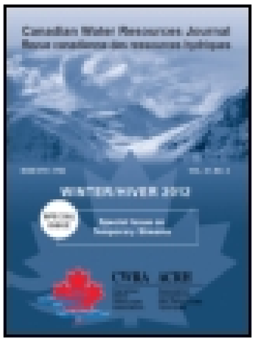

Canadian Water Resources Journal / Revue canadienne des ressources hydriques

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tcwr20

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CANADIAN WATER RESOURCES JOURNAL / REVUE CANADIENNE DES RESSOURCES HYDRIQUES
https://doi.org/10.1080/07011784.2022.2163190

Assessing climate change impacts on North American freshwater habitat of wild Atlantic salmon - urgent needs for collaborative research

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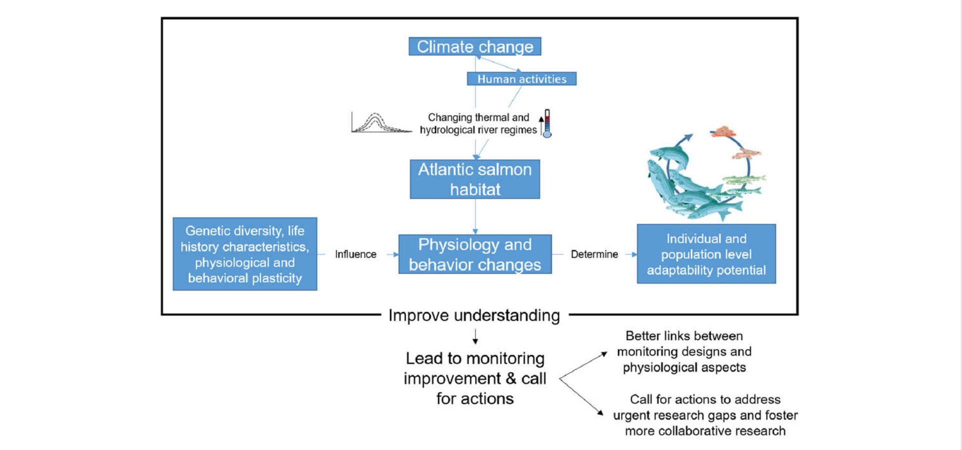
ABSTRACT

Climate change and human activities have dramatically affected all ecosystems inhabited by Atlantic salmon, causing drastic population declines. Change in river temperature dynamics (e.g. daily variability, frequency, and duration of summer maximum, warmer thermal regimes) is of special concern as it impacts growth rates, reproductive success, prey abundance and phenology, timing of migration, and ultimately survival. The Atlantic Salmon Research Joint Venture held a workshop to address the effects of climate change on freshwater habitats of Atlantic salmon and identify research gaps and priorities. Here we summarize the state of the science for three key themes identified by workshop participants: (1) Effects of climate change on in-river habitat conditions, (2) Physiological and behavioral responses of salmon to temperature, and (3) Population-level responses of salmon to climate change. The group highlighted the crucial importance of understanding and monitoring the links between river temperature dynamics and physiological requirements of Atlantic salmon across different life stages and habitat conditions, with a focus on freshwater life stages. Climate change will undoubtedly continue to affect instream habitats across all seasons and render challenging conditions for all freshwater Atlantic salmon life stages. Hence, we call for urgent interdisciplinary collaborations and partnerships among scientists and managers to address the pressing research gaps that require large-scale data integration across life cycle stages and ecosystems. More collaboration between scientists, managers, and interest groups is needed to ensure that fundamental science directly addresses the knowledge-action gap to enhance evidence-based decision-making and conservation.



Climate change and anthropogenic activities are affecting Atlantic salmon habitat characteristics, leading to physiological and behavioral changes that determine both the individual and population level potential for adaptability. Although climate change affects all aspects of the Atlantic salmon life cycle and habitats across the watersheds-ocean continuum, this workshop focused on changes in thermal and hydrological river regimes.

RÉSUMÉ

Les changements climatiques et les activités humaines ont considérablement impacté tous les écosystèmes du Saumon atlantique en provoquant des déclins drastiques de populations. Ces

ARTICLE HISTORY
Received 5 September 2022
Accepted 23 December 2022

KEYWORDS
Atlantic salmon; global change; water temperature; habitat; physiology; research gaps; monitoring; collaboration

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changements modifient la dynamique de la température en rivière tels que la variabilité journalière, la fréquence et la durée du maximum estival et les régimes thermiques plus chauds. Ceci est particulièrement préoccupant puisque la température a un impact sur les taux de croissance, le succès de reproduction, l'abondance et la phénologie des proies, le moment de la migration et, finalement, la survie. Le plan conjoint de recherche sur le saumon atlantique (PCRSA) a organisé un atelier afin d'aborder les effets du changement climatique sur les habitats d'eau douce du saumon atlantique et identifier les lacunes et les priorités en matière de recherche. Dans cet article, nous résumons l'état de la science pour trois thèmes clés identifiés par les participants de l'atelier: (1) Effets du changement climatique sur les conditions d'habitats en rivière, (2) Réponses physiologiques et comportementales du saumon à la température, et (3) Réponses populationnelles du saumon face aux changements climatiques. Le groupe a souligné l'importance cruciale de comprendre et d'assurer le suivi de la température des rivières et les exigences physiologiques du saumon atlantique pour différents stades de vie et conditions d'habitat, tout en mettant l'accent sur les stades de vie en eau douce. Les changements climatiques continueront sans aucun doute d'impacter les habitats en rivière et créer des conditions difficiles pour tous les stades de vie du saumon atlantique, et ce, pour toutes les saisons. Par conséquent, nous faisons un appel d'urgence pour des collaborations interdisciplinaires et des partenariats entre scientifiques et gestionnaires afin de combler les lacunes actuelles de la recherche qui nécessitent une intégration de données à grande échelle pour tous les stades de vie et les écosystèmes. Une plus grande collaboration entre les scientifiques, les gestionnaires et les groupes d'intérêt est nécessaire afin de garantir que la science fondamentale comble directement le fossé entre les connaissances et l'action afin d'améliorer la prise de décisions fondée sur les faits.

Introduction

Atlantic salmon (*Salmo salar)* populations face dramatic changes across all ecosystems they inhabit (de Eyto et al. 2016; Hodgson, Wilson, and Moore 2020; Thorstad et al. 2021). While lower survival at sea is identified as a major cause of Atlantic salmon population decline (ICES 2021; Pardo et al. 2021; Rikardsen et al. 2021), there is increasing awareness that environmental conditions that fish are exposed to in freshwater may play an important role in subsequent mortality at sea (Russell et al. 2012; Thorstad et al. 2021). Changes in freshwater habitats include acidification (Gibson and Bowlby 2009), lack of habitat connectivity (Fay et al. 2006; Kim and Lapointe 2011; Bergeron et al. 2016), and climate-driven habitat changes that influence thermal and hydrological regimes (Dugdale, Bergeron, and St-Hilaire 2013; Kurylyk, MacQuarrie, and Voss 2014; Steel et al. 2019; Beaupré et al. 2020; Wilbur et al. 2020).

River thermal regime is a key environmental factor controlling Atlantic salmon survival-based responses such as activity patterns and growth (Elliott and Hurley 1997; Breau, Weir, et al. 2007; Jonsson and Jonsson 2009), reproductive success (Jørgensen, Sørensen, and Bundgaard 2006; Robinson et al. 2010; Porcelli et al. 2017), prey abundance (Bal et al. 2014) and phenology (Bell et al. 2017; Rossi et al. 2022), and survival (Montgomery et al. 1996; Lobón-Cerviá 2014). Changing thermal regimes can impact the overall river ecology (e.g. food webs, predator-prey dynamics), which can indirectly affect salmonids like Atlantic salmon (Bell et al. 2017; Rossi et al. 2022). Atlantic salmon have a narrow thermal tolerance, and water temperature variations outside of this tolerance range can induce a substantial amount of physiological stress (Breau, Cunjak, and Peake 2011). Changes in river temperature dynamics (e.g. daily variability, frequency, and duration of summer maximum, warmer thermal regimes) pose a distinct threat to Atlantic salmon populations throughout their range (Fay et al. 2006). In North America, Atlantic salmon populations range latitudinally from extirpated, endangered, threatened, of special concern, to not at risk in Labrador and parts of Newfoundland in the northernmost extent of their range (COSEWIC, 2010). Populations at the present-day southernmost extent of their range (i.e. in Maine) are the most affected by warming rivers (e.g. Thorstad et al. 2021).

