	Council Current and predicted ecological impacts of climate change to Atlantic salmon freshwater productivity in the North Atlantic	CNL(23)50 Agenda item: 7a)

Current and predicted ecological impacts of climate change to Atlantic salmon freshwater productivity in the North Atlantic

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1.0 Introduction

1.1 Context

Atlantic Salmon (*Salmo salar*) reproduce in freshwater habitats on both coasts of the Atlantic Ocean (MacCrimmon & Gots 1979). The species' historic native distribution ranges from the Housatonic River in Connecticut, USA, to Ungava Bay in the Nunavik region of Quebec, Canada in North America, and from northern Portugal and Spain to Scandinavia, Finland, and Russia in Europe. The species is also present in Greenland and in the North Atlantic islands (Iceland). Freshwater habitat is of crucial importance for Atlantic salmon to complete several life functions including reproduction, juvenile rearing, and smoltification (Klemetsen *et al.* 2003, Thorstad *et al.* 2012). In addition, successful smolt migration to the sea is thought to be dependent on freshwater habitat quantity and quality. Two key environmental variables affecting freshwater habitat quantity and quality for Atlantic salmon are river discharge and water temperature (Armstrong *et al.* 2003; Jonsson & Jonsson 2009). Discharge, which depends in part on precipitation, evaporation, land use, soil types and local geology, influences the surface area of available habitat, juvenile feeding rates, the speed of upstream and downstream migrations as well as spawning success (Jonsson & Jonsson 2009). Water temperature, which is governed by incoming solar shortwave radiation, net longwave radiation, evaporation, convection and local advection of surface runoff, interflow and groundwater, is the principal controlling factor of metabolism in ectotherms through effects on rates of biochemical reactions, and thus, on physiological and behavioural performance (Fry 1947, 1971; Claireaux & Lefrançois 2007). Thermal tolerance of Atlantic salmon varies with life stage, with incubating eggs/emerging alevin and spawning adults having the narrowest tolerance (0.5–16 °C and 4–12 °C respectively; Gillis *et al.* (2023)), while the optimal range for parr growth is between 16–18 °C (Breau *et al.* 2007; Elliott & Elliott 2010). Throughout the range of Atlantic salmon, climate change is expected to alter the future flow and thermal regimes of salmon rivers (Sundt-Hansen *et al.* 2018) and subsequently impact Atlantic salmon productivity.

1.2 Objective

The objective of this paper is to provide a brief overview of the changes to river discharge and water temperature likely to occur in the freshwater habitat due to climate change and of their potential effects on Atlantic salmon life functions and productivity.

2.0 Trends and scenarios of key abiotic variables

2.1 Discharge

Seasonal patterns of freshwater discharge have been studied in many subregions. Hodgkins *et al*. (2003) investigated trends in 23 unregulated rivers in New England, USA with over fifty years of historical flow data and found that the timing of the spring flood occurred increasingly earlier with time in 11 rivers with nival regime (spring flood produced by snowmelt). Zhang *et al*. (2001) investigated trends in flow characteristics in Canadian Rivers in Quebec and the Atlantic provinces, where Atlantic salmon populations are present. Most hydrometric stations had negative trends for mean annual discharge (MAD), mostly caused by a decrease in summer discharge. However, most stations in the same region showed an increase in annual minimum flows, mainly associated with a possible increase in winter discharge. Stahl *et al*. (2010) investigated trends in stream flows of European rivers and found that over 50% of the time series (1962–2004) showed increasing discharge in the winter months and 60% showed an increasing trend in June. This percentage decreases to 34% in July and 47% in August. Trends in annual discharge for the same period were found to be negative in Northern Spain and Southern France, while past river flows have increased in winter over the last 40 years but no significant summertime trends were found in the U.K. (Watts *et al.* 2015). For Northern Europe, there was no definite spatial pattern in trends, with some stations showing slightly negative trends, while others slightly positive trends in the winter. Summer discharge trends are negative for most stations located in the southern limit of Atlantic Salmon distribution in Europe, including southern parts of the U.K., especially in August and September.

