Council *Current and predicted ecological impacts of climate change to salmon productivity in the North Atlantic, in marine habitats*	**CNL(23)49** **Agenda item: 7a)**

Current and predicted ecological impacts of climate change to salmon productivity in the North Atlantic, in marine habitats

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1.0 Introduction

After spending their early life stages in freshwater habitats, Atlantic salmon (*Salmo salar*) migrate to the ocean to feed, grow, and mature. Salmon move into the ocean as smolts and mature into adults over a 1- to 4-year period. In the Northwest Atlantic, salmon leave rivers in the Northeast U.S. and Canada and migrate to marine feedings areas in the southern Labrador Sea (ICES 2021). After overwintering in the Labrador Sea, individual salmon will either continue their migration to the coast of Greenland to feed for another summer or will initiate their return migration to natal rivers to spawn. Individuals that feed off the coast of Greenland are believed to overwinter in the Labrador Sea the following year with new migrant salmon from the subsequent year's cohort. In the Northeast Atlantic, juvenile salmon from rivers as far south as Portugal, north to Norway, and east to Russia follow a similar pattern after emigration by converging across a broad swath of the Northeast Atlantic, particularly within the Norwegian Sea (ICES 2021). As these postsmolts grow and feed during their first summer and overwinter within these areas, decisions are made to mature and return to natal rivers to spawn as one sea-winter spawners or to remain at sea for another year or more, eventually becoming multi sea-winter spawners. These multi sea-winter spawners will continue their migration to distant summer feeding areas off the west and east coast of Greenland and may overwinter in similar areas with the new migrant salmon from the subsequent year's cohort.

Both North American and European origin salmon have been shown to undergo trans-Atlantic migrations. North American origin salmon have been detected in relatively low numbers within the Norwegian Sea (Gilbey *et al.* 2017), and European origin salmon have been detected along the west and east coasts of Greenland (ICES 2021, ICES 2022) and in the southern Labrador Sea (Bradbury *et al.* 2021). In the Labrador Sea and along the west coast of Greenland, southern European origin salmon are more prevalent than those from northern Europe, whereas east of Greenland potential multi-sea-winter salmon from northern Europe have a more easterly distribution than those from southern Europe (Reddin *et al.* 2012). These stock-specific patterns of marine migration are beginning to emerge more clearly given recent genetic studies (Bradbury *et al.* 2021, Gilbey *et al.* 2021, O'Sullivan *et al.* 2022), stable isotope studies (MacKenzie *et al.* 2011, Almodóvar *et al.* 2020) and tagging studies involving post-spawn migrants (Strøm *et al.* 2017, Rikardsen *et al.* 2021).

In all these marine habitats, physical and ecological conditions affect Atlantic salmon productivity. Since the late 1980's, marine survival rates have declined and remained depressed for many of the monitored populations across both North America and Europe (Olmos *et al.* 2019, ICES 2021), and the coherence of these declines across widespread geographies implicates marine ecosystem conditions as a key driver (Beaugrand and Reid 2003, 2012; Mills *et al.* 2013, Olmos *et al.* 2019, ICES 2021). Temperature, stratification, and ocean currents influence the environmental and ecological conditions experienced by Atlantic salmon, and climate-driven alterations have and will continue to directly and indirectly affect the productivity of Atlantic salmon populations across the species' range.

This paper provides an overview of the key habitat features that influence Atlantic salmon during their marine life stages. It draws upon prior studies to elaborate the direct and indirect pathways by which climate change may affect Atlantic salmon populations. Finally, it synthesizes projected changes in ocean conditions and hypothesizes the potential impacts of climate variability and change on Atlantic salmon productivity.

2.0 Habitat features that influence Atlantic salmon marine life stages

Temperature, stratification, and ocean currents represent key physical variables determining the suitability of Atlantic salmon marine habitats. These variables also influence numerous characteristics of the broader marine ecosystems within which Atlantic salmon are embedded.

Temperature

Ocean temperatures constrain habitat areas Atlantic salmon and other species can occupy, based on the thermal limits, tolerances and preferences of the species. Lower critical temperatures (i.e., the limit of temperatures that can be tolerated) for Atlantic salmon range from 0-7 °C, while upper critical temperatures span 22-33 °C (Elliott 1994 in Jonsson and Jonsson 2009). As migratory species, individual Atlantic salmon may experience a wide range of temperatures, particularly during the riverine-marine transition and over the north-south latitudinal gradient they transit. Despite being able to survive a broad temperature range in laboratory-based thermal tolerance tests, a narrower range of preferred temperature typically constrains their spatial and temporal patterns in the ocean. Atlantic salmon are most commonly found in areas with sea surface temperatures between 3 to 8 °C (Reddin and Shearer 1987) with more recent studies providing more specificity (e.g., 5.0-13.4 °C (Sheehan *et al.* 2012), 3.9-9.7 °C (Minke-Martin *et al.* 2015), 1.6-8.4 °C (Strøm *et al.* 2020)). In addition to absolute temperatures, the seasonal temperature cycle also affects spatiotemporal availability of suitable thermal habitat for salmon and may provide important cues for life history events such as migration to and from rivers or to seasonally used ocean areas (Henderson *et al. in press*).