Climate change-driven increases in river water temperature is among the most cited threats to Atlantic salmon population resilience, with population extinction now considered a real possibility in some regions (Hare et al. 2016; Borggaard et al. 2019). Whereas low levels of heat stress are sufficient to alter physiological functions (e.g. immune system, metabolic rate, Schreck et al. 2016) throughout their life cycle (e.g. Hynes 2001), more persistent exposure to extreme temperatures can lead to mass mortality events in fish populations (Gibson 1966) and local extinction (McGinnity et al. 2009; Piou and Prévost 2013).

Climate change scenarios project changes in precipitation and air temperature that help predict future river discharge and thermal regimes (Van Vliet et al.

2013; Ouellet et al. 2020). Throughout the range of Atlantic salmon, the Coupled Model Intercomparison Project Phase 5 (CMIP5) predicts higher winter discharge (baseflow, max discharge), earlier snowmelt-driven spring freshets, and earlier onset of summer low flow periods (Thibeault and Seth 2014; Demaria, Palmer, et al. 2016; 2016). The CMIP5 also predicts increases in air and water temperatures (Isaak and Rieman 2013; Kwak et al. 2017). Some of these changes are already measurable (Steel et al. 2017) and are further exacerbated by other human activities, including water demands (Van Vliet et al. 2013), and changes in land-use, such as agriculture and urbanization (Haddeland et al. 2014).

The assessment of the effects of climate change on salmon populations is more advanced for Pacific salmon species (*Oncorhynchus spp*), for which models have been developed to predict population-level responses to various combinations of climate change scenarios and proposed management actions (Crozier et al., 2019; Fogel et al. 2022; Fullerton et al. 2022). The lack of comparable quantitative data and model-based approaches currently impedes Atlantic salmon management and conservation planning in the context of climate change. There is an urgent need to improve the understanding of how Atlantic salmon responds to the cumulative impacts of changes in freshwater environmental conditions, their limits for adaptation, and the expected consequences on population persistence.

Experts agree that the most practical way to overcome poor survival at sea is to increase the number of healthy smolts leaving rivers (Thorstad et al. 2021). Consequently, the Atlantic Salmon Research Joint Venture (ASRJV) set a goal of focusing mainly on changing habitat conditions experienced by salmon in freshwater. The ASRJV is a collaborative partnership of Canadian Federal and Provincial agencies, Indigenous organizations and governments, non-governmental organizations, and academia actively engaged in carrying out or supporting research on wild Atlantic salmon. The Joint Venture is now in its 6th year and has demonstrated its potential to be the leading platform for collaborative research and networking within the field of Atlantic salmon research in North America. Through collaborative, inclusive research that strategically links emerging technologies with partnership opportunities, the joint venture can help identify and resolve the questions that were, at one time, prohibitively large and complex.

Because water temperature may be the most important physical variable affecting salmon throughout the life cycle, a thorough and clear understanding of the role of freshwater temperatures in a changing environment on Atlantic salmon is paramount. To meet this critical need, the ASRJV held a workshop in Québec City in March 2018 to address the effects of climate change on Atlantic salmon freshwater habitats in North America. This collaborative workshop brought together 29 scientists from academia (16), industry (1), federal (4) and provincial (1) governments, international (5), and not-for-profit organizations (2) to discuss the current state of the science surrounding Atlantic salmon and their habitats in the context of climate change. Keynote speakers presented the state of the science and developed three priority research themes: 1) climate change effects on in-river habitat conditions, 2) physiological and behavioral responses of salmon to temperature, and 3) population-level response of salmon to climate change. The following sections provide an overview of the information presented at the workshop, an update on the state of the science for each of the three themes, and research gaps and monitoring recommendations generated by workshop participants. We conclude by identifying specific actions to improve collaborative research. Although the workshop focus was on the North American distribution of Atlantic salmon, the recommendations described herein can be applied more broadly across the range of this species.

Climate change effects on in-river habitat conditions

During the workshop, 5 presentations focused on the importance of in-river habitat conditions, with temperature and water discharge being recognized as the most important factors for freshwater fish to complete their life cycles (Juanes, Gephard, and Beland 2004; Jonsson, Jonsson, and Hansen 2007; Jonsson and Jonsson 2009). Hydrological regimes are particularly important because they determine the availability of Atlantic salmon habitats and their associated thermal quality (Mocq, St-Hilaire, and Cunjak 2013). Key drivers of in-river hydrological and thermal regimes that determine salmon habitat conditions and climate resilience are described in Figure 1 and discussed in more detail in this section.

Both hydrological and thermal regimes are determined by meteorological, geomorphological, and landscape features interacting at different spatiotemporal scales to create complex habitat mosaics (Garner et al. 2013; Dugdale, Hannah, and Malcolm 2017).

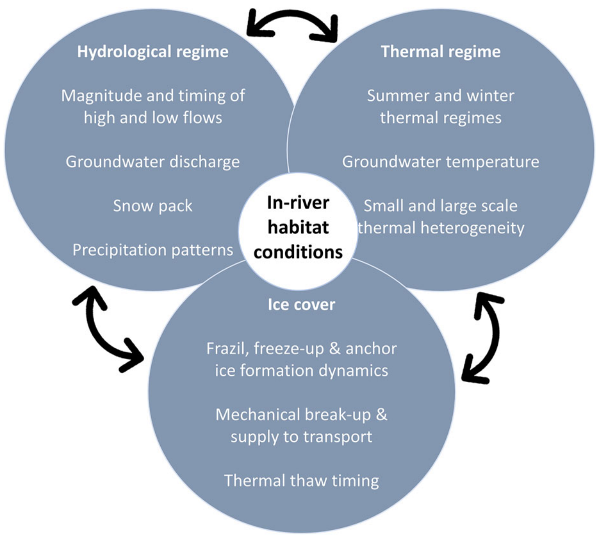

Figure 1. Key components of hydrological, thermal, and ice cover regimes of in-river habitat conditions linked to Atlantic salmon habitat climate resilience. Feedback mechanisms exist between each habitat component.

Anthropogenic activities causing landscape changes (e.g. urbanization, agriculture, deforestation) can alter sub- and surface flow and thermal regimes, which are further altered by climate change (Huntington 2010; Janisch, Wondzell, and Ehinger 2012; Zeiger et al. 2015). Changes in base flow are expected to influence upstream fish migration patterns during summer and fall due to low summer flows and warmer water conditions (Jonsson and Jonsson 2009; Otero et al. 2014; Lazzaro et al. 2017), thereby limiting the ability of mature adults to reach suitable upstream spawning habitats. Caissie et al. (2013) forecasted climate change induced variations in magnitude and timing of summer discharge, which are expected to decrease available instream habitats by 27%. These low flow conditions are often associated with elevated and extended duration of thermal events (Morin, Nzakimuena, and Sochanski 1994; Caissie et al. 2013). Groundwater discharge and air temperature further shape the spatial mosaic of water temperatures (Steel et al. 2017), which allows salmon to select appropriate temperatures based on their life-stage-specific requirements (e.g. Cunjak, Prowse, and Parrish 1998; Breau, Cunjak, et al. 2007). Lower snowpack and earlier timing of snowmelt caused by climate change result in less groundwater discharge in late summer and reduced thermal quality in rivers (Kurylyk, Bourque, and MacQuarrie 2013). Further, groundwater aquifers have been warming in response to atmospheric conditions and climate change, which will ultimately influence rivers' thermal quality and availability of thermal refuges for cold-water fish (Menberg et al. 2014).

An increase in both mean river water temperatures and summer thermal maximums has already been observed in several rivers throughout North America (Kaushal et al. 2010; Isaak et al. 2012) and more locally across the range of Atlantic salmon rivers in eastern Canada (Daigle, Boyer, and St-Hilaire 2019; St-Hilaire et al. 2021; O'Sullivan et al. 2021a). With continued projected warming, the duration and severity of warmer temperatures are expected to increase, which could impact thermal heterogeneity and within river temperature patterns (Van Vliet et al. 2012; Moore, Nelitz, and Parkinson 2013; Jones et al. 2014; Fullerton et al. 2018). Thermal heterogeneity is defined as a mosaic of warm and cool water habitats that allow fish to complete their life cycle (Ebersole, Liss, and Frissell 2003). Although thermal heterogeneity is relevant throughout the year, it is particularly critical during summer because it allows fish to survive warm water temperature events (Dugdale, Bergeron, and St-Hilaire 2015). During low flows and warmer conditions, thermal heterogeneity becomes essential to the resilience and survival of Atlantic salmon. Decreased thermal heterogeneity can have dramatic consequences for Atlantic salmon. For example, when temperatures reach 20-23 °C, thermal stress occurs (Shepard 1995; Wilkie et al. 1997; Breau 2013), and salmons exhibit behavioral thermoregulation to avoid warmer areas by accessing cold water habitat patches called cold-water refuges (e.g. upstream shaded areas, tributaries, groundwater upwelling zones; Breau, Cunjak, et al. 2007; Torgersen, Ebersole, and Keenan 2012; Barrett and Armstrong 2022). This ability to thermoregulate behaviourally becomes limited as thermal heterogeneity decreases and cold-water patches become less available (Frechette et al. 2018; Corey et al. 2020; O'Sullivan et al. 2021a). The distribution, abundance, and persistence of these cool water patches are critical to the resilience of catchments to sustain wild Atlantic salmon populations.

