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Reply to 'Response of chinook salmon to climate change'

Muñoz *et al.* reply — In their Correspondence, Mantua *et al.*¹ have highlighted the complexity underlying the susceptibility of salmon to climate change. We certainly agree with the authors that behavioural responses, enacted through changes in phenology, can be important for salmon populations to adapt to warming temperatures. However, we disagree with their assertion that behavioural responses to climate change are categorically more important than physiological responses. Mantua *et al.*¹ ignore the well-documented importance of the salmonid heart in ensuring performance in a wide range of thermal conditions, with the heart and circulatory system responding both plastically and evolutionarily to temperature^{2,3}. Given that such forms of physiological performance are crucial in allowing wild populations to cope with natural thermal variation, they are also likely to be part of the mechanisms used to cope with anthropogenic changes in thermal conditions. Behaviour must, after all, operate within the capacity set by physiology. Moreover, there are limitations in the potential for phenological responses to warming, which also help to highlight some of the complexity in assessing susceptibility.

As described by Mantua *et al.*¹, phenological responses by chinook salmon populations involve both earlier juvenile migrations to the ocean, thereby avoiding the warmest river temperatures of the spring, and delayed adult migrations to freshwater spawning sites, thereby avoiding the warmest river temperatures of the summer or fall. This change in phenology — the timing of migration out of or into the river — seems like an elegant response; simply avoid the river when temperatures are intolerable. However, warmer temperatures during embryonic development advance the timing of not only downstream migration, but also of juvenile emergence from the gravel bed, after which the juveniles must feed exogenously for a period in their freshwater habitat. As described in a study⁴ co-authored by one of the authors of Mantua *et al.*¹, anomalously high temperatures can create

a mismatch between the optimal and actual dates of emergence, with overly early emergence predicted to result in a loss of fitness due to exposure of juveniles to peak water flows, scarce resources or increased predation⁴. Furthermore, earlier entry into the ocean can exacerbate this effect because of the disruption of trophic interactions; different trophic levels within marine pelagic communities respond differently to warming⁵, which can reduce the energy flow (that is, food availability) to higher trophic levels, including to fish⁶. For example, the abundance of Atlantic salmon populations in the North Atlantic Ocean is dependent upon the availability of marine zooplankton, and different responses to temperature anomalies among zooplankton and salmon can lead to an insufficient food base for early-entering smolts (that is, post-ocean entry salmon)⁷. Delayed adult migration, on the other hand, should delay subsequent juvenile migrations to the ocean⁸, which could work against the ability of juveniles to behaviourally avoid the high river temperatures of the spring. Though we recognize that such phenological responses are utilized by populations to cope with thermal variation, as Mantua and colleagues have previously presented^{9,10}, we do not think such adjustments can match rising temperatures without some limitations.

What our study has shown is that within a specific river system, the Quinsam River, there is an apparent limit to the developmental and evolutionary potential of the heart in chinook salmon to function in warmer temperatures¹¹. Based on IPCC models for the region, this limit in thermal tolerance may be breached this century. Behavioural responses may lessen susceptibility in this and other salmon populations, particularly for those that have access to habitat heterogeneity^{9,12}. However, we disagree with the claim by Mantua *et al.* that, “the premise that the persistence of the genus, or any one of the *Oncorhynchus* species, is now threatened by rising temperature is not supported by other empirical evidence” given the now well-documented susceptibility of these cold-water species to high temperatures^{11–15}.

Nevertheless, Mantua *et al.*¹ do raise the important point: that responses to climate change will be complex. Physiological capacity and behaviour are two of many considerations that underpin a comprehensive understanding of the adaptive potential of species faced with climate change¹⁶. Study of these considerations in salmonid populations that inhabit thermal extremes, such as the redband trout, may prove fruitful in this respect. More broadly, we certainly advocate for more comprehensive models of climate change susceptibility that include aspects of physiological capacity and behavioural responses, as well as species and trophic interactions. Our data¹¹, as well as studies of phenology¹⁰, will help to seed such models and hopefully will increase certainty on the biological consequences of climate change. □

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