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Abstract

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A literature review of climate change on salmonid fish species was made with a special interest on regulated rivers. As a case study, the effect of expected climate change on fish in the River Vuoksi was assessed. The overall impact of climate change on salmonids in the River Vuoksi was considered negative. Being a lowland river, maximum water temperatures in summer may already exceed critical limits for brown trout and landlocked salmon parr, and grayling at all life-stages. Expected increase in winter and early spring discharge of the River Vuoksi in the following decades was considered harmful especially for brown trout and landlocked salmon juveniles. Expected decrease in summertime discharge accompanied with low water velocities will aggravate the loss of riffle habitat preferred by *Salmo* spp. young especially in these restored riffle areas. In contrast to salmonids, several warm-water species (e.g., pikeperch and many cyprinids) dwelling mostly outside the few remaining rapids and riffles in the River Vuoksi are anticipated to benefit from the climate change.

The River Vuoksi was considered to carry a special risk of a self-sustaining rainbow trout establishment in warming climate because of its southern location, expected changes in yearly discharge, relatively high and stable pH and large size of the river. Even without establishing a self-sustaining population, the widely detected spawning behavior of introduced rainbow trout with redd construction may be harmful to the reproduction of brown trout and landlocked salmon. Hence, stocking of put-and-take rainbow trout to the River Vuoksi was considered as a risk.

As mitigation measures for the adverse effect of climate chance on the salmonid species can be suggested restoration of the existing riffles, increased connectivity and new reproduction areas by construction of bypass channels for the fish to pass dams, shadowing tree canopy to possible bypass channels, dampening of hydropeaking, and more effective control of the fishermen in obeying the fishing restrictions especially in the lower reaches of the River Vuoksi.

Keywords: Climate change, salmonids, Vuoksi, global warming

Contents

1. Introduction

Ongoing anthropogenic climate change increases water temperatures and alters precipitation, evaporation and hydrology patterns, consequently affecting fundamental habitat conditions for fish and other freshwater species (Regier & Meisner 1990, Wenger *et al*. 2011). Freshwater communities are particularly vulnerable to this change because fresh waters are naturally fragmented in stream networks or water bodies, and many species have limited dispersal ability to cope with habitat alterations (Woodward *et al*. 2010, Filipe *et al*. 2013). Many streams and lakes may become too warm for the persisting cold-water fish. Migrating salmonids, that change their habitat between life stages, are especially vulnerable to environmental changes (Vagg & Hepworth 2006). All Finnish salmonids are classified as cold- or cool-water species (e.g., Logez *et al*. 2012) being threatened by increasing temperatures with climate change.

RiverGo project seeks to promote preservation of biodiversity and nature values along the River Vuoksi on the Finnish and Russian sides of the border. The project also strives to increase discussion and mutual understanding among the cross-border authorities and enhance environmental awareness of local inhabitants and visitors on both sides of the border. In fisheries, the main activities are to assess the state and structure of salmonid populations, survey potential reproduction areas of salmonids, and to evaluate the impact of hydropower construction and discharge regime changes on the salmonid populations of the River Vuoksi.

As one of the RiverGo project objectives, in this paper we assess the effect of climate change on the fish populations in the River Vuoksi basing on the expected warming of climate and altered flow patterns, and autecology of the present fish species. Although our focus is in the most valuable salmonid species, landlocked salmon, brown trout and grayling, also other native fish species and the introduced rainbow trout are concerned.

2. The River Vuoksi and its catchment

The River Vuoksi runs from the largest Finnish lake, Lake Saimaa, to the largest European lake, Lake Ladoga (Laatokka) in Russia, with total length of about 150 km (Figure 1). Of the 72 m drop in altitude about 60 m is realized in the upstream 25 km stretch of the river, whereas mid- and downstream are characterized by long lake-like sections. The catchment area, covered mostly with coniferous forest, is 68 500 km^2, about which 52 700 km^2 lies on the Finnish side (Figure 2). The mean discharge of the River Vuoksi is the highest of the rivers in Finland, about 600 m^3, expressing relatively high stability over the year. The river is harnessed by four hydroelectric power stations in the upper reaches, two on the Finnish side, and two on the Russian side (Figure 1). Only some rapids run nowadays freely in the lower reach of the river. Water quality of the River Vuoksi is good especially in the upper reach with high oxygen levels, stable pH near to 7, and low concentrations of nutrients and solids (Vehanen *et al*. 2022).

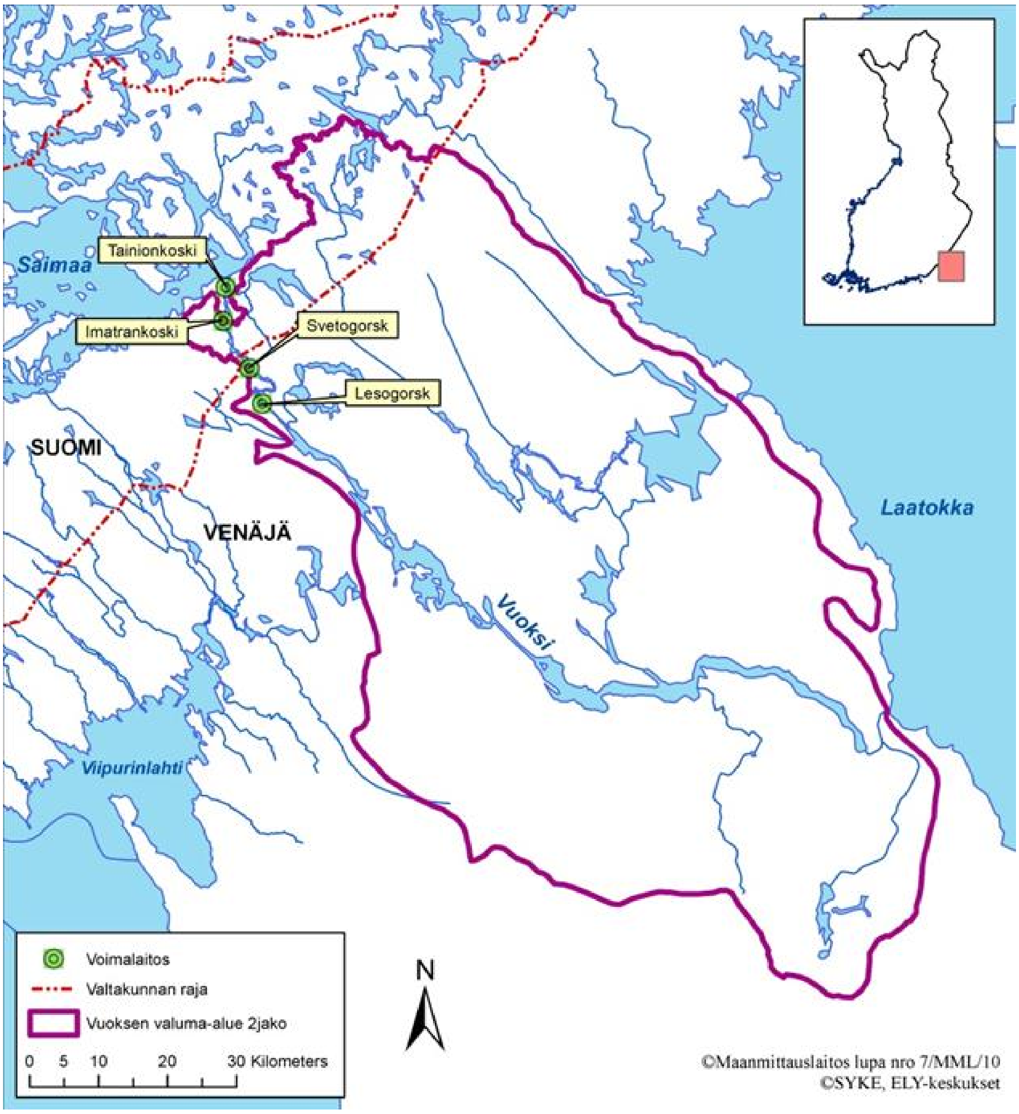

Figure 1. Map of the River Vuoksi and its near catchment. There are two hydropower plants on the Finnish side (Tainionkoski and Imatrankoski) and two on the Russian side (Svetogorsk and Lesogorsk).

