

# A synthesis of US Atlantic salmon habitat requirements and implications for future suitability under a changing climate

M. E. Henderson <sup>1,2</sup>, K. E. Mills <sup>1</sup>, M. A. Alexander<sup>3</sup>, M. Barajas <sup>1</sup>, M. J. Collins<sup>4</sup>, M. Dzaugis<sup>1</sup>, D. Kircheis<sup>4</sup>, and T. F. Sheehan<sup>5,\*</sup>

<sup>1</sup>Gulf of Maine Research Institute, Portland, ME 04101, USA

<sup>2</sup>Monterey Bay Aquarium Research Institute, Moss Landing, CA 95039, USA

<sup>3</sup>NOAA Physical Sciences Laboratory, Boulder, CO 80301, USA

<sup>4</sup>NOAA Fisheries, Gloucester, MA 01930, USA

<sup>5</sup>NOAA Fisheries, Woods Hole, MA 02543, USA

\*Corresponding author: tel: 508.603.9610; e-mail: [tim.sheehan@noaa.gov](mailto:tim.sheehan@noaa.gov).

The Gulf of Maine hosts the southernmost remaining population of North American Atlantic salmon. Despite extensive hatchery supplementation since the late 1800s, and more recent riverine habitat restoration efforts and fishing restrictions, US-origin Atlantic salmon populations continue to decline and have remained at low abundance over recent decades. Climate change has been identified as a critical threat to the future of US Atlantic salmon. In this study, we synthesized available information on how habitats used by Atlantic salmon across all their life stages will be affected by climate change as well as the suitability of future conditions for salmon's persistence in the region. Maintaining sufficient cool water refugia during increasing summer temperatures in riverine habitats is required for sustaining salmon in the future. Changes in groundwater quantity and temperature, which will depend on future precipitation and temperature, will be critical factors for river temperatures, as will land use and land cover. While Atlantic salmon's freshwater life stages are heavily documented, the marine phase is relatively less studied. Climate models predict basin-scale changes over the next century, but impacts to salmon are difficult to predict. Furthermore, disparate drivers and differential rates of change between freshwater and marine habitats could present an obstacle to the transition between phases in the future. We have a general understanding of migration patterns and prey preferences but lack a clear picture of how salmon respond to habitat and ecosystem-level changes associated with climate change progression. More research to understand freshwater habitat changes and salmon's marine spatiotemporal distribution responses will enhance capacities to evaluate future risks and predict impacts of climate change to US-origin Atlantic salmon.

**Keywords:** Atlantic salmon, climate change, climate projections, Maine, salmon, streamflow.

## Introduction

Atlantic salmon (*Salmo salar*) in the United States once occupied streams as far south as the Hudson River, New York (Danie *et al.*, 1984), and north to the Canadian border. Declines have been most dramatic at the southern boundary of Atlantic salmon's distribution (Gephard and McMenemy, 2004; Juanes *et al.*, 2004), and today salmon persist in just eight of Maine's 34 historic Atlantic salmon rivers (Beland, 1984; USASAC, 2021a). In 2000, the remnant United States population of Atlantic salmon in the Gulf of Maine (GOM) was identified as the GOM Distinct Population Segment (DPS) and declared "endangered" under the Endangered Species Act (Ginbar, 2009). In 2009, the listing was revisited, and the geographical range of the GOM DPS was redefined (Federal Register, 2009). The new listing covers all naturally spawned and conservation hatchery populations of anadromous Atlantic salmon whose freshwater range occurs in the watersheds from the Androscoggin River north and east along the Maine coast to the Denny's River, including those that were already listed in 2000 (Figure 1). Hereafter, we will refer to the GOM DPS Atlantic salmon as "salmon."

US Atlantic salmon's declining abundances and shifting distributions have been caused by several factors, including

damming of rivers, pollution, fishing pressure, warming water temperatures, ecosystem changes, and reduced marine survival and productivity (Mills *et al.*, 2013; Borggaard *et al.*, 2019). Hare *et al.* (2016) concluded that Atlantic salmon is among the most vulnerable managed fish species to climate change on the Northeast US continental shelf. In response, in 2017, the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service hosted an Atlantic Salmon Climate Scenario Planning Workshop where key considerations in developing effective management for Atlantic salmon under climate change progression were identified (Borggaard *et al.*, 2019). This paper addresses one recommendation from that workshop by bringing together established knowledge of salmon habitat and climate projections to infer how habitat suitability for US salmon populations may or may not change in the future.

## Life cycle overview

Atlantic salmon have a complicated life history that includes critical transitions between distinct freshwater and marine environments and vast migrations, both within freshwater from headwaters to river mouths and in the ocean from nearshore

Received: 9 June 2022; Revised: 18 March 2023; Accepted: 25 March 2023

© The Author(s) 2023. Published by Oxford University Press on behalf of International Council for the Exploration of the Sea. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.



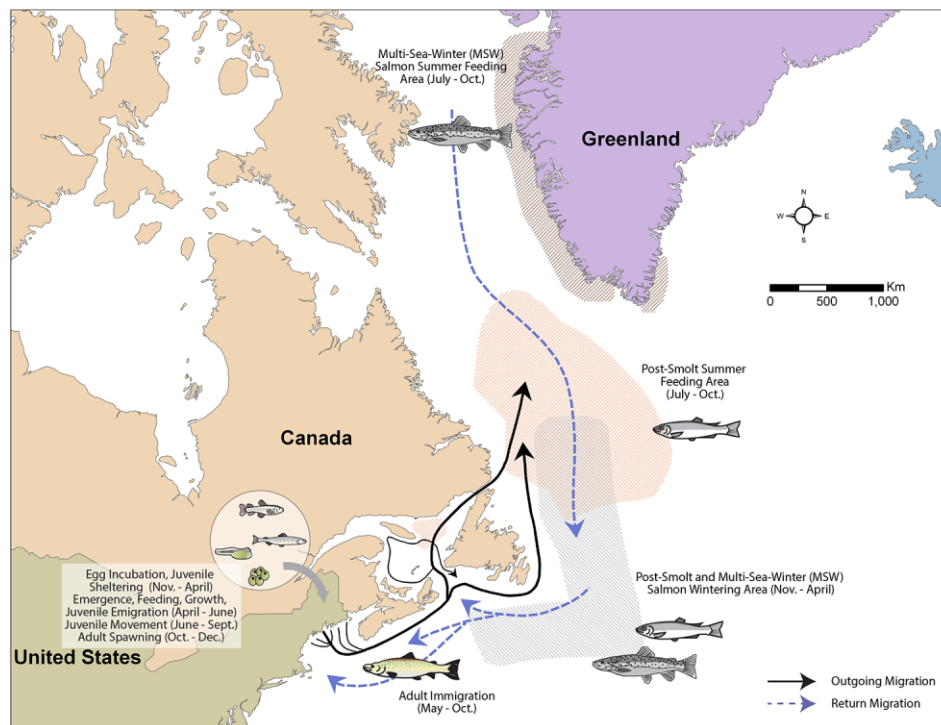
**Figure 1.** Historical US Atlantic salmon rivers. The GOM watershed (green shading) hosts the only remaining US-origin Atlantic salmon. Three individual rivers containing stocks of US-origin Atlantic salmon are identified: (1) Narraguagus River, (2) Penobscot River, and (3) Sheepscot River.

to high seas feeding areas (Figure 2). Life stage duration, transitions, and survival are all contingent on numerous habitat variables and seasonalities. Here, we summarize the Atlantic salmon life history and underscore associations with specific habitat features and times of year. The following summary is drawn from Thorstad (2011), unless otherwise noted.

Anadromous Atlantic salmon spend a significant portion of their life at sea, feeding and growing, before returning to streams to spawn from May through October. Salmon migrate upstream to find suitable spawning habitat. Following a resting period, the digging of gravel nests—called redds—by females in well-oxygenated moving waters is triggered by a combination of photoperiod and temperature. This typically occurs during October and November (USASAC, 2021b), when temperatures reach a critical threshold where egg survival is optimal. The timing of ovulation is dictated by seasonal changes in photoperiod and therefore less likely to change with climate change progression (Scott, 1990). Eggs are deposited and immediately fertilized by males. Yolk-sac-feeding salmon, called alevin, hatch in spring after approaching the critical threshold of accumulated thermal units (ATU) necessary for embryo development. In Maine, eggs are known to hatch from April to early May (Danie *et al.*, 1984). For a three- to eight-week period, alevin live in the gravel, hiding from predators and living on their yolk sac reserves. During this period, the young salmon transition to first-feeding fry as the yolk sac is used up. This transition period is a critical period during which fry need appropriate and sufficient food (Hjort, 1914; Cushing, 1990). Fry quickly develop into parr with dark, vertical bands on their bodies to disguise themselves from predation in the freshwater environment. Most US-origin salmon parr will stay in freshwater for two years,

with a small proportion staying for only one year or greater than two years (Fay *et al.*, 2006). A few males termed “precocious part” will mature early and stay in freshwater their entire lives (Letcher *et al.*, 2002).

At the end of this freshwater growth, parr smoltify over a one- to two-month period (Hoar, 1976). During smoltification, salmon undergo a series of physiological, morphological, and behavioural changes to prepare them for surviving the marine environment (McCormick and Saunders, 1987; McCormick *et al.*, 1998). As smolts enter the marine environment during May and June, they are referred to as post-smolts, and they endure a series of challenges, including osmotic stress, new prey sources, and new predators, including seals and larger fish (Baum, 1997; Beland *et al.*, 2001; Jonsson and Jonsson, 2004). Morphological changes include body colouration and shape to camouflage and navigate the marine environment (McCormick *et al.*, 1998; Kocik and Friedland, 2002; Saunders *et al.*, 2006). Physiological changes most notably include olfactory senses, vision, and osmoregulatory function to handle the quick (two to three week) transition to saltwater (McCormick *et al.*, 1998; Saunders *et al.*, 2006). Smoltification is catalyzed by a variety of environmental cues, including photoperiod, stream temperature, and water flow (McCormick and Saunders, 1987; Metcalfe and Thorpe, 1990; McCormick *et al.*, 1998). The “decision” to smolt is made several months in advance and is typically accompanied by increased feeding to fuel the metabolic costs of smoltification (Metcalfe and Thorpe, 1990). Warming temperatures are known to affect smoltification timing as well as the relative impact of other environmental cues for smoltification. Laboratory studies indicate that warming mean daily temperatures from 2 to 10°C can advance smolting by up to a month (McCormick *et al.*, 1999). Conversely, low temperatures (<3°C) restrict the effect



**Figure 2.** Overview of US-origin Atlantic salmon location and timing of various life stages and their marine migration. Figure from NOAA Fisheries and modified by Borggaard *et al.* (2019).

of photoperiod as a cue for smolting (Fry, 1971; McCormick *et al.*, 1995).

Salmon spend one to three years at sea growing. On average (2001–2020), ~25% of US-origin salmon return to rivers after one winter at sea (1SW), 74% return after two winters (2SW), and 1% remain at sea for three winters (USASAC, 2021b). 1SW salmon are termed “grilse,” while 2SW+ are referred to as “multi-sea winter” (MSW). The grilse returning to US waters are almost exclusively male, whereas the male/female ratio increases in higher latitudes (Hutchings and Jones, 1998). Likewise, the proportion of grilse in the returning population also increases at higher latitudes (Hutchings and Jones, 1998). Throughout the marine phase, salmon feed on a variety of prey, including sandlance, capelin, and zooplankton (Thorstad *et al.*, 2012). During the first year at sea, post-smolts move along the Scotian shelf to summer in the southern part of the Labrador Sea (Figures 2 and 3). In winter, these post-smolts are thought to migrate south to the Grand Banks and southern Labrador Sea, where they join MSW salmon that spent the summer feeding along the West Greenland coast. After overwintering in this area, the MSW salmon are assumed to continue their migration south to their natal river prior to spawn. The post-smolts will either return to their natal rivers as 1SW fish or will migrate north to the coast of Greenland to spend the summer feeding, eventually migrating back to the overwintering areas and joining the next cohort of post-smolts.

