{1,55} = 2.267$, $P = 0.138$; $F_{1,56} = 1.198$, $P = 0.278$, respectively). Slopes were not significantly different for FAS ($F_{1,55} = 0.004$, $P = 0.948$), but elevations were ($F_{1,56} = 29.73$, $P < 0.001$).

from the Firesting O_2 system during the respirometry trials. Calculations of $\dot{M}O_2$ of each individual were based on linear regressions between oxygen concentration and time for each measurement period between flush cycles, taking into account respirometer volume (minus fish mass to adjust for water displacement). Maximum metabolic rate (MMR) was determined from the steepest slope occurring in any 3-min period over the entire trial, which typically occurred during the first sealed cycle after the fish were placed into the respirometers postexercise. Standard metabolic rate (SMR) was calculated as the average of the lowest 10% of $\dot{M}O_2$ measurements (from a minimum of 100 measurements) after excluding outliers (outliers considered as ±2 SDs from the mean).

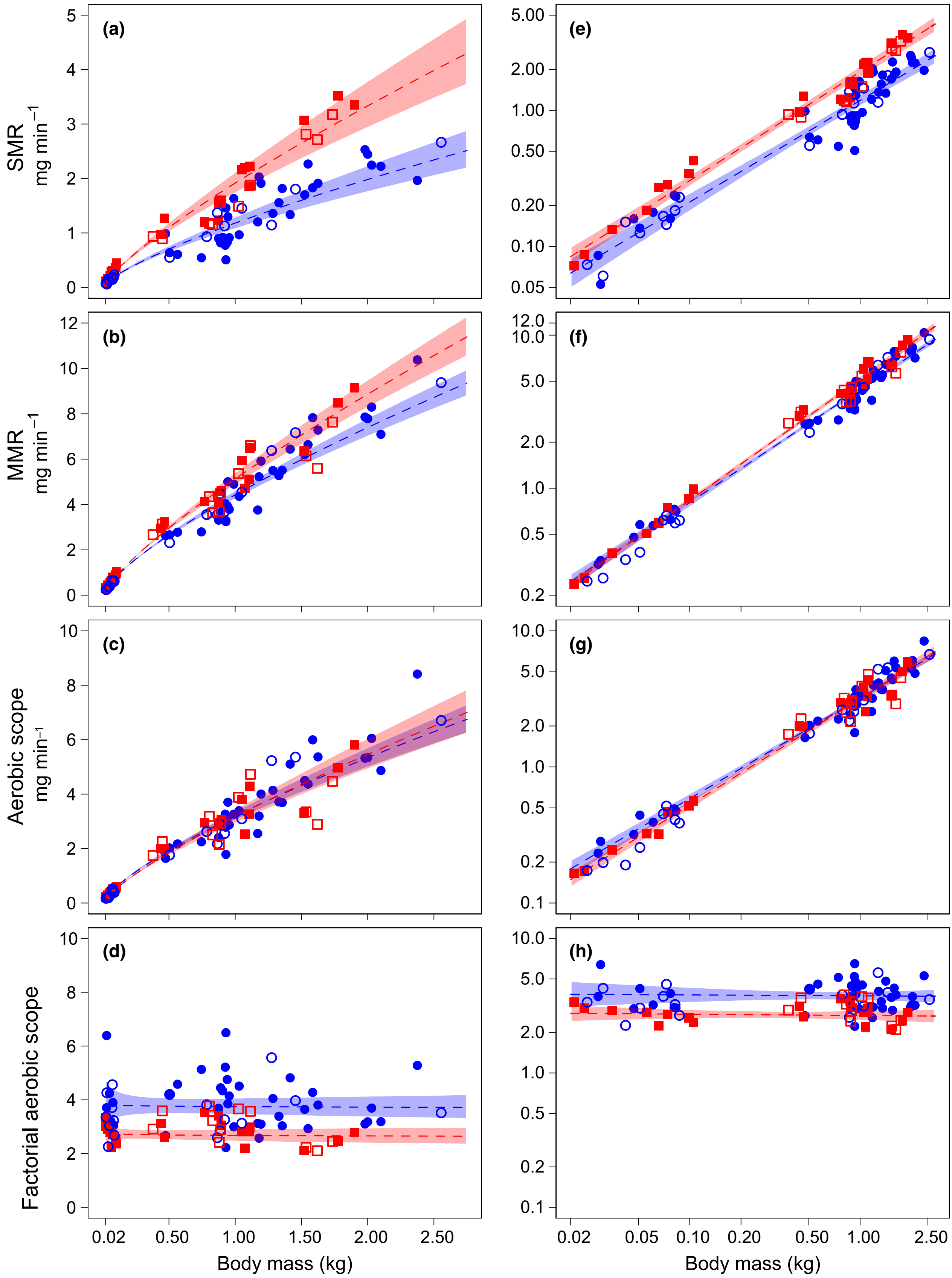
Previously established temperature coefficients (Q_{10}) for *P. leopardus* were applied to SMR and MMR data ($Q_{10} = 2.0$ for SMR and $Q_{10} = 1.0$ for MMR; Pratchett *et al.*, 2013) to account for natural fluctuations in water temperature around the target values of 28.5 °C (27.3–29.3 °C) and 33 °C (32.0–33.2 °C). Temperature-standardized data for SMR and MMR are used herein. Aerobic scope (AS) was calculated as MMR-SMR, and factorial aerobic scope (FAS) was calculated as MMR/SMR.

