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Editorial: Patterns, causes and consequences of intraspecific variation in environmental tolerance in fishes

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Editorial on the Research Topic
Patterns, causes and consequences of intraspecific variation in environmental tolerance in fishes

Intraspecific variation in the functional traits of organisms is a fundamental component of biodiversity, which is of particular significance in an era of human-induced rapid environmental change [HIREC; (1–3)]. The vulnerability of fish species to environmental stresses is influenced by the extent of intraspecific variation in functional traits, especially in physiological tolerance traits [(4–6); Babin and Rees]. Possessing a broad range of tolerance phenotypes among populations, and also within them, can reduce a species' immediate sensitivity to environmental stressors through a number of ecological mechanisms (1, 7). If there is a link between phenotypic variation and underlying genetic diversity in the species, this can foster adaptability and evolvability over the longer term, by providing genotypes for selection as the environment changes (7–9). Furthermore, plasticity during early development can sometimes help cope with stressors encountered later in life, and parents can even pass on this tolerance via intergenerational plasticity involving non-genetic inheritance (Audet et al.). When fish species are challenged by environmental stressors, such as those that arise from HIREC, population sensitivity and adaptability become major determinants of a species' relative vulnerability and resilience (1, 9). There is a need, therefore, for research to understand the *Patterns, causes and consequences of intraspecific variation in environmental tolerance in fishes*. This Research Topic comprises two review articles and three original research articles in the field of fish experimental biology.

Hypoxia (low dissolved oxygen) is a major environmental stressor for fishes, which is growing in extent and severity due to HIREC (10). Babin and Rees reviewed and synthesized research on intraspecific variation in hypoxia tolerance in fishes. They discussed major metrics of hypoxia tolerance, ranging from physiological such as the critical oxygen partial pressure (P_{crit}) for regulating the standard metabolic rate, to behavioral such as the oxygen tension that elicits aquatic surface respiration. Importantly, they also reviewed how tolerances vary (1) among different geographic locations; (2) among genetic strains; (3) with acclimation, and (4) among individuals. Intraspecific variation in hypoxia tolerance is wide-ranging at scales from populations down to individuals, and is driven by both genetic and environmental (plastic) factors. The crucial message is that different fish species/populations utilize different strategies for tolerance, which depend on their evolutionary history and environmental context. There is an urgent need for greater standardization of methods, attention to negative and individual-level data, and development of new, ecologically meaningful metrics. Future research is important because understanding which traits predict survival under hypoxic episodes can inform conservation, aquaculture strain selection, and management strategies.

Along with hypoxia, thermal stress due to global warming is another major challenge to fishes (11). Nati et al. investigated patterns of variation in tolerance to hypoxia and warming among the three genetic populations of European seabass *Dicentrarchus labrax*, that occupy the Atlantic, the Western, and Eastern Mediterranean. Tolerance was evaluated using sub-lethal physiological metrics such as P_{crit} (or critical oxygen saturation, S_{crit}) and critical thermal maximum for swimming [CTS_{max}; (12)]. The populations exhibited complex patterns of variation with no clear evidence that tolerance varied as might be expected from broad-scale thermal gradients across their ranges. Among individuals, there was no clear evidence of functional associations between tolerance of hypoxia vs. warming, or of a dependence of tolerance on body size or metabolic rate. Nonetheless, these results are useful for identifying the most robust populations for cage mariculture farming of this species, a major industry that must adapt to HIREC.

Patterns of interpopulation variation in tolerance of acute warming were also the focus of the study by Zillig et al.; their study examined populations of chinook salmon *Oncorhynchus tshawytscha* from seven restocking hatcheries spanning diverse ecoregions along the West Coast of the United States. Thermal tolerance was evaluated as critical thermal maximum (CT_{max}) in juveniles of each population acclimated to three temperatures, to test the thermal trade-off hypothesis, whereby individuals or populations with higher absolute tolerance have a reduced capacity for acclimation of tolerance. There was evidence of the trade-off among individuals, but not when comparing populations. Among populations, tolerance was broadly related to their latitudinal range and natural rearing temperatures. These results can help identify hatchery populations at risk of thermal stress and highlight the need to consider populational diversity when projecting the responses to HIREC by economically important species.

The report by Hoots et al. considered an altogether different type of stress in fishes, the social environment of gregarious species. The study manipulated the social groupings of juvenile inanga *Galaxias maculatus*, a temperate estuarine fish, to demonstrate that social environment and metabolic rates both mediate individual diversity in growth performance. The effects were context-dependent and questioned the assumption that slow growers are typically subordinate. These results are interesting from a fundamental perspective, but they also have implications for selecting fast-growth phenotypes in aquaculture or stock enhancement.

In the final contribution, Audet et al. synthesized two decades of collaborative research on the brook charr, *Salvelinus fontinalis*, in a tribute to the great fish biologist Louis Bernatchez. Their research focused on charr strains and ecotypes from Québec, Canada, which differ in life history strategies such as whether they are resident or migratory. The study investigated how genetic, epigenetic, and environmental factors interact to shape broad diversity in the populations' developmental and physiological plasticity. These populations were found to differ markedly in their responses to environmental changes and adaptive potential, such that conservation planning for brook charr in an era of HIREC requires population-specific approaches. The review demonstrates that the brook charr is an excellent model for understanding how the interaction between the genome and environment can sustain phenotypic plasticity in fishes in a rapidly changing world.

Overall, these contributions demonstrate that exploring intraspecific diversity in tolerance of environmental stressors in fishes has fundamental biological interest but also important potential applications for management and conservation of fish diversity, along with the resources that fishes represent to humans. We would like to thank the contributors and hope that readers will find the articles interesting and useful for their fish biology research.

Author contributions

DM: Conceptualization, Writing – original draft, Writing – review & editing. KA: Conceptualization, Writing – original draft, Writing – review & editing.

Conflict of interest

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