

EVOLUTIONARY ECOLOGY

Survival of the fittest

Evolutionary adaptation will help some animals cope with future climate change, but for juvenile salmon there may be limits to how far the thermal tolerance of cardiac function can adapt.

Philip L. Munday

Which animal populations will persist in a future warmer world depends, in part, on their ability to adapt to higher temperatures. As the world warms, populations can move to track preferred temperatures, they may acclimate to warmer temperatures through phenotypic plasticity, or they may become better suited to the new environment through evolutionary adaptation¹. There are many examples of how projected future temperatures could dramatically affect the performance of a wide range of different plant and animal species, but whether these species will adapt over the longer term is largely unknown, especially in aquatic environments^{2,3}. Writing in *Nature Climate Change*, Muñoz *et al.*⁴ show that physiological traits important to the survival of juvenile chinook salmon have both plasticity and genetic potential to adapt to warmer temperatures. However, the news is not all good, because one key trait — the upper thermal limit for heart function — appears to lack plasticity or significant genetic variation. As a result chinook populations face an increasing

risk of catastrophic population loss if river temperatures continue to warm.

A powerful way to examine evolutionary potential is to use quantitative genetic breeding designs, where a number of different males are each cross-bred with a number of different females and the phenotypic variation of the offspring is compared within and among family lines^{1,2}. Using this technique it is possible to partition phenotypic variation in the offspring to that due to fathers, mothers, the interaction between mothers and fathers, and non-genetic environmental sources. Mothers contribute both their genes and nutritional provision to their babies in the egg. Fathers, however, just contribute their genes. By estimating the phenotypic variation due to fathers, and comparing it to the total phenotypic variation, one can estimate if there is heritable genetic variation in a trait of interest. This is exactly what Muñoz *et al.* did with chinook salmon, to test for heritable variation in thermal tolerance. They also went one step further: by rearing the baby salmon under two different temperature

regimes, one matching current day river temperatures, and one matching projected future temperatures, they were also able to test for developmental plasticity in thermal tolerance.

In fish and other aquatic animals, the capacity to supply sufficient oxygen to the tissues may set the upper limits for thermal tolerance⁵. The heart is the primary organ that sends oxygenated blood to the tissues and it beats faster at higher temperatures to supply more oxygen. Muñoz *et al.* tested for plasticity and genetic variation in key aspects of cardiac function in the juvenile salmon at higher temperatures, including the maximum heart rate achieved, the optimum temperature for heart rate, and arrhythmic temperature (the point of cardiac failure)⁶. First, they found plasticity in maximum heart rate and the optimum and maximum temperatures for heart rate. Juvenile salmon reared at projected future temperatures had a higher maximum heart rate (180 versus 153 beats per minute), a higher optimum temperature for heart rate, and a higher temperature at which maximum heart rate was achieved. In other words, the heart performed better at higher temperatures in the fish that had grown up at the higher temperatures — a process known as developmental acclimation⁷. However, not all cardiac traits exhibited this plasticity. There was no difference in the arrhythmic temperature between the two temperature groups. This means that the temperature at which the heart fails did not respond to developmental acclimation in the same way as the other cardiac traits.

Importantly, Muñoz *et al.* also found significant additive genetic variation in maximum heart rate and the optimum temperature for heart rate. This means there is significant potential for evolutionary adaptation of these traits as river temperatures increase. Salmon in the future may inherit a higher peak heart rate and higher optimum temperature for heart rate that will help them cope with warmer water temperatures. However, the arrhythmic temperature did not exhibit significant genetic variation. This is bad news for the salmon because there was neither plasticity



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Chinook salmon, Pacific Coast from California to Alaska.

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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WARMING TRENDS

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.

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When 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