



Introduction

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Physiological diversity, biodiversity patterns and global climate change: testing key hypotheses involving temperature and oxygen

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Documenting and explaining global patterns of biodiversity in time and space have fascinated and occupied biologists for centuries. Investigation of the importance of these patterns, and their underpinning mechanisms, has gained renewed vigour and importance, perhaps becoming pre-eminent, as we attempt to predict the biological impacts of global climate change. Understanding the physiological features that determine, or constrain, a species' geographical range and how they respond to a rapidly changing environment is critical. While the ecological patterns are crystallizing, explaining the role of physiology has just begun. The papers in this volume are the primary output from a Satellite Meeting of the Society of Experimental Biology Annual Meeting, held in Florence in July 2018. The involvement of two key environmental factors, temperature and oxygen, was explored through the testing of key hypotheses. The aim of the meeting was to improve our knowledge of large-scale geographical differences in physiology, e.g. metabolism, growth, size and subsequently our understanding of the role and vulnerability of those physiologies to global climate warming. While such an aim is of heuristic interest, in the midst of our current biodiversity crisis, it has an urgency that is difficult to overstate.

This article is part of the theme issue 'Physiological diversity, biodiversity patterns and global climate change: testing key hypotheses involving temperature and oxygen'.

One of the greatest challenges for scientists today is to assess the impacts, and implications, of anthropogenic climate change on biodiversity [1–4]. In particular, there is considerable interest in how the physiology of organisms responds to environmental variation along biogeographic gradients, and what this means for demographic processes and distributions [5,6]. Particularly important is the question voiced by Spicer & Gaston [7, p. 193]: 'How important is physiological differentiation between-individuals, between populations or between-species, in determining persistence in a changing environment (e.g. with climate change)?' This question is driven by the view that a better mechanistic understanding of how animals work may improve our predictive power, enabling us to forecast the outcomes for biodiversity of different climate scenarios [8–12].

Macrophysiology arose against the background of this challenge and these questions. It is still relatively new but developing rapidly [13–17]. Central to the field is the comparison of physiological traits between individuals, populations and species possessing different geographical distributions. This is set within the framework of the hierarchical structure of biodiversity and aims to uncover

the mechanisms that produce, or constrain, these patterns. Its growth is driven by the challenge of understanding what determines species distributions and how global climate change will alter those distributions. Its development is fuelled by the emergence of technology that allows non-invasive measurement of function and the appearance of novel techniques for analysing these large-scale patterns.

That abiotic environmental factors such as temperature and oxygen, in particular, may play key roles in structuring macrophysiological patterns, together with the rapid development of databases and analysis techniques, was the basis for a Satellite Meeting of the Society of Experimental Biology Annual Meeting (*The height, breadth and depth of physiological diversity: Variation across latitudinal, altitudinal and depth gradients*), held in Florence, Italy in July 2018. This theme issue is the primary output from that meeting. How mechanisms underpinning these patterns may be probed by testing some long-standing overarching hypotheses about how biological organisms work and/or are constrained (e.g. oxygen limitation) has raised the possibility of producing unified physiological principles for explaining spatial gradients in biodiversity. Even if not entirely successful, probing and critically evaluating such principles should inform some of the key questions and paradigms in macrophysiology. Some examples are the list of questions that conclude Spicer & Gaston's [7, pp. 192–193] *Physiological diversity*, six of the seven challenges to mechanistic physiologists to broaden their work to macrophysiological questions set out by Gaston *et al.* [16] in the major synthesis paper *Macrophysiology: a conceptual reunification*, and challenges 2, 3, 6 and 7 of the 10 major challenges set out by Chown & Gaston [17] in their paper on progress and prospects for that conceptual reunification. Thus a theme issue is the perfect vehicle through which to communicate such advances to those interested in macrophysiology and its interactions with global climate change.

