nor substantial genetic variation in this important physiological trait. Juvenile salmon may literally have a heart attack if river temperatures in the future exceed the arrhythmic temperature (24.5 °C).

To test the vulnerability of future chinook populations to climate change, Muñoz *et al.* estimated the likelihood that future river temperatures would reach the arrhythmic temperature, the point at which the heart fails causing death. They concluded that there was at least a 5% chance of catastrophic population loss by 2075 and up to a 98% chance by 2100. Not great odds for the salmon if global warming continues unchecked.

One positive, however, is that the quantitative genetic breeding design revealed significant variation in the arrhythmic temperature of juveniles that could be attributed to mothers. This suggests that the way mothers allot resources to their eggs can influence the cardiac function of their offspring. For example, larger eggs may produce fitter offspring with stronger hearts. This provides some hope that plasticity and heritability of maternal provisioning could potentially help juvenile salmon adapt to higher temperatures in the future. It may be mothers, not fathers, that hold the key to chinook population survival.

Most studies investigating the effects of climate change on aquatic species still focus on testing the acute effects of high temperatures and extrapolating these results to populations in the future. However, there is an increasing realization of the need to incorporate an evolutionary perspective if we are to reliably predict the success of future populations^{2,3}. Key questions remain about the scope for evolutionary adaptation to climate change, and the pace of adaptation compared with the pace of environmental change. Also, how important is phenotypic plasticity compared with genetic evolution in responding to climate change? And what are the limits to adaptive responses? An important message from this study is the need to consider a range

of phenotypic traits when examining evolutionary potential. While the salmon exhibited considerable plasticity and heritable genetic variation in most of the traits examined, this variation was absent in one key physiological trait. It may be that one trait, which has been honed by natural selection in the past, that determines the fate of chinook salmon in the future.

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Adapting to nonlinear change

As atmospheric carbon dioxide concentrations rise, some regions are expected to warm more than others. Now research suggests that whether warming will intensify or slow down over time also depends on location.

Alexandra K. Jonko

hen we need to wrap our head around a very complex problem, it is helpful to simplify and make approximations. Many of the methods we currently employ to understand climate change, arguably one of the most complex problems around, use approximations of linearity and aggregation of regional effects to global averages. In reality, all natural systems are nonlinear, and none of us live in a global average world. Deviations from these assumptions are particularly important when we are concerned with climate change adaptation strategies. However, integrated assessment models¹ — the tools developed to inform adaptation decisions - are often based on linear approximations of climate change. As they report in Nature Climate Change, Peter Good and colleagues² investigate sources of regional nonlinearities in climate model projections of future warming.

Integrated assessment models are important decision tools for policy

makers. They represent the complex relationships between the earth system and social and economic realms³. Because they include so many different processes, their representation of the earth system is necessarily very simple, often consisting of only a few equations. Many of these models assume linearity in the response of climate to an external forcing.

In a linear system, doubling a perturbation doubles the response. In the context of global warming, the perturbation might be an increase in carbon dioxide concentrations. The resulting increase in surface temperatures is the system response. In a linear climate, the temperature response to a doubling of carbon dioxide levels would be exactly the same as the temperature response to a subsequent doubling. Making this approximation proves powerful when we are interested in the general behaviour of the climate system. However, when making decisions about adaptation and strategies, projections based on linear global assumptions are of limited use, and we need to take a closer look at how well they hold up in different locations and for different climate change scenarios. This is what Good *et al.*² have done using a framework, developed in previous work⁴, that allows them to separate the climate's response to an external forcing (such as a doubling or quadrupling of atmospheric carbon dioxide) into its linear and nonlinear components.

Nonlinearities in climate have previously been studied both in observational warming trends⁵ and in future model projections⁶. What distinguishes the work of Good *et al.*² from previous studies is their focus on regional patterns of nonlinearity. The metric they use to quantify nonlinearity is a spatially varying 'doubling difference' — the difference between the temperature change caused by the first and that caused by the second doubling of carbon dioxide. Positive doubling differences imply that the second doubling of carbon dioxide leads to a stronger warming than the first

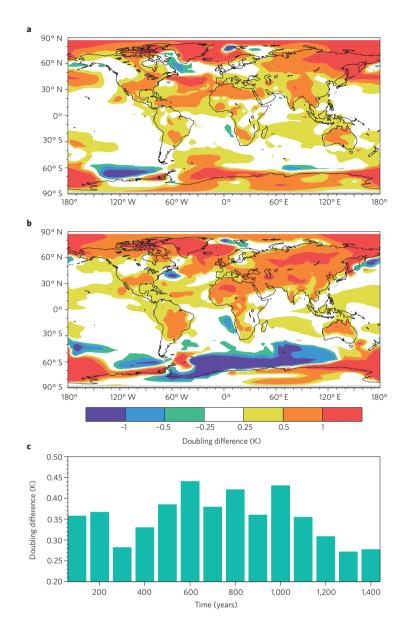


Figure 1 | Doubling differences in 1,500-year Community Climate System Model version 3 simulations, computed by taking the difference between the surface temperature change resulting from two doublings of carbon dioxide concentrations. The first doubling is with respect to present levels and the second doubling is with respect to two-times present levels. **a**, Doubling difference in kelvin for 50-149 years (compare to Fig. 2a in Good *et al.*²) **b**, Doubling difference in kelvin for 1,350-1,449 years. The doubling difference becomes negative over parts of the Southern Ocean, whereas it is amplified over some land regions. **c**, Global average doubling differences for each century of the simulation. No clear trends are discernible.

(Fig. 1). Good *et al.*² make use of doubling difference patterns to identify physical mechanisms driving nonlinear regional warming, including the Atlantic Meridional Overturning Circulation, an ice surface reflectivity feedback in the high latitudes and evapotranspiration over land. The authors focus their analysis on the Met Office Hadley Centre climate model, but corroborate their results using four other global climate

models. Adding the four models to their analysis shows that nonlinearities increase the spread in projected warming among the models. As the forcing increases, so does the uncertainty associated with the climate's response.

The message of the study is timely and relevant. However, there are some caveats to keep in mind. First, the authors have only carried out a full analysis with one

climate model. It is because of the spread in model projections of future climate that results from any one model cannot be interpreted as representations of the actual climate system. Further, the model simulations used are relatively short (150 years) compared with the response timescale of a fully coupled climate model to a doubling or quadrupling of carbon dioxide concentrations (2,000-3,000 years due to the relative sluggishness of the ocean circulation⁷). Fully coupled models are very expensive to run, and few long simulations are available. The 150-year quadrupling simulations have become part of the Coupled Model Intercomparison Project experimental design⁸ and are widely used for this type of research.

But could the relatively short timescale affect the patterns of nonlinearity? To find out, I computed a doubling difference using 1,500-year-long equilibrium simulations performed with the Community Climate System Model version 3. The differences between 50-149 years (the century used by Good et al.2) and 1,350-1,449 years, shown in Fig. 1a and Fig. 1b respectively, demonstrate that different processes may be responsible for nonlinearities at different stages of the simulation. The largest differences are visible over the Southern Ocean. Figure 1c shows global average doubling differences for 14 consecutive centuries. Although the doubling difference towards the end of the 1,500 years is smaller than at the beginning, no clear trend is discernible. This temporal variability in the spatial patterns of doubling differences may call into question the robustness of the processes identified by Good et al.² as being responsible for driving regional nonlinearity.

In summary, Good *et al.*² show that we need to use caution with the assumptions we make in climate prediction. By oversimplifying our methods of assessment of future warming, we can miss important regional details. And regional information is vital for adaptation approaches, as none of us live in a global average world.

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