The effects of body mass on each of the metabolic variables and CTmax were investigated using linear regression models in the R statistical software package (version 3.1.2). We followed guidelines outlined by Xiao *et al.* (2011) to determine whether the error distribution of the data better fitted nonlinear regressions or linear regressions of log-transformed data. Likelihood analyses revealed that linear regressions of log-transformed data were the most appropriate method, and they were subsequently used for all analyses. Linear mixed-effects models (LME; with fish ID as a random factor to account for repeated measures of some individuals) were used to test for differences in the mass–metabolism relationships between the short-term and long-term acclimated groups. ANCOVAS and repeated-measures ANCOVAS were used where appropriate to test for common slopes and elevations for the different metabolic parameters between 28.5 and 33 °C. Significance was considered at $P < 0.05$. Residuals of all models met assumptions of normality.

Results

Captivity and thermal acclimation

Standard metabolic rate (SMR) and maximum metabolic rate (MMR) scaled allometrically with body mass that spanned two orders of magnitude (0.02–2.56 kg), at both temperatures and in both short-term (3–5 days) and long-term (4–5 weeks) acclimated animals (Table 1). At 28.5 °C, there was no effect of time (i.e. 3–5 day vs. 4–5 week measurements) on the slope or intercept of the relationship between body mass and each of SMR, MMR or AS (LME: $n = 52$; factor 'log (mass)*time', $P > 0.091$ in all cases; factor 'time', $P > 0.098$ in all cases), indicating no effect of captivity on fish metabolism. These patterns were the same within the 33 °C trials (only data for adults available at 4–5 weeks), except that the intercept for SMR was higher in fish measured at 3–5 days compared with those measured at 4–5 weeks (LME: $n = 31$; factor 'time', $F_{8,19} = 14.321$, $P = 0.005$). This finding is consistent with thermal compensation of SMR due to acclimation. Subsequent analyses focus on the data from 3 to 5 days to ensure a broad range in body mass (i.e. inclusion of juveniles and adults), bearing in mind that longer thermal acclimation reduces the intercept but not the slope of the SMR–mass relationship at 33 °C, but does not influence any of the other metabolic parameters. Nonetheless, data from the trials at 4–5 weeks are still presented in figures for comparative purposes.


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
SMR mg min⁻¹
MMR mg min⁻¹
Aerobic scope mg min⁻¹
Factorial aerobic scope
0
1
2
3
4
5
0
2
4
6
8
10
12
0.05
0.10
0.20
0.50
1.00
2.00
5.00
0.2
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12.0
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0.02
0.05
0.10
0.20
0.50
1.00
2.50
Body mass (kg)
Body mass (kg)

Fig. 1 Top to bottom: effects of body mass (kg) on absolute standard metabolic rate (SMR), absolute maximum metabolic rate (MMR), absolute aerobic scope (AS) and factorial aerobic scope (FAS) in *P. leopardus* at 28.5 °C [after 3–5 days (blue filled circles) and 4–5 weeks (blue open circles) of exposure] and 33 °C [after 3–5 days (red filled squares) and 4–5 weeks (red open squares) of exposure]. Left (a–d) panels show the relationships on linear scales; right (e–h) panels show the relationships on log scales. Each dashed line represents the modelled scaling relationship (power function based on linear regression model of log-transformed data) between body mass and each of the metabolic parameters (blue lines for 28.5 °C and red lines for 33 °C). Only data from the experiments performed at 3-5 days are used in regressions (see text). The shaded areas represent 95% confidence intervals. Regression information is provided in Table 1.

Thermal effects on metabolic scaling

Model estimates based on data from 3 to 5 days revealed that SMR increased approximately 36-fold across a mass range of 0.021–2.555 kg at 28.5 °C, and approximately 46-fold across the same mass range at 33 °C (Fig. 1). Correspondingly, MMR increased approximately 35-fold across the mass range at 28.5 °C, and approximately 44-fold across the mass range at 33 °C (Fig. 1). Absolute aerobic scope also scaled strongly with body mass at both temperatures (Fig. 1, Table 1), increasing by about 35-fold and 43-fold across the mass range at 28.5 and 33 °C, respectively (Fig. 1).

The mass scaling exponent (slope) was similar for SMR and MMR within each temperature, indicating that factorial aerobic scope was not dependent on body mass (Fig. 1, Table 1). The differences in scaling exponents between temperatures for SMR and MMR were similar, but the difference for SMR (0.75 ± 0.04 and 0.80 ± 0.03, respectively) did not reach statistical significance due to greater variation in SMR than MMR. The intercept for SMR was significantly higher at 33 °C than at 28.5 °C (Fig. 1, Table 1), indicating that SMR increased with temperature across the mass range. The scaling exponent of the MMR–mass relationship increased significantly from 0.74 ± 0.02 at 28.5 °C to 0.79 ± 0.01 at 33 °C (Fig. 1, Table 1). Thus, MMR changed to a greater extent with body size at the higher temperature. Elevation of the MMR–mass relationship could not be compared between temperatures, as the mass scaling exponents were significantly different. However, the 95% confidence intervals for MMR at 33 °C were higher than, and did not overlap with, those at 28.5 °C (Fig. 1). Absolute aerobic scope (AS) did not change with temperature, as no differences in slope or elevation of the AS–mass relationships were observed between 28.5 and 33 °C (Fig. 1, Table 1). Factorial aerobic scope decreased by 30% from 3.87 ± 0.15 at 28.5 °C to 2.70 ± 0.09 at 33 °C (Fig. 1, Table 1).