The main characteristics of winter habitat that drive salmon distributions and densities are flow, channel morphology, ice cover, temperature, and water quality (Armstrong et al. 2003; Huusko et al. 2007; Stickler et al. 2007). Climate change-driven shifts in winter air temperatures also influence the extent and duration of ice cover, which is currently decreasing and is expected to decrease in the future (Vincent et al. 2015). Climate change is likely to affect the timing of freeze-up and breakup, snowpack, rain-on-snow events, frequency, and timing of frazil ice formation, and decrease in the persistence of the ice cover at the regional scale. Warming trends in winter air temperature have been linked to changes in the seasonality of streamflow; including earlier snowmelt runoff (Ellwood et al. 2013; Horton et al. 2014; Olmos et al. 2020), resulting in earlier winter-spring seasonal streamflow (Hodgkins and Dudley 2006; Vincent et al. 2015; Dudley et al. 2017). Sharma et al. (2019, 2021) showed that according to the global scale predictions, the average ice duration in the northern hemisphere will decrease by 16.7 days by 2100, thus contributing to rivers warming earlier and faster during the spring. A shift to wetter winters with precipitation occurring more frequently as rain than snow further alters winter baseflow and the ice cover integrity, resulting in changes in the timing, severity, and frequency of ice breakup (Magnuson 1990; Beltaos and Burrell 2003; Spierre and Wake 2010). Ultimately, these changes in winter temperature and ice cover influence the availability and quality of winter habitat (Cunjak, Prowse, and Parrish 1998; Armstrong et al. 2003; Morse and Hicks 2005). In eastern Canada, the frequency and intensity of dynamic winter ice breakups have increased by up to 50%, rendering an unstable winter ice cover that can be disruptive to overwintering salmon (Turcotte and Morse 2017; Turcotte, Morse, and Pelchat 2020). Ice cover dynamics can alter habitat availability for salmon during winter and decrease survival of all juvenile freshwater life stages (Cunjak, Prowse, and Parrish 1998;; Hedger et al. 2013; Roussel et al. 2004). Reduced ice cover also alters the function of aquatic ecosystems, such as timing and duration of primary production (Mejia et al. 2019), nutrient pulses (Casson et al. 2019), and macroinvertebrate community structure (Huusko et al. 2007); changes that can ultimately all affect salmon populations throughout the year (Thellman et al. 2021).

Climate change effects on physiology and behavior

Eight workshop participants gave presentations detailing Atlantic salmon's physiological and behavioural responses to water temperature at different life stages. Atlantic salmon are cold water, obligate ectotherms with a narrow thermal tolerance (Pörtner and Farrell 2008; Jonsson and Jonsson 2009). Although factors such as population origin and life stage, experimental conditions, and methodology are known to influence study outcomes, it is generally accepted that Atlantic salmon prefer water temperatures ranging from 16 °C to 18 °C (Elliott and Elliott 2010; Breau, Cunjak, and Peake 2011). The range of thermal tolerance is life-stage specific (i.e. each life stage has a thermal optimum range at which growth is maximized), and a temperature range that drives the onset and timing of different behaviors (e.g. foraging, competition, migration, aggregation; Zabel et al. 2006; O'Sullivan et al. 2022). Thermal tolerance is also sensitive to the duration of thermal exposure and past thermal experience. Figure 2 depicts the relative thermal tolerance for Atlantic salmon based on field studies, when available, complemented by controlled laboratory studies where required. Spawning adults, incubating eggs, and emerging alevin have the narrowest tolerance range, followed by migrating smolts (Pörtner and Farrell 2008). The developmental phenology of Atlantic salmon populations is likely to change under a changing winter climate since hatch timing depends on incubation temperature (Rooke, Palm-Flawd, and Purchase 2019). Unless spawning times compensate for changing temperatures, fry emergence may coincide with unfavorable environmental conditions (Winder and Schindler 2004; Rooke, Palm-Flawd, and Purchase 2019) or adjustments in spring conditions may provide suitable conditions sooner, leading to a prolonged growing season for juvenile salmon.

Among the different life stages, Atlantic salmon fry have the highest thermal tolerance and may be more tolerant to warmer temperatures than larger parr. In the Miramichi River (NB), parr aggregated in cool water sites at daily water temperatures ranging between 23 and 30 °C. However, fry were not observed aggregating during those same temperatures (Breau, Weir, et al. 2007). It was later shown that salmon parr attained maximum aerobic capacity (i.e. maximum measured oxygen consumption rate) when exposed to constant water temperatures of 24 °C to 28 °C whereas fry did not reach their maximum aerobic capacity at those temperatures (Breau, Cunjak, and Peake 2011). The onset of aggregation behaviour has been related to the number of degree hours that a salmon parr experiences above 28 °C, noting that water temperatures above 28 °C are considered lethal to salmon parr (Breau, Cunjak, and Peake 2011; Dugdale et al. 2016).

The upper thermal limit for juvenile salmon feeding in the lab and in the wild is 22 °C–24 °C (Cunjak et al. 1993; Breau, Cunjak, and Peake 2011), whereas the optimal temperature for growth in juvenile salmon, determined under controlled conditions, is lower, ranging from 15 °C to 20 °C (Elliott and Hurley 1997; Jonsson et al. 2001; Elliott and Elliott 2010). In the Little Southwest Miramichi River, the daytime activity level (with 'active' defined as a fish present on its feeding territory) for 0+ salmon was highest at 23 °C and leveled

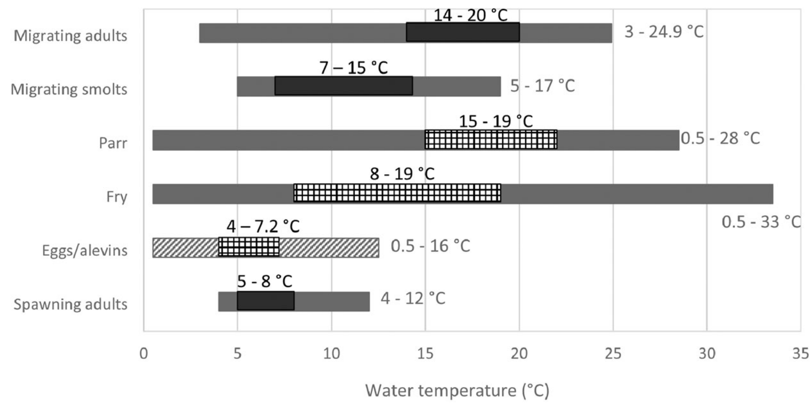

Figure 2. Relative thermal tolerance of Atlantic salmon by life stage. Data were predominantly from field studies (solid bars); findings from controlled experiments are denoted by dashed bars. Black bars (solid and checkered) represent the optimal water temperature range for activity; grey bars (solid and dashed) represent the lower and upper water temperature boundaries. Values collated from: Elson (1969); Danie, Trial, and Stanley (1984); Alabaster, Gough, and Brooker (1991); Grande and Andersen (1991); Jensen, Johnsen, and Heggberget (1991); Elliott (1991); Shepard (1995), Elliott and Elliott (1995); Elliott et al. (1998); Elliott and Elliott (2010).

off at temperatures between 23 and 27 °C, whereas the daytime activity of 1+ salmon exhibited a dome-shaped curve with a peak in activity at 20.7 °C (Breau, Weir, et al. 2007).

Although salmon can survive elevated water temperatures during the summer, repeated thermal stress during the growth season can lead to reduced or even no growth. After a period of growth rate reduction, an organism can restore its growth trajectory by compensatory growth if conditions become favorable. Several factors can lead to compensatory growth in fish, such as periods of low food availability, hypoxic conditions, and unseasonably cool or warm water temperatures (Ali, Nicieza, and Wootton 2003; Jonsson and Jonsson 2009). Higher frequency of thermal stress events in freshwater, resulting from climate change and other human-induced activities, is expected to reduce growth rates (e.g. Swansburg et al. 2002), with potential adverse effects on survival in freshwater and marine environments.