More generally, The Intergovernmental Panel on Climate Change's (IPCC) trend analyses on drought have been qualified as uncertain for Eastern North America, Greenland, positive for Western and Eastern Europe, but possibly negative for Northern Europe, though highly uncertain. For floods, trends are uncertain in Eastern North America, somewhat positive in Greenland (medium uncertainty), possibly negative in Northern Europe and uncertain in Russia (https://interactive-atlas.ipcc.ch/regional-synthesis).

Future discharge scenarios can be obtained by coupling hydrological models to climate models. The seminal work of van Vliet *et al*. (2013) provides a global overview of discharge scenarios for the 2071–2100 horizon under two different greenhouse gas emission scenarios. At the coarse scale of their model, little change in MAD is expected in North American and North European rivers in which Atlantic salmon occur, while slight increases in MAD are predicted for Northern Spain and Southern France. What may be more important is the predicted increase in MAD variability, i.e., indicating that more extremes are to be expected, especially in regions where a slight mean increase is expected. By categorising the discharge values as low, medium, and high flow scenarios, the models indicated that low flows are likely to decrease in most Atlantic salmon rivers, except for the northernmost regions. Increased seasonality (i.e., higher peak flows and lower low flows) is projected for most of New England, Atlantic Canada, and Eastern Quebec, as well as for Northern France, the U.K., Denmark, and southern Sweden. Increased winter flows are also expected in many sub-regions, including the U.K. (Kay, 2021). It should be noted that van Vliet *et al*. (2013) modelled relatively few stations in Eastern Canada and New England and therefore, projections from this study should be considered more uncertain for these sub-regions.

2.2 Temperature

According to the IPCC, trends for extreme heat events (defined by the IPCC as the maximum daily temperatures that were exceeded on average once during the previous a 10-year period) are uncertain for Eastern North America, but positive elsewhere (https://interactive-atlas.ipcc.ch/regional-synthesis). River temperature trends have been examined in different subregions of Atlantic salmon distribution. In general, trends are positive, especially for extreme (maximum and minimum) temperatures towards the southern limits of the Atlantic salmon's range, with some local exceptions. Reasons for local exceptions include local climate variability, anthropogenic mitigation, and poor statistical power for trend detection related to sample size.

One of the most extensive works on temperature trend analyses in Atlantic salmon rivers was completed by one of the co-authors (Daigle) in Québec (Canada) rivers. The trend analysis was performed on 34 time series from 24 different Atlantic salmon rivers, with lengths varying from 21 to 44 years. Positive trends were identified for >75% of time series between June and October, with between 3–26% of trends statistically significant, depending on the method. The significant increases vary between 0.7–0.9 °C per decade. Shifts were also detected in the thermal regimes shape and seasonality (Daigle *et al.* 2019): annual maxima were found to be reached later in the season in 70% of the time series (median of 1,2 day/decade), and to increase (median of 0,6°C/decade) in all time series for which statistically significant trends were detected (40% of the cases).

Kelleher *et al*. (2021) investigated temperature trends in U.S. rivers. For the Northeast region, they found positive summer trends for 13 out of 20 stations. Positive trends were also found for nearly all 20 stations in the winter months. Orr *et al*. (2014) analysed trends in rivers of England and Wales and found an average increase in mean temperature of 0.3 °C/decade between 1900–2006, while Pohle *et al*. (2019) estimated a similar annual temperature increase 0.2 °C/decade for Northeast Scotland (River Spey) between 1912–2016. Mean river temperature in English rivers cooled by −0.4 °C/decade between 2000–2018, but summer temperature increased by +0.6 – +1.1 °C/decade in central/northern parts of the country, according to Wilby *et al*. (2020). Historical mean temperature increases of ~1 °C/decade have been measured across a range of coastal salmonid-bearing streams in France over a 20-year period (Bal *et al.* 2014). Moatar and Gailhard (2006) suggested that the Loire River, France only warmed by ~0.8 °C between 1881–1976, whereas the post 1980s temperature increased at a much faster rate. In France, future increases in mean river temperature are projected to be between 1.2–2.0 °C by 2045–2065, in relation to a 1961–1991 baseline period (*Ministère de l'écologie, du développement durable et de l'énergie*, 2012).

