

# Rapid transgenerational acclimation of a tropical reef fish to climate change

J. M. Donelson<sup>1,2\*</sup>, P. L. Munday<sup>1</sup>, M. I. McCormick<sup>1</sup> and C. R. Pitcher<sup>3</sup>

**Understanding the capacity of species to acclimate and adapt to expected temperature increases is critical for making predictions about the biological impacts of global warming, yet it is one of the least certain aspects of climate change science<sup>1–4</sup>. Tropical species are considered to be especially sensitive to climate change because they live close to their thermal maximum and exhibit limited capacity for acclimation<sup>5–7</sup>. Here, we demonstrate that a tropical reef fish is highly sensitive to small increases in water temperature, but can rapidly acclimate over multiple generations. Acute exposure to elevated temperatures (+1.5 °C and +3.0 °C) predicted to occur this century caused a 15% and 30% respective decrease in individual's maximum ability to perform aerobic activities such as swimming or foraging, known as aerobic scope. However, complete compensation in aerobic scope occurred when both parents and offspring were reared throughout their lives at elevated temperature. Such acclimation could reduce the impact of warming temperatures and allow populations to persist across their current range. This study reveals the importance of transgenerational acclimation as a mechanism for coping with rapid climate change and highlights that single generation studies risk underestimating the potential of species to cope.**

Ocean temperatures are expected to become adverse for many marine species within the next 50–100 years because of global warming<sup>8,9</sup>, however acclimation and adaptation could allow future populations to adjust to increased temperatures<sup>4,5,10</sup>. Although acclimation of physiological processes, such as metabolic function, usually occurs within a generation<sup>11</sup>, parental effects (influences on offspring phenotype that are not solely due to offspring genotype) can also facilitate some acclimatory processes between generations (termed transgenerational effects<sup>12,13</sup>). Tropical species are expected to have less capacity for thermal acclimation than temperate species because they have evolved in a more stable thermal environment<sup>5–7</sup>. There is also some evidence that plasticity and capacity for genetic adaptation may be linked<sup>14</sup>, indicating that limited capacity for thermal acclimation may relate to restricted potential for long-term adaptation to global warming.

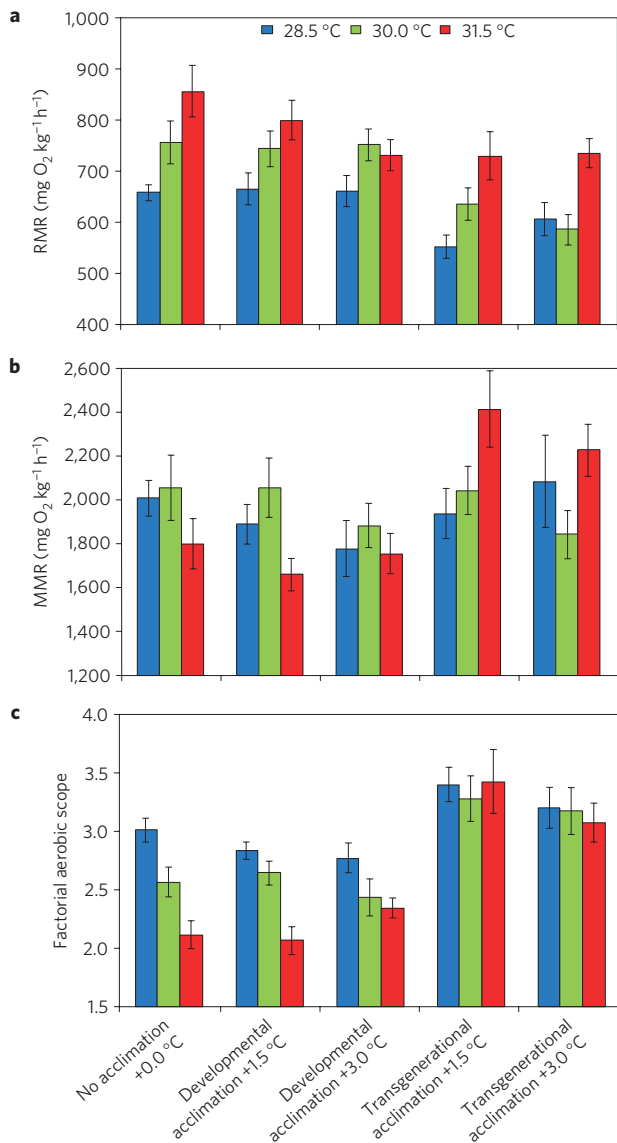
For water-breathing ectotherms, such as fish, the capacity to meet increased oxygen demands at elevated temperature will determine their persistence across locations with ocean warming<sup>15</sup>. Specifically, as ambient temperature increases, a greater rise in resting metabolic rate (RMR) occurs relative to maximum metabolic rate (MMR), reducing scope for aerobic activity<sup>15</sup>. This decline in aerobic scope affects critical biological functions, including behaviour, growth and reproduction, owing to limited capacity of circulatory and ventilatory systems to match oxygen demands<sup>15,16</sup>. At present we have a limited understanding of how aquatic species might be able to alter their

physiology over multiple generations to enable persistence in a warmer environment<sup>4,17</sup>.