For ectotherms like Atlantic salmon, temperature also exerts a strong direct influence on metabolism. Metabolism rises as temperature increases, resulting in higher energy costs (Jonsson and Jonsson 2009). These costs can be multiplied during active life phases, such as migration windows when Atlantic salmon must exert energy for swimming. In general, whether these rising energetic demands can be satisfied depends on the abundance and quality of prey available to Atlantic salmon (Renkawitz *et al.* 2015), which also may be indirectly affected by temperature. Similarly, temperature influences the spatial and temporal distributions of Atlantic salmon predators, which may alter encounter frequency and modify natural mortality rates (Friedland *et al.* 2012). As such, temperature-related effects on species across the marine ecosystem can disconnect or concentrate interactions between salmon and other species (e.g., predators, prey) that ultimately affect vital rates such as growth and mortality.

Stratification

Rising sea surface temperature and declining salinity strengthen ocean stratification, which in turn may affect primary productivity and zooplankton composition in ways that influence trophic relationships across the ecosystem (MERCINA Working Group 2012). In the North Atlantic habitat areas occupied by Atlantic salmon, temperature and salinity changes have historically been driven by changes in ocean circulation that modulate the influence of ocean currents with different salinity properties. For example, the relative balance of Labrador Sea water (colder, relatively less saline) versus Gulf Stream water (warmer, relatively more saline) entering Northwest Atlantic shelf ecosystems affects both salinity and temperature, thereby determining the strength of stratification (MERCINA Working Group 2012). In general, changes in the Gulf Stream and Arctic circulation affect temperature, salinity, and stratification across much of the North Atlantic Ocean used by Atlantic salmon (Meyer-Gutbrod *et al.* 2021, Vollsett *et al.* 2022), which creates cascading impacts that can positively or negatively affect Atlantic salmon productivity and abundance (Mills *et al.* 2013).

Ocean currents

As described above, large-scale ocean circulation patterns associated with major current systems influence ecosystem conditions and dynamics in the North Atlantic region. These broad circulation patterns and other environmental conditions (e.g., wind, river discharge) also affect current strength at local scales within the North Atlantic. The strength of local currents is particularly important for Atlantic salmon during their ocean-going migration as postsmolts, when altered currents may impact the efficiency of migration by increasing or decreasing their swimming time and distance traveled (Friedland *et al.* 2012, Mork *et al.* 2012, Byron *et al.* 2014). As adults, Atlantic salmon are strong swimmers that are unlikely to be significantly deflected from their migration route, although swimming against stronger currents imposes a higher energetic demand. The altered metabolic cost of migration for both postsmolt and adults may divert energy from growth, and may be compounded by conditions such as warmer temperatures, foraging quality and predation risk (Friedland *et al.* 2012, Byron *et al.* 2014), ultimately influencing both growth and survival.

Ecosystem changes

The above descriptions of how physical habitat variables affect Atlantic salmon during their time at sea introduce some indirect mechanisms through which these variables alter ecosystem conditions. Yet it is valuable to highlight that these underlying physical variables exert a strong influence on the development of the entire marine ecosystem. Their variability affects the magnitude and timing of phytoplankton blooms, composition of the zooplankton community, abundance and quality of prey fish, and the spatiotemporal distribution of predators, all of which may indirectly influence population dynamics such as growth, maturity, fecundity, and survival of Atlantic salmon during their marine life stages.

3.0 Impacts of ecosystem change on Atlantic salmon

A number of studies from the Northwest and Northeast Atlantic have demonstrated relationships between changing ecosystem conditions and Atlantic salmon population characteristics and dynamics. Direct effects of temperature have been associated with spatial distribution and run timing of Atlantic salmon smolts and adults. Warming and broader ecosystem changes have been associated with changes in growth, productivity, and abundance of Atlantic salmon populations.

Temperature range and spatial distribution

As noted earlier, marine spatial and temporal patterns of Atlantic salmon are generally constrained by a relatively narrow range of preferred temperatures. Salmon have evolved to depend on the ecosystem dynamics that are represented within this range, and alterations of these spatial and temporal patterns may have consequences for Atlantic salmon productivity. Generally speaking, it is hypothesized that salmon seek a preferred temperature range and that their marine distribution may shift both inter-annually and over the long-term in response to short and longer term warming trends (Strøm *et al.* 2020).

A recent large-scale tagging study on Atlantic salmon has helped define the marine migration patterns of post-spawned adults from across Europe and Iceland (Rikardsen *et al.* 2021). Salmon from different populations utilized different migration routes and areas, with differing temperature profiles, but they consistently migrated to areas of high productivity located between North Atlantic and cold polar water frontal areas. Increased diving activity indicated these areas to be important feeding areas. If the locations of these boundary areas change over time, it is unclear how populations will respond in terms of migration routes and timing. If the location of these areas moves northward because of ocean warming, southern populations may be especially challenged given increased migration distance, time and energy demands. Although Rikardsen *et al.* (2021) investigated post-spawned adults, the dynamics seen may also be indicative of dynamics for early marine phase Atlantic salmon.