A critical period of high mortality is the migration of juvenile salmon from freshwater to the marine environment in spring, as it involves specific physiological, behavioral, and osmoregulatory changes that must occur within an optimal timing window for entering saltwater (McCormick et al. 1998). This optimal timing window differs among regions, latitudes, and rivers, with the onset and duration of migration driven by photoperiod, water temperature, and discharge (McCormick and Saunders 1987; Metcalfe and Thorpe 1990; Bjerck et al. 2021), with water temperature acting as a primary driver (Jonsson and Ruud-Hansen 1985; Hvidsten, Heggberget, and Jensen 1998). The process of smoltification is size-dependent, with freshwater conditions directly affecting growth, body size, and survival in both freshwater and marine environments.

The entry of smolts into the ocean is a critical stage where biotic and abiotic conditions in the receiving environment must be favorable to allow smolts to feed, grow and adapt to the saltwater. This transition phase is a period of high mortality when smolt physiology and behavior are controlled by cumulative degree-days (McCormick et al. 1998) which was shown to explain 75% of the gill Na+,K+-ATPase activity and loss of smolt morphological characteristics in salmon smolts (McCormick, Regish, and Christensen 2009). The study showed that a reduction in gill Na+,K+-ATPase activity in salmon smolts was related to degree-days and occurred earlier during warm years.

In recent decades, many studies have shown earlier smolt emigration timing from freshwater environments linked to earlier onset of spring conditions (Kennedy and Crozier 2010; Russell et al. 2012; Carr-Harris et al. 2018). For instance, throughout the range of Atlantic salmon, smolt out-migration timing advanced by 2.5 days per decade between 1961 and 2010 (Otero et al. 2014). Although water temperature in the marine environment is increasing, the difference in environmental conditions between freshwater and the marine environment is also increasing, creating a mismatch in optimal conditions for survival and food availability (Kennedy and Crozier 2010; Wilson et al. 2021) but also with the migratory timing of other fishes that currently buffer predation (Saunders, Hachey, and Fay 2006; Ouellet et al. 2022). Climate change models predict continued warmer and earlier springs (IPCC 2014), exacerbating these sub-optimal conditions for smolts upon seawater entry.

Upon returning from sea, riverine upstream migration of adult Atlantic salmon depends on water discharge and consists of a migration phase, search phase, and holding phase (Aas et al. 2011) until suitable spawning conditions are met during fall (Fleming et al. 1996). Although many environmental factors potentially influence the riverine upstream migration of Atlantic salmon (Banks 1969), water temperature, in addition to water discharge, was shown to be influential (Alabaster 2006). During the summer, many rivers reach water temperatures deemed stressful (>20 °C) or lethal (>26 °C) to adult salmon (Gibson 1966; Shepard 1995; Wilkie et al. 1997; Elliott and Elliott 2010; Breau 2013). Both low and high-water temperatures reduce salmon swimming ability (Beamish 1978; Booth et al. 1995; Gerlier and Roche 1998), impeding upstream migration of salmon. This is especially true in systems where salmon migrate upstream of obstacles or barriers to reach spawning grounds (Frechette, St-Hilaire, and Bergeron 2019). Although exposure to elevated water temperature (on the order of a few hours) did not impede upstream migration of Atlantic salmon in the Miramichi River (New-Brunswick, Canada; Elson 1969), the effects of longer duration thermal stress (many hours or days) on riverine upstream migration are unknown.

Adult salmon holding in the Rivière Sainte-Marguerite Nord-Est (Québec, Canada) exhibited behavioral thermoregulation when river temperatures were between 17 °C and 23 °C and maintained internal body temperatures within a narrow range (16 °C to 20 °C) despite access to warmer and sometimes cooler ambient water temperatures (Frechette et al. 2018). The temperature at which salmon initiated cool refuge use appeared to be linked to acclimation temperatures, with salmon in a cooler river reach initiating behavioral thermoregulation at cooler (17 °C) temperatures than fish in a warmer river reach (23 °C) (Frechette et al. 2018).

In combination with photoperiod, water temperature determines spawning time in many salmonids, including Atlantic salmon (Klemetsen et al. 2003), with the spawning season for Atlantic salmon in Eastern Canada ranging from mid-October to January, depending on the population. Adult salmon typically select spawning sites in pool/riffle sequences having specific habitat characteristics (depth, water velocity, and substrate; Louhi, Mäki-Petäys, and Erkinaro 2008). Exposure of Atlantic salmon spawners to elevated water temperatures during the spring and summer before spawning, when gametogenesis occurs, has been shown to reduce maternal investment and gamete viability (Pankhurst and King 2010). Spawners held at elevated water temperatures of 13-14 °C during the spawning season, followed by a temperature reduction to 8 °C, had ovulation delayed, and 43% of females did not ovulate (Taranger and Hansen 1993).

Oxygen concentration, water exchange, and water temperature are all variables controlling the developmental rates of eggs (Hamor and Garside 1979; Gendaszek and Sheibley 2021), with development rates increasing with water temperature. The optimal temperature for developing Atlantic salmon eggs varies between 4 to 12 °C (Jensen, Johnsen, and Saksgård 1989; Crisp 1993), whereas water temperatures below 0 °C and above 16 °C are lethal at this life stage (Elliott 1981). Emergence of alevin is temperature-driven, with the timing of reproduction synchronized such that offspring emergence coincides with optimal feeding conditions (Brannon 1987; Heggberget, Hansen, and Naesje 1988). Higher substrate temperatures may result in earlier emergence of alevin, which may be problematic if unfavorable conditions are encountered (e.g. low food abundance; Heggberget, Hansen, and Naesje 1988; Jonsson and Jonsson 2011).

Atlantic salmon are an iteroparous species that can survive to spawn multiple times during an individual's lifetime. Surprisingly, very little is known about the dynamics and movements of post-spawned salmon, also referred to as kelts or black salmon, in freshwater during the winter months. In recent years, repeat spawners have become an increasingly important component of the spawning population entering the Miramichi River (New Brunswick, Canada), where this spawning component of the population has increased from less than 5% prior in 1995 to over 10% in recent years (Douglas et al. 2022).

Regarding winter survival, the specific requirements of the three distinct freshwater stages (egg, juvenile, kelt) relate to the characteristics of the three biophysical phases: beginning of winter (drop in temperature and freezing), mid-winter (ice formation and changes in available habitat) and the thaw and warming phase. In this sense, a large proportion of the embryo incubation period in most Atlantic salmon rivers coincides with the winter low flow period and the presence of an ice cover, which has been shown to influence recruitment (Linnansaari and Cunjak 2010). A recent study assessed juvenile growth rates under treatments of varying ice cover and found that although energetic costs were greater under a no ice-cover scenario, they do require compensatory growth that may impact timing of migration and survival

(Härkönen et al. 2021). Little information is available on the behavior of individuals during periods of dynamic thermal melting. However, juveniles and kelts are known to take refuge in interstices that prevent physical damage from dislodged ice and sediment transport during ice-out (Harwood et al. 2002). During ice-out and early spring, water quality and increased water temperature can severely impact eggs, juveniles, and kelts. Too sudden an exposure to contrasting temperatures can, if not acclimatized, dramatically increase salmon mortality (Cunjak, Prowse, and Parrish 1998).

Population-level responses to climate change

The workshop participants examined the potential for Atlantic salmon to adapt to changing climate with three presentations summarizing the information on genetic diversity, life history characteristics, physiological, and behavioral plasticity at the individual-level required for adaptation. Migratory fish are particularly vulnerable to climate change as transitions between habitats are finely tuned to specific environmental cues, and these transitions have consequences for subsequent life stages (Crozier et al. 2008; 2019). Moreover, they utilize numerous habitats from freshwater headwaters to distant ocean; all habitats that are being impacted by climate change (Hare et al., 2016). The adaptive capacity of a population to respond to climate change can be enhanced by life history diversity and reproductive strategies that can buffer its vulnerability to warmer water conditions. Factors that have been shown to reduce this diversity are: modification and reduction in habitat heterogeneity, hatchery propagation practices, fishing practices, habitat fragmentation, and other human-caused stressors (Beever et al. 2016; Herbold et al. 2018; Thorstad et al. 2021; Claussen and Philipp 2022). Life history traits and genetic diversity are key components of Atlantic salmon climate resilience as they can buffer the vulnerability to warmer water, i.e. represent a higher potential for adaptation against adverse conditions (Erkinaro et al. 2019). Management could identify resilient populations and prioritize their conservation, while improving the fast uptake of scientific advances. An important research gap remains regarding the artificial selection that can result from such management actions. As data are collected and new information is gained, management needs to undergo an adaptive process to improve management strategies and priorities (Figure 3).