We reared siblings from eight wild parental lineages of the tropical damselfish *Acanthochromis polyacanthus* for two generations in present-day (+0.0 °C) and predicted future increased water temperatures (+1.5 and +3.0 °C) to test their capacity for metabolic acclimation to ocean warming. The metabolic performance of F2 (second generation of offspring) fish at their summer average rearing temperature was influenced by whether individuals had the opportunity for no acclimation, developmental acclimation or transgenerational acclimation (Fig. 1). For fish with no opportunity to acclimate, an increase in temperature caused an increase in RMR, a decline in MMR at the warmest temperature, and a progressive decline in factorial (MMR/RMR) and net aerobic scope (MMR–RMR), which are common trends for tropical coral reef fish<sup>18,19</sup>. Developmental acclimation significantly reduced RMR, compared with no acclimation, but only for +3.0 °C fish at 31.5 °C (Fig. 1a). A lack of increase in MMR for developmental acclimation fish (Fig. 1b) resulted in no significant increase in factorial aerobic scope (Fig. 1c). A similar result was observed for net aerobic scope (Supplementary Information). In contrast, transgenerational acclimation enabled fish to completely restore their aerobic scope (Fig. 1c and Supplementary Fig. S1). Transgenerational acclimation individuals achieved increased scope, compared with fish not acclimated, at 30.0 °C by reducing RMR and at 31.5 °C by both reducing RMR and increasing MMR (Fig. 1). The magnitude of the reduction of RMR in developmental and transgenerational acclimation +3.0 °C fish at 31.5 °C was similar; possibly indicating that physiological mechanisms to reduce RMR may be limited. Increased MMR was exhibited only by transgenerational acclimation groups at 31.5 °C (Fig. 1b). Changes in tissue mitochondrial densities or key oxygen transport characteristics, such as cardiac capacity and blood transport ability, are likely explanations of differences in RMR and MMR, and consequently of differences in aerobic scope<sup>20</sup>. Acclimation of oxygen transport and utilization to warmer temperatures has been observed in temperate marine fishes<sup>21,22</sup>. Furthermore, some evidence exists for adaptation of cardiac capacity between populations with varying thermal regimes<sup>10</sup>, indicating that modifications to oxygen delivery may be critical in coping with climate change.

Not only did the performance of fish at their average summer temperature differ between acclimation groups, but so did their performance across the three testing temperatures (Fig. 1 and Supplementary Table S1). The most striking difference was that the transgenerational acclimation group, at both +1.5 and +3.0 °C, maintained scope across all temperatures, whereas no other treatment groups did (Fig. 1c and Supplementary Fig. S1). The mechanism for maintaining aerobic scope could be through a widening of the thermal performance breadth (the range of temperatures

<sup>1</sup>ARC Centre of Excellence for Coral Reef Studies, and School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia, <sup>2</sup>Climate Adaptation Flagship CSIRO, Hobart, Tasmania 7001, Australia, <sup>3</sup>CSIRO Marine and Atmospheric Research, Brisbane, Queensland 4000, Australia. \*e-mail: jennifer.donelson@myjcu.edu.au.



**Figure 1 | Metabolic performance of acclimation groups across all summer treatment temperatures.** Resting metabolic rate (RMR) (a), maximum metabolic rate (MMR) (b), and factorial aerobic scope (c) of fish across the three summer average temperatures depending on acclimation treatments (mean  $\pm$  s.e.m.).

over which an organism performs well<sup>23</sup>). This is likely, because thermal optima often do not shift readily with temperature<sup>24</sup> and research on the present species found no evidence of season shifts in metabolic thermal optima<sup>19</sup>. This increase in aerobic scope was achieved by a reduction in RMR at all temperatures (Fig. 1a), relative to fish with no acclimation, and an increase in MMR at 31.5 °C (Fig. 1b). Fish with developmental acclimation, at either +1.5 °C or +3.0 °C, did not differ in their response across test temperatures compared to non-acclimated fish for most metabolic measures (except RMR of +3.0 °C at 31.5 °C). The difference in performance between developmental and transgenerational acclimation fish demonstrates that parental influences may be critical in coping with future temperatures, by allowing MMR and subsequently aerobic scope to be maintained. Furthermore, increases of only +1.5 °C are enough for F1 parents to produce offspring with superior metabolic performance at all summer temperatures.