Run timing

The timing of emigration of Atlantic salmon smolts and immigration of adults is shifting, and temperature has been identified as an influential factor. Smolts leaving rivers in the Northwest and Northeast Atlantic have migrated seaward 2.5 days earlier per decade, on average (Otero *et al.* 2014). However, smolt migration timing is variable across rivers, with smolts from southern rivers migrating earlier than northern ones (Hvidsten *et al.* 1998) and Northeast Atlantic populations migrating earlier than Northwest Atlantic populations at analogous latitudes (Otero *et al.* 2014). Differential migration timing has been associated with freshwater and sea surface temperatures; although photoperiod also cues smoltification and migration, river temperature enables salmon to refine the timing of ocean entry to encounter optimal ecosystem conditions (Otero *et al.* 2014). Recent studies have further investigated the complex relationship of these and other drivers of smolt emigration (Vollset, *et al.* 2021, Simmons *et al.* 2021, Frechette *et al.* 2023). As the seasonality of annual temperature cycles shifts, the influence of photoperiod on migration timing may create disconnects between salmon smolts and their prey or may intensify interactions with their predators (Friedland *et al.* 2012). Further, differential warming between freshwater and marine environments could result in cues that cause smolts to enter the ocean at unfavorable times or under unideal conditions.

Return migration timing of adult Atlantic salmon has been changing in many rivers in which this phenomenon has been studied. Analysis of long-term recreational catch data have suggested that the timing of adult returns across France has been delayed by 20-40 days (Bal *et al.* 2017), and a study in Scotland indicates stable median adult return dates in some rivers but delayed returns in others (Todd *et al.* 2012). However, in other locations, advances in adult return dates have been observed. A study of Atlantic salmon adults observed in monitoring stations on 28 rivers across France estimated that return dates have advanced 2.9 days per decade (Legrand *et al.* 2021). In the Burrishoole catchment (Ireland), 50% of returning Atlantic salmon are arriving 1-2 months earlier than in the 1970s: a rate of 0.75 days earlier per year (de Eyto *et al.* 2022). In the Penobscot River (Maine, USA), the median date of adult Atlantic salmon migration has advanced 0.7 days per year from 1978-2001 and 1.3 days per year from 1986-2001 (Huntington *et al.* 2003, Juanes *et al.* 2004, Staudinger *et al.* 2019). These advances in return migration date have been concentrated at the end of the run, with the 75th and 90th percentiles of the run experiencing the most rapid advances (Mills *et al.*, *in prep.*). In both the Burrishoole and Penobscot systems, limited change has been noted for the start of the run, but advancement of the end has resulted in a contraction of the total length of the run (de Eyto *et al.* 2022; Mills et al, *in prep.*). This shorter return period reduces the potential for buffering unfavorable conditions that could be gained if the returning population is spread out over a longer time period. However, if stress is induced by the duration of exposure to unfavorable ocean conditions, a tighter and earlier return period facilitates escapement from these conditions. The different return timing responses and how they are distributed over the course of the run may indicate multiple drivers of return migration timing, which may be acting at basin and local scales.

Growth

Many studies have examined changes in growth of Atlantic salmon based on measures of circuli from salmon scales, with an interest in also understanding how changes in growth are related to marine survival rates and to environmental conditions, particularly temperature. Generally, these studies have focused on the post-smolt stage (through the end of the first calendar year at sea) and have found contrasting results for Northeast and Northwest Atlantic salmon populations. In the Northeast Atlantic, the influence of post-smolt growth on subsequent survival has been detected in some populations (Peyronnet *et al.*, 2007, Friedland *et al.*, 2009a), whereas no similar relationship has been found for Northwest Atlantic populations (Friedland *et al.*, 2009b, Hogan and Friedland, 2010, Izzo and Zydlewski, 2017).

Correlations between temperature and growth are nuanced. The optimum temperature for growth of post-smolts in the ocean has been estimated to be 13 °C based on experimental tests (Handeland *et al.* 2003) and 14.8 °C based on bio-energetic modelling (Smith *et al.* 2009). However, temperature does not act in isolation to determine growth; food resources, particularly plankton and prey fish, are also necessary to support growth (Friedland *et al.* 2009b, Vollset *et al.* 2022). For some populations at the northern extent of the range of Atlantic salmon, warmer sea surface temperatures have been associated with faster growth (Jensen *et al.* 2011). However, for most populations, rising sea surface temperatures have been associated with declines in Atlantic salmon growth (McCarthy *et al.* 2008, Todd *et al.* 2008, Friedland *et al.* 2009b). Most studies have considered growth during the post-smolt life stage, but a recent study found significant declines in growth during the second winter at sea for MSW Atlantic salmon, with the most substantial declines occurring during the warmest period of the time series (Barajas *et al.* 2022). In contrast, marine growth from a French population has demonstrated declines in growth over the first summer only, but also provided evidence on the complex relationship between sex, marine growth and maturation (Tréhin et al 2021). This relationship between growth, survival and maturation is complicated and deserves further attention given its interconnectedness in determining overall population productivity (ICES 2023).

Recent studies provided new insights into relationships between ecosystem conditions, growth, and marine survival of Atlantic salmon, highlighting complex non-stationary relationships. Vollset *et al.* (2022) studied salmon returning to rivers across Norway and found substantial, sudden declines in early marine growth and increases in the proportion of MSW salmon (i.e., later maturity) after 2004. These changes coincided with broader oceanographic and ecosystem changes, including an increase in spring sea surface temperature, reductions in zooplankton biomass, and declines in prey fish abundance, all of which reflect a regime shift in the Northeast Atlantic ecosystem that impacted Atlantic salmon. In addition, Tillotson *et al.* (2021) examined Atlantic salmon from multiple North American stocks feeding off West Greenland and found that while marine growth has generally increased, a strong non-stationary relationship between growth and survival emerged. Growth was positively related to marine survival prior to the 1990s, but the relationship broke down after 1990 when a regime shift affected multiple levels of the North Atlantic ecosystem, indicating that mechanisms controlling marine survival changed. These studies both show direct, indirect, and interacting climate influences on affect Atlantic salmon growth and survival, but these relationships need to be examined in an ongoing matter as ocean ecosystem regimes change.

