

campus. Moving from the baseline (pre) to the competition period, the direction of the trend changes significantly, visibly shifting downward (β change = -111.21 , $t = -3.88$, $P < 0.01$, 95% CI: -168.69 , -53.74). What is particularly interesting, however, is that there is another significant trend change: as soon as the competition ends the positive effect of the intervention is reversed and energy usage bounces right back to the baseline consumption level before the competition was launched (β change = 88.81 , $t = -5.01$, $P < 0.01$, 95% CI: 53.25 , 124.38).

While competitions of this kind are usually well-intended (for example, they may help raise awareness), a competition by its very nature is an extrinsically motivated incentive that leverages people's intention to act in their self-interest (winning, in this case). Yet, what Fig. 1 illustrates is a fundamental characteristic of nearly all extrinsically sourced incentives; once they disappear, so does the positive impact on behaviour. There is a pervasive tendency in both public policy-making and social science to conceptualize our thinking and experiments around short-term motivators of behaviour change. Unfortunately, plenty of behavioural research has shown that extrinsic incentives often crowd out (that is, undermine) intrinsic motivation^{12,13}. For example, emphasizing the monetary benefits of an energy-savings programme

can actually decrease environmental concern and reduce overall willingness to participate⁹.

Back to warm glow. When people decide to act pro-environmentally because they believe it is the right thing to do, because they are intrinsically motivated (and physically and psychologically rewarded for doing so) — change is much more likely to be sustained over time. The value of this line of research is not to simply demonstrate that people light up when they are doing something good. The real message lies in the fact that long-term environmental problems call for long-term motivators of pro-environmental behaviour.

While my evaluation of the energy conservation intervention does not directly speak to how behaviour change may be sustained, it does clearly highlight the inherent limitations of extrinsic incentives and serves as an example to encourage a shift in current thinking about how to most effectively promote durable behaviour change. I argue that harnessing people's hard-wired biological capacity to care about others and the environment is likely to far outlive the utility of trying to sway the public with short-sighted incentives. There is good evidence that people are intrinsically motivated to forge a more conserving and sustainable society^{7–9,11}. Future research may be well advised to explore this promising line of inquiry. □

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Additional information

Supplementary information is available in the [online version of the paper](#).

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CORRESPONDENCE:

Response of chinook salmon to climate change

To the Editor — Muñoz *et al.*¹ present some interesting and valuable experimental data about the physiological responses of chinook salmon (*Oncorhynchus tshawytscha*) to changes in developmental temperature. Especially notable is the way they develop quantitative genetic data to evaluate the adaptive potential of cardiac performance to different temperature regimes. Pacific salmon clearly have the ability to develop population-specific adaptations in cardiac performance over evolutionary time scales², but they found relatively little capacity for adaptive genetic or plastic responses in one

key performance measure, the arrhythmic temperature, in the population they studied. However, we raise concerns about their extrapolation from a small study to broad conclusions about vulnerability of the entire species to climate change. They claim that “rising temperatures now threaten the persistence of [salmon]”¹. While it is true that many individual salmon populations and some regional population groups are at risk, threats to persistence are multifaceted and population-specific³. Moreover, the premise that persistence of the genus, or any one of the *Oncorhynchus* species, is

now threatened by rising temperature is not supported by other empirical evidence. We are also concerned that this study ignored the documented capability of salmonids to respond to environmental change with plastic and evolutionary changes in behaviour, such as upstream (adult) and downstream (juvenile) migration timing⁴. Changes in phenology, rather than physiological tolerances, provide greater capacity for resilience to climate change in salmonids⁵ and other taxa more generally⁶, although the two clearly interact and the relative importance of

behavioural and physiological responses may vary across taxa or contexts (such as geographic locations)⁷.

The Quinsam River population used in the experiment by Muñoz *et al.* inhabits a watershed where average water temperatures seasonally increase by about 7 °C from April to June⁸. Warmer temperatures are associated with more rapid development and earlier downstream migration for juvenile salmonids⁴. If juvenile migration advanced by a month, which is well-within the capacity for a rapid plastic response in chinook salmon, this behavioural shift would prevent exposure to 4 °C of warming in June temperature. A four-year study of juvenile migration timing in chinook salmon in Oregon's Umpqua River showed that median migration dates in two tributaries advanced 40 days when spring water temperatures were 5 °C higher⁹. Given that egg development is also likely to be advanced under warmer temperatures (Muñoz *et al.* themselves found that entry into the juvenile phase occurred 50 days earlier in their +4 °C treatment group), juvenile development in fresh water need not be cut short by earlier ocean entry. Of course, timing changes at any one life stage may pose fitness challenges in subsequent life stages, so advanced ocean migration timing might come with fitness costs¹⁰.