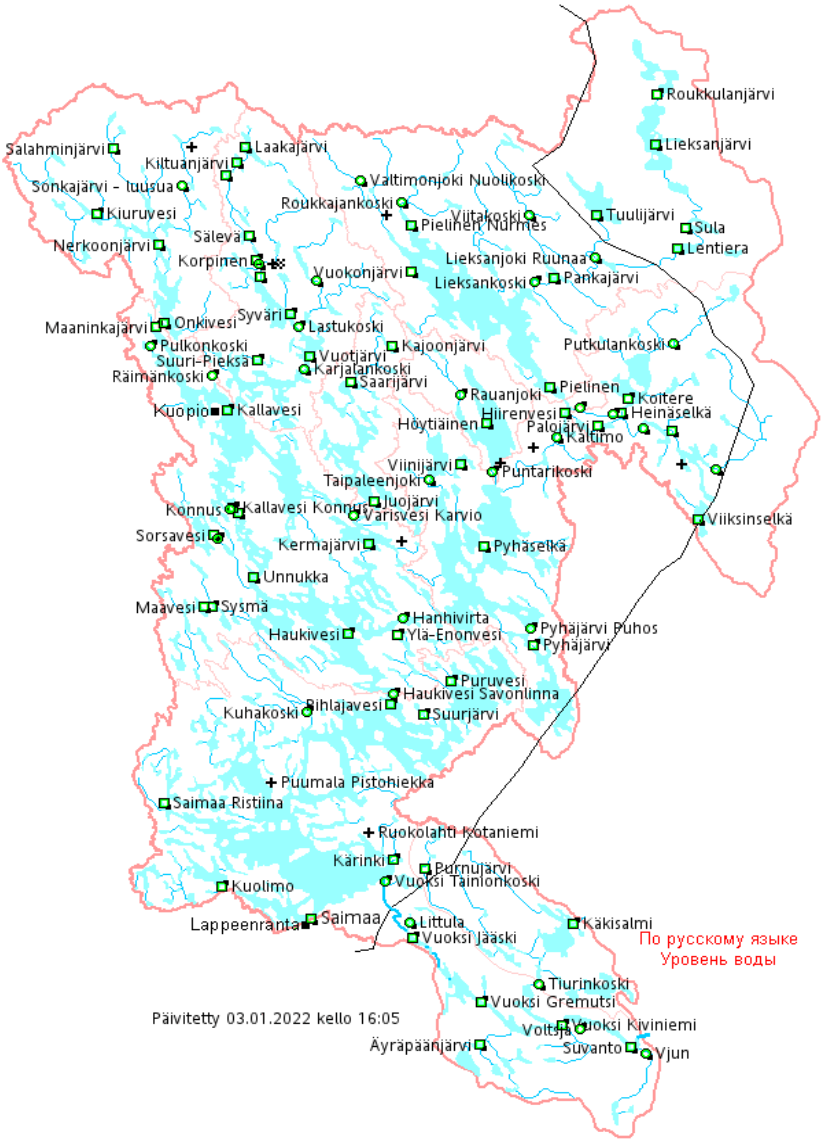

Figure 2. Vuoksi water system including River Vuoksi in the southeastern corner (outlined by a red line). Black line indicates the border between Finland and Russia. (www.vesi.fi)

3. Valuable salmonid populations in the Vuoksi drainage basin

Landlocked salmon

Atlantic salmon (*Salmo salar*) populations in the Baltic Sea are significantly differentiated from the other Eastern Atlantic populations and possess generally lower genetic variability than the Atlantic stocks (Koljonen *et al.* 1999, Verspoor *et al.* 1999, Nilsson *et al.* 2001, Gross *et al.* 2003). In the Baltic Sea rivers, a clear dichotomy was observed between stock groups from southeastern (Russia, Estonia, Latvia, southern Sweden) and northwestern (northern Finland, northern Sweden) drainage basins, corresponding to the postglacial colonization of the Baltic Sea by two phylogeographic lineages, one from the east (the Ice Lake lineage) and one from the west (the Atlantic lineage) (Koljonen *et al.* 1999).

In general, anadromous salmon populations can migrate from river to river via the open seas (straying versus homing), but landlocked salmon (*Salmo salar m. sebago*) populations are restricted within their specific lake basin. One of the key generalizations that can be made is that compared with their anadromous counterparts, freshwater salmon populations tend to exhibit lower genetic diversity within and higher genetic differentiation between populations (Tonteri *et al.* 2007, Ozerov *et al.* 2010). This is due to the combination of a lower effective population size (rivers accommodating landlocked subpopulations tend to be shorter and offer fewer spawning and nursery areas) and a lack of migration and gene exchange between populations (Tonteri *et al.* 2007, Lumme *et al.* 2015).

Landlocked salmon in Lake Saimaa shows low genetic variation (Vuorinen 1982, Säisä *et al.* 2005). The average allelic diversity and heterozygosity in landlocked populations (samples from the River Svir and Lakes Vänern, Saimaa, Onega, and Ladoga) were significantly lower than in the anadromous Baltic Sea populations (Säisä *et al.* 2005).

Landlocked Saimaa salmon and anadromous Neva salmon are genetically different and Saimaa salmon has lost genetic diversity due to its long isolation and small population size (Koljonen 1989, Säisä *et al.* 2005, Koljonen *et al.* 2012). Landlocked Saimaa salmon in Vuoksi water system is critically endangered (Urho et al. 2019), as well as the landlocked salmon population migrating to spawn to River Vuoksi from Lake Ladoga. Landlocked populations have been influenced by legal and illegal fishing owing to the proximity of human settlements (Ozerov *et al.* 2012 reviewed by Lumme *et al.* (2015), and poaching on the Ladoga landlocked salmon, as well as other salmonids in the lower reaches of the River Vuoksi, seems to continue in the 2020s (Menna *et al.* 2022).

Brown trout

In general, in brown trout *(Salmo trutta*) the genetic distances between the anadromous stocks follow the geographical distances between the river mouths and the form of the coastline (Koljonen *et al.* 2013). There are genetically two different main groups in the eastern Gulf of Finland; Bay of Vyborg group including rivers running from Finland to Russia and group of Russian rivers including rivers of Karelian Isthmus (Koljonen *et al.* 2013).

In the Vuoksi water system, there are both migratory and local (non-migratory) trout stocks, which reproduce in the streams connecting lakes (Piironen *et al.* 2016). Hatchery-reared trout juveniles are also largely released in the lakes of the Finnish side of the Vuoksi water system. Brown trout sampled from River Vuoksi and its side streams are genetically near to the hatchery reared brown trout of Vuoksi (Koljonen *et al.* 2022). According to Piironen *et al.* (2016), in future, spatially genetically different stocks should be used in the releases; in the northern lakes (Pielinen trout) and the more southern lakes (Heinävesi trout) (Piironen *et al.* 2016). Status of brown trout in the waters south of the 67th parallel in Finland is endangered (EN) (Urho *et al.* 2019). In the Russian part of the Vuoksi river basin, landlocked trout is included in the Red Book of the Leningrad region and the Red Book of the Russian Federation with a category 2, as decreasing in number (Red Book of the Leningrad Region 2018, Decree of the Ministry of Natural Resources and Ecology of the Russian Federation, 2020).

Grayling

The European grayling (*Thymallus thymallus*) is a salmonid fish native to Europe, with a distribution ranging from England and France to the Ural Mountains of north-western Russia (Swatdipong *et al.* 2009). Majority of grayling populations inhabit freshwater rivers and lakes, but some populations also occupy brackish water in northern parts of the Baltic Sea (Koskinen *et al.* 2000, Vehanen *et al.* 2003, Swatdipong *et al.* 2009). Grayling stocks in Finland are clustering into three genetically different groups largely corresponding to the northern, Baltic and south-eastern geographic areas of Finland (Swatdipong *et al.* 2009).

Lake Saimaa is currently inhabited by a number of genetically substantially differentiated grayling populations that form five main groups (Lieksanjoki, Pielinen Vuoksi, Puruvesi, Etelä-Saimaa) coinciding relatively well with the geographic origins of the samples (Koskinen et al. 2002). Despite these clear genetic imprints of stocking, the contemporary populations exhibited evolutionary relationships congruent with the sampling locations, and up to 73% of contemporary individuals were identified to be of pure indigenous origin (Koskinen *et al.* 2002).

Grayling sea populations are considered critically endangered (CR) in Finland (Urho *et al.* 2019). The status of grayling in the freshwater bodies south of the 65th parallel in Finland is considered vulnerable (VU) (Urho *et al.* 2019). The population sizes of grayling inhabiting the Lake Saimaa water system have been declining in recent decades mainly because of destruction of suitable spawning habitat, pollution and overfishing (Makkonen *et al.* 2000). In the most of the European part of Russia, grayling has not a special protection status, including populations of the lower reaches of the Vuoksi river system, mainly due to lack of scientific data about them. Though, in the South-East of the European part of Russia, grayling population of the river Ural is under protection - it is listed in the Red Book of the Russian Federation with status 2 - decreasing in number and prohibited for catch (Decree of the Ministry of Natural Resources and Ecology of the Russian Federation 2020).

4. Climate change affects the distribution and abundance of salmonids

4.1. Climate change

Human activities are estimated to have caused approximately 1.0°C of global warming above pre-industrial levels (from 1880 to 2017), with a likely range of 0.8°C to 1.2°C. Global warming is likely to reach 1.5°C at about 2030 if temperature continues to increase at the current rate (IPCC 2021).

Sea surface temperature (SST) changes are one of the most important sources of uncertainty in future climate change. SSTs exert important local and remote influences on the global climate through the distribution and transport of heat and moisture. Variations in global and regional SST patterns influence zonal and meridional circulations, which in turn affect the precipitation and temperature patterns across the globe. Records of SSTs from the past 25 years show progressive warming trends that have been formally attributed to anthropogenic forcing both globally and regionally. Associated with these changes in SSTs are changes in global mean temperatures, global circulation patterns, sea levels, temperature and precipitation extremes and sea-ice extent (reviewed by Ashfaq *et al.* 2010).

Increasing global surface temperatures are very likely to lead to changes in precipitation and atmospheric moisture because of changes in atmospheric circulation, a more active hydrological cycle, and increases in the water-holding capacity throughout the atmosphere. Overall, global land precipitation has increased by about 2% since the beginning of the 20th century. There have been marked increases in precipitation in the latter part of the 20th century over northern Europe, with a general decrease southward to the Mediterranean. Dry wintertime conditions over southern Europe and the Mediterranean and wetter than normal conditions over many parts of northern Europe and Scandinavia (Hanssen-Bauer and Førland, 2000) are linked to strong positive values of the North Atlantic Oscillation (NAO), with more anticyclonic conditions over southern Europe and stronger westerlies over northern Europe (reviewed by Dore 2005).