Productivity and abundance

Atlantic salmon have experienced population declines across their North American and European range, with particularly strong declines in post-smolt survival, productivity, and abundance observed in the early 1990s (Beaugrand and Reid 2003, 2012; Mills *et al.* 2013, Olmos *et al.* 2019, 2020). These declines have been coherent across North American and European regions (Olmos *et al.* 2019, 2020), but the greatest declines have been experienced by populations at the southern extent of the range (ICES 2021). Moreover, declines have been more severe for fish that spend more time in the marine environment (i.e., multi-sea-winter fish), including those that migrate longer distances.

These multi-population studies have identified relationships between population declines and environmental conditions such as sea surface temperature and changing dynamics of ocean currents (Beaugrand and Reid 2012, Mills *et al.* 2013, Olmos *et al.* 2020, Vollset *et al.* 2022). However, the concurrent broader ecosystem conditions may exert stronger influences on Atlantic salmon populations via indirect mechanisms acting through bottom-up or top-down processes. A recent bioenergetics modelling study concluded that increases in ocean temperatures will result in significant indirect impacts (e.g., prey quality and abundance) to individual Atlantic salmon productivity compared to the direct impacts of temperature on physiological performance (Strøm *et al.* 2023). The authors suggest their conclusions may be applicable to many northern Atlantic salmon populations, but possibly not southerly populations given that they are already experiencing warmer temperatures compared to than their northern conspecifics.

Bottom-up trophic mechanisms have received the greatest attention in existing studies. A major trophic shift in the 1990s on both sides of the North Atlantic. This shift resulted in changes in phytoplankton and zooplankton communities (Pershing *et al.* 2005, Beaugrand and Reid 2003) and reductions in the abundance and energetic quality of prey (Mills *et al.* 2013, Renkawitz *et al.* 2015), which have contributed to changes in productivity and abundance of Atlantic salmon populations (Beaugrand and Reid 2003, 2012; Mills *et al.* 2013). In addition, shifts in the distribution and phenology of predators may enhance their overlap with and mortality of Atlantic salmon, particularly during certain critical life stages such as estuarine and coastal migrations (Friedland *et al.* 2012).

4.0 Projected climate-driven changes and impacts to Atlantic salmon

Projected climate-driven changes in physical ocean conditions

Climate projections indicate that physical features of the North Atlantic region inhabited by Atlantic salmon will change over the coming decades, and these physical changes are expected to drive ecological changes in the region. The magnitude of change will be influenced by greenhouse gas emission trajectories, and results presented below contrast two extreme scenarios using the most recent Intergovernmental Panel on Climate Change's (IPCC) Coupled Model Intercomparison Project 6 (CMIP6) model ensemble (Eyring *et al.* 2016). The SSP1-2.6 scenario is based on substantial global CO_2 emission cuts that achieve net-zero emissions around 2070, with temperatures stabilizing around 1.8 °C warmer at the end of the century. In contrast, the SSP5-8.5 scenario assumes a future with continued rapid economic growth and CO_2 levels doubling by 2050, resulting in a 4.4 °C increase in global temperature by 2100 (IPCC 2021, Table SPM.1). Oceanographic responses under these scenarios begin to diverge by mid-century (2040-2069), but the differences are most apparent at the end of the century (2070-2099).

Sea surface temperature is projected to increase over much of the North Atlantic under both scenarios, with the strongest warming expected south of Newfoundland to the Gulf of Maine in the Northwest Atlantic and in the Norwegian Sea in the Northeast Atlantic. In these areas, sea surface temperatures are projected to warm by more than 1.6 °C by mid-century and 2.0 °C by end-of-century under the SSP1-2.6 scenario and by up to 2.5 °C by mid-century and 4.8 °C by end-of-century under the SSP5-8.5 scenario (Figure 1). However, Arctic and Greenland ice melt and other factors are expected to contribute to weakening of the Atlantic Meridional Overturning Circulation (AMOC, the global ocean conveyer belt that brings warm water north and cold water south), creating a "warming hole" south of Greenland, one of the only places in the ocean that is projected to *cool* in future decades under certain scenarios (Bakker *et al.* 2016, Ceasar *et al.* 2018, Keil *et al.* 2020). Cooling is projected to be as great as 0.6 °C under the SSP1-2.6 scenario at the end of the century. Under the SSP5-8.5 scenario, this area is projected to warm modestly (up to 0.8 °C by the end of the century), yet far less than surrounding portions of the North Atlantic.

Salinity is projected to decline across the North Atlantic region (Figure 2). Under both the SSP1-2.6 and SSP5-8.5 scenarios, sea surface salinity is projected to be 0.5-0.6 practical salinity units (psu) fresher in the Labrador Sea, east of Newfoundland, and in the North Sea at mid-century. By end-of-century the area experiencing the strongest freshening will expand to cover more of the North Atlantic, and salinity is projected to decline by 0.5-0.7 psu under the SSP1-2.6 scenario and by 1.4-1.8 psu under the SSP5-8.5 scenario.