Critical thermal maxima and links with metabolism

Critical thermal maxima (CTmax) of adult *P. leopardus* correlated negatively with body mass (Fig. 2, Table 2). Model estimates indicated that CTmax ranged from 38.3 °C in the smallest individuals (0.45 kg) to 37.5 °C in the largest individuals (2.82 kg). Notably, the first signs of thermal stress (e.g. more erratic swimming/escape behaviour) were observed at several degrees below the CTmax. Short-term fluctuations in starting (ambient) temperature between morning and afternoon trials had no effect on CTmax (Table 3), possibly because all fish were acclimated to the same average daily temperatures.

To investigate whether the decline in CTmax with body mass was linked with metabolism, we calculated mass-specific metabolic parameters for animals with similar body mass to those used for the CTmax trials (Fig. 2). No significant relationships between body mass and mass-specific SMR, MMR or aerobic scope were observed at 28.5 °C, nor for SMR at 33 °C (Fig. 2, Table 2). However, MMR and AS declined to a greater extent with body mass at 33 °C compared with 28.5 °C (Fig. 2, Table 2), indicating that the influence of body mass was disproportionately greater at the higher temperature.

Discussion

Climate change is expected to have significant impacts on fisheries production in the world's oceans, owing largely to projected shifts in the distribution of marine species (Cheung *et al.*, 2010; Bell *et al.*, 2013) and the degradation of benthic habitats (Pratchett *et al.*, 2014; Rogers *et al.*, 2014). However, increasing temperatures may also lead to declines in maximum size of species (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Forster *et al.*, 2012; Ohlberger, 2013), which will further impact on fisheries productivity. Given that warming-induced reductions in body size appear to be more prevalent in aquatic than terrestrial species, at latitudinal extremes (poles and tropics), and most pronounced in larger-bodied species (Daufresne *et al.*, 2009; Forster *et al.*, 2012; Horne *et al.*, 2015), tropical fishes and fisheries are likely to be particularly vulnerable. While the temperature–size phenomenon in fishes has been widely documented, very few studies have empirically investigated the underlying mechanisms (but see Clark *et al.*, 2012). Our results show that larger individuals of the predatory and commercially important reef fish, *Plectropomus leopardus*, are more sensitive to acute temperature increases than smaller-bodied conspecifics, as CTmax