From the F1 generation, 64% of fish reproduced in +0.0 °C, 54% in +1.5 °C and 36% in +3.0 °C. Successful reproduction in

fish is linked to energy storage<sup>25,26</sup>. An indicator of the amount of stored energy, and physical condition of fish generally, is the liver to body weight ratio (hepatosomatic index = HSI; ref. 27). The mean HSI of all F1 fish was significantly higher in elevated temperature treatments (Table 1). Furthermore, although the HSI of breeding and non-breeding F1 fish in either the +0.0 °C or +1.5 °C treatments did not differ, those F1 fish that reproduced at +3.0 °C had significantly greater HSI than non-breeders at the same temperature (Table 1). This indicates that a larger amount of stored energy may be required for reproduction at elevated temperatures, possibly because the liver is critical in the production of vitellogenin<sup>28</sup>. However, those F1 fish in +3.0 °C, with greatest HSI, were significantly shorter and lighter than fish from +0.0 °C or +1.5 °C (Table 1).

Eight genetic lineages from the F0 wild stock were evenly represented in the F1 population, allowing the investigation of the potential for genetic selection (adaptation). Evidence of rapid selection for particular genetic lineages was observed at the F1 +3.0 °C temperature, with 75% of all pairs that reproduced at this temperature comprising offspring of wild pair #41, whereas this genetic lineage was less prominent among reproducing pairs at +1.5 °C and +0.0 °C treatments (57% and 44% respectively). The selection of a genetic lineage at +3.0 °C indicates that, in addition to transgenerational acclimation, rapid selection of genotypes tolerant to thermal regimes could also occur in tropical marine fishes. Importantly, the increased contribution of wild pair #41 to the F2 generation did not affect our interpretation of complete acclimation in aerobic scope by transgenerational acclimation groups, because the improved performance seen in F2 transgenerational acclimation was observed across all lineages, not just offspring from #41 grandparents (Supplementary Table S2).

The rapid transgenerational acclimation observed in our experiments to temperatures expected by 2050–2100, including complete restoration of aerobic capacity, could allow species to persist across their present locations. The ability to acclimate and maintain aerobic capacity would also be expected to maintain performance in characteristics such as growth and swimming ability at elevated temperatures<sup>15,16</sup>. Non-genetic parental effects or epigenetic inheritance (phenotypic differences not originating from variations in DNA base sequences<sup>29</sup>) most likely explain the transgenerational acclimation to increased temperature. As the magnitude of response in the transgenerational +1.5 °C and +3.0 °C F2 offspring were equivalent, it is likely that the same mechanism operated in both treatments. Furthermore, it indicates that an increase of only +1.5 °C in the parental generation may be sufficient to ‘prepare’ offspring and enhance performance at +3.0 °C. One likely mechanism by which parents influenced the performance of offspring in the present study is through variation in their epigenetic state, which effects gene expression, potentially producing offspring of phenotypes more suited to their environment<sup>30</sup>. Another possible mechanism is by selection within the F1 generation for particular genotypes, which produce progeny with enhanced metabolic performance because of genetic differences. Although detailed physiological and genetic investigations would be needed to identify the means of transmission, these results clearly show that the attributes of progeny have been altered compared with their parents in response to elevated temperatures.

This study provides evidence that, contrary to some expectations, a tropical marine species has the capacity for acclimation and adaptation to temperature increases over timescales much shorter than the rate of anthropogenic climate change. Genetic diversity was reduced at the warmest temperature, owing to differential breeding success among familial lineages, which has a range of implications for future populations, including disease resistance and plasticity to further environmental changes<sup>31</sup>. Furthermore, physiological modifications involved in acclimation and adaptation may come at a cost to other attributes, such as growth<sup>11,19</sup>. Nevertheless, the discovery