Northern Eurasia (north of approximately 40°N) shows widespread and statistically significant increases in winter precipitation during 1921–2015, with values exceeding 1.2–1.6 mm mo^{-1} per decade west of the Ural Mountains and along the east coast, while southern Europe exhibits coherent albeit weaker amplitude drying trends that attain statistical significance over the eastern Mediterranean. These precipitation trends occur in the context of changes in the large-scale atmospheric circulation, with negative SLP (Sea Level Pressure) trends over northern Eurasia and positive SLP trends over the central North Atlantic extending into southwestern Europe (Guo *et al.* 2019)

The magnitude of climate change is considered to be dependent on the atmospheric load of the two most important greenhouse gases, carbon dioxide (CO_2) and methane (CH_4). The terrestrial biosphere plays an important role in the global carbon balance. In boreal zones, forests and peatlands are an important part of the global carbon cycle. Recent temperature increases have been associated with increasing fire activity in Canada since about 1970 and exceptionally warm summer conditions in Russia during the 2010 fire season (Reviewed by Terrier *et al.* 2013)

Climate change impacts and will impact on water resources and lake regulation in Vuoksi watershed in Finland following the scenarios. Climate change will alter snow accumulation and melt and therefore cause large seasonal changes in runoff and water levels. Runoff from Lake Saimaa to River Vuoksi, and thereby the discharge in the River Vuoksi, will decrease during summer and increase during winter (Marttunen *et al.* 2010, Veijalainen *et al.* 2010a).

4.2. Large-scale spatial distribution and abundance changes in salmonids

Salmon

Atlantic salmon is distributed form northern Portugal (42°N) to River Kara in northern Russian in Europe (Kazakov 1998), and West Atlantic salmon is distributed from Connecticut River to Ungava region of northern Quebec. Anadromous brown trout is distributed from Portugal to the White Sea (MacCrimmon 1971, referred by Jonsson & Jonsson 2009a). Southern Atlantic salmon populations have declined dramatically and face the highest risk of extinction as global warming moves its thermal niche northwards (Nicola *et al.* 2018).

The stock complex of Atlantic salmon in Europe has experienced a multidecadal decline in recruitment, resulting in the lowest stock abundances observed since 1970. Friedland *et al.* (2009) support the hypothesis that increased sea surface temperature (SST) affects negatively survival and growth of post-smolts inducing low recruitment of salmon.

Atlantic salmon abundance and productivity show similar patterns of decline across six wide-spread regions of North America (Mills *et al.* 2013). Abundance declined in late 1980s and early 1990s after which it remained stable at low levels. Climate-driven environmental factors, as changes in plankton communities and prey availability and warmer ocean temperature were linked to low productivity of North Atlantic salmon populations (Mills *et al.* 2013).

Lajus *et al.* (2005) demonstrated, using historical catch data, a positive relationship between salmon catches and temperature in the Barents and White Seas areas. Salmon catches tended to decrease during relatively cold periods in these northern regions.

Atlantic salmon abundance in the Baltic Sea is associated with longer-term patterns in the climate. During maritime, temperate climate periods salmon were larger in size but low in abundance, with contrasting characteristics during continental, cold climate periods (Huusko & Hyvärinen 2012).

Landlocked European populations of salmonids are found in Norway, Sweden, Finland and Russian Karelia (Berg 1985, Kazakov 1992, Ozerov *et al.* 2010, Lumme *et al.* 2015). The landlocked stocks of salmon have declined throughout their whole distribution range (Kazakov 1992, Leinonen *et al.* 2020).

Brown trout

Brown trout is native to Europe and Asia where anadromous populations are found from Portugal to the White Sea (Jonsson & Jonsson 2009a). In future, the survival conditions for trout will probably decrease in the southern part of the current distribution. In the northern part of their current distribution, global warming may improve feeding opportunities, growth and survival conditions (Jonsson & Jonsson 2009a).

According to Filipe *et al.* (2013), brown trout distribution will become progressively and dramatically reduced in European watercourses in future. Their forecasts indicated that the greatest changes in suitable habitats will occur in the southern Europe.

Generally, the status of the natural brown trout (sea trout) population is considered poor in the Finnish coast (Jutila *et al.* 2004). Also, the wild stocks of brown trout in Finnish inland waters collapsed during the 20th century mainly because building of dams prevented upstream migration, and low water quality and stream dredging weakened reproduction and finally overfishing decreased spawning stocks (Syrjänen & Valkeajärvi 2010).

Grayling

The distribution of grayling is widespread from west Wales throughout Europe to the Barents, White and Kara Seas in the north (Shilin 2001). It is found in the Northern Hemisphere, 40° – 70°N, at altitudes up to 500 m in the Alps and 1000 m in the Carpathians. Grayling is native to Europe and the former USSR inland waters, the NE Atlantic, Mediterranean and Black Sea (www.fishbase.org.uk, 1999) (reviewed by Ingram *et al.* 2000). Regionally the species suffers from dam constructions, river regulation, pollution, and eutrophication (HELCOM-Red-List 2013).

The abundance of sea-spawning grayling in the coastal areas in the Gulf of Bothnia has decreased during the last twenty years in Sweden and in Finland. The exact degree of this decrease is difficult to estimate because the stocks have not been monitored properly. The situation of sea-spawning grayling is much worse than that of anadromous grayling. Sea-spawning grayling is rather unique in the world (HELCOM-Red-List 2013, Keränen 2015). The abundance of grayling in the Vuoksi water system has also decreased after 1960s (Sundell 2008).

Shilin (2001) has reported the distribution, habitats, abundance and protection of grayling in Russian Federation. Grayling inhabits basins of rivers flowing into the Baltic, Barents, White and Kara seas, basins of upper and middle Volga (including the basin of Kama) and basin of the Ural River (reviewed by Shilin 2001).

Reduction in the number of European grayling populations in the basin of the Volga River was noted back in the 19th century. In the basin of the Ural River, the species lived in the past in the left-bank tributaries, where it is now absent. The decline and disappearance of individual populations primarily concerns the large forms (river and lake ecotypes). The small form (brook ecotype), due to its small size (not so attractive for fishermen) and short-term cyclicity (the rate of reproduction increases), more successfully resists anthropogenic impact and therefore remains in a number of places. Apparently, only the brook ecotype is able to withstand the intense anthropogenic impact, which contributes to the formation of short-cycle populations consisting of small individuals; this allows the species to survive, but its gene pool is apparently becoming impoverished. The brook ecotype is represented by isolated, small populations inhabiting streams, rivers, and upper reaches of rivers. The number of individual populations, apparently, does not exceed several thousand breeders. The main limiting factors are intensive fishing by the local population, pollution of rivers and streams by various flows. It is necessary to make an inventory of the remaining populations and assess their current state, to carry out cryopreservation of genomes, to organize specially protected natural areas in the habitats of endangered populations (reviewed by Shilin 2001).

5. Life-history and environmental preferences of salmonids

5.1. Life history and habitats

Salmon and brown trout

Salmo salar (sea salmon or landlocked salmon) and *Salmo trutta* (sea-run trout, lake-run trout, brown trout) live in a variety of habitats such as brooks, rivers, lakes and coastal waters (Jonsson 1989, L'Abee-Lund *et al.* 1989, Klementsen *et al.* 2003, Ozerov *et al.* 2012, Harvey *et al.* 2020). Landlocked salmon (*Salmo salar m. sebago*) live in large lakes, like Lake Saimaa or Lake Ladoga (Säisä *et al.* 2005, Hutchings *et al.* 2019, Leinonen *et al.* 2020, Ozerov *et al.* 2010, Valetov 1999). The spawning area and nursery area for young salmon or trout are always in flowing fresh water (Jonsson 1985, 1989, Syrjänen *et al.* 2008, Piironen *et al.* 2016). Spawning grounds of the brown trout can also be located in the lake areas with ground water influx (Brabrand *et al.* 2002). *Salmo* spp. spawn in autumn when the water is cold (Jonsson *et al.* 2005). The incubation of eggs during the winter takes several months (Finstad & Jonsson 2012). The eggs hatch in spring and newly hatched alevins remain in the gravel nest where they utilize their yolk reserves for growth. After a few weeks the alevins have used most of their yolk and develop into fry. After that fry emerge from the gravel nest and start to feed on invertebrates (Elliott *et al.* 2000, Jonsson *et al.* 2005). The young, called parr, live in fresh water for one or more years before smoltification and migration to sea or lake for feeding in a richer environment (Klementsen *et al.* 2003, Jokikokko & Jutila 2004). After smoltification process that physiologically adapts fish to sea life, smolts leave the home stream (Skilbrei 1991). Both species may have sea-run and lake-run populations (Hutchings & Myers 1988, Näslund 1993, Klemetsen *et al.* 2003). Part of salmon males in the anadromous population may mature as parr and live their entire life cycle in the river (Hutchings & Myers 1988, Kazakov *et al.* 1988). Also, some individuals of brown trout may stay in the stream their entire life span, although major part of the population performs feeding migration (Jonsson 1985, 1989).

Salmon females usually spend two or more years at sea or lake before maturation and return to home river, but majority of males may mature after one sea year (Jokikokko *et al.* 2004, Jonsson *et al.* 2016). Sea trout females also spend more pelagic life than males (Jonsson 1985). The sea-run trout may return to their home river as immature fish and spend winter months in fresh water (Jonsson 1989). Feeding migration of salmon may exceed 500-900 km in the Baltic Sea, but trout seldom migrate over 100 km from their home river (Kallio-Nyberg *et al.* 1999, 2002).

Landlocked salmon inhabit structurally complex Lake Saimaa (61°15′N, 28°15′E) in the Vuoksi water system, spawning during the latter half of October in River Pielisjoki (67 km) and its tributary Ala-Koitajoki (25 km) running from the north into the lake (Piironen, J. unpublished data). After 2–3 years, smolts (17–19 cm) migrate from late May to late June to Lake Saimaa where they feed mainly on vendace and smelt. Interestingly, compared with males that migrate to the lake, females mature at a younger age (2–4 years; 3–5 years for males) and smaller size (65–80 cm and 3–5 kg; 70–90 cm and 4–8 kg for males) (Hutchings *et al.* 2019). Landlocked salmon also descended from Lake Saimaa to spawn to River Vuoksi before its harnessing to hydropower production.