The first seven contributions to this theme issue either forward, or test, hypotheses about the mechanisms animals have evolved to cope with spatial and temporal thermal heterogeneity. First, Sunday *et al.* [18] present latitudinal and elevational clines in both upper and lower thermal tolerance limits of organisms based on the largest global dataset yet amassed (937 species in total). They hypothesize that differences in patterns of episodic thermal extremes across biological realms could explain the fundamentally different patterns of thermal limits found among them, thus providing realm-specific updates to global macrophysiological 'rules' [16]. There are a number of hypotheses explaining how ectotherms cope with a reduction in environmental temperature with increasing latitude [5,6]. Kreiman *et al.* [19] have tested one of these, the metabolic homeostasis hypothesis [20], using amphibians. This hypothesis states that species should display the greatest thermal sensitivity in their metabolism at the colder end of the environmental temperatures they experience *in situ*. Maclean *et al.* [21] tested a number of key hypotheses about thermal tolerance and performance using 22 fruit fly (*Drosophila*) species, i.e. temperate species are more cold-tolerant, less heat-tolerant, more plastic, have broader thermal performance curves, and lower optimal temperatures, compared to tropical species. Staying with latitude Jurriaans & Hoogenboom [22] examine the thermal performance of Great Barrier Reef coral species widely distributed along a latitudinal gradient. They test whether species with broad geographical distributions are thermal

generalists that perform well across a broad range of temperatures, or whether there are subpopulations of locally adapted thermal specialists [5–7]. And then investigating what determines latitudinal patterns of voltinism (i.e. the number of generations produced annually), Kong *et al.* [23] attempt to reconcile two different models that have been advanced: one in which egg development and voltinism are seen as thermally determined traits, and another where the evolution of dormancy and the thermal sensitivity of development are independent influences on life history.

Challenging the idea of thermal niche conservatism [24], Bennett *et al.* [25] investigate the often overlooked possibility of intra-specific variation in thermal sensitivity (owing to phenotypic plasticity and/or local adaptation) that could result in too conservative an estimate of how marine ectotherms will respond to ocean warming. Following the theme of taking variation into account, only this time methodologically, there is a paper by Rezende & Bozinovic [26] on thermal performance curves. Such curves are commonly used to describe how environmental temperature affects various aspects of an ectotherm's biology. However, Rezende and Bozinovic highlight that there is no agreed formal framework to characterize these performance curves and explore which factors contribute to their variation; they address how biological integration and different levels of organization respond to thermal environments in ectotherm animals and plants. Therefore, they develop a nonlinear regression approach, and using it put forward the hypothesis that the thermal range for elevated performance should decrease at higher organization levels.

The remaining four contributions all involve oxygen in some way, with all but one focusing on oxygen limitation. Despite the widely held assumption that animal energetics must be of ecological significance, attempts to construct hypotheses that link aerobic scope (i.e. the capacity for aerobic metabolism), whole-organism performance and altered abundance and distribution of aquatic ectotherms in a changing climate have proved elusive. The oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis has been extremely useful in marshalling tests of how to probe these links but its generality remains controversial [27–29]. Against this backdrop, Ern [30] proposes his mechanistic framework for integrating a range of experimental traits for assessing metabolism and range boundaries of aquatic ectotherms in response to rising sea temperatures and progressive aquatic hypoxia. This novel approach could be construed by some as a challenge to OCLTT hypothesis, although others may view it as development of, or from, the OCLTT hypothesis. Asking whether giant polar amphipods be first to fare badly in an oxygen-poor ocean, Spicer & Morley [31] test three hypotheses that link oxygen to body size, namely the oxygen limitation hypothesis [32], the symmorphosis hypothesis [33] and the respiratory advantage hypothesis [34]. Leiva *et al.* [35] test the hypothesis that larger ectotherms, and particularly those belonging to aquatic taxa, will be more vulnerable to thermal extremes, and therefore will be more severely impacted by global warming, compared to smaller individuals [36]. This is predicated on the assumption (tested by Spicer & Morley [31]) that enhanced temperature vulnerability of large species is attributable to oxygen limitation. Leiva *et al.* [35] also postulate that such a limitation will be more prevalent in water than air.