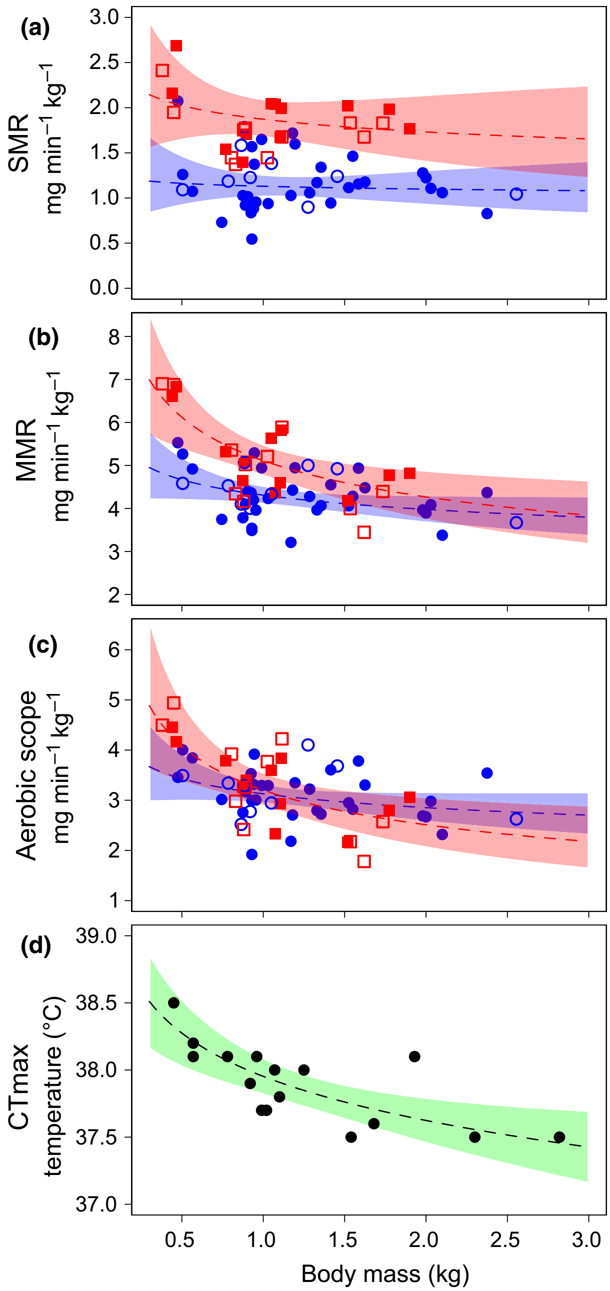

Fig. 2 Effects of body mass (kg) on mass-specific (a) standard metabolic rate (SMR), (b) maximum metabolic rate (MMR) and (c) aerobic scope for *P. leopardus* at 28.5 °C [after 3–5 days (blue filled circles) and 4–5 weeks (blue open circles) of exposure] and 33 °C [after 3–5 days (red filled squares) and 4–5 weeks (red open squares) of exposure]. The scaling relationships are based on linear regression models of log-transformed data and are represented by the fitted lines. Only data from the experiments performed at 3–5 days are used in regressions (see text). (d) Effects of body mass (kg) on the critical thermal maximum (CTmax). The linear regression model of log-transformed data incorporated the starting temperature, but this did not have a significant effect (Table 3). The shaded areas represent 95% confidence intervals in all graphs. Regression information is provided in Table 2.

decreased from 38.3 to 37.5 °C as body mass increased from 0.45 to 2.82 kg.

Aerobic metabolic processes have been proposed as possible drivers for thermal tolerance in aquatic ectotherms because of the temperature dependence of oxygen supply capacity, which above a given temperature is no longer able to meet increasing demand (Gillooly *et al.*, 2001; Pörtner & Knust, 2007; Ern *et al.*, 2015; Verberk *et al.*, 2016). Based on these ideas, the size-dependent thermal tolerance of *P. leopardus* could be due to the limited capacity for large-bodied individuals to increase mass-specific maximum metabolic rate (MMR) in warm conditions (Fig. 2). That is, the size-dependent thermal tolerance in *P. leopardus* may be linked with changes in metabolic scaling relationships across temperature, as scaling exponents increased from 0.75 ± 0.04 to 0.80 ± 0.03 for SMR (nonsignificant) and from 0.74 ± 0.02 to 0.79 ± 0.01 for MMR (significant) as temperature increased from 28.5 to 33 °C. A reduction in mass-specific MMR with body size at 33 °C is consistent with slower swimming speeds and longer resting times found in large *P. leopardus* at elevated temperature (Johansen *et al.*, 2014).

It is important to recognize that the qualitatively similar relationships between body mass and each of mass-specific MMR and CTmax could be correlative rather than causal. Indeed, thermal tolerance across body mass may not be linked with oxygen supply and metabolic capacity at all and instead may be a consequence of factors such as ionic imbalance, mitochondrial dysfunction and/or neuronal failure (Iftikar & Hickey, 2013; Vornanen *et al.*, 2014; Devor *et al.*, 2016). While the metabolic scaling exponents for *P. leopardus* are consistent with those reported for other fishes (White *et al.*, 2006; Clark *et al.*, 2012; Norin & Clark, 2016), conflicting reports in the literature regarding the thermal dependence of metabolic scaling exponents highlight the need for further work on this topic (Glazier, 2005; Killen *et al.*, 2010; Ohlberger *et al.*, 2012; Verberk & Atkinson, 2013; Carey & Sigwart, 2014). In any event, our findings for CTmax suggest that we might see a reduction in body size in *P. leopardus* with predicted global warming, particularly in warmer (lower latitude) regions of its distribution.

Previous studies on the relationship between body size and CTmax have shown mixed results (e.g. Ospina & Mora, 2004; Recsetar *et al.*, 2012), but generally involved smaller-bodied fishes than the size range in *P. leopardus* examined here. These contrasting results based on acute thermal challenges may be explained by the suggestion that thermal effects on body size are stronger in larger-bodied species (Daufresne *et al.*, 2009; Forster *et al.*, 2012; Peck *et al.*, 2013). While CTmax is not typically representative of actual

Table 2 Log-linear relationships between body mass and mass-specific standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) for adult *P. leopardus* at 28.5 °C (ambient temperature) and 33 °C following 3–5 days of exposure. Log-linear relationship between body mass and CTmax for fish acclimated to ambient temperature is also presented (Fig. 2)

Variable (y)	a (SE)	b (SE)	R^2	df	F	P
SMR (28.5 °C)	0.122 ± 0.053	−0.041 ± 0.125	0.004	1, 29	0.107	0.747
SMR (33 °C)	0.627 ± 0.050	−0.113 ± 0.115	0.088	1, 10	0.960	0.350
MMR (28.5 °C)	1.461 ± 0.024	−0.115 ± 0.057	0.125	1, 29	4.138	0.051
MMR (33 °C)	1.632 ± 0.032	−0.260 ± 0.072	0.565	1, 10	13.00	0.005
AS (28.5 °C)	1.141 ± 0.031	−0.133 ± 0.073	0.102	1, 29	3.276	0.081
AS (33 °C)	1.164 ± 0.047	−0.351 ± 0.107	0.518	1, 10	10.74	0.008
CTmax	3.636 ± 0.001	−0.012 ± 0.003	0.604	1, 14	20.84	<0.001

Equations are solved as $y = \exp(a) \times \text{mass}^b$. ANCOVAS were used to test for common slopes and elevations between temperatures within a metabolic variable. For SMR, slopes were not significantly different ($F_{1,55} = 1.152$, $P = 0.288$), but elevations were ($F_{1,56} = 37.24$, $P < 0.001$). Slopes were significantly different for MMR ($F_{1,55} = 4.730$, $P = 0.034$). Slopes and elevations were not significantly different for AS ($F_{1,55} = 2.257$, $P = 0.139$; $F_{1,56} = 1.205$, $P = 0.277$, respectively).