Although limited, there is evidence of phenotypic plasticity in response to elevated water temperatures in Atlantic salmon at the population, family, and individual levels. At the population-level, key elements of climate change vulnerability are plastic responses that can occur in migration timing, spawn timing, growth, body size, age at maturity, age at smolting, fecundity, and juvenile survival (Crozier and Hutchings 2014; Crozier et al. 2021). Piou and Prévost (2013) developed a demo-genetic model predicting that extinction of southern salmon populations should not occur based solely on spatial environmental conditions in freshwater. Flow regimes in rivers and growth conditions in the ocean were forecasted to be more influential contributors to low population persistence in southern salmon populations relative to river temperature over the next 30 years.

In Hare et al. (2016), Atlantic salmon scored very high on the biological sensitivity scale to overall climate vulnerability as they are exposed to climate change in both freshwater and marine habitats. Near shore, ocean water temperatures and ocean acidification were the climate exposure factors with the greatest magnitude of change expected by 2055 (Hare et al., 2016). Across their latitudinal range, salmon populations at higher latitudes will benefit from warmer thermal regimes by having greater food availability and a higher mean thermal experience, thus allowing physiological processes to be closer to the optimal range (Anttila et al. 2013).

Two wild Atlantic salmon populations (southern and northern European rivers) with similar acclimation regimes showed similar cardiac responses to acute warming (Anttila et al. 2014). Eyed eggs acclimated at 12 °C from both populations had cardiac collapse at 21 °C–23 °C with acute warming, whereas the two groups acclimated at 20 °C had cardiac collapse at 27.5 °C. This cardiac plasticity in fish from different thermal regimes shows differential acclimation capacities, with the northern population having more capacity for acclimation. Anttila et al. (2013) found variations in thermal tolerance and hypoxia tolerance among 41 Atlantic salmon families with critical thermal maximum (CTmax), a measure of upper thermal tolerance, correlating with hypoxia tolerance at the family level. Individual fish with higher CTmax had larger ventricle mass and ventricular myoglobin levels. These results support the idea that genetics play an important role in thermal tolerance in salmon.

Adaptive phenotypic plasticity distinguishes genetic effects (threshold) from environmental effects (cue).

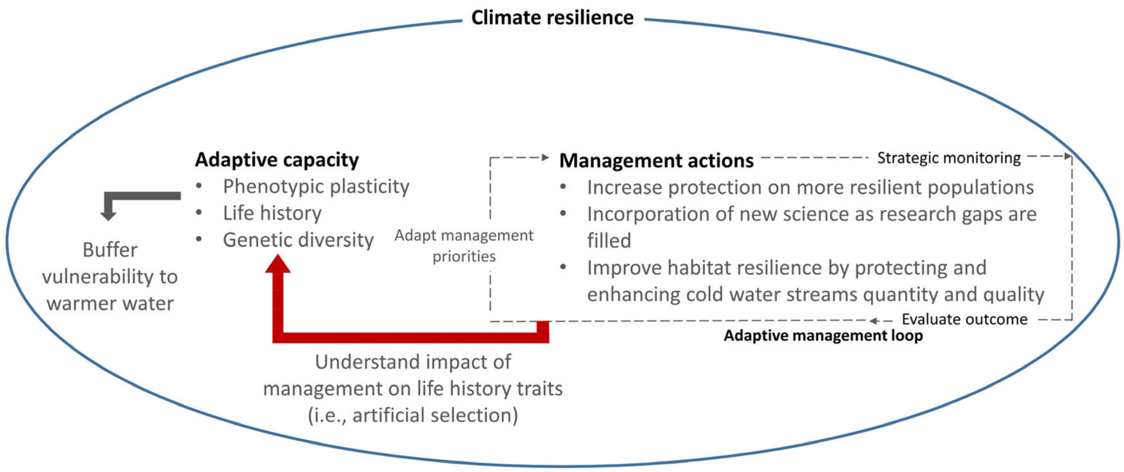

Figure 3. Schematic of how climate resilience of Atlantic salmon populations (encompassing circle) is influenced by both adaptive capacity, targeted management actions and how these actions can in turn impact the adaptive capacity.

To a large extent, life history decisions are dictated by the individual energetic status in salmon as the energetic requirement for the smolting process is energetically costly and strongly influenced by environmental conditions (Buoro, Gimenez, and Prévost 2012). The individual response to environmental changes by means of phenotypic plasticity, trait transmission, and genetic adaptation result in trade-offs for energetic allocations. Under high environmental stochasticity but low predictability, phenotypic plasticity did not allow demographic responses to adjust to environmental fluctuations (Reed et al. 2010). The study quantitatively demonstrated that phenotypic plasticity is a possible mechanism by which populations can maintain stable population dynamics over time if there is some environmental predictability (also see Caswell 1983).

Another interesting research avenue is the use of relative telomere length as a biomarker of past thermal stress. The relative telomere length in young-of-the-year brown trout exposed to various thermal environments was negatively related to body size and thermal exposure (Debes et al. 2016). Conversely, McLennan et al. (2018) found that fluctuations in water temperature did not drive telomere length in early developmental stages of Atlantic salmon in the laboratory. This adaptive capacity to restore the length of their telomeres may showcase greater resiliency to climate change in Atlantic salmon than in other salmonids. In Bull trout populations, allelic richness was shown to be positively related to habitat patch size and complexity while being negatively related to maximum summer temperature and the frequency of winter flooding, a situation shown to reduce genetic diversity under future climate change scenarios (Kovach et al. 2015). Heat shock proteins (HSP) are also a known biomarker for heat-induced physiological stress in fish and have been used in juvenile Atlantic salmon field and lab studies to determine protein damage (Lund et al. 2002; Corey et al. 2017).

Genetic composition and environmental exposure experienced by eggs to young juveniles can influence morphology, physiology, and life history (Jonsson, Jonsson, and Finstad 2013). The importance of parental contributions has been demonstrated on the phenotypic plasticity of organisms and their evolutionary significance (Jonsson and Jonsson 2009). Epigenetic effects include phenotypic changes caused by environmental influence early in life and have potential heritability components, thus may play a significant role in how organisms adapt to a rapidly changing environment. Epigenetic effects, involving differential DNA methylation patterns, may affect individual capacity to adapt to changing conditions (Burgerhout et al. 2017; Moghadam et al. 2017; Jonsson, Jonsson and Jonsson 2019; Gavery et al. 2018). Jonsson, Jonsson, and Finstad (2013) demonstrated that life-history characteristics in adult salmon were affected by the thermal exposure of these fish during egg development, suggesting plasticity in traits. In addition, female Atlantic salmon with a fast growth rate in the early life stages produced more and smaller eggs than conspecifics (Jonsson, Jonsson, and Fleming et al. 1996). In Chinook salmon, females with larger eggs produced offspring with higher thermal tolerance than conspecifics (Muñoz et al. 2014), which suggests maternal contribution to thermal adaptation. Consequently, female Atlantic salmon with larger eggs may produce offspring with greater thermal adaptation to a warming environment and thereby have greater fitness. Sävilammi et al. (2021)

provided evidence that methylation played an evolutionary role in the adaptation of European grayling populations to different thermal regimes. They showed a plastic response in the cytosine methylation process providing the plastic material required for adaptation. However, plasticity may not always lead to local adaptation, and the understanding of this concept is crucial in determining the future resilience of Atlantic salmon populations in the context of global change.

Research gaps, urgent needs, and recommendations

At the workshop, after reviewing the state of the knowledge on the Atlantic salmon, the participants focused on identifying research priorities and knowledge gaps to guide collaborative research needed to adaptively manage salmon populations in the face of climate change. Here, we summarize the key points discussed and integrate them into a framework to guide Atlantic salmon monitoring and research throughout the freshwater life cycle (Figure 4). The information is organized in Table 1 with the identified research gaps, and associated data needs to be addressed.

