without net greenhouse-gas emissions. As people are known to do a poor job of considering worst cases, it is likely that the IPCC estimates are conservative in that regard. Expanding the worst cases considered might significantly affect the distance between the cumulative emissions targets implied by Drouet and colleagues' expected utility and maxmin criteria.

The conditions that favour a 2 °C target might also expand if such an analysis considered a broader range of decision frameworks. For instance, Drouet *et al.* employ only a utilitarian social welfare function that weights all individuals equally. If the analysis added a so-called prioritarian social welfare function[7] that judged policies more by their impact on the poor than on the rich, the conditions that favour low climate targets would include a focus on not only worst cases or low discount rates, but also the amount of attention paid to the poorest among us.

Drouet and colleagues also shed light on the difficult challenge of iterative climate risk management. Combined with uncertainty about outcomes, differing values lead to different global climate targets. But to the extent that policy learning will rely on direct observations of actual system behaviour, we all might prefer to reduce uncertainty by directly exploring the tails of the mitigation cost distribution rather than the tails of impacts distribution, if only because experiments towards the former can be made more localized and reversible.

As such, this analysis suggests that robust climate policy — consistent across many values and uncertainties — might prioritize aggressive efforts aimed towards encouraging and rewarding technological, institutional and social innovations that could forge a path to a zero-emissions economy. ❒

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References

1. Drouet, L., Bosetti, V. & Tavoni, M. *Nature Clim. Change* **5,** 937–940 (2015).
2. IPCC *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. *et al.*) (Cambridge Univ. Press, 2013).
3. IPCC *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects* (eds Field, C. B. *et al.*) (Cambridge Univ. Press, 2014).
4. IPCC *Climate Change 2014: Mitigation of Climate Change* (eds Edenhofer, O. *et al.*) (Cambridge Univ. Press, 2014).
5. Bankes, S. C. *Oper. Res.* **41,** 435–449 (1993).
6. Weaver, C. P. *et al. Wiley Interdiscip. Rev. Clim. Change* **4,** 39–60 (2013).
7. Adler, M. *Well-Being and Fair Distribution: Beyond Cost-Benefit Analysis* (Oxford Univ. Press, 2012).

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CLIMATE CHANGE ECOLOGY

Salmon behaving badly

Projected future CO_2 levels reduce the growth of juvenile salmon and alter their behaviour, with implications for the productivity of coastal ecosystems unless populations can adapt.

Philip L. Munday

Pink salmon (*Oncorhynchus gorbuscha*) are anadromous fish that start life in fresh water but spend the majority of their juvenile and adult lives out at sea. Writing in *Nature Climate Change*, Ou *et al.*[1] report that CO_2-induced acidification of aquatic habitats could dramatically affect the performance of young pink salmon during the transition from a freshwater to marine lifestyle.

Pink salmon are remarkable fish — they hatch from eggs buried in the gravel of rivers and streams, emerging into a freshwater environment. The tiny hatchlings, with a yolk sac still attached to their belly, remain close to their birth place for a few months. Once the yolk sac is consumed they migrate downstream to the ocean, where they transition to a saltwater lifestyle. The juvenile salmon grow rapidly in the ocean and in less than two years they return as adults to their natal streams where they spawn and complete their lifecycle[2]. All of the complex physiological changes that enable juvenile salmon to survive in saltwater, after starting life in fresh water, occur while they are just a few centimetres long and weigh less than a quarter of a gram. This is a time of rapid change in the salmon's life and they are also at high risk of predation from larger fishes and other predators.

Ou *et al.*[1] observed reductions in growth, yolk conversion efficiency and maximal capacity for oxygen uptake in juvenile salmon reared at projected future CO_2 levels. Furthermore the juvenile salmon exhibited significant alterations in olfactory preferences and anti-predator behaviour. Salmon have enormous cultural significance in the northern Pacific, they support commercial and recreational fisheries, and they are fundamental to the function and productivity of coastal ecosystems[3]. Consequently, any effects of elevated CO_2 on the growth and survival of juvenile salmon could have far-reaching ecological, economic and social consequences.

When research into the biological effects of ocean acidification started in earnest, a little over ten years ago, fishes were assumed to be largely immune to rising CO_2 and declining pH in the ocean because they have well-developed physiological mechanisms to defend against CO_2-induced acidosis of their blood and tissues. However, carefully designed experiments have since shown that even relatively small increases in ambient CO_2, consistent with climate change projections, can affect the growth, development and survival of some marine fishes, especially during their larval and juvenile stages[4,5]. Even more surprising was the discovery that near-future CO_2 levels can impair sensory functions and alter the behaviour of juvenile fishes[6,7]. A wide range of behaviours are now known to be affected by permanent exposure to elevated CO_2 in marine fishes[5]. A major knowledge gap, however, is the potential effects of rising CO_2 levels on freshwater fishes[8] and those species that start life in fresh water before moving to the sea, such as salmon. Do these species suffer the same impacts of CO_2-induced acidification as marine fishes?