Table 3 Results of log-linear regression models for the relationship between body mass and critical thermal maximum (CTmax) including starting temperature and the best model based on model selection (Fig. 2d)

	Estimate	SE	t-value	P-value
Full model ($R^2 = 0.604$, adj. $R^2 = 0.543$, $F_{2,13} = 9.912$, $P = 0.002$, AIC = −165.45)				
Intercept	3.677	0.0946	38.853	<0.001
Body mass	−0.0118	0.0027	−4.452	<0.001
Start temperature	−0.0124	0.0285	−0.434	0.671
Best model ($R^2 = 0.598$, adj. $R^2 = 0.570$, $F_{1,14} = 20.84$, $P = <0.001$, AIC = −154.63)				
Intercept	3.636	0.0013	2811.176	<0.001
Body mass	−0.0117	0.0026	−4.565	<0.001

temperatures that can be tolerated during long-term thermal exposures, it represents a standard acute screening technique that has been shown to provide a relative index of thermal tolerance at lower heating rates (Paladino *et al.*, 1980; Beitinger & Mccauley, 1990; Mora & Maya, 2006; Chown *et al.*, 2009). Therefore, the qualitative relationship between body mass and CTmax for *P. leopardus* is likely to persist at lower heating rates and reflect the relative thermal tolerance of individuals experiencing transient temperature spikes in the natural environment (Sunday *et al.*, 2012). It must be noted, however, that heating rates are influential in CTmax tests and should be taken into account when comparing across studies (Rezende *et al.*, 2014). Many tropical animals, including coral reef fishes, appear to already live close to their thermal limit, such that the forecasted increases in the frequency and severity of heatwaves are likely to increasingly compromise animal fitness (Hoegh-Guldberg *et al.*, 2007; Munday *et al.*, 2008; Tewksbury *et al.*, 2008; Dillon *et al.*, 2010; Pearce & Feng, 2013; Wernberg *et al.*, 2013).

Standard metabolic rate (SMR) of *P. leopardus* displayed thermal compensation, whereby individuals at 33 °C exhibited a significantly reduced SMR following 4–5 weeks of acclimation compared with the same individuals after only 3–5 days of acclimation. Despite this, the thermal compensation was incomplete, such that long-term acclimated animals at 33 °C maintained higher SMR than animals acclimated to 28.5 °C. This finding is consistent with established literature on the thermal effects on SMR in ectotherms (Bullock, 1955). As a result, greater food intake and/or lower activity levels would be required at the higher temperature to maintain the same energy balance as at the cooler temperature (e.g. energy for maintenance and somatic/reproductive investment). Although *P. leopardus* has been reported to increase the frequency of food intake at higher temperatures when fed *ad libitum* in experimental tanks (Johansen *et al.*, 2015), presumably to offset increased metabolic demands, prey availability can be inconsistent in the natural environment and a greater investment of energy may be required to support higher foraging rates. However, activity levels and swimming speeds of *P. leopardus* were reported to decrease at higher temperatures in experimental tanks (Johansen *et al.*, 2014), such that increased metabolic demands may be jeopardized by a decrease in foraging activity. If so, with climate warming, we expect that growth rate and maximum body size will be compromised in favour of other critical and energetically demanding processes, such as reproduction (e.g. Sheridan & Bickford, 2011). Given that fecundity is positively correlated with body size in fish, thermally mediated changes in maximal body size represent a meaningful change in a key life-history parameter that will likely influence demography.

Absolute aerobic scope was size-dependent but maintained across the temperature range in the present study. However, a maintenance of absolute aerobic scope at 33 °C, a temperature 3 °C above current summer maxima, should not be perceived as complete thermal tolerance to these elevated temperatures; thermal limits for other vital processes and overall fitness may differ substantially from the thermal limits for aerobic scope (Clark *et al.*, 2013b,c; Jutfelt *et al.*, 2014; Norin *et al.*, 2014). Despite the maintenance of absolute aerobic scope across temperatures, there was a decrease of approximately 30% in factorial aerobic scope at 33 °C compared with 28.5 °C. While there is little consensus in the literature whether aerobic or factorial aerobic scope has greater relevance to the energetics and fitness of fishes in the natural environment (Clark *et al.*, 2013b), the decrease in factorial aerobic scope due to increasing SMR with temperature in *P. leopardus* indicates that a larger proportion of energy must be allocated to the maintenance of basic body functions, and the proportional capacity to accommodate simultaneous energy-demanding processes (e.g. swimming, digestion) may be compromised at higher temperatures.