Further, shallower mixed layer depths are projected across much of the North Atlantic (Figure 3). Shallowing of the mixed layer reflects enhanced water column stability (i.e., stratification) that is influenced both by warming of the surface waters and reduced salinity. Mixed layer depths are projected to shoal by 110 m across much of the North Atlantic, from the southern part of the Labrador Sea to Ireland, at mid-century under both scenarios. At end-of-century, the same areas will experience the greatest shallowing of mixed layer depth, with a projected shoaling of as much as 120 m under SSP1-2.6 and 200 m under SSP5-8.5.

Implications for Atlantic salmon populations

Climate change will push ocean conditions in the North Atlantic beyond bounds that have been experienced during the observational record for Atlantic salmon. Ocean temperatures are projected to rise substantially in certain areas, including the Gulf of Maine, Gulf of St. Lawrence, Scotian Shelf and southern Newfoundland Shelf, Iceland Sea, and Norwegian Sea. Many of these areas are primary Atlantic salmon marine habitat and these increased temperatures, combined with potential ecosystem changes that affect Atlantic salmon feeding success and predation rates, may significantly impact the marine productivity of this species. These impacts may particularly threaten the survival of populations at the southern extent of the range, as these stocks will not only experience the highest-magnitude temperature increases, but also have the largest migration distances to reach marine feeding areas.

In addition to increasing temperatures, Atlantic salmon will experience stronger temperature gradients and changing seasonality, which may affect their migrations from southern areas of the Northwest Atlantic to the Labrador Sea and from Europe to the Norwegian Sea. In particular, in the mid-North Atlantic, the cooling (SSP1-2.6) and less dramatic warming (SSP5-8.5) effects associated with a slowdown of the AMOC will disrupt temperature gradients across much of the area south of Greenland and Iceland. This disrupted temperature gradient may interfere with migration cues and the ability of salmon to effectively navigate through feeding, overwintering, and other habitats in the ocean. Changing seasonality of spring warming and fall cooling will also shift migration cues, creating the potential for mismatch between the needs of salmon and the ecosystem conditions they encounter. Further, shifting seasonality will alter the length of the summer feeding and overwintering periods, which will have energetic implications for Atlantic salmon. This varied temperature gradient will likely create a complex mosaic in which contemporary direct and indirect drivers of salmon productivity are changing in vastly different directions and magnitudes across the spatial marine range of the species. The impact of these varied changing conditions could range from strongly negative, to neutral to strongly positive. Collectively, this will create a future salmon marine ecosystem that is difficult to predict and even more difficult to forecast the impact it may have on the productivity of Atlantic salmon populations across the species entire range. These scientific limitations will require managing salmon populations within a context of greater uncertainty.

Although temperature, salinity and stratification are key physical properties that will be affected by climate change, it is critical to recognize that most of the impacts to Atlantic salmon will not be attributable to one variable acting directly or in isolation of other variables. The interactive effects of multiple changes and their indirect effects through the ecosystem will exert the greatest effects on Atlantic salmon. Physical changes that alter primary productivity, zooplankton composition, prey fish, and predators will all affect Atlantic salmon. Bottom-up effects may accrue through changes in species overlap and interactions, or they may emerge through changes in energy pathways and energy density. As such, future success of Atlantic salmon in terms of growth, productivity, and survival may not be determined only by changes in prey composition but also by changes in the quality of the prey items in terms of energetic value (Renkawitz *et al.* 2015). Top-down effects may emerge as predators of Atlantic salmon shift their spatiotemporal distributions and experience different encounter rates (Friedland *et al.* 2012). In addition, changing overlap between Atlantic salmon and fishing fleets could occur if fleets shift their locations as their target species move.

The Atlantic salmon marine environment is extremely complex and is changing at a rapid pace, which is projected to continue with climate change. The expected changes are varied within regions of the North Atlantic used by Atlantic salmon, and the magnitude of these changes is not yet known given uncertainty in future global greenhouse gas emissions and interconnectedness of the ecosystem. However, even with this uncertainty, rising temperatures, changing stratification, shifts in ocean currents, and other climate-related changes will act directly and indirectly on Atlantic salmon to:

(1) Shift spatial distributions, which may:
   a. Increase risk of extirpation, as southern portions of range may exceed bioenergetic thresholds or tolerance limits
   b. Increase potential for northerly range expansion and enhanced productivity of stocks within the northern portion of the range
   c. Shift locations of preferred habitats

(2) Shift temporal distributions, which may:
   a. Alter smolt migration timing, resulting in different ecosystem conditions at sea-entry (potential predator-prey mismatch)
   b. Alter dates of return from sea, with evidence of both earlier and later returns emerging from studies in different systems
   c. Shift the timing of transition between various marine phases (e.g., overwintering, summer feeding)

(3) Alter growth, maturation, and survival schedules:
   a. Increase or reduce metabolic demand due to changes in temperature, currents, and other conditions, which would affect the quantity and quality of prey salmon need to satisfy their energetic requirements
   b. Influence growth of Atlantic salmon during all marine phases, with changes during post-smolt and late marine phases being most tightly associated with marine survival (based on prior studies)

c. Alter maturation decisions, creating the potential for slower maturation with lower marine growth or earlier maturation with faster growth

Prior studies of how warming and other ecosystem changes have affected Atlantic salmon populations lead us to expect mostly negative effects of continued climate change. However, it is possible that some effects may be positive, particularly the potential for the northward expansion of favorable habitats. In addition, if warming causes alternative high-energy prey species to increasingly overlap in distribution with Atlantic salmon, positive indirect effects of warming could be realized (Strøm *et al.* 2023). However, multiple sources of uncertainty associated with future climate scenarios, magnitude of physical and ecosystem changes, and how those will affect Atlantic salmon across their mosaic of ocean habitats and life stages limit our ability to confidently project the future of Atlantic salmon under climate change.