In the experiment with released juveniles in the river Ala-Koitajoki, smolts left the river when water temperature rose to 12–16 °C and mean weight and length of smolts were 48 g and 18.4

cm, respectively (Makkonen *et al.* 1995). Landlocked salmon in Vuoksi water system display a corresponding smoltification like sea-run Atlantic salmon stocks, although landlocked salmon live their entire life in freshwater (Piironen *et al.* 2013).

The landlocked Saimaa salmon was nearly lost in the mid-1900s because of the construction of hydroelectric power plants into its home rivers. Currently, the population is mainly maintained by broodstocks and releases of hatchery-reared juveniles or smolts (Makkonen *et al.* 1995). Stocking experiments show that by transporting maturing parents to the restored river stretch (In River Ala-Koitajoki), natural production can be increased (Leinonen *et al.* 2020). The smolts from the river Pielisjoki migrate downwards to the feeding area, which is the chain of lakes. They can reach most of southern Saimaa (migration distance about 250 km) within some months (Makkonen *et al.* 1995).

Landlocked salmon and trout inhabit Ladoga Lake and spawn in rivers flowing into the lake and their tributaries, including the Vuoksi water system (Shustov & Veselov 2005, Valetov 1999). Salmon spawning migrations were observed earlier in 34 rivers of the Ladoga Lake basin (Valetov 1999). However, salmonid populations essentially decreased due to diverse anthropogenic impacts, including influence of hydropower stations (HPSs) and poaching. Several HPSs were constructed already in the 1930s there. To compensate their negative impact on salmonid populations, five hatcheries were built in the Ladoga Lake basin. One of them (Svirskiy hatchery) is still operating and releases landlocked salmon and trout. However, according to estimates, the total spawning stock of these populations decreased approximately to about 20 % of the potential and the density of juvenile salmon in the Ladoga rivers was considered to be 25–50 % of the potential (Valetov 1999).

The landlocked Ladoga trout migrate for spawning into rivers from August to mid-October (Shustov & Veselov 2005). Adults migrate back to the lake and spend there from 2 to 4 years, commonly 3 years (Dyatlov 2002, cited by Shustov & Veselov 2005). Trout diet in the lake is mainly focused on vendace (Shustov & Veselov 2005).

Landlocked salmon smolts from rivers flowing into the western part of the Ladoga Lake have a mass from 16 to 44 g and age 1–2 years (Valetov 1999). Lake salmon spawns in age from 2 to 11 years, age 5-6 years is the most common for migrating fish (Valetov 1999).

Grayling

European grayling is a marine water intolerant species with diverse life cycles, including the occurrence of river and lake spawning forms, as well as anadromous populations which may spend several years in a brackish environment before returning to freshwater to spawn (reviewed in Koskinen *et al.* 2000).

European grayling are spring spawners. Spawning takes place just after snowmelt in European countries (Sundell 2008). Grayling may conduct a feeding migration in lakes. In Finland, they ascend to the home stream to spawn in May or June. Grayling may also descend to spawn to a river from a lake, as was the case in River Vuoksi before its harnessing to hydropower production (Seppovaara 1984). During spawning, the water temperature ranges from 3 to 11°C. Grayling spawn at depths of 10–40 cm hiding their eggs under gravel. Water depth at the spawning site of grayling is shallower than that of trout. After spawning, the fertilized eggs remain in the gravel for approximately 22 days at about 8 °C after which they hatch. After dwelling 4–5 days within the gravel and consuming their yolk sac, fry emerge. Complete reabsorption of the yolk sac takes place after 12 days (reviewed by Ingram *et al.* 2000).

Grayling display various forms of movement and migration. These range from spawning migrations such as river to tributary, lake to tributary, sea to river, foraging trips, and diel migrations to shifts in habitat with age. Grayling often make a short-term foraging trip and return to a specific 'spot' in their own territory, occupying what is known as a home range. Movements are also seasonal (reviewed by Ingram *et al.* 2000).

Trout and grayling can live in the same stream. However, a high degree of microhabitat segregation occurs between salmonids (Table 1). For example: (1) Brown trout and salmon are autumn spawners whereas grayling are spring spawners, (2) grayling eggs are buried at shallower depths than those of salmon or trout, (3) emergence and displacement times are shorter for grayling than salmon, (4) brown trout and salmon are common in pelagic areas whereas few grayling are found in pelagic zones (reviewed by Ingram *et al.* 2000).

Table 1. Water depth (cm) favoured by different sizes of grayling and brown trout in a stream (Greenberg et al. 1996).

Fish size (cm)	Water depth (cm) / Grayling	Water depth (cm) / Brown trout
2–8	105–180	<45
9–18	45–90	30–60
19–50	75–165	60–135

There are several naturally spawning grayling populations in the Vuoksi water system (Koskinen et al. 2002), but grayling is partly maintained by broodstocks and releases of hatchery-reared juveniles in the upper reaches of the River Vuoksi (Sundell 2008). Current natural populations are weak. One reason may be predation by other fish species (Sundell 2008).

5.2. Critical and preferred temperatures

Salmon and brown trout

Water temperature is likely the most important abiotic factor influencing survival, growth and reproduction of fish species (Elliott & Elliott 2010). In the Baltic Sea region, warming is likely to exceed its global average, particularly in winter and in the northern parts of the area (Räisänen 2017). Temperature affects the physiology and behavior of a fish (Cunjak *et al.* 1998, Borgwardt *et al.* 2020, Dempson *et al.* 2017, Russell *et al.* 2012) and also other conditions as suitable food for salmon (Friedland *et al.* 2009).

Salmonids have been classified as cold- or cool-water species (e.g., Logez *et al.* 2012). They have low tolerance to high water temperatures because warm water has low solubility of oxygen (Jonsson & Jonsson 2009a). Temperature tolerance varies in the different stages of salmon and brown trout (Elliott & Elliott 2010). Thermal limits are narrower for eggs and alevins (hatched fish with yolk sac) than for parr, smolt or adult (Elliott & Elliott 2010). Salmon spawn usually at 1–5°C, and brown trout at 2–6°C water temperature (Jones 1959, Heggberget 1988). According to a review by Elliott & Elliott (2010), critical temperature limits (°C) for survival of brown trout eggs are from 0°C (lowest) to 13 °C (Table 2). For survival of brown trout, the optimal range of water temperature is 8–10°C, both from fertilization to hatching and from hatching to the beginning of feeding (Ojanguren & Brana 2003). The eggs and alevins, which live in gravel nest in the stream during autumn and winter months, are more sensitive for high temperature than parr, which can move to colder water (Jonsson & Jonsson 2009a, Elliott & Elliott 2010). Salmon has higher tolerance for high temperatures than brown trout (Elliott & Elliott 2010).

Table 2. Critical temperatures (°C) for survival of different life stages of salmon and brown trout according to a review by Elliott & Elliott (2010).

Stage	Salmon		Brown trout	
	Lower	Upper	Lower	Upper
Eggs	0	16	0	13
Alevins:				
incipient	0–2	23–24	0–1	20–22
ultimate	0–1	24–25	0	22–24
Parr+smolt:				
incipient	0–2	22–28	0–0.7	22–25
ultimate	-0.8	30–33	-0.8	26–30

Estimated optimum temperature for growth of Atlantic salmon parr was between 16 and 20°C in Norwegian rivers (59°N–70°N) (Jonsson *et al.* 2001). Experiments with four populations showed that 0+ year brown trout started growing at c. 5 °C, growth peaked at 13.5 °C and growth ceased at c. 23 °C (Forseth *et al.* 2009).

Salmon and brown trout smolts migrate to the feeding areas in spring (Jutila et al. 2005, Jokikokko *et al.* 2016, Kallio-Nyberg *et al.* 2007). The timing of migration of salmon smolts is affected among other things by physiological development of smolts, water temperature and discharge (Whalen *et al.* 1999). In the West River, Vermont, salmon smolt migration began in late April and early May when water temperature reached 5 °C, peak movements occurred in early and mid-May at temperatures exceeding 8 °C (Whalen *et al.* 1999). In River Simojoki, in the northern Baltic Sea, the survival of Carlin tagged wild salmon smolts was the highest when the average SST was 9–11.9 °C (Jutila *et al.* 2005). The post smolts tend to pass the Simojoki estuary fast (within 1–2 days) if the mean SST is high (12–14 °C) (Jutila *et al.* 2009).

Most researchers consider the temperature and water level in the river to be the main factors provoking the downstream migration of Atlantic salmon smolts (Valetov 1999). In the tributaries of Lake Ladoga, the downstream migration begins in the second half of May - early June at a water temperature of 7–13°C, with older (3+) and larger smolts migrating first (Valetov 1999). The duration of the downstream migration is not strictly regulated, and depending on hydrometeorological conditions in the studied rivers, it lasts from 20 to 40 days (Valetov 1999). No clear dependence of downstream migration intensity on temperature and water level was found. Apparently, these factors limit only the duration of the migration and, to a lesser extent, the peaks. It was observed that downstream migration proceeds in a short time with a pronounced peak in conditions of pronounced amplitude of water level fluctuations and elevated water temperature. In opposite conditions, the migration is extended, and the peak of the downstream migration is not clearly expressed. In 1973 in the River Hiitolanjoki, the smolt migration was observed to increase after thunderstorms, which may be due to an increase in water turbidity, which reduces the hunting capabilities of predators. The period of mass downstream migration of Ladoga salmon smolts occurs at a water temperature of 12–17°C and a progressive decrease of water level (Valetov 1999).

Recapture rate of the reared sea trout released as smolt (Gulf of Finland) was the highest when the water temperature was 4–15.9 °C in the release site compared to lower (0–4 °C) or higher (16–19.9 °C) water temperature conditions (Kallio-Nyberg *et al.* 2007).

Anadromous salmon migrate from freshwater river to sea for rapid growth in a habitat with high productivity. An increase of temperature at sea usually increases growth rate of salmon. The growth of one-sea-winter salmon in the North Sea was higher in years with relatively high water temperature and high North Atlantic oscillation index (NAOI) in May, the month when the smolts moved to sea (Friedland *et al.* 2000, Jonsson & Jonsson 2004).