**Table 1 | Average size and condition of F1 adults in temperature treatments.**

Temperature treatment	SL	Weight	HSI	HSI breeders	HSI non-breeders	Mann-Whitney U HSI breeder versus non-breeders
+0.0 °C	78.82 ± 1.23	21.55 ± 1.14	0.93 ± 0.05	0.93 ± 0.08	0.93 ± 0.05	Z = 0.33 n = 24 p = 0.75
+1.5 °C	79.13 ± 1.09	21.10 ± 0.91	1.09 ± 0.05	1.07 ± 0.08	1.09 ± 0.07	Z = 0.46 n = 25 p = 0.64
+3.0 °C	74.79 ± 1.18	17.73 ± 1.00	1.32 ± 0.05	1.51 ± 0.08	1.21 ± 0.05	Z = 12.05 n = 22 p = 0.007
ANOVA difference b/w treatments	<b>F<sub>2,69</sub> = 4.73</b> p < 0.01	<b>F<sub>2,69</sub> = 4.22</b> p = 0.019	<b>F<sub>2,69</sub> = 11.99</b> p < 0.001			

Mean (±s.e.m.) standard length (SL; mm), weight (g) and hepatosomatic index (HSI) of F1 adults at the conclusion of the experiment are shown. Bold indicates significant differences between temperature treatments (analysis of variance (ANOVA)) and between breeding and non-breeding fish within a temperature treatment (Mann-Whitney U).

that advantageous offspring phenotypes are produced within two generations could indicate that some tropical marine species are more capable of coping with global warming than has been suggested and illustrates a potential limitation of short-term experiments in predicting the long-term impacts of climate change<sup>32</sup>.

## Methods

We reared two generations of the damselfish *A. polyacanthus* in environmentally controlled conditions to investigate the potential for transgenerational effects to mediate the impact of expected temperature increases. To allow investigation of genotypic-driven effects, sibling fish from eight wild-caught parents were used to commence the experiment. Replicate clutches of F1 siblings were divided into three groups and reared until maturity with three seasonally cycling temperature treatments (+0.0 °C, +1.5 °C and +3.0 °C; Supplementary Fig. S2). F2 offspring produced by +0.0 °C F1 adults were divided into the three treatment temperatures at hatching and reared for three months at summer average temperatures (Supplementary Fig. S2; see Supplementary Methods for details). F2 offspring raised at +0.0 °C had 'no acclimation' and thus demonstrate the acute effects of temperature, whereas offspring raised at +1.5 °C and +3.0 °C could demonstrate 'developmental acclimation'. The F2 offspring produced by +1.5 °C and +3.0 °C treatment F1 adults comprised the 'transgenerational acclimation' treatment. At three months, the metabolic performance of all acclimation groups was tested using closed respirometry<sup>18,19</sup> at their own summer average temperature (+0.0 °C = 28.5 °C, +1.5 °C = 30.0 °C and +3.0 °C = 31.5 °C) and then one of the two other summer average temperatures (Supplementary Fig. S2).

Received 16 June 2011; accepted 9 November 2011;  
published online 4 December 2011

## References

- Hughes, T. P. *et al.* Climate change, human impacts, and the resilience of coral reefs. *Science* **301**, 929–933 (2003).
- Bradshaw, W. E. & Holzapfel, C. M. Evolutionary response to rapid climate change. *Science* **312**, 1477–1478 (2006).
- Munday, P. L., Jones, G. P., Pratchett, M. S. & Williams, A. J. Climate change and the future for coral reef fishes. *Fish Fish.* **9**, 261–285 (2008).
- Hofmann, G. E. & Todgham, A. E. Living in the now: Physiological mechanisms to tolerate a rapidly changing environment. *Annu. Rev. Physiol.* **72**, 127–145 (2010).
- Stillman, J. H. Acclimation capacity underlies the susceptibility to climate change. *Science* **301**, 65 (2003).
- Wright, S. J., Muller-Landau, H. C. & Schipper, J. The future of tropical species on warmer planet. *Conserv. Biol.* **23**, 1418–1426 (2009).
- Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. Putting heat on tropical animals. *Science* **320**, 1296–1297 (2008).
- Poloczanska, E. S. *et al.* Climate change and Australian marine life. *Oceanogr. Mar. Biol. Annu. Rev.* **45**, 407–478 (2007).
- Munday, P. L. *et al.* Climate change and coral reef connectivity. *Coral Reefs* **28**, 379–395 (2009).
- Elaison, E. J. *et al.* Differences in thermal tolerance among sockeye salmon populations. *Science* **332**, 109–112 (2011).
- Angilletta, M. J. Jr *Thermal Adaptation: A Theoretical and Empirical Synthesis* (Oxford Univ. Press, 2009).
- Mousseau, T. A. & Fox, C. W. The adaptive significance of maternal effects. *Trends Ecol. Evol.* **13**, 403–407 (1998).
- Rossiter, M. Incidence and consequence of inherited environmental effects. *Annu. Rev. Ecol. Syst.* **27**, 451–476 (1996).
- Lucassen, M., Koschnick, N., Eckerle, L. G. & Pörtner, H. O. Mitochondrial mechanisms of cold adaptation in cod (*Gadus morhua* L.) populations from different climatic zones. *J. Exp. Biol.* **209**, 2462–2471 (2006).