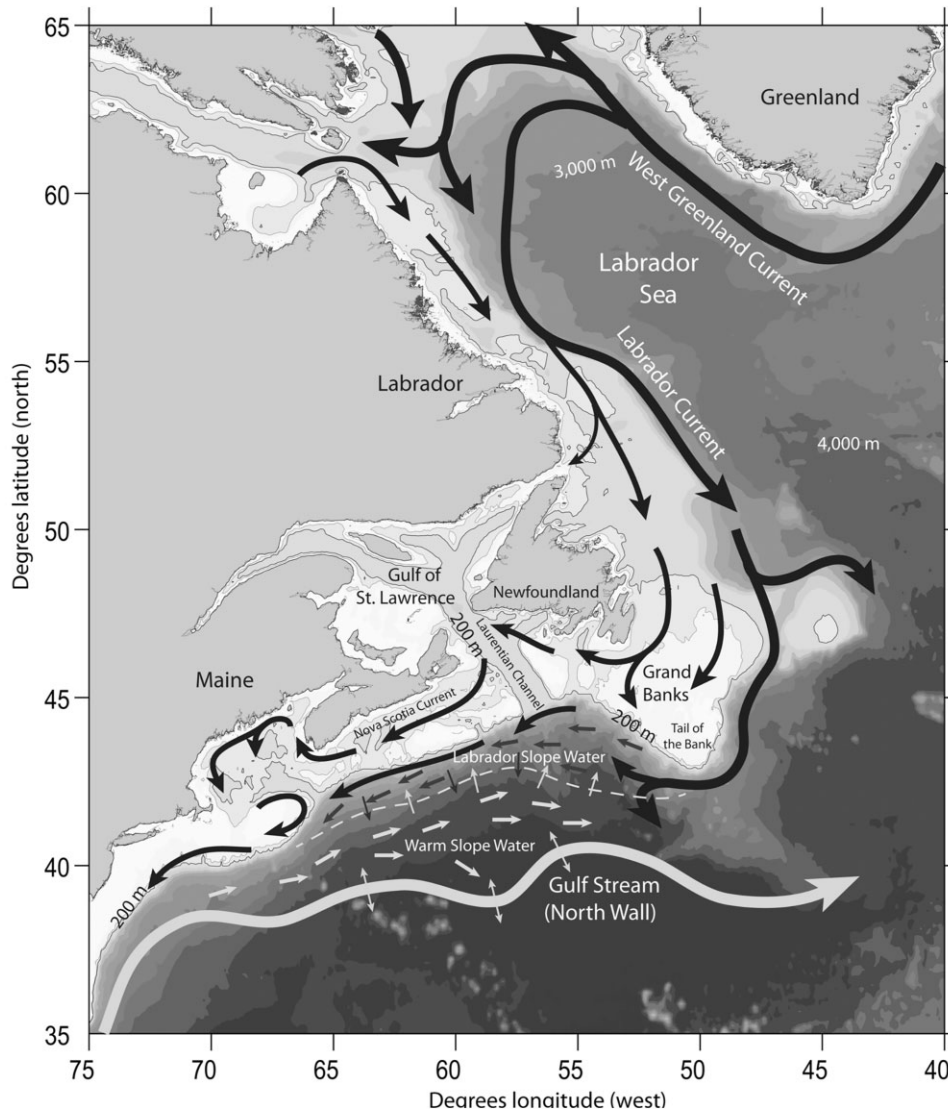
When salmon migrate back to freshwater, they return to natal rivers with astonishing accuracy (Stabell, 1984). It is generally accepted that salmon use sequential imprinting during their seaward migrations to establish homing patterns for their eventual return (Harden Jones, 1968; Jonsson *et al.*, 1990). Salmon’s homeward migration is thought of in two phases: (1) at sea and (2) near and within rivers (Stabell, 1984). In the second navigational phase, salmon navigate pri-

marily based on olfactory signatures that are imprinted during river egress as young smolts (Stabell, 1984; Jonsson *et al.*, 1990). Hatchery-reared, smolt-released salmon will return to the rivers in which they were released—not the river from which they genetically originated (Jonsson *et al.*, 1990). Spawning site fidelity strengthens local adaptations to river habitats. However, genetic diversity within riverine metapopulations is bolstered when a few returning smolts stray to rivers other than their origin (Rieman and Dunham, 2000).

Unlike Pacific salmon species, which spawn just once before dying, Atlantic salmon are iteroparous, meaning they can spawn multiple times in their life. After first spawning, either in the fall or the following spring, salmon that have survived return to the sea to recover their energy reserves. Some salmon return to spawn the following year (consecutive spawners), while others spend more than one year feeding at sea before returning (alternate spawners; Klemetsen *et al.*, 2003). Since 1970, repeat spawners have represented just over 1% (on average) of the US adult salmon returns (Maynard *et al.*, 2018). The low numbers of repeat spawners are thought to be attributed to low marine survival and dams, which limit migration and cause mortality in some rivers (Maynard *et al.*, 2018; April *et al.*, 2021). Females generally comprise a greater proportion of repeat spawners than males (Mills, 1989; Hubley and Gibson, 2011).

### Paper objective

Our goal was to characterize the US GOM DPS Atlantic salmon habitat across its full range, from headwaters in Maine to the coast of Greenland, and assess the influence of projected habitat conditions on the population’s productivity and persistence over the next century. Well-documented declines in salmon’s range and survival are linked to habitat changes,



**Figure 3.** Map of the Northwest Atlantic with major surface (black arrows) and subsurface (grey arrows) circulation features. Warmer waters are coloured light grey, and colder waters are coloured black. The general mixing region between subsurface waters (Labrador Slope Water and Warm Slope Water) is indicated by the dashed line (Figure 3 from Townsend *et al.* (2015)).

both anthropogenic and natural, and future changes are expected to continue to alter habitat and impact salmon in potentially novel ways. In this paper, we document habitat conditions Atlantic salmon need during different life stages and characterize how those conditions may change over the next century based on a literature synthesis, output from climate models, and expert opinion. We also consulted with leaders in relevant fields of hydrology, geomorphology, climate science, oceanography, and Atlantic salmon ecology. Where available, life stage-specific preferences and tolerances are compared with habitat projections to make inferences about future productivity and persistence. Our basis of assessing future scenarios entailed using outputs from an ensemble of climate models run under “stabilization” (RCP 4.5) and “business as usual” (RCP 8.5) carbon concentration scenarios in the Coupled Model Intercomparison Project Phase 5 (CMIP5).

For this review, we make general statements about regional physical dynamics. It is important to understand that many variables, for example, streamflow and temperature, may vary considerably both between watersheds and within a watershed.

### Freshwater phase

Atlantic salmon pass through sensitive early life stages in freshwater, wherein they require life stage-specific habitats. We focus on two major freshwater habitat variables, streamflow and temperature, that influence productivity at multiple freshwater life stages. Past changes and future projections of streamflow and temperature are more widely studied and readily available than other freshwater habitat variables, such as streambed features, dams, water chemistry, and forestation. While the influence of dams on riverine connectivity has been well studied (Magilligan *et al.*, 2016; Bellmore *et al.*, 2017),

and river dams are ubiquitous throughout the Northeast US, the number of dams removed thus far is small compared to how many remain. It is reasonable to assume that dams and other barriers will continue to substantially impact habitat connectivity over the time frame we consider in this paper.

## Streamflow

Streamflow is a major component of Atlantic salmon freshwater habitat, which affects salmon directly and indirectly throughout their freshwater life stages (Table 1). Flow magnitude, sources, and hydraulics influence streambed habitat characteristics (e.g. streambed sediment mobility that impacts redd building and cold-water refugia for parr), oxygenation for developing eggs, and river temperature.

Total streamflow consists of two major components: baseflow and stormflow (Smakhtin, 2001). Baseflow comes from wetlands, lakes, and groundwater. These hydrologic storage basins temporarily hold precipitation from snowmelt and rainfall events and slowly release it to streams (Hodgkins and Dudley, 2011). During summer, groundwater-derived baseflow is generally colder than surface water, and therefore baseflow moderates warming. Stormflow is water that reaches a stream rapidly during and shortly after a precipitation or snowmelt event (Smakhtin, 2001; Hodgkins and Dudley, 2011). Stormflow includes shallow subsurface flow generated by infiltrated precipitation and overland flow that occurs when falling precipitation exceeds the soil infiltration rate or saturates the soil completely (Dingman, 1994). Baseflow is most represented by freshwater climate projections and is generally the more critical component to salmon life history. As such, this paper generally focuses on baseflow.

The baseflow component of total streamflow is particularly important to salmon during the summer season, when water temperatures warm and relatively cool baseflow provides thermal refugia during peak temperatures (Kurylyk *et al.*, 2015; Lombard *et al.*, 2021). Generally, summer baseflow is negatively correlated with stream temperatures because it is supplied by groundwater and is thus cooler than stormflow that is in contact with seasonally warm air and the land surface. This relationship is contingent on other factors such as land use and land cover (e.g. agriculture and forest cover), dams, and the origin and relative temperature of the baseflow. For example, a river's baseflow may have a large component that is generated from shallow lakes or reservoirs that have seasonally warm water or receive warm stormflow from urban or agricultural areas.

Streamflow in Maine rivers typically peaks during the spring season, when snowpack melts, water tables and soil moisture are high, and precipitation increasingly falls as rain. Streamflow during this period consists of a greater ratio of stormflow to baseflow relative to the other seasons. Through the summer and into early fall, evapotranspiration increases, driving low streamflow that is often primarily composed of storage discharge from riparian aquifers, lakes, wetlands, and dam impoundments (Dudley *et al.*, 2020). Moving into late fall, evapotranspiration declines with cooling temperatures and plant senescence, and streamflow increases from the minima of late summer and early fall. High streamflow can occur during the winter if temperatures warm, causing snow to melt and precipitation to fall as rain as during the spring. In the absence of snow cover, high streamflow can also be generated

in the winter and early spring by rain falling on frozen or saturated soil (Collins *et al.*, 2014).

## Present streamflow conditions

Since the mid-20th century, the northeastern US has experienced generally increasing annual streamflow with some season- and region-specific differences. Across the GOM DPS, winter and fall baseflow and stormflow increased from 1980 through 2010 (Ficklin *et al.*, 2016), whereas summer baseflows decreased (Hodgkins and Dudley, 2011). Annual 7-d low flows increased across New England but not in eastern Maine (Dudley *et al.*, 2020).

Streamflow seasonality also shifted over the last century. With annual warming trends in air temperature, the timing of spring warming on land advanced (Ellwood *et al.*, 2013). Earlier warming air temperatures cause earlier snowmelt runoff, a major seasonal contribution to streamflow that causes earlier winter-spring streamflow maxima throughout New England (Hodgkins and Dudley, 2006; Dudley *et al.*, 2017; Dupigny-Giroux *et al.*, 2018). Earlier winter-spring high streamflow could cause streambed scour that decreases the survival of eggs and sensitive early life stages present at that time of year (Figure 4; Goode *et al.*, 2013). The incidence of high flow events during the warm season (June–October) since the late 20th century (Frei *et al.*, 2015; Collins, 2019) has also increased.

## Future streamflow projections

Demaria *et al.* (2016a) modelled Northeast streamflow conditions under the RCP 4.5 and RCP 8.5 scenarios and concluded that winter streamflow will increase and spring streamflow will decrease, while summer and fall streamflow will not change. Precipitation in the form of rainfall is expected to increase across the Northeast US through the late 21st century (Thibeault and Seth, 2014). Lynch and Thibeault (2016) predicted that precipitation increases would be greatest during the late winter and early spring. Summer precipitation may also increase (by about 10%), but predictions are less confident (Easterling *et al.*, 2017). Increased spring and summer rainfall could partially compensate for the effects of warming air temperatures and increased evapotranspiration on groundwater reserves and baseflow. Since groundwater baseflow is essential to thermal refugia during peak summer temperatures, future changes in rainfall and evapotranspiration could be particularly important to salmon.

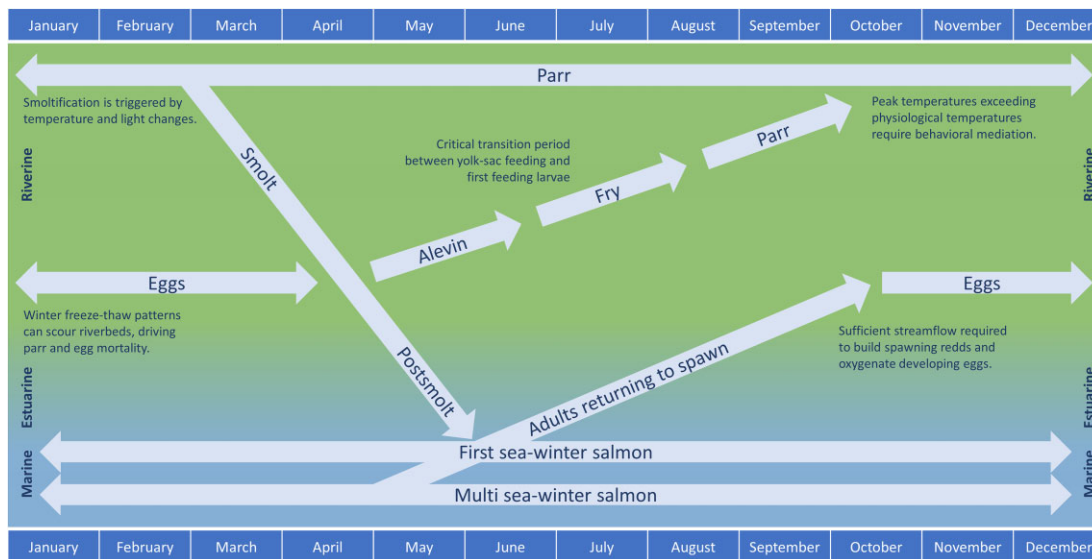
At the individual basin level, predictions for eastern Maine were more ambiguous. At one station, high-flow events—driven largely by stormflow—were expected to rise insignificantly, whereas other nearby stations showed non-significant and significant decreases (Figure 5 in Demaria *et al.*, 2016a). Meanwhile, low-flow—driven by decreased stormflow and baseflow—events show insignificant decreases. Insignificant increases in mean annual baseflows are expected across all Maine stations.

## Potential impacts of streamflow changes

Streamflow affects every aspect of salmon's freshwater life history; we cannot cover every streamflow impact in this paper. This paper focuses on areas that are well covered in the literature and where future impacts can be reasonably foreseen—despite still being uncertain. While most hydrological literature discusses streamflow in annual terms, we need to consider seasonal differences as they pertain to Atlantic salmon's

**Table 1.** Freshwater habitat variables with life stage-specific salmon tolerances, present conditions, future habitat projections, and estimated impacts to salmon productivity and persistence.