Further, just as variables associated with climate change do not act alone, neither does climate change operate as a singular stressor. Climate-related challenges facing Atlantic salmon during their marine life stage cannot be separated from, and in fact will likely be compounded by, climate impacts during their freshwater life stages and by a large suite of anthropogenic stressors, such as habitat degradation, pollutant loads, and fishery interactions. Reducing these other stressors can enhance the resilience of Atlantic salmon to climate impacts, giving them the greatest opportunity to withstand negative impacts of changes in the marine ecosystem during their time at sea.

Uncertainties and research needs

Conserving Atlantic salmon populations as climate change progresses requires managing in the context of uncertainty. Understanding how climate change impacts Atlantic salmon and elucidating mechanisms influencing these impacts necessitates knowing how Atlantic salmon use the marine environment. As salmon populations have declined, the ability to observe individuals in large-scale surveys has been reduced, making it harder to know if and how their spatiotemporal distribution in the ocean is changing. Leveraging newer techniques, such as tagging and genetic identification over larger numbers of individuals, at higher temporal frequency and at larger spatial extents of observation will facilitate a better understanding of the spatiotemporal distribution of salmon and the physical and ecosystem conditions they encounter through their marine life stages.

In addition, many uncertainties exist related to the ecosystem-scale effects of projected physical changes. The direct, indirect, and cascading effects of physical changes on marine ecosystems and species of interest are challenging to predict in most ecosystems. This challenge is especially unique in the North Atlantic, where general ocean warming patterns around the edges of the basin are distinct from projected trends of reduced warming (and even cooling under certain scenarios) in the middle of the basin due to changes in the AMOC. These unique features in the area south of Greenland and Iceland may preserve habitats suitable for *Calanus* and other cold-water lower trophic level species, and this area represents one of few places of the ocean where fish biomass is projected to increase under future climate scenarios (Cooley *et al.* 2022, Figure 3.21). These divergent projections for North Atlantic regions pose unique considerations for Atlantic salmon, given their use of multiple habitat areas across the basin. In addition, critical tipping points associated with melting of the Greenland ice sheet and slowdown of the AMOC are not well characterized, both of which would exert major impacts on the North Atlantic ecosystem, and hence, Atlantic salmon populations.

Research programs directed at resolving these uncertainties can be built collaboratively with institutions that represent broad expertise across the North Atlantic, enhancing the potential for Atlantic salmon-focused studies to leverage other larger efforts. While enhancing understanding of these uncertainties is possible, it will not be possible to pursue conservation and management efforts in the *absence* of uncertainty. As such, managing for resilience through efforts to reduce other stressors affecting Atlantic salmon populations will be an important element of conservation efforts in the context of climate change.

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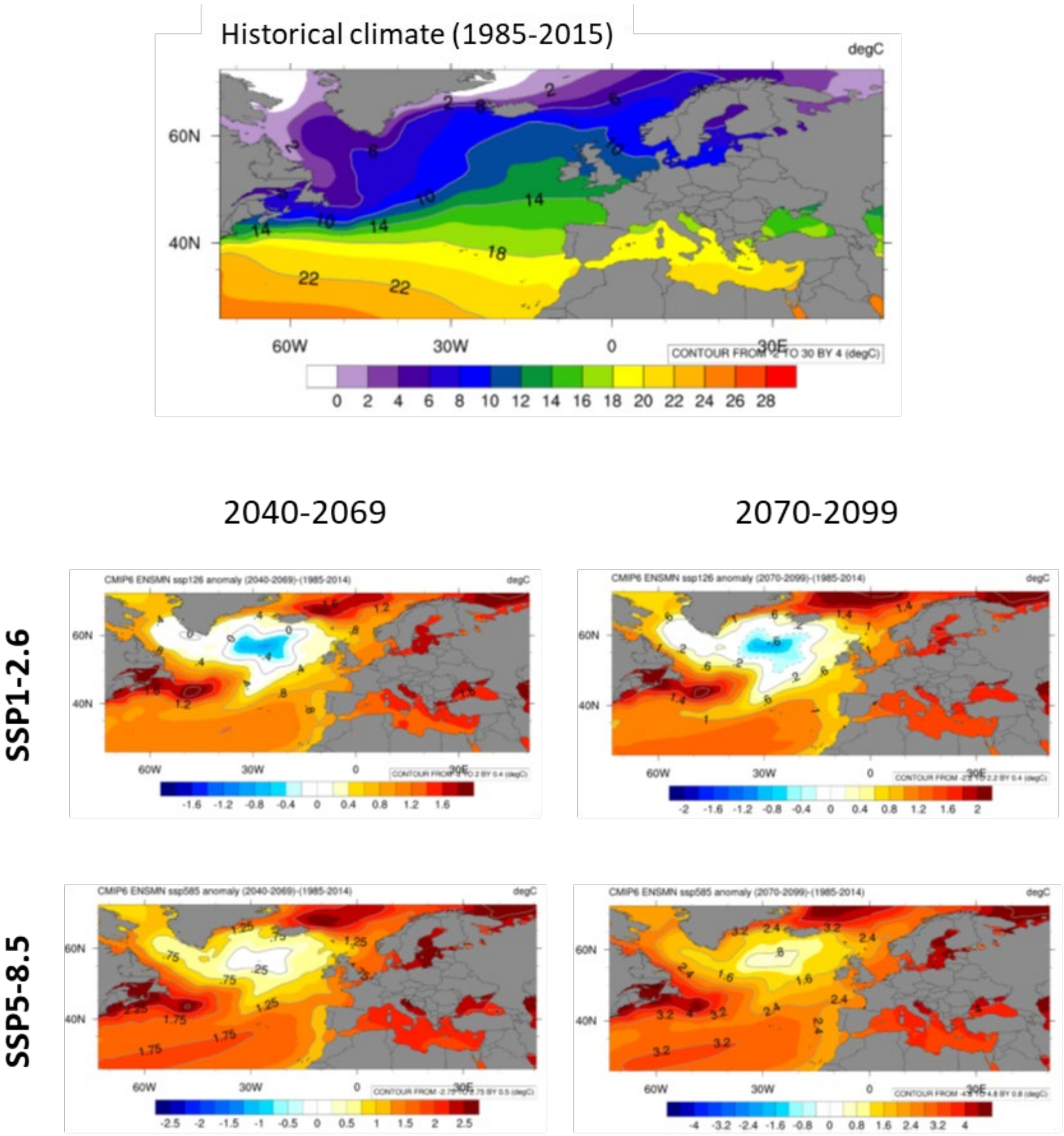