Dmitrieva and Buchik (2021) examined the temperature time series of the Don River in Russia and found mixed results over 70 years, i.e., some positive and some negative trends. Lammers *et al*. (2007) studied river temperature trends in the Russian Pan Arctic region for datasets with a mean length of 40-years and found significant positive trends in the maximum decadal values. Other Pan Arctic work includes the study of Park *et al*. (2017) who used synthetic temperature time series generated by the CHANGE model. Their modelling exercise suggested an average increase of 0.16 °C/decade.

A similar approach to the one used for flow forecasting was used by van Vliet *et al*. (2013) to produce global river temperature scenarios from climate model outputs. Their most optimistic scenario indicated that an increase in mean river temperature would be < 1 °C between the reference period and the end of the century in regions such as northern Quebec and Labrador, as well as most of the coast of Greenland and most of the U.K. Other subregions would have larger temperature increases (1–2 °C) under the more optimistic scenario. However, the more pessimistic scenario (arguably more realistic) predicts increases ≥ 2 °C for most of the distribution area of Atlantic salmon. A number of more geographically focused studies have also been completed in the last two decades, including that of Hrachowitz *et al*. (2010) who investigated temperature changes in the Dee River drainage basin in Scotland associated with two air temperature future scenarios: assuming an increase in air temperature of 2.5 and 4 °C, respectively. At this scale, they were able to identify temperature sensitive zones in the river system.

Some regions, such as Scotland, have a relatively dense river temperature monitoring network and salmon rivers are well-covered (SRTMN, designed for modelling river temperatures across Scotland; Jackson *et al.* 2016). Other regions, such as Eastern Canada are currently constructing a network (RivTemp; www.rivtemp.ca). England and Wales are much more poorly covered by existing temperature records, with the English Environment Agency's surface water temperature archive only providing sporadic longer-term data amongst predominantly spot temperature records. France has some long-term temperature time series, but not in all salmon rivers. Spot or instantaneous records exist in most jurisdictions and recent work (Daigle *et al.* 2022) have shown the usefulness of such data, as well as those gathered by remote sensing. For the latter, progress has been made in North America (e.g., Fakhari *et al.* 2022) and this effort should be expanded throughout the region of interest.

Arevalo *et al*. (2020) investigated bivariate trends (combination of low flows and high temperatures) in six major French rivers and found that all rivers suffered from increases temperatures from spring to fall and most (5 out of 6) were characterized by a negative trend in summer-fall discharge between the latter part of the 20th century and the first 15 years of the 21st century. Bivariate extreme analysis tools such as copulas have been extensively used in hydrology to characterize and model floods (e.g., Latif *et al.* 2020). Some work is underway to develop both parametric and non-parametric copula to jointly estimate return periods of events with high river temperatures and low flows (Latif *et al.* 2023). These tools offer the advantage of estimating joint or conditional probabilities of exceedances of two extremes that can have compounding impacts on Atlantic salmon: stressful temperatures and low habitat availability.

3.0 Effects of changing environmental conditions on Atlantic salmon life stages Atlantic salmon populations are adapted to the environmental conditions of their local river (Dionne *et al*. 2008; Jonsson & Jonsson 2009). Subsequently, the present and projected cumulative changes in environmental conditions in native rivers pose considerable adaptive challenges on Atlantic salmon populations by directly affecting the life functions, fitness, and survival, particularly in the southern range of the distribution. Here, we focus in particular on the effects of river discharge and water temperature on the different life stages and on indirect consequences on Atlantic salmon productivity (Table 1).