		21st century projected change (CMIP5)	Life stage	Salmon tolerances and/or needs	Potential impacts to salmon
Freshwater	Streamflow	<b>Baseflow</b> (Demaria <i>et al.</i> , 2016a): Increasing in winter Decreasing in spring Summer, fall unchanged  <b>Other factors:</b> Earlier spring flow (Demaria <i>et al.</i> , 2016b)  <i>low confidence—wide range of possible outcomes</i>	Egg	Sufficient streamflow to oxygenate water	Reduced survival
			Parr	Prefer 0.6–0.9 m/s stream velocity during high T events	Potentially reduced cold-water refugia and increased aggregating behaviour in summer when refugia is most scarce, especially for older parr with lower thermal tolerance
			Smolt	Spring streamflow cues smoltification	Earlier smoltification
	Temperature	<b>Magnitude:</b> Average warming Hotter peak temperatures  <b>Seasonality:</b> Earlier winter-spring warming Later fall cooling  <i>medium/high confidence</i>	Spawning Adult	Sufficient streamflow to move sediment and build redds	Fall streamflow is not expected to change.
			Egg	0–16°C (Elliott, and Elliott, 2010)	Warmer peak temperatures and later fall cooling could be thermally stressful for developing eggs
			Alevin	0–25°C (Elliott and Elliott 2010)	Metabolic stress could cause a smaller body size, lower fitness, lower survival, and lower fecundity
	Parr	0–28°C (Elliott and Elliott 2010) 14– 27.5°C for 2+ parr (Wilbur <i>et al.</i> , 2020)			

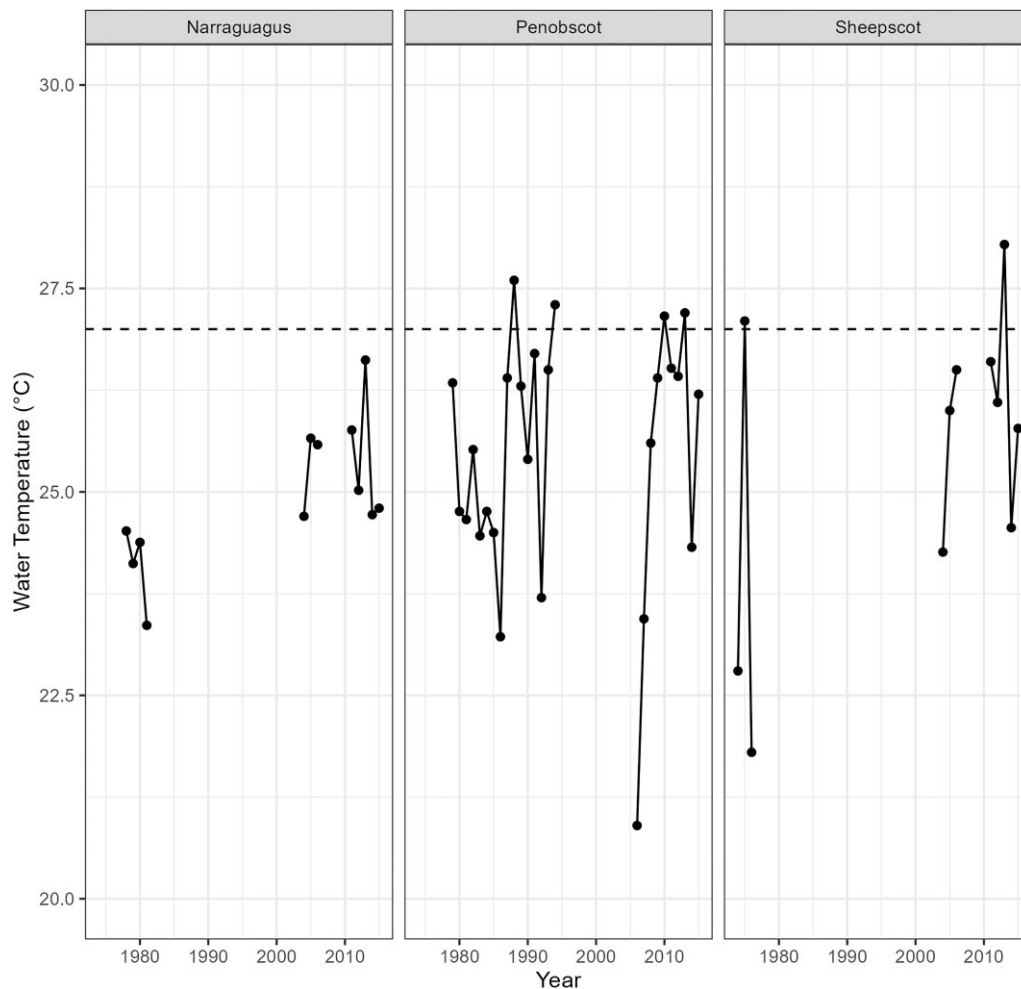


**Figure 4.** Visual summary of major physiological and habitat changes through the Atlantic salmon life history.

life history. Streamflow changes are most likely to occur in the winter and spring and less likely to occur in the summer and fall.

Baseflow provides critical thermal refugia to older parr (2+ years) and adults during peak summer warming and will

become increasingly critical to parr and adults with projected freshwater warming (section “Temperature”). In the fall, total streamflow is important to spawning adults as they build redds to lay eggs because redd placement is a function of stream depth and velocity in relation to appropriate spawning



**Figure 5.** Peak annual 5-d mean water temperatures from USGS stream gauges in 3 Maine rivers from 1970 to 2018 USGS gauge numbers are as follows: Narraguagus = 01022500, Penobscot = 01036390, and Sheepscot = 01038000. Dashed horizontal line drawn at 27°C, the point at which parr exhibit aggregating behaviour in cool water refugia.

substrate that optimizes egg survival (Beland *et al.*, 1982). And for eggs, streamflow is important for oxygen saturation during the late fall through spring hatching. Further, streamflow affects streambed morphology and, subsequently, predation refugia and the ability to build redds. In spring, changes to the timing of seasonal snowmelt may affect the timing and frequency of ice scour events. Table 1 summarizes factors driving streamflow and projections for how streamflow will change over the next 75 years.

Projected increases to winter average daily streamflow magnitudes are not expected to negatively affect oxygenation for developing eggs but may impact overall redd stability due to streambed scour (section “Ice”). If, as predicted, summer average daily streamflow remains relatively unchanged and river temperatures continue to warm, parr—particularly older parr—will increase their dependency on cool baseflow input for thermal refuge. Furthermore, warmer ambient temperatures will dilute the thermal gradient afforded by cooler baseflow, thereby reducing effective refugia.

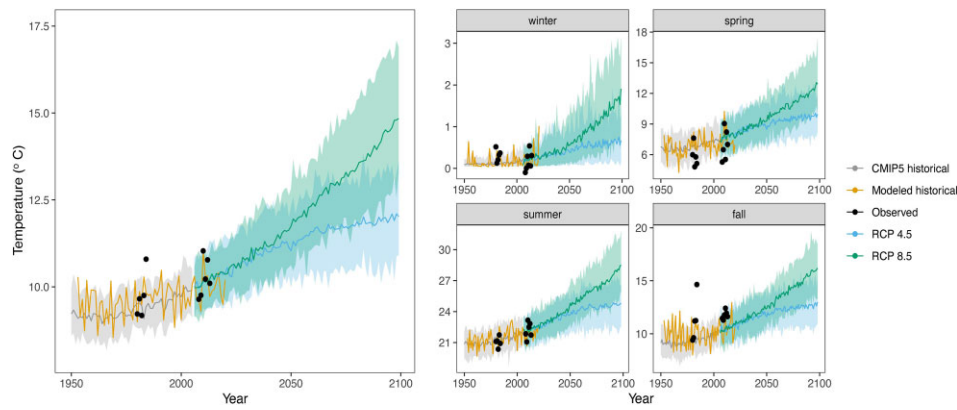
Perhaps most important to salmon, the frequency of low-magnitude floods in New England increased throughout the 20th century and into the 21st century (Armstrong *et al.*, 2012) and is projected to continue increasing (Demaria *et al.* 2016a). Low-magnitude flooding events affect channel

morphology and sediment transport, which in turn impact salmon’s streambed habitat in terms of riverbed mobility and refugia from predation and extreme temperatures. These smaller flooding events have become more frequent, particularly during the warm season (June–October) (Collins, 2019). Changes in streamflow could affect upstream migrations in unpredictable ways, as streamflow during October has been directly linked to salmon’s ability to access headwaters for spawning (Cunjak *et al.*, 2013).

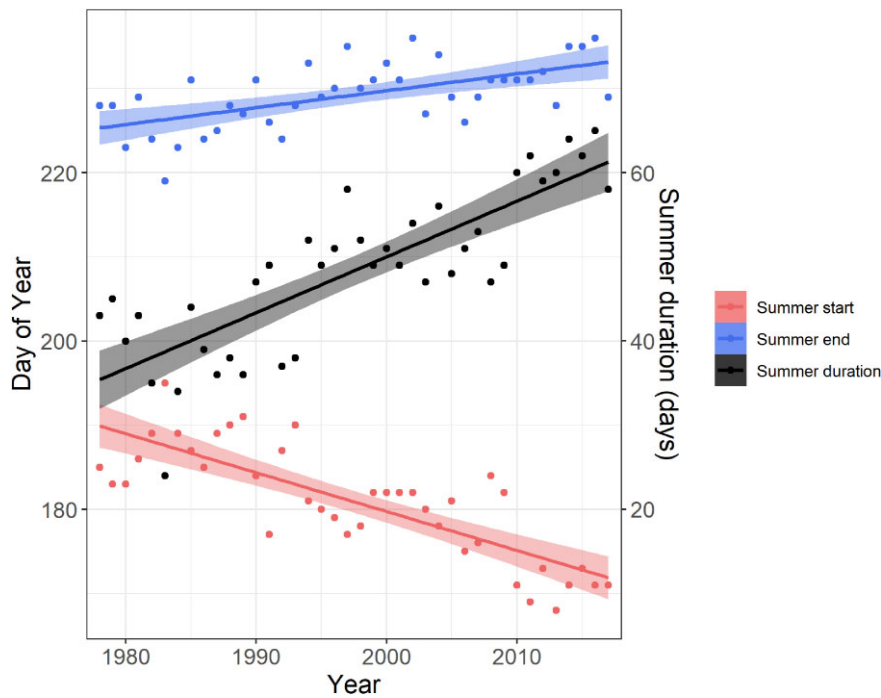
### Temperature

Atlantic salmon, like all fish, have a range of tolerable temperatures but perform best within a preferred temperature range (Pörtner and Knust, 2007). Suboptimal temperatures generate stress and draw metabolic energy from other functions such as growth and reproduction (Sibly and Atkinson, 1994), while beyond certain thresholds, ambient temperatures can become lethal.

River temperatures are influenced by air temperature, solar irradiation, riparian shading, groundwater inflow, and anthropogenic factors including impoundments, impervious cover, and withdrawals/releases (Erickson and Stefan, 2000; Tague *et al.*, 2007; Kaushal *et al.*, 2010; Hodgkins and Dudley, 2011). During summer, an influx of cool groundwater bal-



**Figure 6.** Yearly and seasonally averaged observed Penobscot River (USGS 01036390) temperature (black dots) and modelled river temperature (coloured lines and shaded region) under the CMIP5 “stabilization” (RCP 4.5) and “business as usual” (RCP 8.5) carbon concentration scenarios from 1950 to 2100. The solid lines represent the mean values, and the shaded region indicates the range of the 5th and 95th percentiles for each year. Note the variable y axis scales across all graphs.



**Figure 7.** Temperature seasonality (1978–2017) of the Penobscot River, Maine, as estimated from the USGS gauge (01036390). Metrics include the onset of summer (summer start), the end of summer (summer end), and the duration between the two (summer duration). Summer start and end (on the left y-axis) are defined as the first and last days of the year on which a threshold of 0.5°C below the maximum summer temperature observed was held or exceeded for 8 consecutive days. Summer duration (right y-axis) is the difference between the days of the year associated with summer start and end (Thomas *et al.*, 2017).

ances warming stream temperatures. Localized groundwater discharge locations generate thermal refugia, which can be a particularly important factor during the summer months (Danie *et al.*, 1984; Hodgkins and Dudley, 2011; Lombard *et al.*, 2021).

When temperatures exceed the tolerable range, salmon alter behaviour to mitigate exposure. As with many fish species, salmon thermal tolerances also change with age (Portner and Farrell, 2008; Elliott and Elliott, 2010). In a laboratory study, older parr reached maximum basal (resting) metabolic rates at 24°C; warmer temperatures generated anaerobic metabolism, indicating physiological stress (Breau *et al.*, 2011). Conversely, young parr did not exhibit anaerobic metabolism at the high-

est temperature evaluated (28°C). These age-related metabolic differences drive differences in behaviour. Juvenile salmon are known to deviate from normal territorial behaviour to live in dense aggregations during peak summer temperatures, when suitable thermal habitat is scarce. Parr in a tributary of the Miramichi River (New Brunswick, Canada) have been shown to aggregate in cold water refugia when ambient river temperatures exceed 27°C (Wilbur *et al.*, 2020). Young parr (0+ years) in the Miramichi River tolerate a wide range of temperatures and do not aggregate in cold water refuges (Breau *et al.*, 2007). Adult salmon also thermoregulate by moving to cooler, deeper waters and aggregating in thermal refugia at a lower threshold (17–19°C) than parr (Frechette *et al.*, 2018).



Unusually warm riverine temperatures also have population-level impacts on salmon. Egg incubation temperatures can affect adult migration timing through phenotypic plasticity. Salmon eggs reared in temperatures 3°C warmer than normal produced adults that migrated back to Norwegian rivers from feeding grounds in the North Atlantic two weeks later (Jonsson and Jonsson, 2018). This suggests that salmon may have pathways to adjust for overall warming patterns, but this highlights the potential risk of disparate rates of warming between freshwater and marine habitats. Spawning females exposed to elevated summer temperatures produced smaller eggs of lesser quality and subsequently reduced survival (King *et al.*, 2003). Additionally, females exposed to unseasonably warm temperatures during the fall took much longer to ovulate—if at all—and their eggs exhibited much lower survival (Taranger and Hansen, 1993).

Temperature may also affect critical physiological adaptations for moving between fresh and saline waters. During smoltification, gills increase osmoregulatory function to tolerate saline waters, and this function declines towards the end of the seaward migratory period if salmon have not already exited freshwater. McCormick *et al.* (1999) found that in rivers in the southern part of the range, like the Penobscot River, warm temperatures exacerbate the metabolic costs of ocean adaptation, resulting in decreased salinity tolerance for late migrants. This decrease in salinity tolerance occurs earlier in warm years (McCormick *et al.*, 1999). Decreased osmoregulatory function in late seaward migrants can subsequently reduce marine survival (McCormick *et al.*, 2009a).

### Historical to present river temperatures

Stream temperatures above freezing are generally modelled well with a simple linear relationship to air temperature (Pilgrim *et al.*, 1998; Mohseni and Stefan, 1999; Erickson and Stefan, ; Morrill *et al.*, 2005), though this relationship may be complicated by local and regional influences of land use, dams, forest cover, and agriculture (Rice and Jastram, 2015). In the Northeast US, land cover and land use changed considerably with European settlement and have varied since that time (Irland, 1998; Foster and Hayden, 2004; Thompson *et al.*, 2013). Regardless, river and stream temperatures have warmed in recent decades, and the warming is correlated with warming air temperatures (Kaushal *et al.*, 2010). Although available river temperature records in Maine streams are too short and sporadic to quantitatively evaluate trends in peak annual 5-d mean river temperatures, the available data from US Geological Survey (USGS) gauges do show exceedances of the 27°C threshold that is important for salmon (Figure 5). It is important to note that the location of gauges along the river with respect to dams, lakes, shade, and land use may influence the temperature measurements.

