DOI: 10.1111/jfb.14762

EDITORIAL

JOURNAL OF FISH BIOLOGY fsbi

Effects of global warming on fishes and fisheries

The reality of global warming is now undeniable: many aquatic ecosystems are experiencing progressive increases in seasonal temperatures coupled with wider thermal variation, and an increased incidence of extreme heatwaves (Collins *et al*., 2019; Frölicher *et al*., 2018; IPCC, 2014). The vast majority of fishes are ectotherms so these climactic changes are likely to have strong effects on their physiology, with implications at the individual, population, and species level, and thus on the fisheries they sustain (McKenzie *et al*., 2016; Pörtner & Farrell, 2008; Pörtner & Peck, 2010; Seebacher & Franklin, 2012).

Three major phenomena have been documented as broadscale responses by fishes to the ongoing warming of their habitats: (a) latitudinal shifts in species distributions, with poleward movements by temperate and sub-tropical fishes (Hickling *et al*., 2006; Parmesan & Yohe, 2003; Perry *et al*., 2005; Poloczanska *et al*., 2013); (b) changes in phenology of major life-cycle events, for example the timing of migrations and spawning, or the length of reproductive seasons (Crozier & Hutchings, 2014; Myers *et al*., 2017; Poloczanska *et al*., 2013; Rogers & Dougherty, 2019), and (c) a reduction in average body size, linked to declines in final adult size and an increased proportion of younger and smaller individuals in populations (Audzijonyte *et al*., 2020; Daufresne *et al*., 2009; Gardner *et al*., 2011). The mechanisms underlying these phenomena are far from completely understood but they are assumed to be driven, at least in part, by physiological functions and responses of individual animals, which reflect either phenotypic plasticity or evolutionary processes (Goikoetxea *et al*., 2021; Huey *et al*., 2012; Pörtner & Farrell, 2008; Pörtner & Peck, 2010; Seebacher *et al*., 2015; Stillman, 2019; Wang & Overgaard, 2007).

This Special Issue (SI) follows a previous one published over a decade ago in the Journal of Fish Biology, entitled *Fishes and Climate Change* (Vol. 70 November 2010) and so provides an update on knowledge after the warmest decade since detailed temperature records began. As reflected in the title of this SI, *Effects of Global Warming on Fishes and Fisheries*, we aimed to bring together contributions that ranged from physiology to fisheries biology. Despite, however, casting our net wide among our fish biology colleagues, enthusiasm for further reviews of effects of warming on fish ecology and fisheries was low. On the other hand, our physiologist colleagues were keen to contribute, perhaps because although the significance of physiology for understanding responses by fishes to warming is intuitive, many unknowns remain and this is an active area of research in the fish physiology community.

Exactly how physiological effects of warming translate into ecologically relevant impacts remains a matter of conjecture. One of the most influential papers in the SI on *Fishes and Climate Change* was Pörtner and Peck (2010), which discussed a unifying theory, the Oxygen- and Capacity-Limited Thermal Tolerance (OCLTT) hypothesis (Pörtner, 2002, 2010), to explain how ectotherm physiology could determine their performance and fitness as a function of environmental conditions, especially temperature. Pörtner and Peck (2010) is one of the most highly-cited of all papers in the *Journal of Fish Biology* and the OCLTT theory has stimulated a wave of research by fish physiologists. The outcome has been controversy in the literature (Clark *et al*., 2013; Farrell, 2016; Jutfelt *et al*., 2018; Lefevre, 2016; Pörtner *et al*., 2017) and we have decided not continue the debate in this SI. Instead, we focus on various different aspects of how warming affects the physiology of fishes and how they respond to this, towards a broader overall understanding.

The SI comprises seven reviews and five research articles, and is published both in the normal run off issues but also as a "virtual issue" because some of its contributions were published as a result of a production error in various volumes of the Journal between 2020 and 2021. The general premise, that runs through all of the review articles, is that effects of temperature on physiological systems in individuals will scale up to influence population responses to warming. The consequences for population dynamics and phenology would influence patterns of distribution and abundance of species and communities. That is, because Darwinian fitness acts at the level of individuals, reliable information on thermal physiology is essential for fish biologists that aim to develop mechanistically-based models, to project the fate of fish populations and communities in a warmer world (Seebacher & Franklin, 2012; McKenzie *et al*., 2016).