- Pörtner, H. O. & Knust, R. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97 (2007).
- Pörtner, H. O. & Farrell, A. P. Physiology and climate change. *Science* **322**, 690–692 (2008).
- Skelly, D. K. *et al.* Evolutionary responses to climate change. *Conserv. Biol.* **21**, 1353–1355 (2007).
- Nilsson, G. E., Crawley, N., Lunde, I. G. & Munday, P. L. Elevated temperature reduces the respiratory scope of coral reef fishes. *Glob. Change Biol.* **15**, 1405–1412 (2009).
- Donelson, J. M., Munday, P. L., McCormick, M. I. & Nilsson, G. E. Acclimation to predicted ocean warming through developmental plasticity in a tropical reef fish. *Glob. Change Biol.* **17**, 1712–1719 (2011).
- Perry, S. F. & Gilmour, K. M. in *Respiratory Physiology of Vertebrates: Life without Oxygen* (ed. Nilsson, G. E.) 49–94 (Cambridge Univ. Press, 2010).
- Guderley, H. & Johnston, I. A. Plasticity of fish muscle mitochondria with thermal acclimation. *J. Exp. Biol.* **199**, 1311–1317 (1996).
- Klaiman, J. M., Fenna, A. J., Shiels, H. A., Macris, J. & Gillis, T. E. Cardiac remodelling in fish: Strategies to maintain heart function during temperature change. *PLoS ONE* **6**, e24464 (2011).
- Huey, R. B. & Stevenson, R. D. Integrating thermal physiology and ecology or ectotherms: A discussion of approaches. *Am. Zool.* **19**, 357–366 (1979).
- Guderley, H., Leroy, P. H. & Gagné, A. Thermal acclimation, growth, and burst swimming of threespine stickleback: Enzymatic correlates and influence of photoperiod. *Physiol. Biochem. Zool.* **74**, 66–74 (2001).
- Tyler, C. R. & Sumpter, J. P. Oocyte growth and development in teleosts. *Rev. Fish Biol. Fish.* **6**, 287–318 (1996).
- Brooks, S., Tyler, C. R. & Sumpter, J. P. Egg quality in fish: What makes a good egg? *Rev. Fish Biol. Fish.* **7**, 387–416 (1997).
- Chellappa, S., Huntingford, F. A., Strang, R. H. C. & Thomson, R. Y. Condition factor and hepatosomatic index as estimates of energy status in male three-spined stickleback. *J. Fish Biol.* **47**, 775–787 (1995).
- Matty, A. J. *Fish Endocrinology* (Timber Press, 1985).
- Jablonka, E. & Raz, G. Transgenerational epigenetic inheritance: Prevalence, mechanisms and implications for the study of heredity and evolution. *Q. Rev. Biol.* **84**, 131–176 (2009).
- Bonduriansky, R. & Day, T. Non-genetic inheritance and its evolutionary implications. *Annu. Rev. Ecol. Syst.* **40**, 103–125 (2009).
- Reed, D. H. & Frankham, R. Correlation between fitness and genetic diversity. *Conserv. Biol.* **17**, 230–237 (2003).
- Leuzinger, S. *et al.* Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends Ecol. Evol.* **26**, 236–241 (2011).

## Acknowledgements

This study was supported by the ARC Centre of Excellence for Coral Reef Studies (P.L.M. and M.I.M.), the CSIRO Climate Adaptation Flagship (J.M.D.), the Australian Coral Reef Society (J.M.D.) and the GBRMPA Science for Management Awards (J.M.D.). Thanks to staff at JCU Research Aquarium Facility for logistical support. This project was completed under JCU Ethics A1233 and A1415.

## Author contributions

J.M.D., P.L.M. and M.I.M. designed the experiments. J.M.D. performed all the experiments and analysed the raw data. J.M.D., P.L.M., M.I.M. and C.R.P. wrote the paper. All authors provided intellectual input, read and approved the manuscript.

## Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/natureclimatechange](http://www.nature.com/natureclimatechange). Reprints and permissions information is available online at <http://www.nature.com/reprints>. Correspondence and requests for materials should be addressed to J.M.D.