Ou *et al.* set out to answer this question for juvenile pink salmon, the most abundant salmon species in the northern Pacific. Salmon eggs were placed in fresh water at ambient (450 µatm) and high levels of CO_2 (1,000 and 2,000 µatm), and in an oscillating CO_2 treatment (450–2,000 µatm) mimicking the variation in CO_2 levels that can occur in some freshwater habitats. The embryos and juveniles were reared in their respective treatments for 10 weeks, at which time the yolk sac was mostly absorbed and the fish were ready to begin their life in seawater. The juvenile fish were transferred to seawater in their ambient- and high-CO_2 treatments and then monitored for a further two weeks.

Growth and production efficiency (percentage of the yolk converted into tissue) were lower in high-CO_2 treatments during the freshwater stage. As a result, the fish reared in high-CO_2 waters were shorter and lighter at the end of their yolk-sac stage. Despite being smaller, the high-CO_2 fish were bolder than fish reared in ambient conditions, spending more time investigating a new object. They were also less fearful of conspecific alarm cues, spending more time in water containing alarm cues than their siblings that had been reared in current-day CO_2 conditions. Alarm cues are chemicals released from the skin of prey during a predator attack. Other fish avoid these chemicals because they are a reliable indicator of an immediate risk of predation. If a nearby fish of the same species has just been attacked by a predator, then it's probably a good time to lie low. However, salmon reared at projected future CO_2 levels were less likely to engage in predator avoidance behaviour. This is cause for concern because it could lead to higher rates of mortality. The juvenile salmon also exhibited an impaired ability to recognize amino acids that could be involved in imprinting to natal rivers. Thus, a future high-CO_2 environment might affect not only the probability that a juvenile salmon will live to adulthood, but also whether it will be able to relocate its natal stream when it is ready to spawn.

The effects of high CO_2 on growth were even more pronounced in seawater. Growth was negative at high CO_2 in seawater, with individuals losing weight, whereas fish in ambient conditions grew substantially. Furthermore, the effect of high CO_2 on growth was compounded by exposure to high CO_2 in fresh water. When juveniles experienced high CO_2, both before and after the transition to seawater, they lost weight at double the rate of fish that only experienced high CO_2 in seawater. Maximum capacity for oxygen uptake increased for all fish in seawater, but was approximately 30% lower in the high-CO_2 groups. Reduced growth and capacity for maximum oxygen uptake could be especially detrimental to salmon during their early seagoing life when they are actively feeding and avoiding predators.

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Coho and pink salmon fry.

The results of Ou *et al.*[1] sound a warning that we need to consider the possible effects of CO_2-induced acidification on freshwater fishes, especially species that migrate to the ocean during early life. Some of these fishes may be more susceptible to rising CO_2 levels than we have assumed. At the same time, we also need to consider the potential for fishes to adapt to rising CO_2 levels over coming decades[9]. One positive for pink salmon is that they have very large populations, they are highly fecund, and they complete their lifecycle in just two years. Consequently, there is likely to be genetic variation within existing populations that could assist them in adapting to future high CO_2 levels, and they will have at least 30 generations to do so before the end of this century. Testing the potential for adaptation of growth, metabolism and behaviour to higher CO_2 levels will be the next important step in determining the impacts of CO_2-induced acidification on wild salmon populations. ❒

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References

1. Ou, M. *et al. Nature Clim. Change* **5,** 950–955 (2015).
2. Groot, C. & Margolis, L. *Pacific Salmon Life Histories* (Univ. British Columbia Press, 1991).
3. Quinn, T. P. *The Behaviour and Ecology of Pacific Salmon and Trout* (Univ. Washington Press, 2005).
4. Baumann, H., Talmage, S. C. & Gobler, C. J. *Nature Clim. Change* **2,** 38–41 (2012).
5. Heuer, R. M. & Grosell, M. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **307,** R1061–R1084 (2014).
6. Munday, P. L. *et al. Proc. Natl Acad. Sci. USA* **106,** 1848–1852 (2009).
7. Nilsson, G. E. *et al. Nature Clim. Change* **2,** 201–204 (2012).
8. Leduc, A., Munday, P. L., Brown, G. E. & Ferrari, M. C. O. *Phil. Trans. R. Soc. B* **368,** 20120447 (2013).
9. Munoz, N. J., Farrell, A. P., Heath, J. W. & Neff, B. D. *Nature Clim. Change* **5,** 163–166 (2015).

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