

The Effect of Climate Change on Salmonid Fishes in Rivers

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Climate warming is a serious threat to many organisms, such as cold-adapted ectotherms. Among these, salmonid fishes are highly threatened not only at their southern edge of distribution, but also in large parts of the temperate climate zone. With climate warming, populations go extinct, population sizes decline, and there are sub-lethal effects with genetic, epigenetic, and phenotypic changes as a result. These phenotypic changes include changes in physiology, behaviour, life history, and distributions. For instance, metabolic rates, growth and body size changes, and the tendencies and timings of migrations are altered. In addition, exotic species spread and affect interspecific competition and change threats from parasites, contagious diseases, and predators. Habitats also change in an altered climate. In rivers, this means that flow regimes, feeding opportunities, vegetation, substrate stability, oxygen concentration, particle transport, and the turbidity of the water will change. It is important to document how these alterations influence salmonid populations to reveal causes and effects and make predictions to foresee how salmonid communities will be modified in the future to improve our ability to perform proper management of habitats and populations.

The climate, i.e., the long-term pattern of the weather in a particular area, is constantly changing. We all know how the weather can vary over a day, week, month, and year. In a longer perspective, the weather is also changing, with cold and dry periods followed by mild and wet ones. At least five major ice ages have occurred through the history of the earth, and 10,000 years ago, in the early Holocene at the end of the last Ice Age, surface temperatures in the Arctic were ca. 7 °C warmer than they are today. This was because of the high energy flux from the sun in the atmosphere (radiative forcing) and the intensified inflow of warm Atlantic waters towards the north [1]. The ocean north of Siberia was open, and fish, such as walleye pollock *Gadus chalcogrammus* Pallas and Pacific herring *Clupea pallasii* Valenciennes, spread from the Pacific to the Atlantic Ocean. Then, between 9500 and 8000 years ago, temperatures began to drop in response to freshwater fluxes from melting ice. After that, the climate slowly became colder until a thermal low ca. 200 years before the present, when the climate again changed and has since become gradually warmer. After 1880, the surface temperature of the Earth increased by ca. 1.2 °C; a major part of this increase was after 1975. Thus, the climate has always changed, and will do so in the future, and fish have mechanisms that make them able to sustain climatic variations if they are not extreme. In this volume of *Fishes*, ecologists present knowledge about how salmonids spawning in fresh water react to climate warming, and what may be done to mitigate negative population effects.

Temperature affects the metabolic rates and aerobic scope of fishes; the latter is the difference between the maximum metabolic rate and the standard metabolic rate. Jonsson ([2], this volume) reviewed how metabolic rates are associated with growth, body size, behaviour, and reproduction in salmonid species. In a warmer climate, adult body size is expected to decrease, and the fish attain maturity at a younger age [3]. A younger age at maturity is associated with the faster growth of juvenile fish. In addition to this direct thermal effect, water temperature has an indirect effect, induced during early development, and expressed in a later life stage as a knock-on effect. Among these indirect thermal effects are changed egg sizes and effects on swimming and migratory activities. These



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phenotypically plastic responses may pre-adapt offspring to perform better in the expected future thermal environment. The mechanism allowing this flexibility in ecology is not well known, but epigenetic mechanisms have been a suggested cause [4].

The vulnerability of salmonids to climate warming is associated with their high oxygen demand. The oxygen content in water decreases with increasing temperatures. Thus, the production of salmonids in rivers at low latitudes and elevations has decreased because of warm and stressful thermal regimes. To mitigate these production losses, fishery managers release artificially bred offspring in rivers (supportive breeding). The fitness in nature of the released fish is often low because of their inadequate behaviour [5]. Also, releases may reduce the genetic diversity of natural populations. This may be because a few captive parents produce large numbers of offspring that are released (the Ryman–Laikre effect [6]). Almodóvar et al. ([7], this volume) show how the genetic diversity of Atlantic salmon populations in Spain, at the southern edge of distribution in Europe, has decreased dramatically in the last 70 years because of population reductions associated with climate change and supportive stocking of artificially bred offspring from various, often foreign sources.

Elevated temperature levels also influence the transcriptome (protein coding part of the genome) of the skeletal muscles, thereby influencing the growth and activity of fish. Molina et al. ([8], this volume) show how high temperatures upregulate many of the genes associated with autophagy (breakdown and reuse of cell parts), amino acid transport, and the glutamine metabolic process of rainbow trout *Oncorhynchus mykiss*, but they downregulate several other genes associated with digestion and muscle contraction, which are important for the adaptive processes of fish.