Finally, Tan *et al.* [37] hypothesize that as cephalopods tend to have greater energetic costs of locomotion (as well as shorter lives and more sustained growth) than teleost fish, their ontogenic metabolic scaling will differ and this is reflected in the water depths they inhabit. That the body mass exponent depends on metabolic rate is termed the 'Metabolic-Level Boundaries Hypothesis' [38].

These articles together address the aim of the Florence meeting, to improve our knowledge of large-scale geographical differences in physiology, e.g. metabolism, growth, size and subsequently our understanding of the role and vulnerability of those physiologies to global climate warming.

While such an aim is of heuristic interest, in the midst of our current biodiversity crisis, it also has an urgency and importance that is difficult to overstate [39,40].

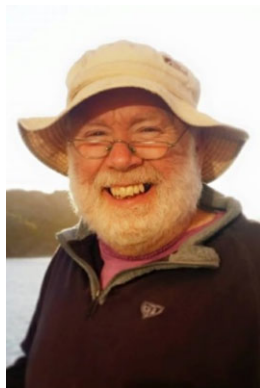
Data accessibility. This article has no additional data.

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Editors' biographies



John Spicer is a Professor of Marine Zoology at the University of Plymouth, UK. He received his PhD in Invertebrate Ecophysiology from the University of Glasgow, Scotland in 1986. His work centres on the response of marine invertebrates to hypoxia, ocean acidification and warming, singly and in combination, with a particular focus on incorporating the early developmental stages of animals into these studies.



Simon Morley is an ecophysiologicalist and part of the Biodiversity, Evolution and Adaptation Team, at the British Antarctic Survey in Cambridge, UK. He has conducted comparative physiological studies on marine ectotherms for more than 10 years. He received his PhD in Fish Ecophysiology from the University of Liverpool, UK in 1998. His work in polar oceans has been a key component of our developing knowledge of how marine ectotherms have evolved to the variability in their environment and how this advances our knowledge of species vulnerability across latitudes.



Francisco Bozinovic is a Professor of Evolutionary and Ecological Physiology at the Catholic University of Chile. He received his PhD from the University of Chile in 1988 for his work on the energetics of endotherms. He has long-standing interests in environmental physiology and evolutionary ecological physiology, and is particularly interested in the light these disciplines throw on the global and local distribution of species and how species cope with environmental variability and oncoming global change.

References

- Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB. 2015 Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science* **348**, 336–340. (doi:10.1126/science.aaa1788)
- Pecl GT *et al.* 2017 Biodiversity redistribution under climate change: impacts on ecosystems and human well being. *Science* **355**, eaai9214. (doi:10.1126/science.aai9214)
- Intergovernmental Panel on Climate Change. 2018 *Global Warming of 1.5°C: An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission*

- pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Geneva, Switzerland: World Meteorological Organization.
4. Lovejoy TE, Hannah L (eds). 2019 *Biodiversity and climate change*. New Haven, CT & London, UK: Yale University Press.
 5. Bozinovic F, Calosi P, Spicer JI. 2011 Physiological correlates of geographic range in animals. *Annu. Rev. Ecol. Syst.* **42**, 155–179. (doi:10.1146/annurev-ecolsys-102710-145055)
 6. Bozinovic F, Naya DE. 2015 Linking physiology, climate, and species distributional ranges. *Integr. Org. Biol.* **2015**, 277–290.
 7. Spicer JI, Gaston KJ. 1999 *Physiological diversity and its ecological implications*. Oxford, UK: Blackwell.
 8. Helmuth B, Kingsolver JG, Carrington E. 2005 Biophysics, physiological ecology, and climate change: does mechanism matter? *Annu. Rev. Physiol.* **67**, 177–201. (doi:10.1146/annurev.physiol.67.040403.105027)
 9. Pörtner HO, Farrell AP. 2008 Physiology and climate change. *Science* **322**, 690–692. (doi:10.1126/science.1163156)
 10. Somero GN. 2010 The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. *J. Exp. Biol.* **213**, 912–920. (doi:10.1242/jeb.037473)
 11. Vázquez DP, Gianoli E, Morris WF, Bozinovic F. 2017 Ecological and evolutionary impacts of changing climatic variability. *Biol. Rev.* **92**, 22–42. (doi:10.1111/brv.12216)
 12. Rilov G, Mazaris AD, Stelzenmüller V, Helmuth B, Wahl M, Guy-Haim T, Mieszkowska N, Ledoux JB, Katsanevakis S. 2019 Adaptive marine conservation planning in the face of climate change: what can we learn from physiological, genetic and ecological studies? *Glob. Ecol. Conserv.* **17**, e00566. (doi:10.1016/j.gecco.2019.e00566)
 13. Chown SL, Addo-Bediako A, Gaston KJ. 2003 Physiological diversity: listening to the large-scale signal. *Funct. Ecol.* **17**, 568–572. (doi:10.1046/j.1365-2435.2003.07622.x)
 14. Chown SL, Gaston KJ, Robinson D. 2004 Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Funct. Ecol.* **18**, 159–167. (doi:10.1111/j.0269-8463.2004.00825.x)
 15. Chown SL, Gaston KJ. 2008 Macrophysiology for a changing world. *Proc. R. Soc. B* **275**, 1469–1478. (doi:10.1098/rspb.2008.0137)
 16. Gaston KJ *et al.* 2009 Macrophysiology: a conceptual reunification. *Am. Nat.* **174**, 595–612. (doi:10.1086/605982)
 17. Chown SL, Gaston KJ. 2016 Macrophysiology – progress and prospects. *Funct. Ecol.* **30**, 330–344. (doi:10.1111/1365-2435.12510)
 18. Sunday J *et al.* 2019 Thermal tolerance patterns across latitude and elevation. *Phil. Trans. R. Soc. B* **374**, 20190036. (doi:10.1098/rstb.2019.0036)
 19. Kreiman LE, Solano-Iguaran JJ, Bacigalupe LD, Naya DE. 2019 Testing the metabolic homeostasis hypothesis in amphibians. *Phil. Trans. R. Soc. B* **374**, 20180544. (doi:10.1098/rstb.2018.0544)
 20. Cossins A, Bowler K. 1987 *Temperature biology of animals*. Dordrecht, The Netherlands: Springer.
 21. MacLean HJ, Sørensen JG, Kristensen TN, Loeschcke V, Beedholm K, Kellermann V, Overgaard J. 2019 Evolution and plasticity of thermal performance: an analysis of variation in thermal tolerance and fitness in 22 *Drosophila* species. *Phil. Trans. R. Soc. B* **374**, 20180548. (doi:10.1098/rstb.2018.0548)
 22. Jurriaans S, Hoogenboom MO. 2019 Thermal performance of scleractinian corals along a latitudinal gradient on the Great Barrier Reef. *Phil. Trans. R. Soc. B* **374**, 20180546. (doi:10.1098/rstb.2018.0546)
 23. Kong JD, Hoffmann AA, Kearney MR. 2019 Linking thermal adaptation and life-history theory explains latitudinal patterns of voltinism. *Phil. Trans. R. Soc. B* **374**, 20180547. (doi:10.1098/rstb.2018.0547)