The effects of climate change on large predatory and commercially important coral reef fishes are attracting considerable research attention, given the proposed vulnerability of tropical fishes and fisheries to ocean warming. Our results indicate that large adults may be less resistant to increases in temperature than smaller individuals, which could result in population-level decreases in body size, especially at lower latitudes where populations may be already approaching their thermal limits. Accordingly, based on modelled growth, *P. leopardus* at the southern (cooler) end of the Great Barrier Reef (GBR) reach a maximum length that is 21% larger than those at the northern end of the GBR (Brown *et al.*, 1994). If climate warming further exacerbates this temperature–size effect and holds true for other large species, the ramifications for fisheries and population dynamics (e.g. reproductive output) will be significant (Baudron *et al.*, 2014). *P. leopardus* is one of the larger predators on coral reefs and plays an important role in structuring fish communities and maintaining ecosystem health (Ritchie & Johnson, 2009; Schmitz *et al.*, 2010; Estes *et al.*, 2011; Ripple *et al.*, 2014). Reductions in body size of this large predator will affect the size of prey that can be ingested with potential effects on size distributions of smaller reef fishes, possible trophic cascades and therefore consequences for ecosystem function. Reductions in body size could also have detrimental implications for this important fishery, as larger female *P. leopardus* are disproportionately important to the reproductive output of the breeding population (Carter *et al.*, 2015). The extent to which our findings may be applied to other regions or systems should be addressed in future studies using similar approaches as used here, but also including additional fitness-related performance metrics at different levels of biological organization (e.g. growth rate, fecundity, swimming capacity, ionic status, neural function).

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References

Angilletta MJ, Dunham AE (2003) The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *American Naturalist*, **162**, 332–342.

Angilletta MJ, Steury TD, Sears MW (2004) Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, **44**, 498–509.

Arendt J (2007) Ecological correlates of body size in relation to cell size and cell number: patterns in flies, fish, fruits and foliage. *Biological Reviews*, **82**, 241–256.

Atkinson D (1994) Temperature and organism size – a biological law for ectotherms. *Advances in Ecological Research*, **25**, 1–58.

Atkinson D, Morley SA, Hughes RN (2006) From cells to colonies: at what levels of body organization does the 'temperature-size rule' apply? *Evolution & Development*, **8**, 202–214.

Baudron AR, Needle CL, Rijnsdorp AD, Marshall CT (2014) Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Global Change Biology*, **20**, 1023–1031.

Becker CD, Genoway RG (1979) Evaluation of the critical thermal maximum for determining thermal tolerance of freshwater-fish. *Environmental Biology of Fishes*, **4**, 245–256.

Beitinger TL, Mccauley RW (1990) Whole-animal physiological processes for the assessment of stress in fishes. *Journal of Great Lakes Research*, **16**, 542–575.

Beitinger TL, Bennett WA, Mccauley RW (2000) Temperature tolerances of North American freshwater fishes exposed to dynamic changes in temperature. *Environmental Biology of Fishes*, **58**, 237–275.

Bell JD, Ganachaud A, Gehrke PC *et al.* (2013) Mixed responses of tropical Pacific fisheries and aquaculture to climate change. *Nature Climate Change*, **3**, 591–599.

Bergmann C (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Studien*, **3**, 595–708.

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, Sams S (1978) Relationships between body size and some life-history parameters. *Oecologia*, **37**, 257–272.

Brett JR, Groves TDD (1979) 6 – Physiological energetics. In: *Fish Physiology* (eds Hoar WS, Randall DJ, Brett JR), pp. 279–352. Academic Press, New York.

Brown IW, Doherty P, Ferreira B *et al.* (1994) Growth, reproduction and recruitment of Great Barrier Reef food fish stocks. Project No. 90/18. Australian Fisheries Research and Development Corporation (FRDC), Canberra.

Bullock TH (1955) Compensation for temperature in the metabolism and activity of poikilotherms. *Biological Reviews*, **30**, 311–342.

Carey N, Sigwart JD (2014) Size matters: plasticity in metabolic scaling shows body-size may modulate responses to climate change. *Biology Letters*, **10**, 20140408.

Carter AB, Carton AG, Mccormick MI, Tobin AJ, Williams AJ (2015) Maternal size, not age, influences egg quality of a wild, protogynous coral reef fish *Plectropomus leopardus*. *Marine Ecology Progress Series*, **529**, 249–263.

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Zeller D, Pauly D (2010) Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology*, **16**, 24–35.

Cheung WWL, Sarmiento JL, Dunne J *et al.* (2013) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, **3**, 254–258.

Chown SL, Jumbam KR, Sorensen JG, Terblanche JS (2009) Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. *Functional Ecology*, **23**, 133–140.

Clark TD, Donaldson MR, Pieperhoff S *et al.* (2012) Physiological benefits of being small in a changing world: responses of Coho salmon (*Oncorhynchus kisutch*) to an acute thermal challenge and a simulated capture event. *PLoS ONE*, **7**, e39079.

Clark MS, Husmann G, MaS Thorne *et al.* (2013a) Hypoxia impacts large adults first: consequences in a warming world. *Global Change Biology*, **19**, 2251–2263.

Clark TD, Sandblom E, Jutfelt F (2013b) Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *Journal of Experimental Biology*, **216**, 2771–2782.

Clark TD, Sandblom E, Jutfelt F (2013c) Response to Farrell and to Pörtner and Giomi. *Journal of Experimental Biology*, **216**, 4495–4497.