Many salmonids are anadromous, i.e., they migrate between rivers and the open ocean and are particularly sensitive to climate warming at the time when they migrate to sea at a life-stage called smolts. Vehanen et al. ([9], this volume) summarise how higher temperatures lead to earlier smolting, which influences their survival at sea. In warmer rivers, the salmonids smolt younger and smaller, and they leave earlier in spring, which may result in a mismatch between migration timing and optimal conditions for survival and growth at sea.

River flow changes with climate. The amount of precipitation increases in the northern and decreases in the southern part of the Northern Hemisphere, and in the north, more precipitation comes as rain instead of snow, with effects on the water flow and thermal climate. Watz et al. ([10], this volume) investigated, with the use of replicated simulations, the effects of increased temperature and discharge on the overwinter growth and mortality of one- and two-summers-old freshwater resident Atlantic salmon and brown trout in a regulated Swedish river. While increased water temperature had a positive effect on growth, the effect of a changed flow depended on the winter temperature and differed between the two species. Thus, climate change may affect the competition between salmon and trout. Ecological models that predict the effects of different environmental conditions may offer insight into such effects when in situ experiments are not feasible.

In temperate parts of Europe, the growth of Atlantic salmon during the first year at sea has decreased [11,12]. Typically, this decrease is accompanied by decreased production caused by younger age at maturity and a decrease in fish size [13]. Less is known about the climatic effects of growth in sub-Arctic parts of Europe. However, Alioravainen et al. ([14], this volume) found that freshwater growth has decreased in the River Teno (Tana), a border river between northern Finland and Norway, which probably holds the largest natural salmon population in the world. However, growth has increased during their first year at sea, contrasting observations farther south in Europe. Post-smolts of northern and southern salmon populations feed in different oceanic areas and may be differently affected by recent environmental changes.

In rivers, salmonids avoid stressful temperatures in thermal refuges. Linnansaari et al. ([15], this volume) summarise how young salmon seek cold tributary plumes, groundwater springs, alcoves and hyporheic upwellings, deep lakes, and artificial impoundments.

Salmonids have very good spatial cognition to locate and re-locate cold-water refuges. There, they may stay close together, although their distribution within the refuge can be hierarchic. With continued climate warming, managers may create new thermal refuges in rivers to protect fish populations.

Climate change may have a dramatic effect on the growth of Arctic charr in the high Arctic. This species is the northernmost freshwater fish in the world and the only fish species present in Arctic lakes on the Svalbard Islands (74–81 °N). Svenning et al. ([16], this volume) investigated the growth of Arctic charr in two Svalbard lakes between 1960 and 2008. The growth rate of young Arctic charr correlated positively with the air temperature, but negatively with the annual snow accumulation. This suggests that Arctic charr may grow better in a future with warmer Arctic lakes. On the other hand, the authors speculate that a loss of glacier rivers in a warmer future may affect the opportunity of anadromous Arctic charr to migrate to and from the sea, where the sub-adults and adults in these populations grow the most. New fish species may also enter northern rivers in a warmer future, influencing the success of Arctic charr because of interspecific interactions [17].

In a warmer northern climate, the ice-covered period will decrease in length, and salmonids will be more exposed to predators in winter. Filipsson et al. ([18], this volume) used experimental flumes to examine how surface ice and light affected the anti-predator behaviour of juvenile brown trout (*Salmo trutta*) in relation to piscivorous burbot *Lota lota* and northern pike *Esox lucius* at 4 °C. Trout had lower foraging and swimming activity and spent more time sheltering when predators were present than when absent. In daylight, the trout's swimming activity was not affected by predators, but in darkness trout were less active when predators were present. Trout consumed more drifting prey during the day when ice was present and positioned themselves further upstream when ice was not present. In the presence of pike, the trout stayed closer to conspecifics under ice. Thus, one may consider not only the potential for adaptation to changes in abiotic factors during climate change, but also how changes in environmental factors can affect behavioural species interactions which influence their survival.

In the last paper of this volume, Crozier and Siegel [19] performed a systematic literature review of climate impacts on Pacific and Atlantic salmon as a resource for stakeholders, managers, and researchers. They review published studies that address climate impacts on salmon from 2010 to 2021. They summarise expected phenotypic and genetic responses and management actions by life stage. They also show the largest research gaps related to species interactions, behavioural responses, and effects across life stages. With this literature collection, one may better perform salmonid management in a changing climate.

Conflicts of Interest: The author declares no conflicts of interest.

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