Maturing salmon return to their home river in summer or in autumn (Jokikokko & Jutila 2004). In the River Imsa in Norway (59°N), maximum ascent of adult Atlantic salmon per day took place at water temperatures between 10 and 12.5 °C (Jonsson *et al.* 2007). Stock origin, fish size and water discharge were important variables influencing the upstream migration of salmon in small rivers. Water temperature had an additional positive effect on ascent in September in the end of upstream migration (Jonsson *et al.* 2007). Trépanier *et al.* (1996) observed that upstream migratory movement was negatively related to changes in river flow, suggesting that fish favour falling water flows for ascent, whereas water temperature appeared to have little effect on migratory movement. However, increasing river flow has as well been found to attract migratory ascent to a river (e.g., Vehanen *et al.* 2020). In large rivers of the Lake Ladoga basin (Taipale, Svir) and rivers regulated by dams (Tulema (Tuulomanjoki), Hiitolanjoki), there is a relationship between the intensity of salmon spawning migration and the water level and discharge regime of the river (Valetov 1999). An increase in the water level during floods, after rains, or due to influence of hydropower station dams, contributes to upstream migrations of salmon, which, for example, was observed in the Hiitolanjoki and Vidlitsa (Vitelenjoki) rivers. However, in anomalously warm dry years, as well as in small and unregulated rivers of the Lake Ladoga basin (Ikhala, Syskyänjoki), especially in years with moderate water discharge, there is no clear relationship between the water level and the intensity of salmon spawning migrations. It was observed that there was an influence of water temperature on the intensity of salmon spawning migration in rivers flowing into northern part of the Lake Ladoga. The most of spawning salmon migrated into rivers when water temperature decreased after its peak values (Valetov 1999).

In hatcheries, landlocked salmon embryos are incubated normally at low temperatures. In the experiment by Kiiskinen *et al.* (2004), early development of landlocked salmon embryos was accelerated by increasing the water temperature gradually from 4 to 8 °C about four weeks after the eyed stage of embryos until 'startfeeding' when the ambient water temperature reached 8 °C.

Grayling

European grayling is generally a freshwater fish but may dwell also in brackish water. Suitable habitats for grayling fry are the rivers or larger streams with cool and well oxygenated water and with gentle slope and riffles and rapids separated by pools and runs (reviewed by Ingram *et al.* 2000). Grayling is threatened by climate change, especially increasing temperatures in its southern distribution area.

Grayling have a minimum oxygen requirement of 5–7 ppm and an upper temperature tolerance of 18–25 °C, preferring a maximum of 18 °C (Crisp 1996) (Table 3). Constant temperature of >5 °C is optimal for spawning. Incubation temperature of embryos is 3–15.0 °C. Hatching of grayling has been found to take place at an optimum temperature range of 7–11 °C (Crisp 1996, reviewed by Ingram *et al.* 2000).

Table 3. The suggested optimum, upper and lower critical temperatures (°C) for grayling in Europe (Crisp 1996).

Range	Temperature °C
Lower critical	0–4
Upper critical	>18
Optimum	4–18

5.3. Preferences of river habitat

Salmon and brown trout

Habitat criteria for spawning sites and eggs of salmon and brown trout are narrower than those for small juveniles. Louhi *et al.* (2008) found salmon to spawn mostly in relatively deep, swift-velocity habitats (20–50 cm, 35–65 cm s^{-1}), whereas trout selected slightly shallower and slower flowing spawning sites (15–45 cm, 20–55 cm s^{-1}). Salmon and brown trout preferred pebbles (16–64 mm) for spawning (Louhi *et al.* 2008).

Salmon parr live in the home stream usually 2–4 years before smoltification and feeding migration (McCormick *et al.* 1998). McCormick *et al.* (1998) have divided the movements of juvenile salmon prior to the smolt transformation into five phases: (1) movement of fry from the vicinity of their redds; (2) establishment and occupation of feeding territories; (3) spawning movements of sexually mature male parr; (4) shifting from summer feeding territories to winter habitat; and (5) descent from nursery streams to lower reaches of some rivers in late autumn as a forerunner or component of smolt migration.

Salmon parr may use different habitat seasonally and velocity is one factor, which affects habitat selection (Enders *et al.* 2007). In comparison to summer (most frequently 40–60 cm s^{-1}), parr used predominately slower flow velocity (0–40 cm s^{-1}) during winter. Significant differences were also observed in the use of substrate between summer and winter. During summer, parr used predominately cobble substrate, whereas during winter, a proportion of the parr (45%) were observed to prefer boulder substrate (Enders *et al.* 2007). Seasonal differences in parr position in relation to shoreline have also been observed in larger rivers by Mäki-Petäys *et al.* (2004), who showed that larger parr occupied territories further from the shoreline in summer and moved closer to the shoreline during winter.

Salmon juveniles of different age also distributed in the stream depending on the velocity (Valetov 1999). In late June - early July, during the formation of scales in juveniles, their behavior changes from swarming to territorial, and each fry is looking for its foraging site. When fingerlings reach a length of 3–4 cm in late July - early August they leave the shallows and move to riffles of depths from 0.2 to 0.5 m and water velocities of 30–50 cm s^{-1} (Valetov 1999). During this period, territorial behavior is finally formed and the conditional boundaries of the individual sites are determined. Yearlings and elder parr inhabit deeper areas of the riffles (from 0.4 to 1.5 m), where the velocity is higher (up to 80 cm s^{-1}) (Valetov 1999).

In an experiment by Vehanen *et al.* (2000), brown trout preferred the highest water velocities (21–29 cm s^{-1}) in early summer, and the lowest (10–17 cm s^{-1}) in winter. In the River Imsa in Norway (59°N), maximum ascent of Atlantic salmon per day occurred at water discharges between 12.5 and 15 m^3 s^{-1} (Jonsson *et al.* 2007).

Thorstad *et al.* (2003) studied upstream migration of Atlantic salmon in large, regulated rivers in Norway in relation to discharge. They concluded that relatively short and small artificial freshets in large regulated rivers may be a waste of water and money in stimulating salmon to pass power station outlets and a water discharge may not be important until the salmon is motivated for migration.

Grayling

Grayling spawn and spend their juvenile lives usually in running water. In general, a moderate velocity, ranging from 20–90 cm/s, is required at spawning sites for grayling. The different life-stages of grayling in the stream require specific habitat types to survive. The distribution of grayling is related to the flow rate. The preferred velocity of grayling juveniles is <10 cm/s whilst older, larger individuals prefer velocities of 20–50 cm s^{-1} (reviewed by Ingram *et al.* 2000, Greenberg *et al.* 1996).

Larval grayling shifted their habitat with growth in the medium-sized river in northern Finland (Nykänen & Huusko 2003). Small (17–21 mm) larvae preferred water depths 10–30 cm, sub-strata dominated by mud or sand (<2 mm), 10–70 % vegetation cover and water velocities <10 cm s^{-1}. Middle-sized (22–25 mm) larvae preferred depths of 30–90 cm, sandy substrata, <40% vegetation cover and velocities <10 cm s^{-1}. Large (26–31 mm) larvae preferred >50 cm depths, substrata dominated by sand or boulders, <20% vegetation cover and 10–50 cm s^{-1} velocities.

In an experiment in a restored stretch in the northern Finland, adult grayling preferred water velocities between 0.20 and 0.45 m s^{-1}, water depths between 0.20 and 1.55 m and coarse substrate (Vehanen *et al.* 2003).

Ingram *et al.* (2000) state that the importance of water velocity relates to the maintenance of grayling eggs below the substrate surface. If velocity is high, the likelihood of egg dislodgement increases. In addition, high flow rates could flush developing larval stages into areas where food abundance is sparse, or to pools which are only accessible at high water (Clark 1992). The temperature of the water may also be decreased as a result of mixing at high velocities which will slow the rate of egg development (Clark 1992). Similarly, increased turbidity affects larval development by reducing feeding efficiency (reviewed by Ingram *et al.* 2000, Clark 1992).

6. Possible impact of climate change on salmonids in their different life history phases

6.1. Hatching and egg incubation

Climatic conditions influence embryonic development and parr growth in Atlantic salmon (Jonsson *et al.* 2005). NAOI correlated positively with parr growth and smolting as 1-year-olds. Juveniles that hatched after mild and wet winter tended to grow larger during the first year and they migrated to sea younger than those born after a cold and dry winter (Jonsson *et al.* 2005).

Wedeking & Kühn (2010) assumed that the changes in water temperatures could have promoted the decline of grayling abundance and earlier spawning season. At the beginning of the spawning season the water temperature was approximately 6 °C every year. This temperature did not differ significantly from year to year, but it was reached increasingly earlier in the period 1948–2009. The change in the timing of spawning has changed the temperatures under which embryos, larvae, and fry develop. Significant temperature reductions over time occurred during embryogenesis, hatching, metamorphosis from larva to fry, and emergence from gravel. In the summer months, temperatures increased significantly from 1971 to 2009. These temperature changes correlated with a decrease in the number of egg-bearing females.