The SI begins with a review by Little *et al*. (2021) on the principal physiological mechanisms that transduce temperature signals and the physiological responses to those signals in fishes. This review provides a grounding of how physiological processes within individuals might drive broader scale effects of global warming on populations and fisheries. Little *et al*. (2021) focus on effects of temperature on energy metabolism and the efficiency of converting oxygen to ATP, as a core mechanism by which changes in temperature affect individual performance. They link across levels of organization from mitochondrial function, to cardiovascular performance, growth efficiency, and locomotor muscle performance. They conclude by considering what is known about the neuroendocrine processes that link environmental signals with the responses of various tissues, including muscle.

Alix *et al*. (2020) provide an extensive review of the impacts of higher-than-optimal temperatures on teleost reproductive development and physiology, with an aim to understand the implications for population dynamics, fisheries, and aquaculture. The authors review how excessive warmth affects reproductive development from puberty to spawning, linked to changes in the brain-pituitary-gonad axis. They consider the environmental and biological factors that can modulate such impacts, and the negative consequences for gamete quality, spermiation/ovulation, and spawning. The review concludes by highlighting knowledge gaps and areas where emerging technologies may help to understand and project climate change impacts on fish reproductive physiology.

Temperature can affect sex determination in many fishes. Therefore, Geffroy and Wedekind (2020) review the various ways that warming can bias sex ratios in wild fish populations, with potentially profound consequences for population dynamics. They consider, in particular, effects on sex determination that act through the stress axis or epigenetic mechanisms, and through temperature-related differential mortality between sexes. A majority of laboratory studies indicate that, if temperature affects sex ratios, warming mostly causes a male bias, with some studies on wild populations confirming this general trend. The authors conclude with the glimmer of hope that transgenerational plasticity might mitigate effects of warming on sex ratios.

Alfonso *et al*. (2021) appraise information about effects of warming on stress physiology in fishes, based on laboratory studies, and how this may provide insight into what can be expected in wild populations. They consider how chronic temperature increase constitutes a physiological load that can alter the ability of fishes to cope with additional stressors, while extreme heatwaves would engender direct stress responses, all with potential consequences for fitness.

Feidantsis *et al*. (2021) propose that studying the impacts of climactic temperature variation, on fishes farmed in offshore cages, can provide valuable understanding of physiological responses in natural populations. Taking the gilthead seabream *Sparus aurata* L. 1758 in the Mediterranean Sea as a case study, they review impacts of natural thermal regimes on a diversity of biochemical and molecular markers of performance and stress, plus behaviours such as responsiveness and appetite. The evidence indicates that farmed seabream are already brought close to their thermal tolerance limits by the seasonal temperatures experienced at their cage sites, with a warmer future having important implications for aquaculture. The results may contribute to more accurate definition of tolerance limits in natural populations.

Morash *et al*. (2021) consider temperate freshwater fishes through the lens of spatiotemporal variation in thermal challenges they face. They review how the physiology, behaviour and overall performance of fishes, notably salmonids, is affected by oscillating temperatures, considering the potential extent of such thermal variation in rivers and impacts growth and metabolism. They also consider the challenges of quantifying the effects of thermal variation, and the scope for fishes to acclimatize or adapt.

McKenzie *et al*. (2021) focus on how intraspecific variation in thermal tolerance can be a key determinant of species vulnerability to global warming. The review considers empirical evidence for three elements of intraspecific variation in tolerance. Firstly, how tolerance varies across life stages, possibly due to universal physiological principles. Secondly, the extensive evidence of phenotypic plasticity in tolerance, where more research is required to understand underlying mechanisms and to reveal whether there are general patterns. Thirdly, the evidence of local adaptation and heritability of tolerance to warming, where the knowledge base is convincing but limited to a few model or emblematic species. The review concludes by considering the ecological and evolutionary significance of these forms of intraspecific variation, and the need for further research.