### Future river temperature projections

Stream and air temperatures collected at a site on the Penobscot River (USGS 01036390) were modelled using a generalized additive model ( $R^2 = 0.883$ ). The model was projected forward to 2100 using air temperature outputs from an ensemble of climate models run under “stabilization” (RCP 4.5) and “business as usual” (RCP 8.5) carbon concentration scenarios in the CMIP5. Annual mean temperatures in the Penobscot River are expected to warm an additional 2–4°C by 2100 (Figure 6). Perhaps more critical to salmon, summer temperatures are expected to warm by about 3–7°C under RCP

4.5 and 8.5, respectively, a disproportionately greater amount than other seasons.

Along with this continued warming, the Northeast US is projected to experience earlier snowmelt runoff, increases in evaporation, increased low flow magnitude, and no significant changes to summer baseflow in the future (Demaria *et al.*, 2016a; Easterling *et al.*, 2017). The exact combined impact of these projections with reference to salmon is difficult to parse, but the general pattern points towards declining habitat conditions. With rising temperatures, the magnitude and relative temperature of baseflow during peak summer temperatures may have significant ramifications for salmon.

The Penobscot River station USGS 01036390 is not representative of all rivers in Maine, especially since it is near the outlet to Penobscot Bay and represents an integration of factors affecting temperature over Maine’s largest watershed—including proximal suburban development and upstream impoundments. Smaller rivers within the GOM DPS, especially those in relatively underdeveloped watersheds that also have frequent contact with sand and gravel aquifers that contribute cooler baseflow, could potentially experience more moderate warming than the Penobscot River (Lombard *et al.*, 2021). Nonetheless, the Penobscot River supports the most substantial Atlantic salmon stock and is therefore an important consideration in the future of salmon in Maine.

Given the generally linear relationship between air temperature and river temperature, observed changes in air temperature seasonality (Ellwood *et al.*, 2013) will influence stream temperatures into the future. This is evidenced by the temperature seasonality from the Penobscot River USGS gauge (Figure 7). From 1978 to 2017, summer onset (as defined in Thomas *et al.*, 2017) shifted earlier by nearly 20 d, and fall onset shifted slightly later, but increases in summer duration were largely driven by spring onset. Spring warming is expected to continue shifting earlier while fall cooling arrives later (Dupigny-Giroux *et al.*, 2018). Across the Northeast US, the duration of annual below-freezing temperatures is expected to shrink by 6–18 d in the next 50 years (Dupigny-Giroux *et al.*, 2018). Indeed, there has been a decline in the duration of ice in New England rivers since the mid-1800s (Dudley *et al.*, 2017). Given projected warming, ice duration will continue to decline during the 21st century.

### Potential impacts of temperature changes

Warming river temperatures are consequential throughout every life stage salmon undergo in freshwater. Given the overwhelming complexity of the influence of temperature on salmon freshwater productivity, we have not addressed all the possible interactions but instead have focused on the aspects that are most confidently predictable and impactful to salmon.

With warming summer temperatures, greater areas of river habitat supporting US-origin salmon will reach temperatures above 27°C, the threshold for behavioural changes in parr. Cold-water refugia during the summer season may become increasingly critical, particularly for older parr, which have a narrower range of thermal tolerance (Table 1). The temperature of cold-water refugia will likely warm with rising air and river temperatures, even if baseflow remains unchanged. Given that salmon do not exhibit physiological adaptation for upper thermal limits (Elliott and Elliott, 2010), we can expect to see the salmon’s southern range shift northward with further warming in the region. There are examples in the literature of warming temperatures benefitting some salmon popu-

lations through faster early life growth rates and better recruitment (Hedger *et al.*, 2013). However, the impacts are overwhelmingly negative, particularly for stocks at the southern extent of the range, where warm temperatures approach the salmon's upper thermal limit.

Conditions that cause delays to migration such as dams, low streamflow, and low oxygen zones will also be more impactful to salmon when smolt windows shorten (McCormick *et al.*, 1999). Across fish species, thermal stress increases metabolic costs, resulting in a variety of impacts, including smaller adult body sizes and reduced fecundity, recruitment, and survivorship (Sibly and Atkinson, 1994; Pörtner *et al.*, 2001; Pörtner and Peck, 2010). Additionally, smaller fish are less metabolically efficient at osmoregulation due to having greater surface-to-volume ratios (Hoar, 1976). With rising temperatures, we expect compounding effects of temperature and osmoregulation on body size, survival, and productivity. Warm rearing temperatures in rivers have also been linked to reduced marine survival in salmon (McCormick *et al.*, 2009a), supporting the idea that thermal impacts in freshwater will manifest later during their marine phase.

Changes in temperature seasonality may also affect transitional periods. For example, spawning is timed to occur after temperatures begin to cool in the fall so that eggs will not be subjected to temperatures above the 16°C lethal limit (Table 1). Therefore, later fall cooling could cause greater egg mortality. Eggs also develop more quickly in warmer temperatures. A warmer winter season could result in earlier hatching, which could subsequently drive a mismatch with prey for first-feeding larvae (Leggett and DeBlois, 1994).

### Other habitat variables

There are several factors other than streamflow and stream temperature that shape Atlantic salmon freshwater habitat quality (Kircheis and Liebich, 2005; Snyder *et al.*, 2009; Wilkins and Snyder, 2011; Wilbur *et al.*, 2020). Here we briefly review a few of these factors, including riverbed morphology, ice cover, and water chemistry. We have a less clear grasp of how these factors will change in the future, though morphology and ice cover are tied to changes in temperature and streamflow. Other factors that are less understood or supported in the literature are not included here (e.g. woody debris).

### Riverbed morphology

Salmon have life stage-specific riverbed requirements. Throughout the year, parr need rocky bottoms with access to interstitial spaces to hide from predators and escape extreme temperatures. In autumn, spawning adults need a mobile streambed to build redds. Each of these needs is partially affected by streamflow.

In some places, riverbeds can become “embedded” with sediment that fills the spaces between rocks, limiting places for parr to hide. The amount of sediment washing into streams is often constrained upland and riparian zone land cover. With the reforestation of Maine since the mid-20th century (Irland, 1998), embeddedness is assumed to be less of a concern today. Furthermore, upstream lakes or wetlands, which are common in glaciated watersheds like those in Maine, are effective sediment traps, reducing the risk of the riverbed downstream becoming embedded. Lake and wetland sediment storage is one of the reasons Northeast US watersheds

have very low sediment yields when compared to other regions of the world (Milliman and Syvitski, 1992; Milliman and Farnsworth, 2011).

Low-gradient rivers like those that are characteristic of the glaciated watersheds of eastern Maine often have insufficient energy to mobilize the bed for salmon to build redds for spawning (Snyder *et al.*, 2013). An immobile riverbed is considered “armored” to change. Armouring results not only from the low energy hydraulics but also because the finer sediments the flow can transport have already been mobilized and the resupply from upstream is low because of lake and wetland storage. Thus, only coarse sediments remain that require greater energy to move. Future changes in average daily streamflow are not expected to occur in the fall season (see 2.1 Streamflow) when salmon are building redds, nor would they likely be large enough to mobilize armoured beds where they occur. However, an increased frequency of small floods, as documented in the region historically and projected for the future, especially if they occur in the warm season, may improve conditions for building redds (Armstrong *et al.*, 2012; Demaria *et al.*, 2016a; Collins, 2019). For similar reasons, embeddedness is unlikely to become an issue unless land use radically changes.

### Ice

Extent of ice cover and volume affects certain freshwater life stages, primarily as it reduces available habitat and alters behaviour. Parr are relatively inactive during winter ice periods, when habitat is reduced (Breau *et al.*, 2011; Cunjak *et al.*, 2011; Linnansaari and Cunjak, 2013). When temperatures are very cold, subsurface ice can extend all the way to the streambed, effectively cutting off portions of habitat (Linnansaari *et al.*, 2009). Juvenile survival (from egg through age 2+ parr) is greatest when streamflow remains high in winter and ice does not reduce habitat accessibility (Cunjak *et al.*, 2011). In winters with mid-winter rain-on-snow events, ice breaks apart, which may cause severe scouring to the riverbeds, disturbing nests and parr habitat. Years with mid-winter ice breakups have dramatically reduced juvenile survival to the following summer (Cunjak *et al.*, 2011).

In the last 150 years, ice duration in New England rivers and lakes has declined (Dudley *et al.*, 2010). Robust projections for future warming indicate that the extent and duration of ice cover will continue to decline. Although salmon may have increased habitat availability during the winter season, more mid-winter rain and ice breakup events (Demaria *et al.*, 2016b) could lead to reduced survival of early life stages (0–2+ years) and disturbed redds due to streambed scour.

### Water chemistry and pollution

Water chemistry—particularly dissolved oxygen and acidity—is also a concern in some GOM DPS rivers. While salmon are resistant to low pH, dissolved inorganic aluminium becomes mobilized in acidic environments and blocks gill membranes that are necessary for osmoregulation (Haines, 1981; Liebich *et al.*, 2011). Smolts are considered the life stage most vulnerable to these impacts (Dill *et al.*, 2002). In rivers with sufficient dissolved organic carbon (DOC), the pH threshold for mobilizing aluminium is greater. Salmon exhibit reduced physiological fitness and increased mortality in acidic rivers with low DOC (McCormick *et al.*, 2009b; Liebich *et al.*, 2011). Most Maine rivers tend to have high DOC concentrations and are therefore less likely to contain free aluminium to interfere

with osmoregulation. Furthermore, Maine rivers experience episodic dips in pH rather than chronically low pH, as occurs in salmon rivers of Nova Scotia and Norway (Dill *et al.*, 2002).

### Summary of combined freshwater impacts

While we have described major freshwater habitat variables individually, future impacts to salmon due to a changing climate will be synergistic. Combined changes in streamflow, temperature, and secondary factors will individually and simultaneously affect salmon. This is complicated by the relative confidence with which we can predict future changes in each freshwater factor. Projections provide high certainty that temperatures will continue to warm and that warming will be greatest during the spring and summer seasons. Warming impacts may be mediated by thermal refugia availability, which is largely controlled by baseflow, which is also expected to warm (Kurylyk *et al.*, 2014; Menberg *et al.*, 2014; Pitz, 2016). Baseflow predictions rely on changes in precipitation and evaporation, among other regional and local variables, and as such are less certain. Generally, we expect that baseflow during the summer, when thermal refugia are most critical, will remain unchanged. However, static summer baseflow concurrent with warming temperatures will likely mean less thermal refugia available to meet increasing needs to escape lethal temperatures. Conversely, winter baseflow is expected to increase as more precipitation falls as rain rather than snow. With warming temperatures, mid-winter ice breakups could also become more common and more severe, subsequently driving reduced survival.

There are also combined factors that we cannot fully characterize in this paper. For example, changing temperature and streamflow could alter salmon phenology, which in turn could affect out migration. Smoltification is cued by several seasonal changes in the environment, including temperature, streamflow, and photoperiod. Indeed, changing migration phenology in response to streamflow and temperature has already been observed in salmon populations throughout the North Atlantic Ocean (Otero *et al.*, 2013). Changing environmental conditions may also result in physiological, morphometric, and behavioural changes that could negatively impact the smoltification process, resulting in increased mortality during this critical transition period (McCormick *et al.*, 1999) or later in the estuarine and marine environments (McCormick *et al.*, 2009a). Additionally, barriers to migration (e.g. dams, temperature, and low oxygen zones) may exacerbate all the above by slowing or stopping migration, preventing smolts from exiting before reverting to pre-smolt condition, making them incapable of transitioning to life in the ocean. The synthesis presented above characterizes average regional dynamics that affect salmon populations, but local factors may cause significant differences between and within watersheds.

### Estuarine

Estuaries are widely considered important ecological areas (Summers *et al.*, 1995). While estuaries provide critical habitat for many fish species, US Atlantic salmon spend relatively little time in this environment while migrating between their freshwater and marine habitats (Kocik *et al.*, 2009). As such, research on Atlantic salmon in the estuarine environment is limited (Hodgson *et al.*, 2020). However, estuaries represent a

major transition period for smolts, where they interact with a new array of biotic (prey and predators) and abiotic (salinity and temperature) factors that are expected to change over the next century.

### Biotic factors

The freshwater to seawater transition that out-migrating salmon smolts experience is known to be a physiologically taxing experience that, coupled with migration through a funneling estuarine environment and exposure to a novel suite of predators, may result in significant levels of predation within a small spatial and temporal window. Some predator species are encountered annually, whereas others vary interannually. As temperatures continue to warm, fish distributions will continue to shift northward (Nye *et al.*, 2009), bringing a variety of new potential smolt predators into the GOM (Friedland *et al.*, 2012; Kleisner *et al.*, 2017; Allyn *et al.*, 2020).

Changes in migration duration and predation dynamics may negatively impact estuarine survival in the future. Striped bass are known to prey on salmon smolts with varying consistency (Blackwell and Juanes, 1998; Beland *et al.*, 2001), and striped bass predation rates within a Canadian estuary were shown to be variable between years (Daniels *et al.*, 2018). The same Canadian estuary contains a recovering striped bass population, raising concerns about increasing predation impacts in the future. In the GOM DPS, salmon abundances declined with simultaneous increases in striped bass (Beland *et al.*, 2001). In a river just south of the GOM DPS, nearly half of all striped bass stomach contents contained smolts (Blackwell and Juanes, 1998). However, striped bass abundance within GOM estuaries is highly variable between years and likely not a primary driver of declines (Beland *et al.*, 2001). Avian predation is also a concern. With recent declines in benthic fish species (e.g. flounder and cod) and regional river herring populations (Limburg and Waldman, 2009), double-crested cormorants may be preying on Atlantic salmon smolts with increasing frequency (Blackwell and Krohn, 1997; Hawkes *et al.*, 2013). We do not know the relative impact of estuarine predation on adult return rates, though it is assumed to be much lower than marine mortality rates (April *et al.*, 2021).