3.1 Egg incubation and alevin emergence

Fluctuating temperatures during winter months leading to freeze and thaw events are likely to affect the discharge and water temperature during the sensitive egg incubation period (Bergeron & Enders 2013). Embryo development is temperature-dependent and emergence is timed with optimal environment conditions for alevin survival (Elliott *et al*. 1987). In general, high discharges during the winter risk disturbing the substrate in which the eggs are incubating and potentially leading to lower survival rates (Levasseur *et al*. 2006). Increased winter temperature will lead to higher metabolic rates and consequently an accelerated development of eggs and early alevin emergence (Elliott 1987; Rahmati 2023). For example, under the IPCC's Representative concentration pathways (RCP) 8.5 climate change scenario (aka 'business as usual'), the number of days of egg incubation may be significantly reduced by more than 20 days in the Tobique River (N.B., Canada; Rahmati 2023). Gregory *et al*. (2020) also indicated recruitment was reduced when spawning temperatures are warmer and flood frequency increases during the pre-emergence and emergence periods.

3.2 Fry and parr rearing

In juvenile Atlantic salmon, growth rate correlates positively with survival rate (Nislow *et al*. 2004), and thus productivity. Juvenile Atlantic salmon typically defend territories, from which they feed on drifting invertebrate prey (Steingrimsson & Grant 2008). Climate change can influence the phenology and distribution of organisms which may cause mismatch in trophic linkages, such as synchrony in invertebrate prey availability and fry emergence (Larsen *et al.* 2016; Winder & Schindler, 2004). Temperature and discharge are therefore important drivers of juvenile productivity, as they affect growth through cascading changes on foraging behavior and physiology.

Discharge is a key driver of productivity through effects on growth, survival, and movement costs. Generally, lower discharge and subsequently lower velocities correlate with lower invertebrate drift concentration (Rashidabadi *et al.* 2022) and can lead to benthic feeding (Nislow *et al.* 1998), ultimately reducing energy acquisition. Higher flows can correlate with higher food availability through invertebrate prey displacement (see Naman *et al.* 2016 for a review), but fish may also exhibit reduced foraging efficiency via increased swimming cost and lower catchability of invertebrate drift (Hill & Grossman 1993).

Atlantic salmon growth follows a bell-shaped curve across temperatures, with optimal growth occurring near 16–18 °C (Forseth *et al.* 2001). Colder (6–16 °C) temperatures result in slower growth through reduced digestion speed, whereas warmer temperatures (18–27 °C) result in reduced foraging efficiency as well as reduced conversion of energy intake into growth (i.e., growth efficiency) through increases in metabolism (Elliott & Elliott 2010), ultimately leading to reduced growth and greater starvation risks. When applying the functional model for growth of juvenile Atlantic salmon developed by Elliott & Hurley (1997) to climate change scenarios, it is expected that salmon growth rates would generally improve in United Kingdom rivers in a low emission scenario but would decrease in a high emission scenario (Davidson *et al.* 2006).

Juvenile Atlantic salmon can, to some extent, regulate temperatures by actively seeking thermal refuges (Wilbur *et al.* 2020) in a process known as ‘behavioural thermoregulation’. Applying different future climate scenarios to five Quebec rivers predicted that most tributaries would likely remain sufficiently cool to be used as refuges by the end of the century, while most river main stems would be characterized by a significant increase in the number of thermally stressful events for the parr life stage (Jeong *et al.* 2013; Daigle *et al.* 2015). However, most climate change scenario studies focus on summer temperature, but changes in winter temperature may also affect juvenile life stages of Atlantic salmon.

3.3 Smolt downstream migration

Anadromous salmonids undergo smoltification to adapt to outmigration and life in saltwater. Abiotic variables such as water temperature and photoperiod regulate smolting process by rate of development (McCormick *et al.* 2002). With increasingly earlier spring temperatures due to climate change, the onset of smolt migration is predicted to occur earlier. Smolts use higher spring discharges for their downstream migration. Changes in discharge, due, for example, to reduced snowpack, may consequently affect and potentially reduce downstream migration rates when smolts are actively searching for high velocity fields (Svendsen *et al.* 2007). Advanced or delayed arrival at sea may lead to a mismatch with optimal ocean survival conditions (i.e., food availability, predator presence, ocean current; Satterthwaite *et al.* 2014).