In addition to immediate plastic responses, evolution of reaction norms (the phenotypic response of a single genotype across a range of environments), as observed in Columbia River sockeye salmon (*O. nerka*) adult migration timing¹¹, allows further modification of these traits. Taking evolution in adult migration timing into account greatly reduces the simulated probability of extinction in a population of sockeye salmon in the Fraser River, British Columbia, Canada, under climate warming scenarios¹⁰ (Fig. 1).

We also disagree with their statement that “climate change mitigation is ... necessary to ensure the future viability of Pacific salmon populations”¹. We believe that the impacts of future climate warming on Pacific salmon will be mixed, and context dependent. Populations now occupying the warmest and most degraded habitats in the range of Pacific salmon are very likely to experience increased stress with future warming that could lead to extirpation¹². In contrast, populations that now occupy the colder parts of salmon habitat might realize increased productivity with future warming¹³. Populations with access to thermally and hydrologically complex

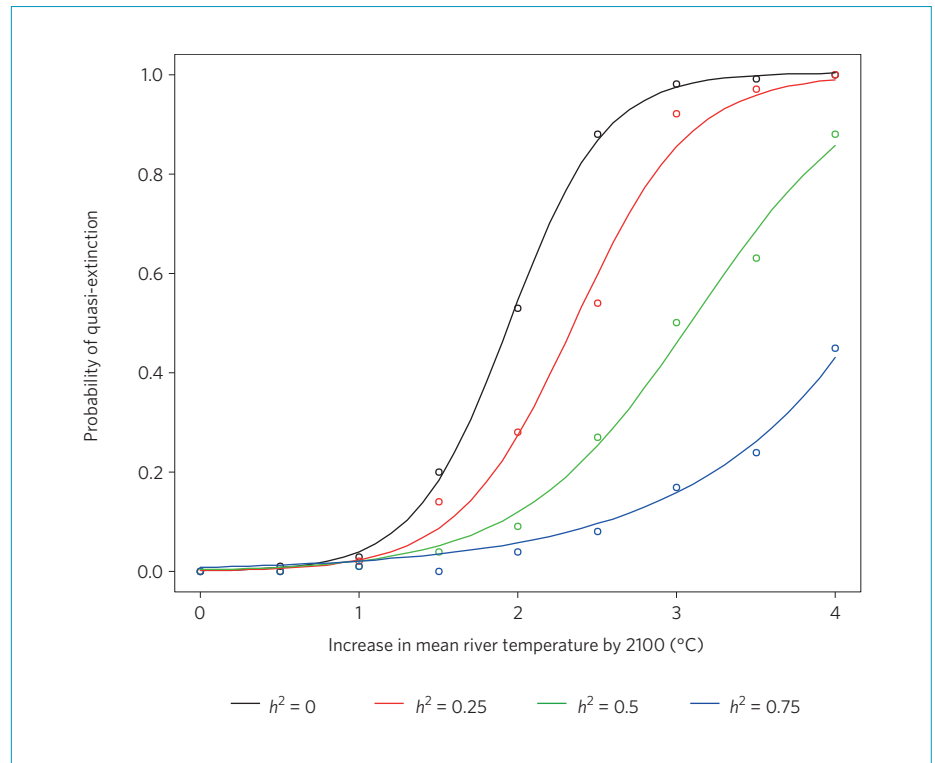


Figure 1 | Effects of evolution on quasi-extinction risk for a modeled population of sockeye salmon. Probability of quasi-extinction is calculated as a function of the rate of river warming and the heritability of adult return migration timing, assuming no flow effects on survival. Heritability is the fraction of phenotypic variation caused by additive genetic effects inherited by offspring from parents. Data points show means of 100 replicates; curves are best sigmoid fits to data. The larger the heritability of migration (h^2), the more rapid the evolutionary response and the lower the quasi-extinction risk. Figure reproduced from ref. 10.

habitats throughout the range of Pacific salmon will have options for behaviourally adapting to a warming climate. Pacific salmon will also colonize some historically inaccessible habitats that become thermally and hydrologically more favourable in a warmer climate and establish new populations, as has been documented in Glacier Bay, Alaska¹⁴.

Heterogeneity in habitat and genetics will produce more resilience in salmon ecosystems than Muñoz *et al.* suggest¹⁵. Without considering adaptation and plasticity in behaviour (migration timing in particular), one misses what are likely to be the most important mechanisms for adapting to climate change within the constraints of physiological limits. Mitigating anthropogenic climate change can help to limit future climate warming and related impacts on biodiversity globally. But even in the best-case scenarios the world is committed to substantial warming¹⁶. Enabling adaptation by maintaining genetic, life-history, and habitat options are practical actions that

can be managed now and that offer the possibility of maintaining the long-term resilience of Pacific salmon to both natural and anthropogenic climate changes^{17,18}. □

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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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