In addition to changes in predation, changes to post-smolt prey abundances in estuaries may also be impacted by a changing climate. In the Penobscot Bay, Atlantic herring juveniles and various invertebrates comprise much of the diet of early marine-phase salmon smolts (Renkawitz and Sheehan, 2011). Atlantic herring juveniles are protein- and energy-dense and may be a necessary fuel source for young salmon entering the ocean phase. Changing climate may alter local environments and make them less suitable for species like juvenile herring, thereby eliminating this important prey source.

### Abiotic factors

Estuarine migration timing and success are dependent on several abiotic factors, including salinity, temperature, and streamflow (Thorstad *et al.*, 2012; Stich *et al.*, 2015, 2015ab). While warmer river temperatures and lower streamflow cause earlier migrations, survival to the sea depends heavily on sufficient smolt development (Otero *et al.*, 2013; Stich *et al.*, 2015a). Warming temperatures also shrink the temporal window during which smolt characteristics (e.g. osmoregulation) are maintained for successful marine entry (McCormick *et al.*, 1999). With increasing temperatures, migration timing and

physiological preparedness could potentially shift out of synchrony, causing increased estuarine mortality.

Estuaries are also a gradient between freshwater and marine systems, which experience climate change through disparate drivers and rates of change. Seasonal and annual changes in river temperature are driven primarily by air temperatures, whereas temperatures in the ocean are controlled by a combination of air temperature and ocean circulation. Given the disparate drivers of these two systems, warming rates may be asynchronous—creating a potential mismatch between changing habitat conditions, both seasonally and annually, and resulting in increased mortality for out-migrating smolts. Spring and summer temperatures in rivers are increasing, and the start of summer is shifting earlier (Figure 7), but the start of summer remains variable in the GOM (Thomas *et al.*, 2017; Alexander *et al.*, 2018). This mismatch is likely to increase and affect migration survival, but the interplay of variables is difficult to tease apart and likely variable across rivers and estuaries. The relative impact of warming on earlier smoltification versus the duration over which smolt characteristics are maintained is not fully understood. Southern populations may experience increased estuarine mortality as warming river temperatures drive earlier migrations and shorten smolt windows. There is some evidence that seaward migrations are advancing in response to ambient temperatures, suggesting that salmon may have the capacity to adapt to climate change-induced warming (Otero *et al.*, 2013). However, it is unclear if the rate of adaptation can match the rate of environmental change, considering that river and marine temperatures are likely to diverge even further by the end of this century.

## Marine phase

Despite extensive freshwater restoration efforts, salmon populations continue to decline across much of the species' range, with poor marine survival being a primary driver (April *et al.*, 2021; USASAC, 2021b). Furthermore, while salmon's freshwater phase is heavily documented, the marine phase is relatively understudied. Salmon survival at sea began to decline in the late 1980s, with another downturn in 1997 (Beaugrand and Reid, 2012; Mills *et al.*, 2013). The decline marked a phase-shift in salmon productivity (Chaput *et al.*, 2005), which resulted in lower abundances ever since, particularly of MSW fish (Jonsson and Jonsson, 2004; Chaput and Benoit, 2012). Atlantic salmon harvest (commercial and recreational) in North America has been greatly reduced and yet abundances continue to decline (ICES, 2020).

Continued low abundance is attributed to a variety of mechanisms. Some studies point to temperature and predation as causes for poor marine survival (Friedland *et al.*, 1993; Reddin *et al.*, 2000; Peyronnet *et al.*, 2007). Others suggest basin-wide processes that affect trophic structure and prey energy density (Mills *et al.*, 2013; Renkawitz *et al.*, 2015). Regardless, marine mortality is considered a primary threat to the recovery of the GoM DPS (ICES, 2016; NMFS, 2018).

## Regional oceanography

Salmon's marine range covers a large swath of ocean that is affected by regional circulation patterns (section "Climate variability"; Figures 2 and 3). The primary range of US salmon extends from the GOM up through the Labrador Sea to the coast of Greenland. Along the Greenland coast, the West

Greenland Current carries cool, relatively fresh water west, around southern Greenland, and then follows the Greenland coast north (Figure 3). The West Greenland Current then bifurcates, feeds the subpolar gyre to the north, and turns south to feed the Labrador Current. The Labrador Current carries surface water south, bathing the Grand Banks in relatively cold water before meeting the warm, north wall of the Gulf Stream and continuing down along the continental shelf. Water from the Labrador Current is brought into the GOM in surface currents. The Northwest Atlantic is heavily influenced by the balance between the northward-flowing, warm waters of the Gulf Stream and the equatorward-flowing, cool waters of the Labrador Current (Figure 3).

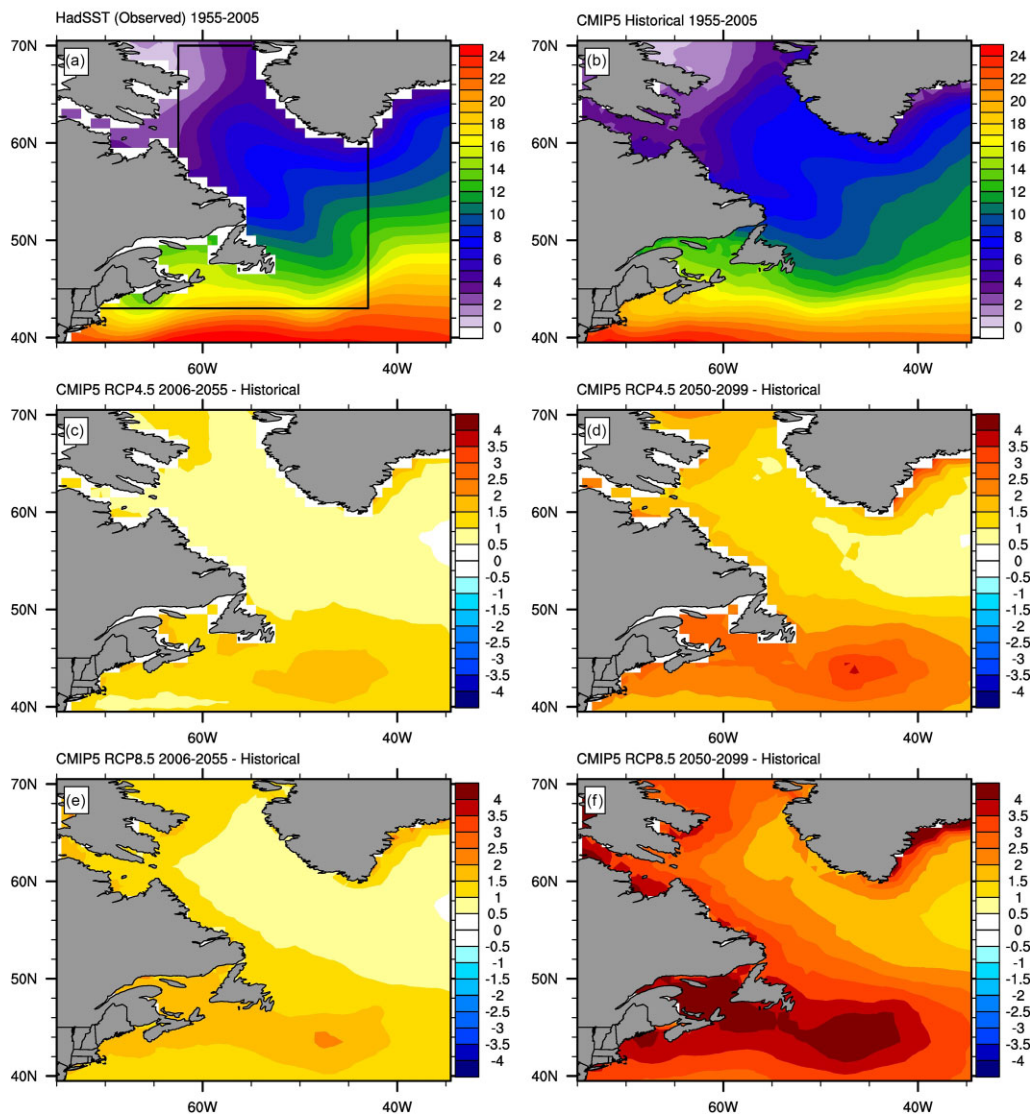
The relative influence of these warm and cool currents drives regional changes in ambient temperatures and is linked to anomalies in the strength of the Atlantic Meridional Overturning Circulation (AMOC) (Gonçalves Neto *et al.*, 2021). While AMOC represents natural oceanographic variability in the region, climate change is pushing conditions beyond those previously observed (Alexander *et al.*, 2020). Since 1982, sea surface temperatures in the Northwest Atlantic have consistently warmed, two-thirds of which are attributed to natural climate variability and the rest to anthropogenic forcing (Chen *et al.*, 2020). There is significant regional variation in warming rates. The shelf waters of the Labrador Sea region warmed at 0.25°C per decade, while the interior Labrador Sea and Greenland coast warmed at 0.5°C per decade (Chen *et al.*, 2020). Meanwhile, the GOM and portions of the Grand Banks have warmed by 0.5–0.75°C per decade.

The exchange of waters with different properties (temperature, salinity, and nutrients) drives regional productivity (Greene and Pershing, 2007; Townsend *et al.*, 2015). General circulation patterns and deviations associated with climate variability and change affect abiotic habitat conditions (e.g. temperature, salinity, and nutrients), which in turn affect productivity and upper trophic level animals, including salmon (Mills *et al.*, 2013).

## Climate variability

Currents and regional circulation are modified by climate variability operating on varying spatiotemporal scales, ultimately impacting basin-wide ecosystem productivity, including salmon. As such, it is potentially helpful to consider how intrinsic variability can alter circulation in the Northwest Atlantic when considering salmon's fate.

The North Atlantic Oscillation (NAO) is the difference in sea-level atmospheric pressure between the Arctic and subtropical Atlantic (Hurrell *et al.*, 2003; Stephenson *et al.*, 2003). The pressure difference is most pronounced during the winter, and therefore the wintertime index is most often used. Changes in the NAO create temperature anomalies in the Labrador Sea, which then propagate along the continental shelf and slope regions, generating a lagged signal in the GOM (Greene *et al.*, 2013). GOM surface temperatures are negatively correlated with the NAO at a 4-year lag (Xu *et al.*, 2015). The NAO is positively correlated with adult salmon mortality in the second year after spawning, but the mechanisms are unclear (Hubley and Gibson, 2011). Positive phases of the NAO are linked with declining zooplankton and forage fish productivity in the eastern Atlantic (Parsons and Lear, 2001). When high-quality prey (e.g. sandlance, capelin, and Atlantic herring) abundances decline, salmon growth rates and survival



**Figure 8.** Differences in North Atlantic summer SST (July, August, September) in degrees Celsius (NOAA Physical Sciences Laboratory [n.d.](https://psl.noaa.gov/ipcc/ocn/), <https://psl.noaa.gov/ipcc/ocn/>). Top row shows average 1955–2005 temperatures from (a) observation and the (b) CMIP5 historical baseline. Middle row contains stabilization (RCP 4.5) projections to (c) mid-century (2005–2055) and (d) the end of the century (2050–2099). Bottom row contains business as usual (RCP 8.5) projections to (e) mid-century and (f) the end of the century.

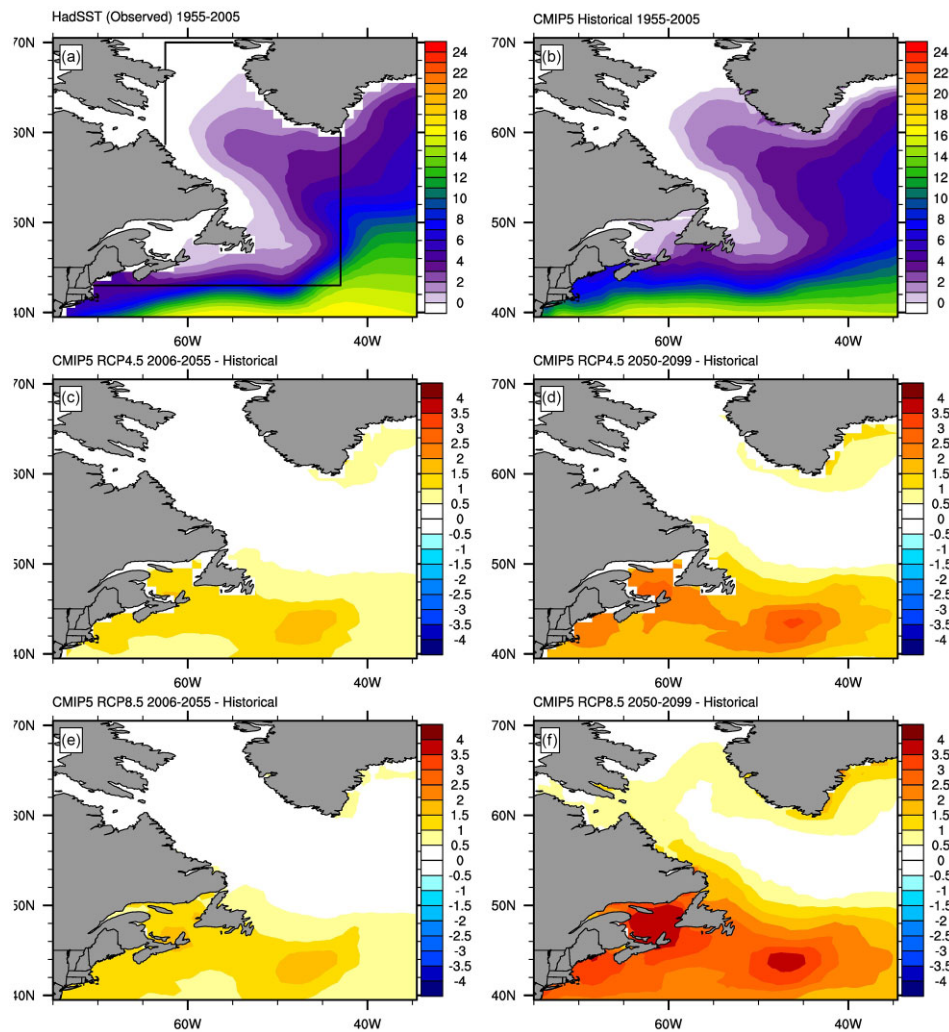
are likely to decline (Barajas *et al.*, 2021). Declining salmon abundances in the early 1990s followed changes in climate and the physical environment, which were also linked to changes in the plankton community and altered prey dynamics (Mills *et al.*, 2013).