The SI then has five research articles, which are dominated by experimental physiology. Christensen *et al*. (2020) investigated how metabolism is affected by temperature and body size in European perch *Perca fluviatilis* L. 1758. They provide evidence that larger animals may perform less well at warm temperatures, with potential implications for effects of warming on perch sizes and distribution. Morissette *et al*. (2021) report that wild Atlantic salmon *Salmo salar* L. 1758 juveniles can tolerate thermal variation near their thermal optimum without effects on growth, metabolism or swimming performance. Musa *et al*. (2020) investigated the single or combined effects of ocean warming and hypoxia on embryonic growth, fitness and survival of an oviparous elasmobranch, the lesser spotted catshark *Scyliorhinus canicula* L. 1758. Results indicate that warming raises embryonic growth rate but leads to smaller animals at hatch, while hypoxia has generally negative effects on survival. Vargas-Chacoff *et al*. (2021) consider how increased freshwater inputs to coastal areas in Antarctica, due to global warming, challenge osmoregulatory homeostasis in a sedentary intertidal notothenioid fish, the Antarctic spiny plunderfish *Harpagifer antarcticus* Nybelin 1947. Results indicate that ongoing freshening causes osmotic imbalances in *H. antarcticus*, due to reduced osmoregulatory capacity in key organs. The SI concludes with a fisheries study, where Lloret *et al*. (2021) consider whether three deep-water species of ling (genus *Molva*) can rebuild populations depleted by fishing pressure, to conclude that this will be most difficult in southern areas of the species' ranges, also as a result of ongoing global warming.

We hope that fish biologists in fields other than physiology will find these reviews and research articles interesting. We hope that they find them informative when developing hypotheses about potential impacts of global warming on fish biology more broadly and fisheries specifically.

David J. McKenzie[1]
Benjamin Geffroy[1]
Anthony P. Farrell[2,3]

[1]*MARBEC, Univ Montpellier, CNRS, IFREMER, IRD, Montpellier, France*
[2]*Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada*
[3]*Faculty of Land and Food Systems, University of British Columbia, Vancouver, British Columbia, Canada*

REFERENCES

Alfonso, S., Gesto, M., & Sadoul, B. (2021). Temperature increase and its effects on fish stress physiology in the context of global warming. *Journal of Fish Biology*, *98*, 1496–1508.

Alix, M., Kjesbu, O. S., & Anderson, K. C. (2020). From gametogenesis to spawning: How climate-driven warming affects teleost reproductive biology. *Journal of Fish Biology*, *97*, 607–632.

Audzijonyte, A., Richards, S. A., Stuart-Smith, R. D., Pecl, G., Edgar, G. J., Barrett, N. S., … Blanchard, J. L. (2020). Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology & Evolution*, *1*, 1–6.

Christensen, E. A. F., Svendsen, M. B. S., & Steffensen, J. F. (2020). The combined effect of body size and temperature on oxygen consumption rates and the size-dependency of preferred temperature in European perch *Perca fluviatilis*. *Journal of Fish Biology*, *97*, 794–803.

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

Collins, M., Sutherland, M., Bouwer, L., Cheong, S.-M., Frölicher, T., Jacot Des Combes, H., … Tibig, L. (2019). Extremes, abrupt changes and managing risk. In H.-O. Pörtner, D. C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, et al. (Eds.), *IPCC special report on the ocean and cryosphere in a changing climate* Retrieved from: Geneva: IPCC. https://www.ipcc.ch/srocc/cite-report.

Crozier, L. G., & Hutchings, J. A. (2014). Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications*, *2014*, 68–87. https://doi.org/10.1111/eva.12135.

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.

Farrell, A. P. (2016). Pragmatic perspective on aerobic scope: Peaking, plummeting, Pejus and apportioning. *Journal of Fish Biology*, *88*, 322–343.

Feidantsis, K., Pörtner, H. O., Giantsis, I. A., & Michaelidis, B. (2021). Advances in understanding the impacts of global warming on marine fishes farmed offshore: *Sparus aurata* as a case study. *Journal of Fish Biology*, *98*, 1509–1523.

Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, *560*, 360–364.

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

Geffroy, B., & Wedekind, C. (2020). Effects of global warming on sex ratios in fishes. *Journal of Fish Biology*, *97*, 596–606.

Goikoetxea, A., Sadoul, B., Blondeau-Bidet, E., Aerts, J., Blanc, M. O., Parrinello, H., … Geffroy, B. (2021). Genetic pathways underpinning hormonal stress responses in fish exposed to short- and long-term warm ocean temperatures. *Ecological Indicators*, *120*, 106937.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D. (2006). The distributions of a wide range of taxonomic groups are expanding Polewards. *Global Change Biology*, *12*, 450–455.

Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. a. M., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*, 1665–1679.

IPCC. (2014). *Climate change 2014: Synthesis report*. Geneva, Switzerland: Intergovernmental Panel on Climate Change.

Jutfelt, F., Norin, T., Ern, R., Overgaard, J., Wang, T., McKenzie, D. J., … Clark, T. D. (2018). Oxygen- and capacity-limited thermal tolerance: Blurring ecology and physiology. *The Journal of Experimental Biology*, *221*, jeb169615.