Figure 1. *Historical (1985-2014) sea surface temperatures (°C) across the North Atlantic are shown in the top panel. The bottom panel shows projected changes in sea surface temperature for a mid-century period (2040-2069; left column) and an end-of-century period (2070-2099; right column) for two scenarios: SSP1-2.6 (top row) and SSP5-8.5 (bottom row).*

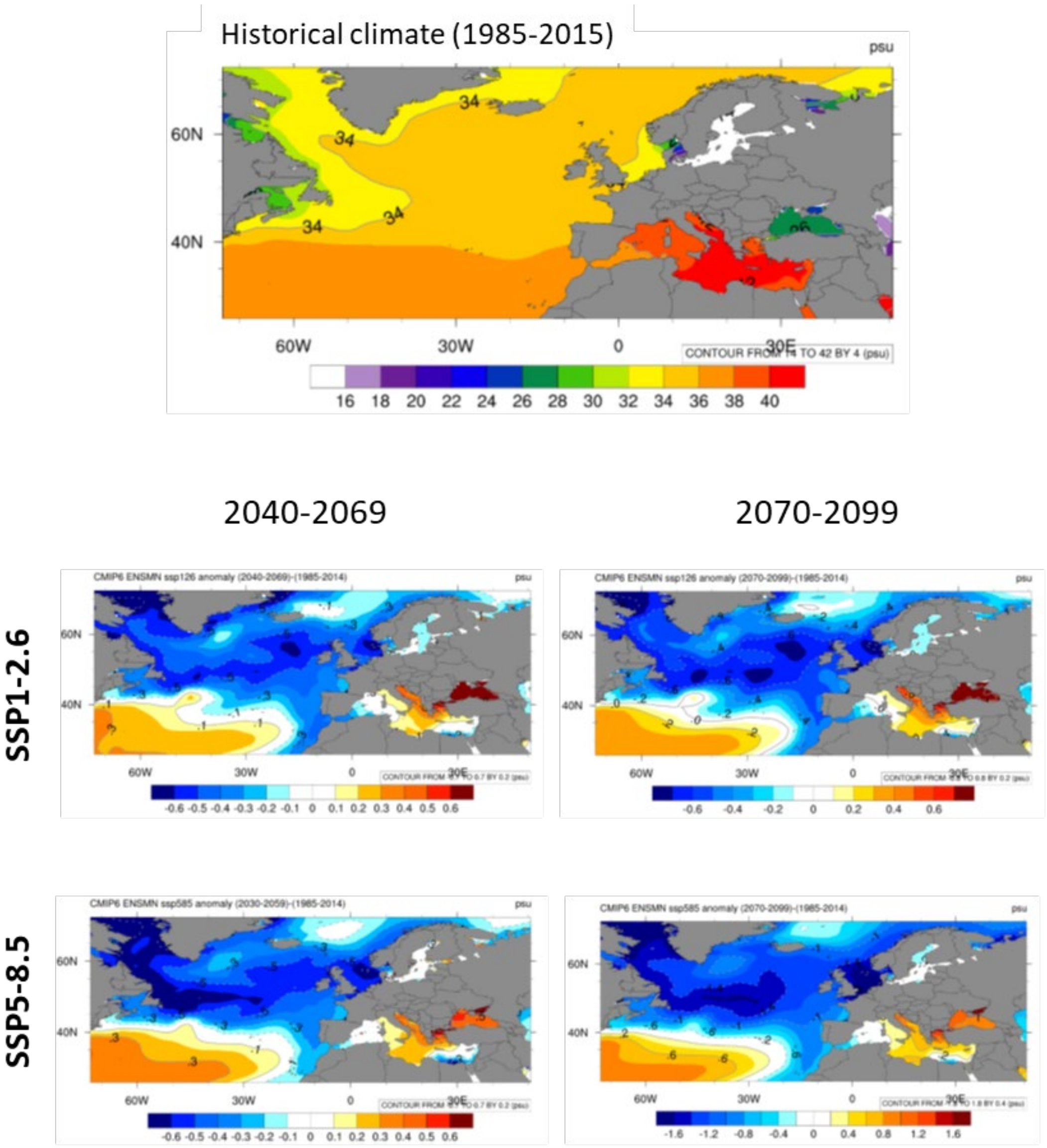

Figure 2. *Historical (1985-2014) salinity (practical salinity units, psu) across the North Atlantic are shown in the top panel. The bottom panel shows projected changes