The Atlantic Multidecadal Oscillation (AMO) is a multi-decadal index of variation in sea surface temperatures over the North Atlantic (typically, 0°–80°N), as indicated by a time series that dates to the 1870s (Drinkwater *et al.*, 2014). The AMO has been thought to oscillate with a periodicity of 60–80 years, though the record is only long enough to observe two full oscillations. Positive AMO phases are associated with warmer surface temperatures and lower North American salmon abundances (Condrón *et al.*, 2005; Mills *et al.*, 2013; Friedland *et al.*, 2014). AMO temperature changes are most pronounced in winter near the Grand Banks of Newfoundland, where salmon overwinter (Condrón *et al.*, 2005). Warming in the region is probably not directly impacting salmon; rather, the AMO is hypothesized to impact Atlantic salmon

populations through temperature-associated ecosystem and food web changes (Mills *et al.*, 2013). AMO dynamics have traditionally been described as oscillatory, and subsequent Atlantic salmon studies have interpreted the metric in this way. However, AMO dynamics may be better represented as red noise with variability across all low-frequency time scales, and many scientists have proposed that the Atlantic Multidecadal Variability (AMV) may be a more appropriate name for the index (Klavans *et al.*, 2022).

#### Projected changes to salmon's marine environment

While projected changes to salmon's freshwater habitat are moderately uncertain, models of temperature changes in the marine environment are generally consistent with warming over most of the North Atlantic and less warming or even cooling to the south of Greenland, although the magnitude of these changes varies (e.g. Alexander *et al.*, 2018). As in the freshwater section, we use the CMIP5 ensemble of climate models under the RCP 4.5 and 8.5 carbon concentration



**Figure 9.** Differences in North Atlantic winter SST (January, February, March) in degrees Celsius (NOAA Physical Sciences Laboratory [n.d.](https://psl.noaa.gov/ipcc/ocn/), <https://psl.noaa.gov/ipcc/ocn/>). Top row shows average 1955–2005 temperatures from (a) observation and the (b) CMIP5 historical baseline. Middle row contains stabilization (RCP 4.5) projections to (c) mid-century (s–2055) and (d) the end of the century (2050–2099). Bottom row contains business as usual (RCP 8.5) projections to (e) mid-century and (f) the end of the century.

scenarios to project marine habitat change over this century. These models include natural variability in projections of a variety of ocean parameters, including temperature, salinity, and stratification. We then make inferences about potential impacts to salmon directly and indirectly, through prey species and habitat changes.

The predicted marine impacts of a changing climate are continually evolving. Some models predict the Gulf Stream will shift northward over the next century, pushing the Labrador Current northward and potentially bathing the Grand Banks salmon overwintering area in warmer water (Saba *et al.*, 2016). This shift was observed in 2008, when the Gulf Stream shifted northward, reduced the supply of cold, oxygen-rich waters to the continental shelf (Gonçalves Neto *et al.*, 2021). The CMIP5 ensemble of climate models indicated that Northwest Atlantic waters would warm over the 21st century (Figure 8) and that this warmer water would likely be transported towards the Northeast continental shelf (Alexander *et al.*, 2020). Given this, the GOM is expected to warm greatly over the 21st century.

Given our incomplete understanding of salmon's marine habitat use, it is difficult to predict how climate change will im-

part migration in the future. Future changes to currents could positively or negatively impact salmon migrations, which often follow basin patterns (Reddin *et al.*, 2000). Weakening surface currents would reduce the metabolic requirements for migration patterns, as salmon would need less energy to migrate to the Labrador Sea. However, if the Gulf Stream does not shift northward, as suggested by Alexander *et al.* (2020), and general warming occurs, the increased metabolic demand associated with warmer ocean conditions could negate any potential advantages from weakened currents. While we cannot know the exact balance of these variables, future warming is highly likely, which is generally expected to subsequently increase salmon's metabolism and caloric needs.

### Seasonal warming differences

Projected warming rates differ across seasons. Shoaling of the mixed layer causes heat to be integrated over a smaller volume of water in the surface layer, driving greater warming rates during the summer season (Alexander *et al.*, 2018). However, differential warming rates across seasons may not be uniformly impactful to salmon. The southern Greenland coast, the summer feeding

**Table 2.** Marine habitat variables with life stage-specific salmon tolerances, present conditions, future habitat projections, and estimated impacts to salmon productivity and persistence.

		Region	21st Century projected change (CMIP5)	Potential impacts to salmon
Marine	Temperature	GOM and Grand Banks	0.2 to 0.5°C per decade warming	Ecosystem-level impacts that result in reduced prey quantity and quality for post-smolt salmon. Potentially novel predator encounters as well.
		Labrador Sea and Greenland	0 to 0.3 5°C per decade warming <i>medium/high confidence</i>	Relatively moderate warming in this region will probably not generate a strong direct impact to salmon.
	Salinity	GOM and Grand Banks	-0.1 to -0.8 ppt freshening	Prey availability changes related to ecosystem-wide impacts of shoaling mixed layer and increased stratification.
		Labrador Sea and Greenland	-0.5 to -1.2 ppt freshening <i>medium/high confidence</i>	Freshening along West Greenland has already and will likely continue to reduce prey quality and abundance in salmon's summer feeding grounds.
	pH	Northwest Atlantic	-0.20 to -0.35 lower pH <i>medium/high confidence</i>	Documented impacts of acidification to forage species in the Northwest Atlantic may affect salmon prey quality and availability. Additionally, acidification may negatively impact salmon's olfactory homing when returning to natal rivers.
Mixed layer depth	Northwest Atlantic	Shoaling by 0 m near coastlines and by over 300 m in the Labrador Sea, particularly near Greenland. <i>medium/high confidence</i>	Impacts to ecosystem productivity and subsequently, salmon prey availability and quality.	

Projected environmental changes gathered from the NOAA Physical Sciences Laboratory's Climate Change Web Portal (<https://psl.noaa.gov/ipcc/ocn/>).

grounds for MSW salmon, will continue to warm at a much slower rate than the rest of the North Atlantic due to ice melt and reduced AMOC (Drijfhout *et al.*, 2012; Cheng *et al.*, 2013; Menary and Wood, 2018). Under RCP 8.5, by the end of this century, summer sea surface temperatures along west Greenland are projected to be around 2.5°C warmer than the historical mean (1956–2005). Meanwhile, summers along the Grand Banks are projected to be 4.5°C warmer (Figure 8). However, salmon spend the winter, not the summer, at the Grand Banks. Winters along the Grand Banks may be around 3°C warmer (Figure 9). Warming projections under RCP 4.5 are lower. The combined effect of salmon migration patterns and the disparate spatiotemporal warming rates could potentially mitigate stress for salmon, or changing cues may lead to mismatches with suitable habitat conditions or prey availability.

Shoaling of the mixed layer could also impact salmon directly through increased metabolic efficiency. Salmon are thought to take energetic advantage of thermal gradients by feeding in shallow, warmer waters where prey is abundant and then retreating to cool waters at depth to metabolize food more efficiently (Hedger *et al.*, 2017). A shallower mixed layer could give salmon an advantage by shortening the vertical migration between warm and cool waters, thereby reducing en-

ergy expenditure, though it is unclear if the potential saved energy would offset the metabolic demands of a warming ocean.

### Temperature and metabolism: direct impacts

Just as in freshwater, salmon's marine distribution is temporally and spatially constrained by a range of physiologically favourable temperatures. Sea surface temperatures ranging from 3 to 8°C have been positively correlated with salmon occurrence in the Northwest Atlantic (Reddin and Shearer, 1987). We know that marine ectotherms generally follow species-specific temperature preferences, and many Northwest Atlantic fish species have shifted distributions northward in response to warming (Nye *et al.*, 2009; Kleisner *et al.*, 2016; Fredston *et al.*, 2020). Salmon are expected to potentially shift northward as well, to follow preferred temperatures and/or prey distributions (Friedland *et al.*, 2014). These range shifts could necessitate longer, more energetically costly migrations (Rikardsen *et al.*, 2021) and may contribute an additional burden to the endangered US Atlantic salmon populations.

### Seasonal changes

In addition to changing temperature, the timing of temperature seasonality will also continue to shift. Surface tempera-

tures along the Northeastern continental shelf of North America will continue to warm throughout the 21st century, with more pronounced warming in summer and fall than winter and spring (Alexander *et al.*, 2018). Changing temperature seasonality will directly alter the spatiotemporal distributions of favourable thermal habitat for salmon and lower-trophic-level species (Thomas *et al.*, 2017; Henderson *et al.*, 2017; Staudinger *et al.*, 2019), potentially affecting overlap between salmon and preferred prey species. Species-specific responses to temperature may indirectly lead to prey deficits for salmon at a time when warming temperatures will result in even greater metabolic demand.

There is also much evidence for the combined impacts of climate change on marine ectotherms (Pörtner and Peck, 2010). Warming, freshening, acidification, and decreased oxygen concentration associated with warming all exert metabolic stresses on ectotherms. Furthermore, the combined effects of these stresses are not always additive. Combined impacts may be greater or less than the sum of individual changes to the environment.

### Indirect impacts to salmon

Based on current evidence, most impacts of marine habitat change to salmon will be indirect (Jonsson and Jonsson, 2004; Thorstad *et al.*, 2020). Growth, survival, productivity, and recruitment are primarily affected by ecosystem-level impacts associated with climate change. Here we identify four of the most prominent variables that are expected to change: temperature, salinity, mixed layer depth, and ocean acidification. All four factors are highly interrelated and, as such, will be discussed collectively.

With global temperatures continuing to rise over this century, the Arctic will experience increased freshwater input via a number of sources, including melting sea ice and increased precipitation (Greene and Pershing, 2007). By the end of this century, surface salinity along the west Greenland coast is expected to freshen by 0.1–1.6 ppt (Table 2). Freshening will be greatest along the west Greenland coast, where glacial ice sheets will continue to melt (Sciascia *et al.*, 2013; Straneo *et al.*, 2016). Freshening surface waters will cause increased stratification, and the mixed layer will shoal (Capotondi *et al.*, 2012; Alexander *et al.*, 2018). Shoaling and stratification changes may be most dramatic during the summer season, when salmon are either in the southern Labrador Sea (post-smolts) or along the Greenland coast (MSW) (Table 2). Therefore, salmon will spend summers along the west coast of Greenland, where freshening and shoaling of the mixed layer will be greatest. Simultaneously with warming and stratification, ocean acidification is expected to increase over this century because of the ocean absorbing atmospheric carbon dioxide emissions (Table 2).

Mixed layer depth and stratification are well linked to phytoplankton blooms and ecosystem productivity, particularly in the Northwest Atlantic (Sverdrup, 1953; Greene and Pershing, 2007; Behrenfeld, 2010). *Calanus finmarchicus* abundance in the Northwest Atlantic is significantly positively correlated with salinity ranging 29–33 ppt (Albouy-Boyer *et al.*, 2016). Low salinity pulses have been associated with the dominance of younger *C. finmarchicus* phases (I–IV) and other small copepods (Greene and Pershing, 2007). Freshening of fjord waters along the coast of Greenland (Straneo *et al.*, 2016) has also been associated with smaller copepod

sizes (GrønkJær *et al.*, 2019). Small copepods do not provide the same level of lipid content as larger, later-stage *C. finmarchicus*, which have served as the foundation of the North Atlantic marine food web (Pershing and Stamieszkin, 2020).

Capelin and other small pelagic species serve as a major energy conduit between copepods and upper trophic levels, including salmon. In the absence of sufficient large copepods, capelin will consume greater abundances of small copepods but may not be able to compensate for the reduced energy content in their diet (Greene *et al.*, 2008; GrønkJær *et al.*, 2019). These changes in capelin energy density affect Atlantic salmon. A study of salmon stomach contents from Greenland found mean capelin energy density declined by nearly 38% after the 1990 phase shift, and it is hypothesized that reduced prey quality may be partially responsible for the decline in salmon productivity (Renkawitz *et al.*, 2015).