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, **68**, 893–905.

Coulson T, Catchpole EA, Albon SD *et al.* (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.

Czarnoleski M, Ejsmont-Karabin J, Angilletta MJ, Kozlowski J (2015) Colder rotifers grow larger but only in oxygenated waters. *Ecosphere*, **6**, 164.

Darveau CA, Suarez RK, Andrews RD, Hochachka PW (2002) Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature*, **417**, 166–170.

Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 12788–12793.

Dawson WR (1975) On the physiological significance of the preferred body temperature of reptiles. In: *Perspectives of Biophysical Ecology*, Ecological Studies (eds Gates DM, Schmerl RB), pp. 433–473. Springer-Verlag, New York.

Devor DP, Kuhn DE, O'brien KM, Crockett EL (2016) Hyperoxia does not extend critical thermal maxima (CTmax) in white- or red-blooded Antarctic notothenioid fishes. *Physiological and Biochemical Zoology*, **89**, 1–9.

Dillon ME, Wang G, Huey RB (2010) Global metabolic impacts of recent climate warming. *Nature*, **467**, 704–706.

Durant JM, Hjermann DO, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.

Eliason EJ, Clark TD, Hague MJ *et al.* (2011) Differences in thermal tolerance among sockeye salmon populations. *Science*, **332**, 109–112.

Ern R, Huong DTT, Phuong NT, Madsen PT, Wang T, Bayley M (2015) Some like it hot: thermal tolerance and oxygen supply capacity in two eurythermal crustaceans. *Scientific Reports*, **5**, 10743.

Estes JA, Terborgh J, Brashares JS *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.

Farrell AP (2009) Environment, antecedents and climate change: lessons from the study of temperature physiology and river migration of salmonids. *Journal of Experimental Biology*, **212**, 3771–3780.

Feary DA, Pratchett MS, Emslie MJ *et al.* (2014) Latitudinal shifts in coral reef fishes: why some species do and others do not shift. *Fish and Fisheries*, **15**, 593–615.

Forster J, Hirst AG, Atkinson D (2012) Warming-induced reductions in body size are greater in aquatic than terrestrial species. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 19310–19314.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R (2011) Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, **26**, 285–291.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.

Glazier DS (2005) Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. *Biological Reviews*, **80**, 611–662.

Glazier DS, Butler EM, Lombardi SA, Deptola TJ, Reese AJ, Satterthwaite EV (2011) Ecological effects on metabolic scaling: amphipod responses to fish predators in freshwater springs. *Ecological Monographs*, **81**, 599–618.

Green BS (2008) Chapter 1 Maternal effects in fish populations. *Advances in Marine Biology*, **54**, 1–105.

Hoegh-Guldberg O, Mumby PJ, Hooten AJ *et al.* (2007) Coral reefs under rapid climate change and ocean acidification. *Science*, **318**, 1737–1742.

Hofmann GE, Todgham AE (2010) Living in the now: physiological mechanisms to tolerate a rapidly changing environment. *Annual Review of Physiology*, **72**, 127–145.

Horne CR, Hirst AG, Atkinson D (2015) Temperature-size responses match latitudinal-size clines in arthropods, revealing critical differences between aquatic and terrestrial species. *Ecology Letters*, **18**, 327–335.

Hou C, Zuo W, Moses ME, Woodruff WH, Brown JH, West GB (2008) Energy uptake and allocation during ontogeny. *Science*, **322**, 736–739.

Iftikar FI, Hickey AJR (2013) Do mitochondria limit hot fish hearts? Understanding the role of mitochondrial function with heat stress in *Notolabrus celidotus*. *PLoS ONE*, **8**, e64120.

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.

Johansen JL, Messmer V, Coker DJ, Hoey AS, Pratchett MS (2014) Increasing ocean temperatures reduce activity patterns of a large commercially important coral reef fish. *Global Change Biology*, **20**, 1067–1074.

Johansen JL, Pratchett MS, Messmer V, Coker DJ, Tobin AJ, Hoey AS (2015) Large predatory coral trout species unlikely to meet increasing energetic demands in a warming ocean. *Scientific Reports*, **5**, 13830.

Jutfelt F, Gräns A, Jonsson E *et al.* (2014) Response to 'How and how not to investigate the oxygen and capacity limitation of thermal tolerance (OCLTT) and aerobic scope – remarks on the article by Grans et al.'. *Journal of Experimental Biology*, **217**, 4433–4435.

Kieffer JD (2000) Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology – Part A: Molecular & Integrative Physiology*, **126**, 161–179.

Killen SS, Atkinson D, Glazier DS (2010) The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecology Letters*, **13**, 184–193.

Kingsolver JG, Huey RB (2008) Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, **10**, 251–268.

Millien V, Lyons SK, Olson L, Smith FA, Wilson AB, Yom-Tov Y (2006) Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**, 853–869.

Mora C, Maya MF (2006) Effect of the rate of temperature increase of the dynamic method on the heat tolerance of fishes. *Journal of Thermal Biology*, **31**, 337–341.

Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for coral reef fishes. *Fish and Fisheries*, **9**, 261–285.