3.4 Adult upstream migration

Atlantic salmon returning to their native rivers are likely to encounter decreased discharge and increased temperature associated with climate change. River entry and, to some extent, upstream movement rates are dependent on discharge (Banks 1969; Thorstad *et al.* 2021), which could potentially lead to a delay in upstream movement with climate change (Solomon *et al.* 1999). Some plasticity in movement behaviour to suboptimal discharge conditions has been observed (Tetzlaff *et al.* 2005). Temperature is also affecting the river entry and upstream migration of adult Atlantic salmon to the spawning grounds in complex ways. High river temperature have been associated with delayed river entry in Southwest England (Solomon & Sambrook 2004). In contrast, the timing of the migration of adult Atlantic salmon is occurring increasingly earlier in Newfoundland and Labrador rivers, with some variability among rivers (Dempson *et al*. 2017). While adult Atlantic salmon are also known to behaviourally thermoregulate in cool water refuges (e.g., Frechette *et al*. 2018), extreme temperatures that approach sub-lethal or lethal limits will decrease spawning success, fitness, and survival.

3.5 Spawning

Exposure of adult female to high temperature (e.g. >22 °C) during egg maturation may lead to lower egg quality and survival (King *et al*. 2003). Aside from these direct effects of temperature on egg development, carry over effects of temperature over the salmon life cycle could influence salmon recruitment. Hedger *et al*. (2013) reported that increased temperatures under future climate regimes will likely result in faster parr growth, earlier smolting, and elevated smolt production in more western and northern rivers. This may lead to an increase in egg deposition, in turn producing a possible increase in recruitment, depending on adult returns. Conversely, in southern locations, density-dependent mortality of parr may be caused by lower flows in the summer (less habitat) and thus reduce future smolt production in comparison to the more northern rivers. It can be inferred, therefore, that climate change may have both positive and negative effects on anadromous fish abundance within the subarctic-arctic rivers according to geographical region. Studies have indicated that the potential of establishment of Atlantic salmon in the Arctic increases with increased water temperature and overlap between Atlantic salmon and Arctic char habitat may lead to interspecific competition (Bilhous and Dundall, 2020).

3.6 Indirect and cumulative effects

In addition to the direct impact on productivity, indirect and cumulative effects are also likely to affect Atlantic salmon productivity. Indirect effects that may be caused by climate changes include for example changes to prey availability, predator abundance, aquatic invasive species presence as well as density-dependent effects. Additional indirect effects may also include an increased prevalence of parasites (e.g., myxozoan parasites causing proliferative kidney disease; PKD) and vulnerability of Atlantic salmon to infections with higher temperature and altered flows in natural habitats (Sterud *et al*. 2007; Forseth *et al*. 2017). Higher temperatures may also impact the concentrations and uptake of organophosphates (AchE; Laetz *et al.* 2014).

Table 1. *Present and predicted effects of climate change on Atlantic salmon by life stage and life function.*

Life stage	**Life function**	**Key period**	**Present**	**Predicted**	**Key references**
Egg	Incubation	Winter	Negatively correlated with precipitation (proxy for discharge)		Gallagher *et al*. (2022)
Egg	Incubation	Winter		Increasing number of freeze and thaw events leading to reduced egg survival	Levasseur *et al*. (2006) Bergeron & Enders (2013)
Egg	Incubation	Winter	Reduced incubation time with higher temperature	Reduced incubation time with higher temperature	Elliott (1987) Rahmati (2023)
Fry, Parr	Rearing	Summer	Discharge correlates with invertebrate drift concentration, feeding behaviour, foraging efficiency	Possible decreased growth rate if temperature exceeds optimal thermal range for growth	Hill & Grossman (1993) Nislow *et al*. (1998) Naman *et al*. (2016) Rashidabadi *et al*. (2022)
Fry, Parr	Rearing	Summer	Increased development rate with temperature Possible periods of no or little development	Possible increased development rate with temperature	Forseth *et al*. (2001) Jonsson and Jonsson (2009) Elliott & Elliott (2010)
Fry, Parr	Movement	Summer	Increased importance of thermal refuge	Increased importance of thermal refuge	Wilbur *et al*. (2020) Breau *et al*. (2007) Corey *et al*. (2020)