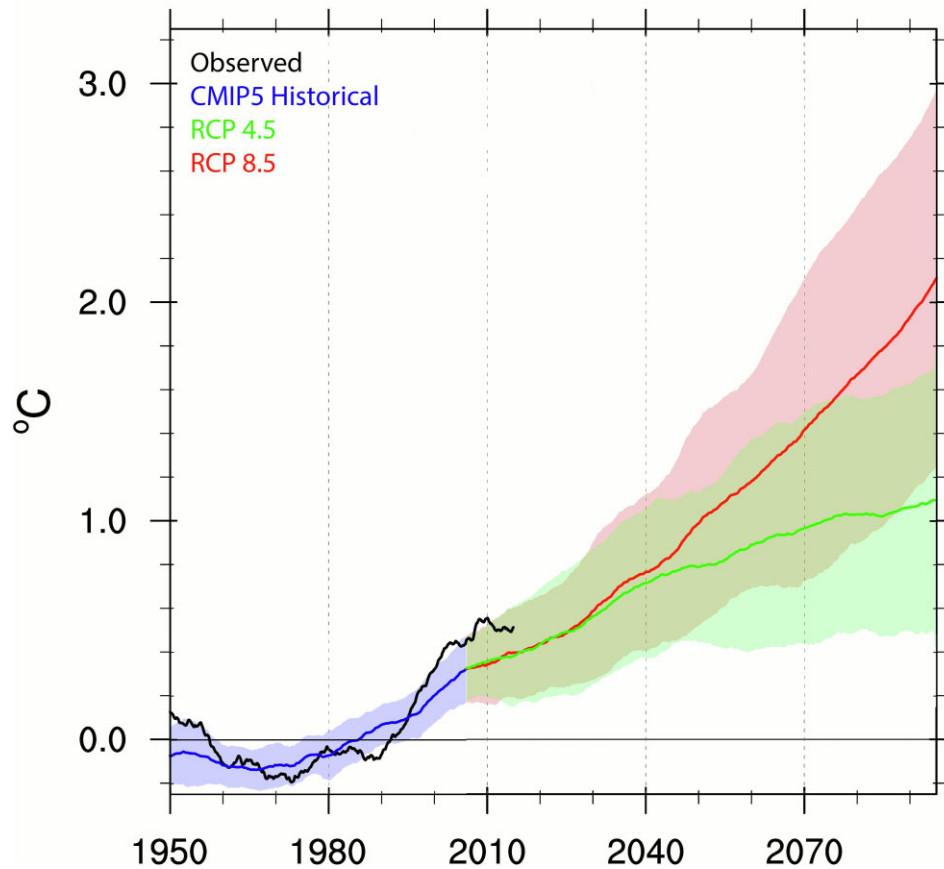
We also know that acidification negatively impacts mid-trophic-level prey species for salmon. Developing sandlance and Atlantic herring may experience reductions in growth and physiological fitness related to ocean acidification levels anticipated by the end of the century (Franke and Clemmesen, 2011; Frommel *et al.*, 2014; Murray *et al.*, 2019; Staudinger *et al.*, 2020). Atlantic herring and sandlance are important prey species for Atlantic salmon (ICES, 2017), and if these impacts extend to other key forage species (e.g. capelin), the result could be that Atlantic salmon will be feeding on smaller and less energy-rich fish into the future across the entirety of its marine phase, potentially resulting in decreased growth and survival during this critical phase (Renkawitz *et al.*, 2015).

In the 1990s, increased transport of relatively fresh water from the Arctic reduced salinity in the Labrador Sea, increasing stratification and shoaling the mixed layer, increasing phytoplankton production and abundance during fall and winter and decreasing during spring and summer (Greene and Pershing, 2007; Pershing and Stamieszkin, 2020). At the same time, *C. finmarchicus*, a critical prey species for its large body size and lipid-rich composition, declined (Pershing *et al.*, 2010). Impacts of climate-generated shifts in lower trophic productivity were seen in upper trophic level animals such as reduced right whale productivity and cod recruitment (Pershing and Stamieszkin, 2020). *Calanus finmarchicus* is a major zooplankton prey species for forage fish that salmon consume, such as Atlantic herring and capelin. Furthermore, recent shifts in *C. finmarchicus* phenology mimic the 1980s/1990s shift (Ji *et al.*, 2010; Pershing and Stamieszkin, 2020), suggesting that copepod phenology could drive major changes in salmon abundance. Projected changes in stratification may be followed by ecosystem-level changes in abundance and seasonality of *C. finmarchicus* and therefore potential changes to salmon prey availability.

### Summary of combined marine impacts to salmon

Salmon's marine habitat will change markedly over the next 75 years. Some changes can be placed into historical context, like the 1980s/1990s ecosystem phase shift associated with basin-scale climate oscillations and ecosystem-wide shifts in trophic structure (Chaput *et al.*, 2005; Mills *et al.*, 2013; Renkawitz *et al.*, 2015). However, the magnitude of warming





**Figure 10.** Northwest Atlantic (same region defined in Figure 8a, black box) SST anomalies ( $^{\circ}\text{C}$ ) observed (black line) and predicted anomalies under the CMIP5, for the historical period (1950–2005, blue line), “stabilization” (RCP 4.5, green line), and “business as usual” (RCP 8.5, red line) carbon concentration scenarios from 1950 to 2100. The anomalies are relative to the 1956–2005 historical mean and smoothed with a ten-year running mean. Shading denotes anomalies with  $\pm$  one standard deviation based on an ensemble of global climate model simulation.

and changes in other physical conditions that are expected by the end of this century is substantial (Figure 10). And while we expect that a highly migratory species like salmon may be able to spatially adjust to accommodate warming, potential spatial and temporal mismatches in habitat connectivity and feeding conditions may dramatically reduce marine growth and survival.

While salmon have direct physiological limits of temperature and other environmental variables, indirect impacts that accrue through ecosystem changes are likely a more significant driver of marine mortality to date and into the future. Changes in prey availability, composition, quantity, and quality may be a significant concern. Salmon’s marine phase is dedicated to eating and growing before maturing and returning to rivers to spawn. Feeding and growth are critical to survival, reproductive success, and subsequent recruitment to the population. Ecosystem changes that result in altered diets and lower energy density will threaten the reproductive success and marine survival of Atlantic salmon and inhibit the recovery of populations existing at low abundance levels.

The early marine phase has traditionally been considered a critical period for Atlantic salmon, particularly in terms of prey availability. Post-smolts undergo accelerated growth (Miller *et al.*, 2014), and metabolic requirements for this growth must be met. Post-smolt salmon typically consume Atlantic herring and krill (Renkawitz and Sheehan, 2011), and the abundance of these lower-trophic-level species affects

salmon feeding and likely productivity. More recently, we are learning that growth later in the marine phase is particularly important to MSW salmon. Reduced growth rates during the late marine stage have been associated with lower return rates of US salmon (Barajas *et al.*, 2021). Salmon also likely feed while migrating through and overwintering in the Labrador Sea, but we do not know as much about salmon during this phase. With warming temperature, lower salinity, and increasing acidification, we know with high certainty that zooplankton and forage fish that currently comprise salmon diets will be negatively impacted. Atlantic salmon tend to specialize in preying on a few species at a time but also exhibit diversification when needed (Dixon *et al.*, 2017). Salmon may not be able to adjust to sharp changes in prey abundance and quality, but we do know that salmon diets change according to the environment (ICES, 2017).

## Discussion

Across the species range, Atlantic salmon have complex spatiotemporal dependencies on a varied array of habitats spanning from riverine headwaters to the coast of Greenland. Given that the US-origin populations occupy the southern extent of the species’ western range, the variability in habitat conditions experienced may exceed that of most populations. Historically, the freshwater, estuarine, and marine habitats that US-origin Atlantic salmon inhabit have not been

static, but given contemporary climate change predictions, these habitats are expected to change in diverse ways. For example, river temperatures and flow regimes will change; cross-habitat transition zones will become more challenging given disparate rates of change; ocean temperatures will warm, circulation patterns may be altered, and other oceanographic effects will result in impacts across all levels of marine ecosystems. The ability of salmon to adapt to these changes is difficult to predict given the uncertainty in some climate projections. As an example, the ability of salmon to adapt to individual stressors in freshwater (e.g. increased river summer temperatures) may be mitigated or exacerbated by other habitat variables that are also expected to change in the future (e.g. availability and quality of cold-water refugia). Outlining the specific impacts of climate change on Atlantic salmon productivity is extremely challenging, but some general conclusions can be made.

**In freshwater**, warming may be partially mitigated by baseflow, but baseflow is also expected to warm. Quantifying the impacts of reduced and warming baseflow is difficult given that there are few detailed streamflow projections available for the study area and they all are associated with large uncertainty. While projections are uncertain, remember that streamflow and temperature dominate the freshwater environment (section “Freshwater phase”). As such, all stages of salmon that occur in freshwater will be impacted by a changing climate in potentially interdependent ways. Disparate environmental cues for freshwater life stages may also diminish early life survival. While photoperiod, the major cue for ovulation, will remain consistent in the future, warming will cause hatching and yolk sac depletion to occur sooner. Finally, dams and other barriers to migration will exacerbate all the above issues by restricting within river movements and by delaying migrations, potentially forcing salmon to miss key physiological and environmental windows.

**In estuaries**, the potential for mismatch between the physical and biological components of freshwater and marine environments could play out as reduced survival of post-smolts during seaward migration. Changes to predator and prey distributions may also negatively or positively impact post-smolts leaving rivers for the open ocean. Larger temperature differences among the cross-habitat transition zones or changes to predator and prey distributions may negatively impact post-smolt survival.

**In the ocean**, we anticipate range shifts given the direct physiological impacts of warming temperatures, but we do not know enough about how salmon behave in the marine environment to accurately predict how their habitat selection and seasonality patterns may change over the 21st century. However, warming temperatures will increase metabolic demands, thus increasing the energy requirements necessary to meet somatic growth requirements for survival (Pörtner and Peck, 2010). We can also expect to see indirect impacts to salmon through changing ecosystem productivity and altered availability, composition, and energy density of prey species.

## Conclusion

While there are a wide range of possible ways in which salmon will be influenced by climate change progression over this century, none of these changes are expected to lead to positive outcomes for US-origin Atlantic salmon (Tables 1 and 2). Salmon are one of the most well-studied anadromous fish

species and yet there are many gaps in our understanding of how they occupy the marine environment. We know a lot about how salmon occupy the freshwater environment, yet have relatively low certainty in our predictions of how riverine environments will change for salmon. The estuarine phase of Atlantic salmon is simply viewed as a transition phase, which may not be accurate, and the dynamics and impacts of projected changes are understood. For their marine phase, there are significant gaps in our understanding of how they occupy and interact with the marine environment. Given the complexities of US-origin salmon life histories and projecting future habitat conditions, there are a myriad of topics that warrant further study to facilitate the development of more robust impact predictions. However, as a starting point, we suggest a few areas that warrant further research and consideration.

Atlantic salmon populations across their range, including US populations, have suffered from reduced marine survival in recent decades. Research and management alike have identified the need for increased focus towards describing the spatiotemporal habitat use and ecology in the ocean. If we know more about how salmon use the marine environment, we can build a clearer picture of how salmon will respond to robustly predicted warming in the marine environment. Specifically, what migration pathways do salmon use (e.g. depth, water properties)? How does migration change in warmer or cooler years? How does a warming ocean impact salmon bioenergetically? How might changing prey availability and quality exacerbate changing metabolic needs associated with warming temperatures? Advancing research on these types of questions will build a better understanding of the scope for behavioural and physiological adaptation, which will influence the nature and magnitude of climate impacts that accrue to US Atlantic salmon. Improved understanding of sensitivity and adaptive capacity as elements of climate risk will reduce uncertainty and enhance confidence in projections of habitat suitability for Atlantic salmon under climate change. Finally, this paper is a current assessment that highlights our gaps in our understanding and how increased focus, effort, and study building from this synthesis will help us to better advise on the impacts of a changing climate in the future.

## Acknowledgements

Funding for this synthesis was provided by NOAA Fisheries’ Atlantic Salmon Ecosystems Research Team, Office of Protected Resources and Office of Science and Technology. We would also like to recognize several researchers for offering their expertise on aspects of this paper: Rob Dudley, USGS; Steve McCormick, USGS; Rick Cunjack, UNB; Noah Snyder, Boston College; Glenn Hodgkins, USGS. Thanks also to Dan Tierney for assistance with some of the figures.

## Author contributions

M.E.H., K.E.M., and T.F.S.: conceptualization and coordination. M.A.A.: marine climate projections. M.B. and M.D.: riverine temperature analyses. M.J.C.: hydrology. D.K.: freshwater ecology. M.E.H.: writing—original draft. K.E.M., M.A.A., M.B., M.J.C., M.D., D.K., and T.F.S.: writing—reviewing, and editing.

## Data availability

This paper is largely a synthesis of published papers which are cited throughout. Publicly available data and climate projections were used to assemble figures of ocean and river temperatures (observed and projected). The sources of this data are included in the manuscript text.