Lefevre, S. (2016). Are global warming and ocean acidification conspiring against marine ectotherms ? A meta-analysis of the respiratory effects of elevated temperature, high CO 2 and their interaction. *Conservation Physiology*, *4*, 1–31.

Little, A. G., Loughland, I., & Seebacher, F. (2020). What do warming waters mean for fish physiology and fisheries? *Journal of Fish Biology*, *97*, 328–340.

Lloret, J., Serrat, A., Thordarson, G., Helle, K., Jadaud, A., Bruno, I., … Rätz, H. (2021). The poor health of deep-water species in the context of fishing activity and a warming climate: Will populations of *Molva* species rebuild or collapse? *Journal of Fish Biology*, *98*, 1572–1584.

McKenzie, D. J., Axelsson, M., Chabot, D., Claireaux, G., Cooke, S. J., Corner, R. A., … Hamer, B. (2016). Conservation physiology of marine fishes : State of the art and prospects for policy. *Conservation Physiology*, *4*, 1–20.

McKenzie, D. J., Zhang, Y., Eliason, E. J., Schulte, P. M., Blasco, F. R., Claireaux, G., … Farrell, A. P. (2021). Intraspecific variation in tolerance of warming in fishes. *Journal of Fish Biology*, *98*, 1536–1555.

Morash, A. J., Speers-Roesch, B., Andrew, S., & Currie, S. (2021). The physiological ups and downs of thermal variability in temperate freshwater ecosystems. *Journal of Fish Biology*, *98*, 1524–1535.

Morissette, J., Swart, S., MacCormack, T. J., Currie, S., & Morash, A. J. (2021). Thermal variation near the thermal optimum does not affect the growth, metabolism or swimming performance in wild Atlantic Salmon *Salmo salar*. *Journal of Fish Biology*, *98*, 1585–1589.

Musa, S. M., Ripley, D. M., Moritz, T., & Shiels, H. A. (2020). Ocean warming and hypoxia affect embryonic growth, fitness and survival of small-spotted catsharks *Scyliorhinus canicula*. *Journal of Fish Biology*, *97*, 257–264.

Myers, B. J. E., Lynch, A. J., Bunnell, D. B., Chu, C., Falke, J. A., Kovach, R. P., … Paukert, C. P. (2017). Global synthesis of the documented and projected effects of climate change on inland fishes. *Reviews in Fish Biology and Fisheries*, *27*, 339–361.

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

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*, 1912–1915.

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., … Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*, 919–925.

Pörtner, H. O. (2002). Climate variations and the physiological basis of temperature dependent biogeography: Systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *132*, 739–761.

Pörtner, H. O. (2010). Oxygen- and capacity-limitation of thermal tolerance: A matrix for integrating climate-related stressor effects in marine ecosystems. *Journal of Experimental Biology*, *213*, 881–893.

Pörtner, H. O., Bock, C., & Mark, F. C. (2017). Oxygen- & capacity-limited thermal tolerance: bridging ecology & physiology. *Journal of Experimental Biology*, *15*, 2685–2696. https://doi.org/10.1242/jeb.134585.

Pörtner, H.-O., & Farrell, A. P. (2008). Physiology and climate change. *Science*, *322*, 690–692.

Pörtner, H. O., & Peck, M. A. (2010). Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *Journal of Fish Biology*, *77*, 1745–1779.

Rogers, L. A., & Dougherty, A. B. (2019). Effects of climate and demography on reproductive phenology of a harvested marine fish population. *Global Change Biology*, *25*, 708–720.

Seebacher, F., & Franklin, C. E. (2012). Determining environmental causes of biological effects: The need for a mechanistic physiological dimension in conservation biology. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*, 1607–1614.

Seebacher, F., White, C. R., & Franklin, C. E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*, *5*, 61–66.

Stillman, J. H. (2019). Heat waves, the new Normal: Summertime temperature extremes will impact animals, ecosystems, and human communities. *Physiology*, *34*, 86–100.

Vargas-Chacoff, L., Dann, F., Pascke, K., Oyarzun-Salazar, R., Nualart, D., Martinez, D., … Navarro, J. (2021). Freshening effect on osmotic response in the Antarctic spiny Plunderfish *Harpagifer antarcticus*. *Journal of Fish Biology*, *98*, 1558–1571.

Wang, T., & Overgaard, J. (2007). Ecology. The heartbreak of adapting to global warming. *Science*, *315*, 49–50.