Climate change effects on in-river habitat conditions

Much of the recent research on the impacts of climate change on freshwater salmon habitats has focused on the summer period. Monitoring temperature, hydrological conditions, and availability of thermal refuge habitats during the summer months is crucial. However, year-round temperature monitoring is also foundational in understanding changes in thermal heterogeneity and the use of this thermal landscape by fish. Furthermore, both the availability of appropriate over-wintering habitats and the interaction with changing winter ice-cover dynamics can severely impact the over-winter survival of parr and kelts. Therefore, there is a need to better understand the impact of an increasingly dynamic river ice regime on the survival rates for different life stages, which could be informed by the development of models that simulate the impact of climate change on ice processes in salmon rivers.

One of the critical needs identified during the workshop was the characterization of abiotic processes affecting salmon habitat across space and time, including during winter (Table 1). First and foremost, temperature monitoring must be expanded to occur year-round, including measurement of both river and groundwater temperatures. To better understand thermal regimes in rivers, dynamic links between groundwater, hyporheic exchanges, and flow regimes need to be evaluated (Corey et al. 2021; O'Sullivan et al. 2021a). Understanding the physio-climatic attributes of watersheds is crucial to ensure that the study sites or monitoring networks adequately capture stream thermal regimes (Boyer et al. 2016; Steel et al. 2017). Daigle et al. (2016) proposed an optimization method that minimizes the number (and density) of temperature monitoring stations while maximizing the information gained. It was recommended to continue promoting and utilizing RIVTEMP, an optimized and highly collaborative water temperature monitoring network, to monitor Atlantic salmon rivers throughout the latitudinal range (see www.rivtemp.ca). Long-term monitoring remains critical, even at higher latitudes where changes in discharge and water temperatures are not seen as current threats, to (1) detect changes before they impact salmon populations, and (2) allow for comparison with other ecoregions. These regions may eventually be the last stronghold for Atlantic salmon, and such monitoring can help tailor early mitigation strategies.

Another important need is a better understanding of hydraulic conditions (i.e. depth and flow velocity) and how they impact salmon habitat use and productivity over a broad range of river discharge, as the few studies conducted to date have focused on habitat use during extreme low flows only (O'Sullivan et al. 2021a). Recent studies have highlighted the importance of flow dynamics during the use of thermal refuges (O'Sullivan et al. 2021b; 2022) or aimed to use modeling to predict baseflow during summer low flows to support conservation and restoration efforts (Lombard et al. 2021). There is still a need to better understand how variations in discharge affect thermal habitat, access to cold water refuges (e.g. during low flows), and population productivity. To prioritize management actions, a better assessment of river thermal sensitivity and flow dynamics under climate change.

Atlantic salmon spend relatively little time in estuaries while migrating between their freshwater and marine habitats. Therefore, estuaries are generally seen simply as migration corridors (Kocik et al. 2009; Ouellet et al. 2022). However, earlier warming of freshwater in spring may alter the timing of the entry of smolts in estuaries. Overall, climate-driven changes in estuarine ecosystems have not yet been properly

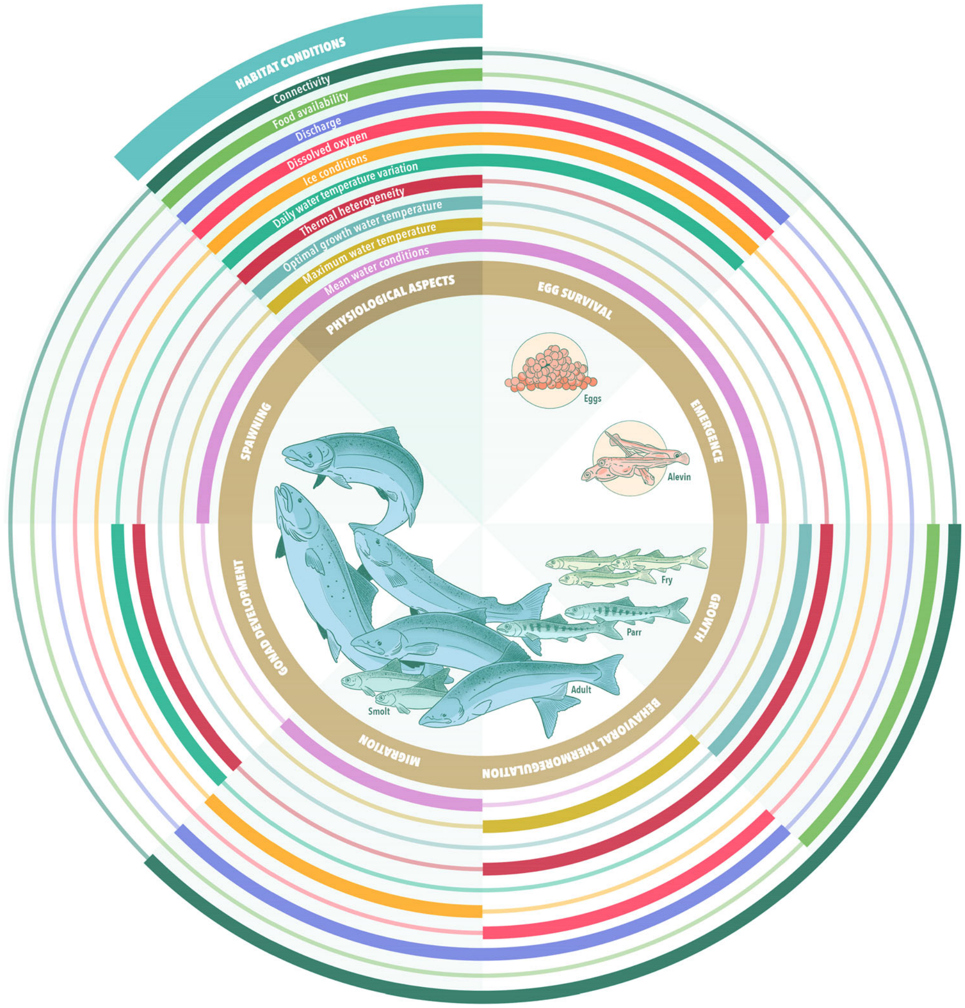

Figure 4. Synthesis of the importance of temperature on physiological aspects and habitat conditions for each Atlantic salmon life stage. Wider lines represent stronger associations between the specific life stage and the physiological aspect that is primarily influenced by habitat conditions. This figure emphasizes the importance of incorporating temperature in study designs, as it drives key processes at each life stage and can have confounding effects in both individual and population-level responses.

assessed regarding the impacts on Atlantic salmon. However, there is increasing recognition of the importance of estuaries for reconditioning salmon kelts between spawning attempts (Lacroix 2013). Warming temperatures may also lead to changes in estuarine assemblages of both predators and other fish species that may buffer salmon from predation and warrant attention because of the associated impacts on salmon populations (Saunders, Hachey, and Fay et al. 2006; Leach et al. 2022). A better understanding of the changing conditions in estuaries will allow to determine whether estuaries are becoming migration barriers or are impacted in other ways that negatively affect salmon migration. Furthermore, the development of cumulative models that integrate climate-driven impacts on salmon across life stages and rearing environments (including estuaries) will help support management actions that ensure habitat suitability and long-term population persistence (Kärcher, Flörke, and Markovic 2021).

Physiological and behavioral responses of salmon to increasing temperatures

Presentations by workshop participants highlighted the need for integrated predictive models of climate impacts on the physiological and behavioral responses of salmon to temperature in freshwater, particularly growth, survival, and smoltification. To this end, workshop participants identified a growing need to develop and use metrics linked to key life cycle stages (e.g. growth, thermoregulation, fitness, egg development, and survival; see Figure 4) to: (1) inform the development of predictive models and (2) monitor behavioral and physiological responses from climate change.

Table 1. Research gaps and associated monitoring needs identified during the workshop.