in salinity for a mid-century period (2040-2069; left column) and an end-of-century period (2070-2099; right column) for two scenarios: SSP1-2.6 (top row) and SSP5-8.5 (bottom row).*

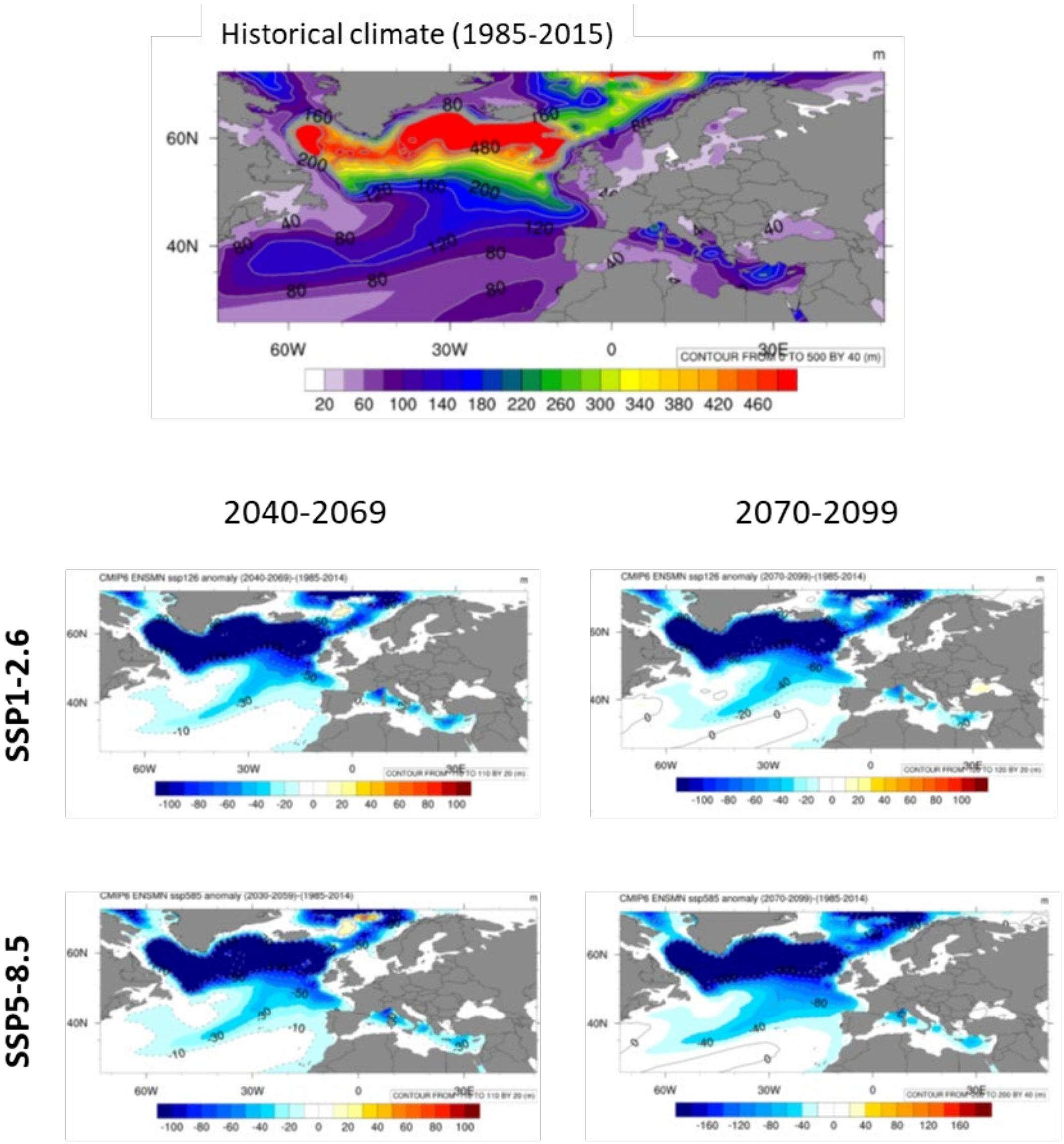

Figure 3. *Historical (1985-2014) mixed layer depth (m) across the North Atlantic are shown in the top panel. The bottom panel shows projected changes in mixed layer depth for a mid-century period (2040-2069; left column) and an end-of-century period (2070-2099; right column) for two scenarios: SSP1-2.6 (top row) and SSP5-8.5 (bottom row).*