6.2. Parr

The water temperature influences the movement of parr. Breau *et al.* (2007) found (in Canada) that 1- and 2-year-old salmon parr aggregated in cool water sites when temperatures exceeded 23 °C, but the younger fish did not move to the cooler sites. Coincident with a decline in daily water temperature below 8–10°C, juvenile Atlantic salmon display an autumnal shift in microhabitat choice and behaviour, moving beneath suitably sized stones during the daylight hours (reviewed in Cunjak *et al.* 1998). Unlike the situation during summer when they are strongly photopositive, young Atlantic salmon become exclusively photonegative in winter, leaving their shelters only during the night (or at dawn/dusk) to feed. The reduced buoyancy of salmon parr at water temperatures <8 °C may be a synchronous adaptation for this cryptic behavior (reviewed in Cunjak *et al.* 1998). Frequency of emergence and nocturnal foraging is unknown, especially in far northern regions that are subject to months of polar darkness. Probably, foraging activity is minimal at such low temperatures because of the reduced metabolic demand and the inability to hold position in moderate water velocities (Rimmer *et al.* 1985, Heggenes & Traaen 1988) although visual acuity is improved at low light levels in winter (Fraser *et al.* 1993). The ability of the young salmonids to swim against strong currents decreases rapidly as the water temperature falls below 6–8°C (Graham *et al.* 1996, Jonsson & Jonsson 2009a). Veselov and Shustov (1991) have suggested that this inability to resist water currents and the reduced fright reaction of overwintering salmon parr may explain the winter hiding behavior – i.e., a tactic to avoid predation and minimize energy expenditure (Cunjak 1996).

Salmonid parr tend to escape too high flow or drought. Movement to the estuary may increase mortality of parrs due to their insufficient physiological adaptation or predation (Jonsson & Jonsson 2009a). The lack of ice cover due to an increase of winter temperature will alter habitat availability for fish. For example, Atlantic salmon are adapted to a complete ice cover during the winter but may suffer from sudden loss of energy when exposed to open-water conditions (i.e., more time spent on escaping predators, less time spent on eating), thus lowering their overwintering survival (Finstad *et al.* 2004).

The availability of habitats suitable for the different size classes of brown trout was clearly depending on the flow rate according to habitat modelling by Yrjänä *et al.* (2002). In the regulated River Siikajoki, there were clearly fewer habitats available for fry under 15 cm in length compared with the other size categories.

Accumulated snow depth and summer temperature were critical factors for recruitment of high mountain populations of brown trout (Borgstrøm & Museth 2005). Climate change with more winter precipitation, as predicted for the present century, may therefore be detrimental to recruitment. Little snow and low temperatures during the winter may have led to recruitment failure, as small nursery streams may freeze completely under such conditions. The mean August temperature in the year of birth of trout was significant for the appearance of strong year-classes (Borgstrøm & Museth 2005).

6.3. Smolt

Salmon and brown trout migrate as smolt usually during spring or early summer from their reproduction area to their growth area at sea or lake (Jokikokko *et al.* 2006, Jonsson & Jonsson 2009b). Prior to the migration salmon and brown trout undergo a major transformation called smoltification. Parr-smolt transformation is associated with increasing temperature in spring, and it is regulated by photoperiod and water temperature (McCormick *et al.* 1998). Timing of smolt migration is affected by water temperature, flow, light conditions or presence of predators (McCormick *et al.* 1998).

Timing of the initiation of smolt migration differs in the different rivers. Otero *et al.* (2014) observed that the initiation of downstream migrations has changed. It has occurred 2.5 days earlier per decade throughout the basin of the North Atlantic. Earlier smolt migration was associated with increase of water temperature both in the river and sea.

Median date of down-migration of salmon smolts has advanced about 10 days in the River Simojoki from 2000 to 2014 (Jokikokko *et al.* 2016). Smolt migration began when suitable temperature (about 13 °C) was reached. Median day temperature during smolt migration did not change over years (Jokikokko *et al.* 2016).

The survival of Atlantic salmon in the Baltic Sea is affected by smolt traits and annual environmental factors. Kallio-Nyberg *et al.* (2004) found that increasing annual sea surface temperature (SST) in July in the Gulf of Bothnia in the smolt year temperature and increased mean smolt size improved survival from smolt to catch size. If the SST was excluded from the model, the NAO index in May to July was also positive effect on survival. Abundance of young herring entered to the model if the SST and NAO was excluded.

Friedland *et al.* (1998) reported positive correlation between post-smolt survival of Atlantic salmon and the SST in May, when smolts enter the sea. The warm water during summer associated negatively with North American Atlantic salmon abundance (Friedland *et al.* 2003).

6.4. Feeding migration

Annual mean individual size (length, mass) of wild one-sea-winter Atlantic salmon from Norwegian River Imsa decreased from 63 cm to 54 cm and from 2 kg to 1.2 kg from cohorts migrating to sea from 1976 to 2010 (Jonsson *et al.* 2016). The length correlated negatively with near-surface temperature in the feeding areas of the present stock. Jonsson *et al.* (2016) suggested that reduced growth may be associated with lower primary and secondary production in the pelagic food web or metabolic costs.

In the Baltic Sea, increasing temperature in the smolt year associated with a smaller grilse size of Atlantic salmon and increasing grilse proportion (Kallio-Nyberg *et al.* 2020). After smoltification, the northern Atlantic salmon usually migrate to the southern parts of the Baltic Sea to feed and return as maturing salmon to their home river. When the post-smolt summer was warm the smolt year class was recaptured more frequently in the feeding grounds closer the home rivers, while colder summers were associated with more recaptures further south (Kallio-Nyberg *et al.* 2020). Zooplankton and herring are abundant during warm springs in the Gulf of Bothnia (Dippner *et al.* 2001), but salmon growth is weaker in the northern feeding ground than in the southern ones.

6.5. Spawning migration

Dahl *et al.* (2004) discovered that the spawning migration peak of salmon in River Dalälven, Sweden, was strongly correlated with mean monthly sea and river temperatures during spring: salmon arrived earlier when temperatures were higher and later when temperatures were lower. River discharge explained little of the variation in timing of migration.

Baisez *et al.* (2011) observed that adult salmon in their spawning migration in the River Allier in France suffered higher mortality if the water temperature in the river was high. The salmon stopped their migration when the mean (±SD) daily temperature of the water reached 15.5 ± 2.7 °C, with a maximum recorded temperature of 22.6 °C and a minimum of 11.2 °C. The salmon that survived the summer period were exposed to a mean temperature of 18.9 °C (± 0.9 °C) during their migration delay, which was significantly lower than that experienced by those that died (mean temperature of 20.4 ± 0.7°C).

7. Ecological responses and adaptation to new thermal conditions

Rolls *et al.* (2017) have summarized the environmental effects of climate change and illustrate the ecological responses of freshwater fishes to these effects, spanning individual, population, and community and ecosystem levels. Decreased size and age of sexual maturation with increasing temperature are widely reported for freshwater fish across contrasting climate regions, including populations inhabiting the subarctic (Blanck & Lamouroux 2007, Daufresne *et al.* 2009). In contrast to decreasing body size of parental fish, individual egg size increases with increasing temperature in autumn-spawning brown trout and Atlantic salmon (Jonsson & Jonsson 2009a) but decreases in spring-spawning roach (Lappalainen *et al.* 2008).

Salmonids can adapt to new thermal conditions (Otero *et al.* 2014, Jonsson & Jonsson 2018). McGinnity *et al.* (2009) showed that the escape of captive bred salmon into the wild can substantially depress recruitment due to crossbreeding, and more specifically, disrupt the capacity of natural populations to adapt to higher winter water temperatures associated with climate variability. The reared salmon are less fit than wild fish under natural conditions. The cultured fish substantially increased the risk of extinction for the studied salmon population within 20 generations. McGinnity *et al.* (2009) proposed that conservation efforts should focus on optimizing conditions for adaptation to occur by reducing exploitation and protecting critical habitats.

Sockeye salmon have been discovered to show remarkable fidelity to their spawning areas and appear to have an optimum temperature for aerobic scope that corresponds to the river temperatures experienced by their antecedents (Farrell 2009). Unfortunately, there is evidence that this potential adaptation is incompatible with the rapid increase in river temperature presently experienced by salmon as a result of climate change. By limiting aerobic scope, river temperatures in excess of the optimum for aerobic scope directly impact upriver spawning migration and hence lifetime fecundity (Farrell 2009).

Temperature in the freshwater period affects life-history traits and behavior of adults (Jonsson & Jonsson 2018). Adult salmon returned about 2 weeks later from feeding ground to the coast, when they developed as embryos in c. 3 °C warmer water than the regular incubation temperature (Jonsson & Jonsson 2018). The warm-water-incubated salmon fed longer at sea before they started return migration (Jonsson & Jonsson 2018). Also, temperature during maturation in the mother generation affects the traits of the next generations (Jonsson & Jonsson 2016). Increased temperature during maturation experienced by female parents increased the size of eggs produced by the offspring (Jonsson & Jonsson 2016).

At population level, increasing winter temperatures are expected to delay and shorten the spawning period of cold-water-adapted subarctic species (putting them at a reproductive disadvantage) and simultaneously stimulate earlier and protracted spawning of cool- and warm-climate species (Karjalainen *et al.* 2015). Community-level response to climate change in freshwaters is a change in competitive advantage between fish species. Where brown trout and Arctic charr (*Salvelinus alpinus*) occur in sympatry, population biomass of brown trout is negatively correlated with ice-cover duration, suggesting that Arctic charr have a competitive advantage during periods of ice cover (Helland *et al.* 2011).

8. Effects of climate change in regulated rivers

Many lakes in Vuoksi watershed are regulated (Veijalainen *et al.* 2010a) and the River Vuoksi, which runs to Lake Ladoga, is regulated by several dams (Korjonen-Kuusipuro 2011). Damming has a dramatic impact on the river environment: it usually changes streaming river habitat to a chain of reservoirs. Damming and reservoirs facilitate rapid changes in water discharge and water level (Puffer *et al.* 2014). These human-induced rapid and frequent fluctuations in water discharge are termed hydropeaking (Vehanen *et al.* 2003) and affect upstream migration of salmon (Vehanen *et al.* 2020). Damming destroys especially rapid and riffle habitats, which are necessary nursery areas for salmonids (Jonsson 1985, McCormick *et al.* 1998, Leinonen *et al.* 2020, Vehanen 2000, 2003). Reservoirs of the dammed river are unsuitable habitat for salmonids compared to natural streams, where the salmonids can find suitable reproduction areas and juveniles can spend territorial life. Damming decreases migration success of downstream-migrating smolts (Huusko *et al.* 2018). Damming has critically destroyed spawning and nursery habitats of the salmonids in the Vuoksi watershed (Hutchings *et al.* 2019, Leinonen *et al.* 2020).