					Morgan & O’Sullivan (2022)
Smolt	Smoltification	Spring	Earlier smolt transition with earlier spring temperatures	Earlier migration with earlier spring temperatures	McCormick *et al*. (2002) Jonsson and Jonsson (2009) Russel *et al*. (2012)
Smolt	Movement	Spring	Higher spring discharges are correlated to successful downstream migration	Decreased spring freshets delayed migration and mismatch with optimal ocean survival conditions	Svendsen *et al*. (2007) Satterthwaite *et al*. (2014)
Adult	Upstream migration	Summer/fall	Earlier run timing	Increased frequency of extreme flows and misleading spawning cues	Thorstad *et al*. (2021) Dempson (2017) O’Keefe *et al*. (2019)
Adult	Reproduction	Fall	Decrease in spawning success with increasing temperatures	Increased risk of unsuccessful spawning due to prevalence of parasites, pathogens, and pollution	Sterud *et al*. (2007) Jonsson and Jonsson (2009) Laetz *et al*. (2014) Forseth *et al*. 2017)

Population	Abundance	n/a	General decrease in recruitment in Europe with increasing temperatures	Decrease at low latitudes / Increase at high latitudes Increase density-dependent parr mortality in southern regions Elevated smolt production in northern and western regions, decrease elsewhere	Friedland *et al*. (2009) Hedger *et al*. (2013)

4.0 Conclusions and recommendations

This brief overview confirms that the observed and predicted changes in river discharge and water temperature have and will continue to have serious impacts on all life stages of Atlantic salmon. The impacts will vary in severity latitudinally. Although coarse scale predictions such as those provided by the IPCC seem to provide a clear signal, our brief overview of local trend analyses and local (downscaled) scenarios of discharge and temperature show more variability. Some of this variability is imputable to relative data scarcity and model uncertainty. However, modelling remains the main tool by which inference on future habitat conditions can be made. In addition, while current modelling efforts are mostly targeted towards providing long term discharge and temperature scenarios, short term forecasts will become increasingly useful for fisheries management. While operational flow forecasting models have been developed (mostly for dam management and flood control) in recent decades, much fewer river temperature forecast models are operational. Models that can investigate the joint impacts of climate change and other anthropogenic impacts such as deforestation, dams and agriculture should be developed and/or implemented across the Atlantic salmon range. The relative paucity of data and available forecasts have been identified as bottlenecks for future Atlantic salmon management efforts (Bull *et al.* 2022).

One key recommendation is to expand and perpetuate river temperature monitoring across the Atlantic salmon's range. The reasons for a spatially denser monitoring network are no to limit trend detection. Other characteristics of the thermal regime (extremes, variability, etc.) need to be fully characterized, and model development (and calibration) requires *in situ* measurements. Effective river monitoring could help the management of Atlantic salmon populations through initiatives such as implementation of in-season closure of recreational fisheries when water temperature exceeds a determined threshold (Breau 2013) and better predict current and future spatial distribution of Atlantic salmon.

Finally, protection of thermal refuges is a key management strategy to mitigate effects of increases in water temperatures in salmon rivers. While the long term impacts of these refuges on individual fitness and population productivity remain to be assessed, their use for behavioural thermoregulation have been demonstrated for Atlantic salmon of all life stages (Breau *et al*. 2007; Frechette *et al*. 2018; Corey *et al*. 2020; Morgan & O'Sullivan 2022). It is thus imperative to identify, protect, and if necessary, restore important thermal refuges in warming salmon rivers. Future research should investigate the bioenergetic benefits of thermal refuge use by Atlantic salmon of all life stages and the variability of thermal onset of movement to thermal refuges among and within populations.

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