 24. Wiens JJ *et al.* 2010 Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.* **13**, 1310–1324. (doi:10.1111/j.1461-0248.2010.01515.x)
 25. Bennett S, Duarte CM, Marbà N, Wernberg T. 2019 Integrating within-species variation in thermal physiology into climate change ecology. *Phil. Trans. R. Soc. B* **374**, 20180550. (doi:10.1098/rstb.2018.0550)
 26. Rezende EL, Bozinovic F. 2019 Thermal performance across levels of biological organization. *Phil. Trans. R. Soc. B* **374**, 20180549. (doi:10.1098/rstb.2018.0549)
 27. Pörtner HO, Bock C, Mark FC. 2017 Oxygen- and capacity-limited thermal tolerance: bridging ecology and physiology. *J. Exp. Biol.* **220**, 2685–2696. (doi:10.1242/jeb.134585)
 28. Jutfelt F *et al.* 2018 Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology. *J. Exp. Biol.* **221**, jeb169615. (doi:10.1242/jeb.169615)
 29. Pörtner HO, Bock C, Mark FC. 2018 Connecting to ecology: a challenge for comparative physiologists? Response to ‘Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology’. *J. Exp. Biol.* **221**, jeb174185. (doi:10.1242/jeb.174185)
 30. Ern R. 2019 A mechanistic oxygen- and temperature-limited metabolic niche framework. *Phil. Trans. R. Soc. B* **374**, 20180540. (doi:10.1098/rstb.2018.0540)
 31. Spicer JI, Morley SA. 2019 Will giant polar amphipods be first to fare badly in an oxygen-poor ocean? Testing hypotheses linking oxygen to body size. *Phil. Trans. R. Soc. B* **374**, 20190034. (doi:10.1098/rstb.2019.0034)
 32. Chapelle G, Peck LS. 1999 Polar gigantism dictated by oxygen availability. *Nature* **399**, 114. (doi:10.1038/20099)
 33. Woods HA, Moran AL, Arango CP, Mullen L, Shields C. 2008 Oxygen hypothesis of polar gigantism not supported by performance of Antarctic pycnogonids in hypoxia. *Proc. R. Soc. B* **276**, 1069–1075. (doi:10.1098/rspb.2008.1489)
 34. Verberk WCEP, Atkinson D. 2013 Why polar gigantism and Palaeozoic gigantism are not equivalent: effects of oxygen and temperature on the body size of ectotherms. *Funct. Ecol.* **27**, 1275–1285. (doi:10.1111/1365-2435.12152)
 35. Leiva FP, Calosi P, Verberk WCEP. 2019 Scaling of thermal tolerance with body mass and genome size in ectotherms: a comparison between water- and air-breathers. *Phil. Trans. R. Soc. B* **374**, 20190035. (doi:10.1098/rstb.2019.0035)
 36. Audzijonyte A, Barneche DR, Baudron AR, Belmaker J, Clark TD, Marshall CT, Morrongiello JR, van Rijn I. 2018. Is oxygen limitation in warming waters a valid mechanism to explain decreased body sizes in aquatic ectotherms? *Glob. Ecol. Biogeogr.* **28**, 64–67. (doi:10.1111/geb.12847)
 37. Tan H, Hirst AG, Glazier DS, Atkinson D. 2019 Ecological pressures and the contrasting scaling of metabolism and body shape in coexisting taxa: cephalopods versus teleost fish. *Phil. Trans. R. Soc. B* **374**, 20180543. (doi:10.1098/rstb.2018.0543)
 38. Isaac NJ, Carbone C. 2010 Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecol. Lett.* **13**, 728–735. (doi:10.1111/j.1461-0248.2010.01461.x)
 39. Kendall HW. 2000 World scientists’ warning to humanity. In *A distant light*, pp. 198–201. New York, NY: Springer.
 40. Ripple WJ, Wolf C, Newsome TM, Galetti M, Alamgir M, Crist E, Mahmoud MI, Laurance WF and 15,364 scientist signatories from 184 countries. 2017 World scientists’ warning to humanity: a second notice. *BioScience* **67**, 1026–1028. (doi:10.1093/biosci/bix125)