Climate change is expected to modify thermal and hydrological regimes, with uncertain consequences for aquatic species (Nicola *et al.* 2018). In the Northern Hemisphere, climate models have predicted an increase in air temperature and winter precipitation, but a decrease in summer precipitation (IPCC 2007, Schneider *et al.* 2013). In the boreal zone, the highest mean winter precipitation increases are projected for 2050s (i.e., +13 %), but also mean summer precipitation is expected to rise by 6 % (Schneider *et al.* 2013). Accordingly, future winter discharges are higher compared to natural flow regime, while summer flows are less impacted (Schneider *et al.* 2013). According to the simulations by Veijalainen *et al.* (2010b), the 100-year floods in Finland in 2070–2099 will change significantly during different seasons and areas. Floods will decrease in spring in part of the central Finland because the increase of temperature causes a decrease in snow accumulation. Water level and flow will increase especially in large central lakes and their outflow rivers in the lake area where the floods are currently long-lasting big floods, and already occur in autumn as well as in springtime. These floods will increase due to increased precipitation and wetter and milder autumns and winters. Winter and early spring discharge in River Vuoksi will increase considerably due to climate change (Veijalainen *et al.* 2010a, Marttunen *et al.* 2010). Veijalainen *et al.* (2010a) state that current regulation practices and limits, which have been based on past hydrology in the Vuoksi watershed, may not be appropriate in future.

Salmonids are vulnerable to diverse anthropogenic disturbances such as river fragmentation and flow and thermal alterations due to their migratory behavior and dependence on environmental cues (Jonsson and Jonsson 2009b, García-Vega *et al.* 2017). Dams, weirs and other river structures can not only hinder or limit the movements of freshwater organisms but also vary the natural flow regime (Nilsson *et al.* 2005, Nyqvist *et al.* 2016). Flow modification may mean daily rapid changes in flow (e.g., hydropeaking) or damping flood peaks (e.g., dams for flood control) (Almodóvar & Nicola 1999). These non-natural flow variations might affect the density, growth, biomass and species composition (Almodóvar & Nicola 1999, Benejam *et al.* 2014, Puffer *et al.* 2015), as well as affect the daily fish behaviour and the time of spawning and migration periods (Karppinen *et al.* 2002).

The effect of future climate change on an Atlantic salmon population in a regulated river was modelled, and bottlenecks for salmon abundance in the warming climate were identified by Sundt-Hansen *et al.* (2018). Future juvenile abundance was reduced in three of four future scenarios (southern Norway). Low water discharge in summer was identified as a possible bottleneck. Reduction in abundance was caused by reduced wetted area in summer periods. Reduced future juvenile abundance can be mitigated in rivers with reservoir capacity by releasing water in critical periods. The age composition of smolts changed; the majority of smolts in the future scenarios were 2+, compared to 3+ and 4+ in the control scenarios.

8.1. Adapting restoration strategy to climate change

Beechie *et al.* (2013) have evaluated habitat restoration plans for salmonids in northwestern USA in relation to climate change scenarios. They present the questions, which are applicable to any salmon restoration effort, and – moreover - generally applicable to restoration of many species or ecosystems. Key elements of adapting any restoration strategy to climate change include (1) understanding the current recovery needs, (2) evaluating whether climate change effects will likely alter those needs, (3) determining whether restoration actions can ameliorate climate change effects, and (4) determining whether restoration actions can increase ecosystem resilience. The key questions that must be answered for any adaptation strategy are as follows: Does climate change alter restoration needs in the future? Can restoration actions increase ecosystem resilience by reducing climate change effects or increasing habitat diversity? Restoring diverse habitats will increase resilience of the riverine ecosystem—thereby increasing the likelihood that a salmon population can recover under a warming climate.

Implementing restoration projects proactively can be used to protect existing resources so that expensive reactive restoration to repair damage associated with a changing climate is minimized. Special attention should be given to diversifying and replicating habitats of special importance and to monitoring populations at high risk or of special value so that management interventions can occur if the risks to habitats or species increase significantly over time. Ensuring environmental flows is needed in adapting restoration strategy to climate change. (Palmer et al. 2009).

9. Whitefish

Whitefish (*Coregonus lavaretus*) is widespread from central and northwest Europe to Siberia (Kottelat & Freyhof 2007). It is clearly a coldwater species (e.g., Logez *et al.* 2012) most probably being disturbed by climate change in Finland (Urho 2011). Whitefish spawn in late autumn and larvae hatch early in spring. In river-spawning populations, whitefish fry descend to river estuary and further to sea or lake during their first summer, while some year later maturing whitefish ascend back to the home river in their spawning migration (Jokikokko *et al.* 2012). In contrast to grayling, brown trout and landlocked salmon, whitefish may avoid the hottest summer in a river if fry manage to drift to lake or sea early enough, which is mostly the case (Koli 1990).

Optimum temperature for growth of whitefish is around 15–18 °C (Siikavuopio *et al.* 2012). Adaptation to shortened winter may be difficult for whitefish, spawning usually in shallow nearshore lake areas or in streams in late autumn. Despite the risen lake water temperatures and shortened ice-cover season the hatching of whitefish larvae should take place in lakes at about the ice-break. This ensures match with the developing zooplankton which is the first food of whitefish larvae. In addition, ontogeny of river-spawning whitefish larvae and young should temporally match the development of zooplankton and insect larvae at first in river, and after some weeks after their descent from the river to the lake (Sutela & Huusko 1998, Straile *et al.* 2007, Karjalainen *et al.* 2015)

Whitefish larvae and young individuals may experience increased predation mortality if perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*) populations as warm-water species grow as a result of climate change (Huusko *et al.* 1996, Jeppesen *et al.* 2012). Increased competition of food resources (zooplankton and macroinvertebrates) by warm-water or eurythermal fish species, for example by roach, may depress whitefish populations in warming environment. Competitive and other interactions of whitefish with other fish species in the warming environment may be diverse, yet mostly negative for whitefish (Jeppesen *et al.* 2012). The decrease of whitefish populations in many Finnish lakes in recent decades (Forsman 2015, Puranen & Ranta 2017) may be linked with climate change.

10. Introduced species: rainbow trout

Rainbow trout (*Onchorhynchus mykiss*) is one of the most widely introduced fish species in the world (Crawford & Muir 2008, Stankovics *et al.* 2015). Introductions are often performed following put-and-take principle, while unintentional introductions as escapees from fish farms are also common. In Europe, rainbow trout have established self-sustaining populations at least in 28 countries (Savini *et al.* 2010). However, the appearance of self-sustaining populations in northern Europe has been rare. In Sweden, there are only a few self-sustaining rainbow trout populations in southern and central Sweden (Stankovics *et al.* 2015). Although spawning behavior has been reported in several Norwegian rivers, there have been only some examples of successful reproduction in recent decades (Stankovics *et al.* 2015). The northernmost naturalized population was located in a remote area north of the Arctic Circle, near the village of Skibotn in Troms County in the 1960´s (Gammelsæter & Dønnum 1994). However, most of the other Norwegian self-sustaining populations persist or have persisted in southern Norway. Despite the intensive put-and-take stocking of rainbow trout in Finland, self-sustaining populations have been known only from a few streams in southern and eastern Finland (Korsu & Huusko 2010, Urho & Lehtonen 2008).

Established populations of rainbow trout have frequently affected native species negatively especially in Japan, New Zealand, and North America (Korsu *et al.* 2008). In the French Pyrenees, rainbow trout significantly affected the habitat selection and apparent survival of native brown trout (Blanchet *et al.* 2007). Competition by rainbow trout, mostly through red superimposition, has been documented for native brown trout from Lake Constance and from Gotland Island (Landergren 1999, Rulé *et al.* 2005). Rainbow trout may represent a severe threat to grayling, showing considerable overlap in habitat use, possible preying on deposited eggs and coincidence of reproduction periods (Wiesbauer *et al.* 1991, Uiblein *et al.* 2000, Uiblein 2001, Stankovics *et al.* 2015).

MacCrimmon (1971) identified water temperature and precipitation as the two most important environmental constraints that could define the natural limits of rainbow trout population establishment and maintenance. Low water temperatures in northern Europe obviously have restrained the establishment of self-sustaining rainbow trout populations (Korsu & Huusko 2010, Stankovics *et al.* 2015). However, warming climate will increase the risk for this establishment. Fausch *et al.* (2001) compared the hydrologic regimes for rivers across the world where rainbow trout invasions ranged from unsuccessful to highly successful. Invasion success was greatest in areas that closely matched flow regimes within the species' native range (i.e., flooding in winter and low flows in summer). Increased wintertime floods and discharges in River Vuoksi induced by climate change (Veijalainen *et al.* 2010a) may thereby also favor natural reproduction and establishment of rainbow trout population.

River Vuoksi carries special risks of self-sustaining rainbow trout establishment for the following reasons. (1) Vuoksi is a southern river in the Finnish perspective. (2) The discharge regime without high spring floods matches with the preferred discharge regime preferred by rainbow trout (see Fausch *et al.* 2001). (3) The high and around the year stable pH in Vuoksi (compared to the average in Finnish streams) is preferred by rainbow trout (Haines 1981, Hulsman *et al.* 1983). (4) Rainbow trout prefers large rivers over small streams and brooks (Korsu *et al.* 2008). Even without establishing a self-sustaining population, the widely detected spawning behavior of stocked rainbow trout with redd construction may be harmful to the reproduction of brown trout (Landergren 1999), landlocked salmon and grayling (Wiesbauer *et al.* 1991, Uiblein *et al.* 2000, Uiblein 2001). Even without rainbow trout put-and-take introductions to the River Vuoksi on the Finnish side of the river, there is a risk for rainbow trout escapees from the fish farms downriver on the Russian side.