Theme	Identified research gaps	Identified data needs
Climate change effects on in-river habitat conditions	• Processes across space and time, including during winter • Thermal sensitivity of catchments • Large-scale processes that make a catchment a thermal refugia • Impact of changing thermal regime on thermal heterogeneity • Impact of an increasingly dynamic river ice regime on the survival rate of salmon eggs, alevin, fry, parr, and pre-smolts and kelts • Models that can be used to simulate the impact of ice processes on salmon habitat • Links between the composition and function of terrestrial habitats on the aquatic environment	• Robust, long-term temperature data sets that span the latitudinal gradient and ecoregions • Year-round temperature monitoring • Groundwater temperature monitoring • Thermal infrared surveys to identify frequency and distribution of potential refuges • Quantification of the bi-directional transfer of nutrients and coupling between different ecosystems • Native forest composition for maintenance of thermal and flow regimes • Data o n river ice dynamics and fish winter movements
Physiological and behavioral responses of salmon to temperature	• Identification of mismatches between life history transitions and environmental cues • Comparison of thresholds of behavioral thermoregulation between populations • Effects of climate change on life histories and fitness • Understand the variations in energetic content of prey and the effects on fish growth	• Robust, long term data sets incorporating physiological and life history parameters and environmental variables (water temperature, prey availability, discharge, dissolved oxygen, etc.) • Temporal and spatial variability in thermal refuge use across life stages • Visual surveys of behavioral thermoregulation • Links between thermal history and epigenetics across life stages. • Monitoring of stress response over time and space • Data on energy content of prey sources and how it varies in space and time across the thermal landscape
Population-level response of salmon to climate change	• Vulnerability assessments across all populations, and subpopulations as applicable, to allow for the prioritization of highly vulnerable life stages and ecoregions in an adaptive framework • Assess components of population-level resilience and vulnerability (e.g. traits and local adaption)	• Identify and prioritize highly vulnerable life stages and populations • Data on various life histories/strategies • Meta-analysis and/or database repositories

Such information is essential for identifying mismatches between life stages and functional habitats and is critical input for modeling population dynamics over the complete life cycle. For example, the timing of key life cycle processes (e.g. hatching, emergence, and smolt outmigration) are all tied to temperatures experienced during the winter (Crozier et al. 2021). However, as previously discussed, winter largely remains a black box (although see Linnansaari and Cunjak 2013). Temperature-mediated changes in egg incubation rates, timing of emergence, and timing of smolt emigration could lead to reduced growth opportunity and reduced survival if they occur out of sync with available food resources or during unfavorable conditions such as high spring flow conditions. Therefore, measuring winter water temperature is a key first step in addressing the match/mismatch hypothesis for different life stages and assess whether phenological mismatches have carry over effects on survival.

Consequently, the greatest monitoring need for assessing the physiological and behavioral responses of salmon to temperature is the development of robust, long-term data sets incorporating biological and environmental parameters. Water temperature data are often collected independently of other variables of interest, making it challenging to understand thermal habitat dynamics or link temperature data to specific physiological observations. Juvenile Atlantic salmon is characterized by periods of rapid growth (e.g. during summer months) and no growth (e.g. in winter). Including these season-specific periods in growth models will improve the ability to assess how climate-driven changes in environmental parameters impact overall growth in freshwater (Pauly et al. 1992). Continuous monitoring of water temperature is also essential for: 1) informing predictive models to understand how thermal conditions are changing and understand their ecological impacts (Ouellet et al. 2020); 2) downscaling thermal changes to local habitats or populations (Isaak et al. 2015); and 3) understanding the role of physio-climactic attributes and their interactions (Daigle et al. 2016).

Furthermore, monitoring networks, such as Rivtemp, need to be designed to incorporate fine-scale temperature monitoring, which is essential for identifying and characterizing thermal refuges as part of large-scale assessment of thermal heterogeneity (Fullerton et al. 2018). Without such fine scale data, it is difficult to fully assess the impacts of climate change on thermal refuge size, distribution, and resilience. More data is needed to inform models and to develop reconstruction techniques of time-series to understand how conditions have changed and predict future thermal mismatches. Although a fair amount of information has been published on the use of thermal refuges by Atlantic salmon, there is still a need to better understand the triggers leading to the use of thermal refuges before water temperatures reach critical values and salmon incur metabolic impacts of thermal stress. These assessments need to be conducted while integrating other variables that can affect refuge use, such as hydrodynamics (O'Sullivan et al. 2021b). Such information is necessary to better understand how and when fish use thermal refuges and inform modelling efforts, which are integral to implementing effective management of thermal refuges.

Finally, it is important to determine how Atlantic salmon use thermal diversity at multiple scales in space and time to increase survival and productivity at the individual, population, and species levels (Armstrong et al. 2021). For example, recent work by Rubenstein (2021) suggests that exposure to an overall warmer thermal regime or reduced access to cool thermal refuges during summer in-river holding can reduce survival to spawning and iteroparity rates which can reduce population productivity. Designing monitoring programs that identify climatically resilient habitats (i.e. river reaches or tributaries that are likely to remain within the thermal tolerance range for salmon) will be essential for prioritizing management actions in a changing climate.

Population-level response of salmon to climate change

Although some life stages are more vulnerable to changes in environmental conditions, the maintenance of all life stages is essential for population persistence, and it is only through understanding the cumulative impacts across life stages that it will become possible to fully explain the current trends in Atlantic salmon abundance and tailor more effective management strategies. One of the more pressing research gaps is to understand climate and habitat vulnerability across populations (Crozier et al., 2019). Genetic and life-history traits are key to adaptation, and are strongly influenced by habitat (e.g. Bradbury et al. 2014); however, this has not been fully characterized for all North American Atlantic salmon populations. It is suggested that this characterization should be conducted for each freshwater ecoregion (as defined by Abell et al. 2008), which would provide a path forward to prioritize highly vulnerable life stages and ecoregions in an adaptive management framework. This would involve characterizing population-level vulnerability based on genetics and a rivers' vulnerability to climate change (Boyer, St-Hilaire, and Bergeron 2021; Crozier et al. 2021). Such thermal sensitivity assessments could then be used to prioritize actions that reduce the vulnerability of catchments to climate change, e.g. using habitat restoration and changes in land-use practices to favor river cooling, increase thermal heterogeneity, and enhance or create thermal refuges.

Resilience needs to be understood at different scales: from stream reach to watershed to ecoregion. Studies should be designed to improve our understanding of the suite of drivers associated with habitat and population resilience across all these scales as well as latitudinally. Researchers have used temperature models to highlight reaches that are vulnerable to warming (e.g. Hill, Hawkins, and Jin 2014; Jackson et al. 2018). However, the links between all relevant habitat variables need to be better understood: 1) how they interact, 2) how these interactions may be modified by climate change, and 3) how this may ultimately affect salmon productivity. This will allow the identification of the most effective management actions to mitigate the expected changes.

The question remains whether salmon populations that are already experiencing thermal conditions at or exceeding upper thermal tolerance have the capacity to adapt to rapidly warming conditions. Monitoring salmon populations and river thermal regimes are needed throughout the entire latitudinal range of Atlantic salmon. There is some monitoring currently ongoing in the southern part of the range, but we need to identify population-level responses to rapidly changing thermal conditions. In contrast, few populations are currently monitored in the northern part of the range, and monitoring of these northern populations should be increased to evaluate population dynamics in relation to water temperature and assess if the rate of change is similar latitudinally or not.

Minimally, monitoring efforts should include discharge and water temperature, but there is also a need to monitor other abiotic and biotic conditions, especially dissolved oxygen, air temperature, and precipitation to assess within and between year thermal, hydrological, and population variability. Such comprehensive, multiyear datasets will be critical for identifying life stages that are highly vulnerable to climate change. Such databases could also be used to help prioritize areas for collecting data and analyzing trends. Pilot projects can be developed to address research gaps at all scales, thereby allowing researchers to assess how conditions are changing at local scales and across the global range of Atlantic salmon. For example, at the watershed scale, Teichert et al. (2020) found that integrating temperature and photoperiod with river discharge explained much of the variation in inter-annual differences in migration timing of smolts in the Ourthe River (Belgium) and predicted that outmigration timing could advance 6 to 51 days because of climate change. At larger geographical scales, winter air temperature, which is more readily obtained than water temperature, was a significant predictor for the onset of smolt outmigration across watersheds and even latitudinal gradients (Vollset et al. 2021, Frechette et al. in review) .

In addition to collecting more and better data, the synthesis, reporting, and data availability needs to be improved (Diack et al. 2022). For instance, water temperatures are typically summarized in terms of summer maximum, resulting in studies that overlook the sub-lethal effects of thermal stress. More detailed forecasts via improved downscaling of regional climate models and improved incorporation of riverine dynamics will facilitate going beyond seasonal and annual predictions of changing freshwater habitats. Truly understanding how salmon are affected by climate change will require building models that incorporate the brief and extreme abiotic disturbances that are likely to occur in freshwater as climate change alters river temperature and discharge.

Increasing collaboration

Workshop participants identified a growing need to improve collaboration between marine and freshwater ecologists at the global level. Effects of climate change on salmon populations during freshwater life stages influence survival at sea and *vice versa*, but research that integrates across marine and freshwater environments remains relatively uncommon. Therefore, increasing collaborative research efforts to holistically examine the effects of temperature on salmon across life stages and ecoregions is necessary for predicting population vulnerability (and persistence), thereby enabling managers to prioritize highly vulnerable life stages and ecoregions in an adaptive framework. To help foster these interdisciplinary collaborations, we proposed a list of call for actions (Table 2).