Norin T, Clark TD (2016) Measurement and relevance of maximum metabolic rate in fishes. *Journal of Fish Biology*, **88**, 122–151.

Norin T, Malte H, Clark TD (2014) Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. *Journal of Experimental Biology*, **217**, 244–251.

Ohlberger J (2013) Climate warming and ectotherm body size – from individual physiology to community ecology. *Functional Ecology*, **27**, 991–1001.

Ohlberger J, Mehner T, Staaks G, Holker F (2012) Intraspecific temperature dependence of the scaling of metabolic rate with body mass in fishes and its ecological implications. *Oikos*, **121**, 245–251.

Ospina AF, Mora C (2004) Effect of body size on reef fish tolerance to extreme low and high temperatures. *Environmental Biology of Fishes*, **70**, 339–343.

Paladino FV, Spotila JR, Schubauer JP, Kowalski KT (1980) The critical thermal maximum – a technique used to elucidate physiological stress and adaptation in fishes. *Revue Canadienne De Biologie*, **39**, 115–122.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pearce AF, Feng M (2013) The rise and fall of the "marine heat wave" off Western Australia during the summer of 2010/2011. *Journal of Marine Systems*, **111**, 139–156.

Peck LS, Webb KE, Bailey DM (2004) Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology*, **18**, 625–630.

Peck LS, Clark MS, Morley SA, Massey A, Rossetti H (2009) Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology*, **23**, 248–256.

Peck LS, Souster T, Clark MS (2013) Juveniles are more resistant to warming than adults in 4 species of Antarctic marine invertebrates. *PLoS ONE*, **8**, e66033.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science*, **308**, 1912–1915.

Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, **315**, 95–97.

Pratchett MS, Messmer V, Reynolds A *et al.* (2013) Effects of climate change on reproduction, larval development, and adult health of coral trout (*Plectropomus* spp.). Project No. 2010/2554. Australian Fisheries Research and Development Corporation (FRDC), Canberra.

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Current Opinion in Environmental Sustainability*, **7**, 37–43.

Ray C (1960) The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology*, **106**, 85–108.

Recsetar MS, Zeigler MP, Ward DL, Bonar SA, Caldwell CA (2012) Relationship between fish size and upper thermal tolerance. *Transactions of the American Fisheries Society*, **141**, 1433–1438.

Reidy SP, Nelson JA, Tang Y, Kerr SR (1995) Postexercise metabolic-rate in atlantic cod and its dependence upon the method of exhaustion. *Journal of Fish Biology*, **47**, 377–386.

Rezende EL, Castaneda LE, Santos M (2014) Tolerance landscapes in thermal ecology. *Functional Ecology*, **28**, 799–809.

Righton DA, Andersen KH, Neat F *et al*. (2010) Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. *Marine Ecology Progress Series*, **420**, 1–13.

Ripple WJ, Estes JA, Beschta RL *et al.* (2014) Status and ecological effects of the world's largest carnivores. *Science*, **343**, 1241484.

Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**, 982–998.

Roche DG, Binning SA, Bosiger Y, Johansen JL, Rummer JL (2013) Finding the best estimates of metabolic rates in a coral reef fish. *Journal of Experimental Biology*, **216**, 2103–2110.

Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, **24**, 1000–1005.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Schmitz OJ, Hawlena D, Trussell GC (2010) Predator control of ecosystem nutrient dynamics. *Ecology Letters*, **13**, 1199–1209.

Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. *Nature Climate Change*, **1**, 401–406.

Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*, **213**, 912–920.

Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan KS, Lima M (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.

Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

Taylor SG (2008) Climate warming causes phenological shift in Pink salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Global Change Biology*, **14**, 229–235.

Tewksbury JJ, Huey RB, Deutsch CA (2008) Ecology – putting the heat on tropical animals. *Science*, **320**, 1296–1297.

Verberk W, Atkinson D (2013) Why polar gigantism and Palaeozoic gigantism are not equivalent: effects of oxygen and temperature on the body size of ectotherms. *Functional Ecology*, **27**, 1275–1285.

Verberk W, Overgaard J, Ern R, Bayley M, Wang T, Boardman L, Terblanche JS (2016) Does oxygen limit thermal tolerance in arthropods? A critical review of current evidence. *Comparative Biochemistry and Physiology – Part A: Molecular & Integrative Physiology*, **192**, 64–78.

Vindenes Y, Edeline E, Ohlberger J, Langangen O, Winfield IJ, Stenseth NC, Vollestad LA (2014) Effects of climate change on trait-based dynamics of a top predator in freshwater ecosystems. *American Naturalist*, **183**, 243–256.

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2561–2569.

Vornanen M, Haverinen J, Egginton S (2014) Acute heat tolerance of cardiac excitation in the brown trout (*Salmo trutta fario*). *Journal of Experimental Biology*, **217**, 299–309.

Walther GR, Post E, Convey P *et al*. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wernberg T, Smale DA, Tuya F *et al.* (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, **3**, 78–82.

White CR, Phillips NF, Seymour RS (2006) The scaling and temperature dependence of vertebrate metabolism. *Biology Letters*, **2**, 125–127.

Xiao X, White EP, Hooten MB, Durham SL (2011) On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. *Ecology*, **92**, 1887–1894.

Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecology Letters*, **13**, 1–10.