11. Expected effects of climate change on the fish species of River Vuoksi

In a big picture, fish populations in the River Vuoksi are not especially vulnerable to climate change because of the large size of the river. Flow and water temperature changes following global warming are most striking in small and shallow streams, and thereby fish species living in small headwater streams are most vulnerable to climate change (Buisson *et al.* 2008, Buisson & Grenouillet 2009). As described in chapters 5.2 and 6.3, salmonids can adapt to warming climate by delaying their spawning run in autumn, precipitating smoltification in spring and other temporal adjustments in their life-span. However, valuable populations of salmonid species in the River Vuoksi are expected to weaken in the long run because their optimal temperatures (see chapter 5.2, Hari *et al.* 2006, Logez *et al.* 2012) are exceeded in midsummer. Globally quite northern location of the River Vuoksi would suggest that its salmonid populations could possibly even benefit from climate change (Jonsson & Jonsson 2009a). However, being a lowland river, the maximum summertime water temperatures of the River Vuoksi are already high (even >25 °C, Figure 3) in comparison to highland and mid-altitude rivers of the same latitudes for example in Norway. In the Alps, the effect of elevation on stream water temperatures, and the upstream shift of optimal temperature zones for brown trout along climate change was documented by Hari *et al.* (2006). High summer temperatures in the River Vuoksi may stress and even induce extra mortality especially among grayling and *Salmo* spp. individuals having quite low optimum and critical temperatures (see chapter 5.2, Elliott & Elliott 2010, Hari *et al.* 2006, Logez *et al.* 2012).

When thinking about critical life history phases of *Salmo* spp. (see chapter 6, supplemented with critical temperatures in chapter 5.2), we consider alevin and parr most vulnerable. In a big river like the River Vuoksi, practically no thermal refugees are offered by springs like in small brooks. Furthermore, shadowing tree canopy in the restored nursery areas for salmonids in the River Vuoksi is minimal in comparison to most tributaries. During their feeding migration to Lake Saimaa or Lake Ladoga, post-smolt and older landlocked salmon and brown trout may find cool water in abysses even in midsummer.

As a potential benefit of warming climate, even higher percentage (nowadays about 90 %) of *Salmo* spp. young in the River Vuoksi may reach smoltification at the age of two years thereby probably increasing survival to smolts and total number of produced smolts. However, we expect the introduced negative effects of warming water temperatures to overrule this positive effect.

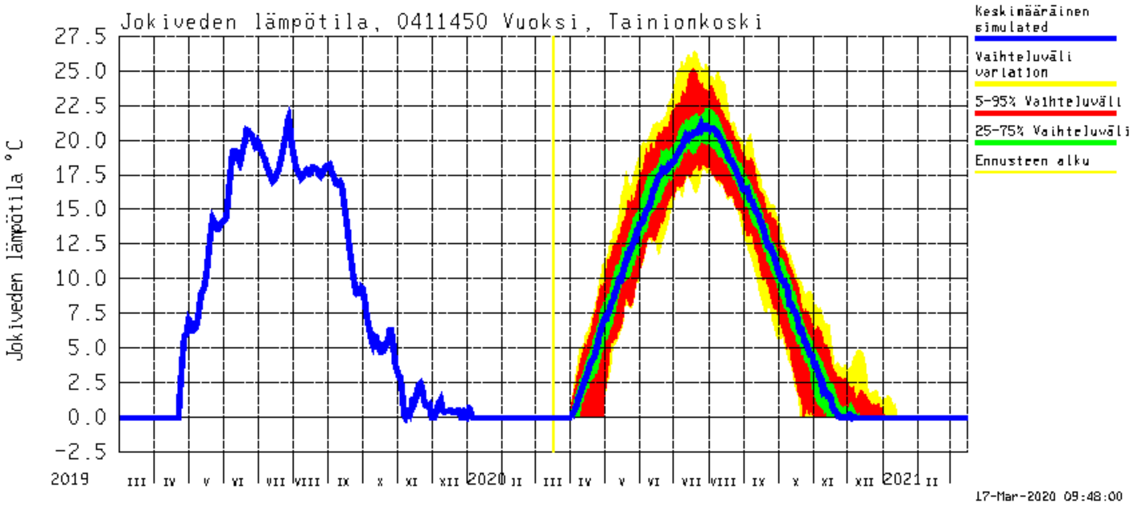

Figure 3. Water temperatures (°C) in the River Vuoksi (Tainionkoski). Blue line refers to simulated mean, yellow total range of variation, red 5–95 % range of variation, green 25–75 % range of variation, and vertical, thin yellow line refers to the start of applying a predictive model. (www.ymparisto.fi)

Late summer runoff from Lake Saimaa to the River Vuoksi is expected to decrease considerably due to climate change especially during the latter part of this century (Figure 4). This means lower discharges, water velocities and water levels in the River Vuoksi in summer. Habitat of *Salmo* spp. young is expected to diminish when shallow natural or restored riffles are run dry in expanded areas. Being territorial, young *Salmo* spp. specimen are reluctant to shift to deeper areas even when water level decreases to an unbearable level. With the restored riffles in the regulated upper reach of the the River Vuoksi, there seldom is any stony, sheltered riverbed habitat available at the nearby deeper areas. Therefore, low water velocities accompanied with low discharge will aggravate the loss of riffle habitat preferred by *Salmo* spp. young especially in these restored riffle areas.

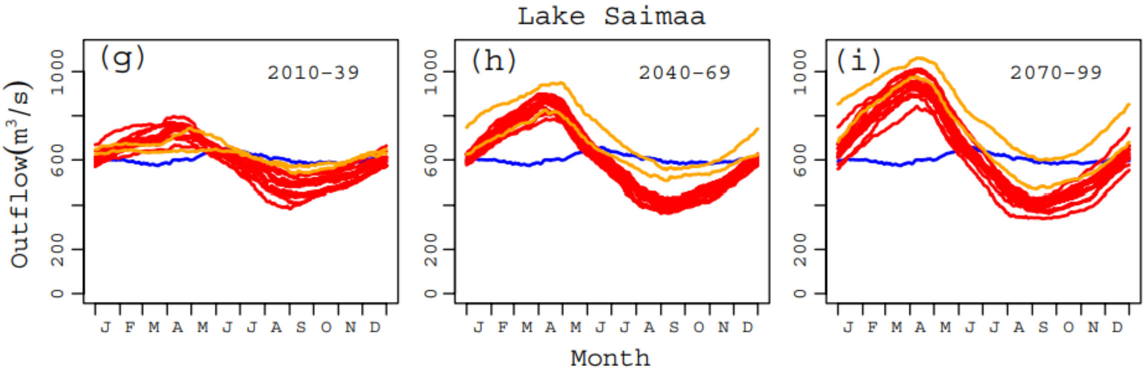

Figure 4. Predicted outflow from Lake Saimaa to the River Vuoksi at three consecutive periods in this century (Veijalainen *et al.* 2010a).

Winter and early spring discharge in the River Vuoksi will increase considerably due to climate change (Figure 4). In the River Vuoksi, the relative wintertime discharge in comparison to average discharge is already high compared to most natural Finnish rivers. While the demand of hydropower is highest in the coldest winter months, there is also a financial motive for the hydropower companies to maintain high wintertime discharge in the River Vuoksi. Increasing wintertime discharge and water velocity due to climate change may be harmful for young salmonids. As described earlier in chapter 5.3, the ability of the young salmonids to swim against strong currents decreases rapidly as the water temperature falls below 6–8°C (Graham *et al.* 1996, Jonsson & Jonsson 2009a), and salmonid parr prefer in winter slower current than in summer (Enders *et al.* 2007). Young salmonids in small-sized restored habitats of the River Vuoksi with marginal area of stony, deeper area nearby, may be confronted with too high velocities as wintertime discharge expands due to climate change. Also reduced ice cover in the River Vuoksi following climate change may be harmful for the overwintering salmonid young (Finstad *et al.* 2004, see chapter 6).

Considering the effects of rising maximum water temperatures in summer and the changes in seasonal discharges in the River Vuoksi, we assess that the gross impact of climate change is clearly negative on salmonids. Besides *Salmo* spp., also populations of grayling and whitefish (see chapter 8) as cold-water species are expected to decline.

In contrast to salmonids, several warm-water species (e.g., pikeperch, perch, many cyprinids) dwelling mostly outside the few remaining rapids and riffles in the River Vuoksi are anticipated to benefit from the climate change. In cyprinids, some nowadays relatively rare warm-water species in the River Vuoksi, like European carp (*Cyprinus carpio*), asp (*Aspius aspius*) and sichel (*Pelecus cultratus*) are expected to strengthen their populations. Of the riffle species, stone loach (*Barbatula barbatula*) favors relatively high temperatures in Finnish streams (Sutela *et al.* 2021), and is thus expected to benefit from climate change, whereas bullhead (*Cottus gobio*) and burbot (*Lota lota*) as cold-water species (Logez *et al.* 2012, Sutela *et al.* 2021) are expected to decline.

12. Recommendations for mitigation measures

As mitigation measures for the adverse effect of climate chance on the salmonid species can be suggested 1) restoration of the existing riffles, 2) increased connectivity and new reproduction areas by construction of bypass channels, 3) shadowing tree coverage to possible bypass channels and 4) more effective control of the fishermen in obeying the fishing restrictions. Furthermore, 5) hydropeaking should be dampened. 6) put-and-take introductions of rainbow trout to the River Vuoksi should be banned to reduce the risk of self-sustaining populations or merely redd construction likely harming the reproduction of grayling, brown trout and landlocked salmon.

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