Predicting and mitigating climate change's effects on Atlantic salmon will require meaningful co-production knowledge, such as monitoring and applied research efforts. Alignment between researchers and practitioners is key to tackling long-term and spatially widespread data acquisition. Although indigenous knowledge can refer to deep baselines of past river conditions, scientists have only been monitoring salmon rivers for 30 years across most of the range of Atlantic salmon, thus both knowledge systems providing insights into how rivers are changing. However, it is difficult to compare rivers and ecoregions since knowledge has not been documented yet, and data are not always compatible because of differences between monitoring protocols and/or temporal changes in the protocols and instrumentation used for monitoring. We cannot stress enough that long-term monitoring and comparable data sets are the most critical sources of information needed to understand how salmon habitat is changing and improve the understanding of the global impacts of climate change on Atlantic salmon and their habitats. This necessitates collaboration to develop homogenized data collection protocols and use best practices such as logger casing shading and series correction that account for differences in equipment and methods (Caissie and El-Jabi 2020). Many avenues for unifying approaches exist, including organizing online and in-person workshops, and leveraging conferences to hold special sessions or additional meetings; but champions for these opportunities are needed. Fortunately, the ARSJV can help lead these efforts.

A better integration of how changing thermal conditions are affecting life cycle aspects and behaviour is also needed for all seasons, but the data gaps are especially important for winter. There is quite a strong understanding of acute thermal stress, but a lack of knowledge exists on the impacts of stress at sublethal values and the capacity to detect post-stress. Similarly, we do understand thermal behaviour during thermally stressful conditions, but we lack the dynamic understanding of what is the postspawning behavior of kelts during winter, how foraging behavior changes with thermal conditions, or how behaviours are affected during thermally dynamic periods such as snowmelt. There is also a need to improve the understanding of intra- and interspecific interactions (prey phenology and buffering, predator-prey interactions) and how these interactions change with changing thermal conditions. Such knowledge can provide essential information to refine bioenergetic models.

This call for action requires urgent collaborative action, including a better integration of local and Indigenous knowledge through participatory governance and knowledge co-production, e.g. through a Two-eyed Seeing approach (Cooke et al. 2021; Reid et al. 2021;

Table 2. Specific call for actions to improve our knowledge on the impacts of climate change on Atlantic salmon.

Objective	Call for actions
Data mobilization to create large-scale data sets that can support evidence synthesis across the distributional range of Atlantic salmon	1) Promote analysis of existing data sets with new approaches and use them more broadly, the design of new questions, and develop targeted data acquisition plans to address gaps 2) Develop common data acquisition protocols
Improve understanding and detection of thermal stress, especially below lethal limits	Develop new techniques and markers (e.g. relative telomere length as a biomarker of past thermal stress and broaden the use of heat shock proteins for tracking *in situ* thermal stress at the reach or catchment scale)
Improve understanding of behaviour	Track: 1) behaviour of individuals during periods of dynamic thermal melting 2) dynamics and movements of post spawned salmon (kelts), in freshwater during the winter months 3) foraging behavior under different thermal conditions 4) thermoregulation behavior, such as aggregations
Improve understanding of inter- and intra-species interactions	1) Revisit how food availability is defined and used and the implications for individual growth 2) Study interactions with predators/competitors (especially in thermal refuges) 3) Assess prey phenology and buffering in different habitats
Improve understanding of bioenergetics	1) Development of complex growth models that account for rapid growth (e.g. during summer months) and no growth (e.g. in winter) to delineate periods in relation to seasonal changes of specific environmental parameters 2) Account for changing foraging behavior and prey energy content
Improve Indigenous inclusion	Implement participatory governance that includes indigenous knowledge and western science using a Two-Eyed seeing approach

These actions prioritize research gaps currently impeding Atlantic salmon management and conservation efforts. We acknowledge that these are short to medium-term priorities and that more actions are needed to address both the range of climate change impacts on Atlantic salmon and long-term objectives. Nonetheless, this list provides a starting point towards fostering urgent international collaborations over the distributional range of Atlantic salmon.

House et al. 2023). Although these approaches are part of a growing trend, more transparency and accountability are needed to ensure that implementation is effective and respectful by including everyone at the decision-making table. Participatory monitoring can improve data collection, while also increasing participation of historically marginalized groups (House et al. 2023). There is also a need to re-establish and foster community support and connections with Atlantic salmon and rivers (Liebich, Kocik, and Taylor 2018), which could be achieved by leveraging cultural ecosystem services (Ouellet et al. 2022). Furthermore, implementing iterative processes that allow for program adjustments as data are collected and new knowledge becomes available can help maintain and further develop collaborative research between academia, government, NGOs, and indigenous organizations and communities. As Atlantic salmon populations are in decline in North America, such collaboration is urgently needed to address the numerous research gaps that currently impede salmon conservation.

Conclusion

Atlantic salmon have a complex life cycle, spanning multiple ecosystems that are changing at different rates and affecting specific life stages differently (Hare et al. 2016; Crozier et al. 2019, Crozier et al. 2021). Atlantic salmon are facing unprecedented changes to both marine and freshwater habitats and have been flagged as a species of high vulnerability to climate change (Crozier et al. 2008; Hare, Morrison, et al. 2016; Farr et al. 2021; Thorstad et al. 2021). Indeed, the impacts of climate change on Atlantic salmon phenology are already being observed. Currently, no model addresses the cumulative impacts of climate-driven changes on salmon freshwater habitat. It is challenging to 1) assess which changes are having the greatest effects on salmon populations and 2) implement management strategies that mitigate the impacts of these changes. More than ever, it is critical to coordinate collaborative, holistic research that spans the full range of Atlantic salmon to tackle these pressing issues. Maintaining sustainable population persistence will require conservation of different life histories and heterogeneous habitats (Schindler, Armstrong, and Reed 2015; Link 2021). Although the present call for actions focuses on freshwater ecosystems, there is a need to do this exercise across all the ecosystems that Atlantic salmon populations need for their survival. Such holistic assessment will help better understand how climate change and other human activities contribute to salmon population declines and prioritize actions for collaboration. These questions cannot be answered by solely looking at a single ecoregion or one phase of salmon life cycle. They require large-scale data integration and knowledge across life cycle stages, rivers, and ecoregions, thus bridging scales and bringing scientists together in interdisciplinary collaborations to understand the broader picture. Involving managers early in the process will ensure that the insights gained from the new science will directly meet the need for evidence-based decision-making of managers and interest groups.

Therefore, we call for increased interdisciplinary collaboration among scientists and managers to address the urgent research gaps associated with the impact of thermal dynamics on growth, migration, reproduction, and survival of Atlantic salmon.

Acknowledgements

This paper is the outcome of a workshop that was led by Dr. Normand Bergeron (INRS) and Dr. Carole-Anne Gillis (Gespe'gewaq Mi'gmaq Resource Council, GMRC). The event was part of a series of workshops financially supported by the Atlantic Salmon Research Joint Venture (ASRJV) initiative. Additional logistical support was provided by the Centre interuniversitaire de recherche sur le saumon atlantique (CIRSA).

We thank all participants for their contributions, listed here by affiliation at the time of the workshop: Dalhousie University: Barret Kurylyk; Department of Fisheries and Oceans Canada: Daniel Caissie, Guillaume Dauphin, Patricia Edwards; Hydro-Québec: Patricia Johnston; Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement: Mathieu Buoro; INRS-CIRSA: André St-Hilaire, Anik Daigle, Claudine Boyer, Sébastien Ouellet-Proulx, Yannis Terranti; Memorial University: Marie Clément; Ministère des Forêts, de la Faune et des Parcs: Julien April; Mount Allison University: Andrea Morash, Suzie Currie; National Oceanic and Atmospheric Administration - Fisheries: Lisa Crozier; Norwegian Institute for Nature Research: Bror Jonsson; Nova Scotia Salmon Association: Edmund Halfyard; United States Geological Survey: Christian Torgersen; Université Laval: Benoit Turcotte; University of Massachusetts: Stephen McCormick; University of New Brunswick Canadian Rivers Institute: Allen Curry, Antoin O'Sullivan, Emily Corey, Tommi Linnansaari. Finally, we thank Emilie Beaulieu, the graphic designer who brought our ideas to life for Figure 4.

Disclosure statement

The authors have no conflict of interest to declare

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Data availability statement

This paper summarizes the information presented in the workshop and provides additional original material supported by the listed references. All figures are original work from the authors. Specific information about the workshop (agenda and presentation summaries) is available upon request.

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