## References

- Albouy-Boyer, S., Plourde, S., Pepin, P., Johnson, C.L., Lehoux, C., Galbraith, P.S., Hebert, D *et al.* 2016. Habitat modelling of key copepod species in the Northwest Atlantic Ocean based on the Atlantic Zone Monitoring Program. *Journal of Plankton Research*, 38: 589–603.
- Alexander, M.A., Scott, J.D., Friedland, K.D., Mills, K.E., Nye, J.A., Pershing, A.J., and Thomas, A. C. 2018. Projected sea surface temperatures over the 21 st century: Changes in the mean, variability and extremes for large marine ecosystem regions of Northern Oceans. *Elementa: Science of the Anthropocene*, 6: 9.
- Alexander, M.A., Shin, S.I., Scott, J.D., Curchitser, E., and Stock, C. 2020. The response of the Northwest Atlantic Ocean to climate change. *Journal of Climate*, 33: 405–428.
- Allyn, A.J., Alexander, M.A., Franklin, B.S., Granier, F.M., Pershing, A.J., Scott, J.D., and Mills, K. E. 2020. Comparing and synthesizing quantitative distribution models and qualitative vulnerability assessments to project marine species distributions under climate change. *PLoS ONE*, 15: 1–28.
- April, J., Ahlbeck-bergendahl, I., Bardarson, H., Bolstad, G.H., Buoro, M., Chaput, G., Dauphin, G *et al.* 2021. Working group on North Atlantic salmon (WGNAS). *ICES Scientific Reports*, 3: 417.
- Armstrong, W.H., Collins, M.J., and Snyder, N. P. 2012. Increased frequency of low magnitude floods in New England. *Journal of the American Water Resources Association*, 48:306–320.
- Barajas, M.F., Sheehan, T.F., Haas-Castro, R.E., Ellingson, B., and Mills, K. E. 2022. Retrospective analysis of marine growth and relationships to return rates of Penobscot River Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*. 79(6): 863–874.
- Baum, E. 1997. *Maine Atlantic Salmon: A National Treasure*. Atlantic Salmon Unlimited: Hermon, ME.
- Beaugrand, G., and Reid, P. C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science*, 69: 1549–1562.
- Behrenfeld, M. J. 2010. Abandoning sverdrup's critical depth hypothesis on phytoplankton blooms. *Ecology*, 91: 977–989.
- Beland, K. F. 1984. Strategic plan for management of atlantic salmon in the state of maine. Atlantic Sea-Run Salmon Commission.
- Beland, K.F., Jordan, R.M., and Meister, A. L. 1982. Water depth and velocity preferences of spawning Atlantic salmon in Maine rivers. *North American Journal of Fisheries Management*, 2: 11–13.
- Beland, K.F., Kocik, J.F., VandeSande, J., and Sheehan, T. F. 2001. Striped bass predation upon Atlantic salmon smolts in Maine. *Northeastern Naturalist*, 8: 267–274.
- Bellmore, R.J., Duda, J.J., Craig, L.S., Greene, S.L., Torgersen, C.E., Collins, M.J., and Vittum, K. 2017. Status and trends of dam removal research in the United States. *Wiley Interdisciplinary Reviews: Water*, 4: e1164.
- Blackwell, B.F., and Juanes, F. 1998. Predation on Atlantic salmon smolts by striped bass after dam passage. *North American Journal of Fisheries Management*, 18: 936–939.
- Blackwell, B.F., and Krohn, W. B. 1997. Spring foraging distribution and habitat selection by double-crested cormorants on the Penobscot River. *Maine USA. Colonial Waterbirds*, 20: 66–76.
- Borggaard, D., Dick, D., Star, J., Alexander, M., Bernier, M., Collins, M., Damon-Randall, K *et al.* 2019. Atlantic Salmon (*Salmo salar*) Climate Scenario Planning Pilot Report. Gloucester. 1–89pp. <https://www.greateratlantic.fisheries.noaa.gov/policyseries/index.php/GARPS/article/view/15/14>. Last accessed date: January 15, 2022.
- Breau, C., Cunjak, R.A., and Bremset, G. 2007. Age-specific aggregation of wild juvenile Atlantic salmon *Salmo salar* at cool water sources during high temperature events. *Journal of Fish Biology*, 71: 1179–1191.
- Breau, C., Cunjak, R.A., and Peake, S. J. 2011. Behaviour during elevated water temperatures: can physiology explain movement of juvenile Atlantic salmon to cool water? *Journal of Animal Ecology*, 80: 844–853.
- Breau, C. 2020. Atlantic Salmon in a warming environment : Challenges to Atlantic Salmon in a warming environment : Challenges to salmon, considerations for managing fisheries By Cindy Breau Fisheries and Oceans Canada. in: Ed. by E. B. Thorstad, D. Bliss, and H Hanson. [https://www.researchgate.net/profile/Cindy-Breau/publication/341680693\\_Breau\\_C\\_2020\\_Atlantic\\_Salmon\\_in\\_a\\_warming\\_environment\\_Challenges\\_to\\_salmon\\_considerations\\_for\\_managing\\_fisheries\\_In\\_EB\\_Thorstad\\_D\\_Bliss\\_K\\_Damon-Randall\\_H\\_Hanson\\_G\\_Horsburgh\\_N\\_O\\_Maoileidigh\\_SG\\_Sutton\\_V/links/5ef1e0c8458515814a77624a/Breau-C-2020-Atlantic-Salmon-in-a-warming-environment-Challenges-to-salmon-considerations-for-managing-fisheries-In-EB-Thorstad-D-Bliss-K-Damon-Randall-H-Hanson-G-Horsburgh-N-O-Maoileidigh-SG.pdf](https://www.researchgate.net/profile/Cindy-Breau/publication/341680693_Breau_C_2020_Atlantic_Salmon_in_a_warming_environment_Challenges_to_salmon_considerations_for_managing_fisheries_In_EB_Thorstad_D_Bliss_K_Damon-Randall_H_Hanson_G_Horsburgh_N_O_Maoileidigh_SG_Sutton_V/links/5ef1e0c8458515814a77624a/Breau-C-2020-Atlantic-Salmon-in-a-warming-environment-Challenges-to-salmon-considerations-for-managing-fisheries-In-EB-Thorstad-D-Bliss-K-Damon-Randall-H-Hanson-G-Horsburgh-N-O-Maoileidigh-SG.pdf).
- Capotondi, A., Alexander, M.A., Bond, N.A., Curchitser, E.N., and Scott, J. D. 2012. Enhanced upper ocean stratification with climate change in the CMIP3 models. *Journal of Geophysical Research: Oceans*, 117: 1–23.
- Chaput, G., and Benoit, H. P. 2012. Evidence for bottom-up trophic effects on return rates to a second spawning for Atlantic salmon (*Salmo salar*) from the Miramichi River, Canada. *ICES Journal of Marine Science*, 69: 1656–1667.
- Chaput, G., Legault, C.M., Reddin, D.G., Caron, F., and Amiro, P. G. 2005. Provision of catch advice taking account of non-stationarity in productivity of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. *ICES Journal of Marine Science*, 62: 131–143.
- Chen, Z., Kwon, Y., Chen, K., Fratantoni, P., Gawarkiewicz, G., and Joyce, T. M. 2020. Long-term SST variability on the Northwest Atlantic continental shelf and slope. *Geophysical Research Letters*, 47(1): 1–11.
- Cheng, W., Chiang, J. C. H., and Zhang, D. 2013. Atlantic meridional overturning circulation (AMOC) in CMIP5 models: RCP and historical simulations. *Journal of Climate*, 26: 7187–7197.
- Collins, M. J. 2019. River flood seasonality in the Northeast United States: characterization and trends. *Hydrological Processes*, 33: 687–698.
- Collins, M.J., Kirk, J.P., Pettit, J., Degaetano, A.T., McCown, M.S., Peterson, T.C., Means, T. N *et al.* 2014. Annual floods in New England (USA) and Atlantic Canada: synoptic climatology and generating mechanisms. *Physical Geography*, 35: 195–219.
- Condron, A., DeConto, R., Bradley, R.S., and Juanes, F. 2005. Multi-decadal North Atlantic climate variability and its effect on North American salmon abundance. *Geophysical Research Letters*, 32: 1–4.
- Cunjak, R.A., Linnansaari, T., and Caissie, D. 2013. The complex interaction of ecology and hydrology in a small catchment : a salmon 's perspective. *Hydrological Processes*, 27: 741–749.
- Cunjak, R.A., Prowse, T.D., and Parrish, D. L. 2011. Atlantic salmon (*Salmo salar*) in winter: 'the season of parr discontent'? *Canadian Journal of Fisheries and Aquatic Sciences*. 55(S1):161–180.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match-mismatch hypothesis. *Advances in Marine Biology*, 26: 249–293.
- Danie, D.S., Trial, J.G., and Stanley, J. G. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—Atlantic salmon. FWS/OBS-82/11.22, Maine Cooperative Fishery Research Unit: Maine University, Orono, ME, USA.
- Daniels, J., Chaput, G., and Carr, J. 2018. Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic

- telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*, 75: 1811–1822.
- Demaria, E. M. C., Palmer, R.N., and Roundy, J. K. 2016a. Regional climate change projections of streamflow in the Northeast and Midwest U.S. *Journal of Hydrology: Regional Studies*, 5: 309–323.
- Demaria, E. M. C., Roundy, J.K., Wi, S., and Palmer, R. N. 2016b. The effects of climate change on seasonal snowpack and the hydrology of the northeastern and upper Midwest United States. *Journal of Climate*, 29: 6527–6541.
- Dill, R., Fay, C., Gallagher, M., Kircheis, D., Mierzykowski, S., Whiting, M., and Haines, T. 2002. Water quality issues as potential limiting factors affecting juvenile Atlantic salmon life stages in Maine Rivers. Report to the Maine Atlantic Salmon Technical Advisory Committee by the Ad Hoc Committee on Water Quality. Bangor, ME. pp 1–29. Last accessed January 15, 2021.
- Dingman, S. L. 1994. *Physical Hydrology*. MacMillan Publishing Company, New York, NY.
- Dixon, H.J., Dempson, J.B., Sheehan, T.F., Renkawitz, M.D., and Power, M. 2017. Assessing the diet of North American Atlantic salmon (*Salmo salar* L.) off the West Greenland coast using gut content and stable isotope analyses. *Fisheries Oceanography*, 26: 555–568.
- Drijfhout, S., van Oldenborgh, G.J., and Cimadoribus, A. 2012. Is a decline of AMOC causing the warming hole above the North Atlantic in observed and modeled warming patterns? *Journal of Climate*, 25: 8373–8379.
- Drinkwater, K.F., Miles, M., Medhaug, I., Otterå, O.H., Kristiansen, T., Sundby, S., and Gao, Y. 2014. The Atlantic Multidecadal Oscillation: its manifestations and impacts with special emphasis on the Atlantic region north of 60°N. *Journal of Marine Systems*, 133: 117–130.
- Dudley, R.W., Hodgkins, G.A., Shanley, J.B., and Mack, T. J. 2010. Quantifying Effects of Climate Change on the Snowmelt-Dominated Groundwater Resources of Northern New England. 3104, U.S. Geological Survey Fact Sheet. [https://pubs.usgs.gov/fs/2010/3104/pdf/fs2010-3104\\_dudley\\_508.pdf](https://pubs.usgs.gov/fs/2010/3104/pdf/fs2010-3104_dudley_508.pdf) Last accessed October 15, 2019 .
- Dudley, R.W., Hirsch, R.M., Archfield, S.A., Blum, A.G., and Renard, B. 2020. Low streamflow trends at human-impacted and reference basins in the United States. *Journal of Hydrology*, 580:124254.
- Dudley, R.W., Hodgkins, G.A., McHale, M.R., Kolian, M.J., and Renard, B. 2017. Trends in snowmelt-related streamflow timing in the conterminous United States. *Journal of Hydrology*, 547: 208–221.
- Dupigny-Giroux, L.A., Mccray, E.L., Lemcke-Stampone, M.D., Hodgkins, G.A., Lentz, E.E., Mills, K.E., Lane, E.D *et al.* 2018. Northeast. In *Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment*, 2, pp. 669–742. Ed. by D.R. Reidmiller, C.W. Avery, D.R. Easterling, K.E. Kunkel, K. L. M. Lewis, T.K. Maycock, and B.C Stewart. U.S. Global Climate Change Research Program, Washington, D.C.
- Easterling, D.R., Kunkel, K.E., Arnold, J.R., Knutson, T., LeGrande, A.N., Leung, L.R., Vose, R. S *et al.* 2017. Precipitation change in the United States. In *Climate Science Special Report: Fourth National Climate Assessment*, 1, pp. 207–230. Ed. by D.J. Wuebbles, D.W. Fahey, K.A. Hibbard, D.J. Dokken, B.C. Stewart, and T.K Maycock. U.S. Global Climate Change Research Program, Washington, D.C.
- Elliott, J.M., and Elliott, J. A. 2010. Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology*, 77: 1793–1817.
- Ellwood, E.R., Temple, S.A., Primack, R.B., Bradley, N.L., and Davis, C. C. 2013. Record-breaking early flowering in the eastern United States. *PLoS ONE*, 8: 1–9.
- Erickson, T.R., and Stefan, H. G. 2000. Linear air/water temperature correlations for streams during open water periods. *Journal of Hydrologic Engineering*, 5: 317–321.
- Fay, C., Barton, M., Craig, S., Hecht, A., Pruden, J., Saunders, R., Sheehan, T *et al.* 2006. Status Review for Anadromous Atlantic Salmon (*Salmo salar*) in the United States: 294. <http://www.nmfs.noaa.gov/pr/species/statusreviews.htm%5Cn2>. Last accessed 15 December 2019.
- Federal Register. 2009. Department of the Interior Fish and Wildlife Service Department of Determination of Endangered Status for the Gulf of Maine Distinct Population. *Federal Register: Rules and Regulations*, 74(117): 29344–29387.
- Ficklin, D.L., Robeson, S.M., and Knouft, J. H. 2016. Impacts of recent climate change on trends in baseflow and stormflow in United States watersheds. *Geophysical Research Letters*, 43: 5079–5088.
- Foster, C. H. W., and Hayden, R. M. 2004. Forests in time: the environmental consequences of 1,000 years of change in New England. *Journal of Interdisciplinary History*, 36:270–271.
- Franke, A., and Clemmesen, C. 2011. Effect of ocean acidification on early life stages of Atlantic herring (*Clupea harengus* L.). *Biogeosciences*, 8: 3697–3707.
- Frechette, D.M., Dugdale, S.J., Dodson, J.J., and Bergeron, N. E. 2018. Understanding summertime thermal refuge use by adult Atlantic salmon using remote sensing, river temperature monitoring, and acoustic telemetry. *Canadian Journal of Fisheries and Aquatic Sciences*, 75: 1999–2010.
- Fredston, A., Pinsky, M., Selden, R., Szuwalski, C., Thorson, J., Halpern, B., and Gaines, S. 2020. Range edges of North American Marine Species are Tracking Temperature Over Decades. *Global Change Biology*, 27(13): 3146–3156.
- Frei, A., Kunkel, K.E., and Matonse, A. 2015. The seasonal nature of extreme hydrological events in the northeastern United States. *Journal of Hydrometeorology*, 16: 2065–2085.
- Friedland, K.D., Manning, J.P., Link, J.S., Gilbert, J.R., Gilbert, A.T., and O’Connell, A. F. 2012. Variation in wind and piscivorous predator fields affecting the survival of Atlantic salmon, *salmo salar*, in the Gulf of Maine. *Fisheries Management and Ecology*, 19: 22–35.
- Friedland, K.D., Reddin, D.G., and Kocik, J. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES Journal of Marine Science*, 50: 481–492.
- Friedland, K.D., Shank, B.V., Todd, C.D., McGinnity, P., and Nye, J. A. 2014. Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems*, 133: 77–87.
- Frommel, A.Y., Maneja, R., Lowe, D., Pascoe, C.K., Geffen, A.J., Folkvord, A., Piatkowski, U *et al.* 2014. Organ damage in Atlantic herring larvae as a result of ocean acidification. *Ecological Applications*, 24: 1131–1143.
- Fry, F. E. L. 1971. The effect of environmental factors on the physiology of fish. *Fish Physiology*, pp. 1–98.
- Gephard, S., and McMenemy, J. 2004. An overview of the program to restore Atlantic salmon and other diadromous fishes to the connecticut river with notes on the current status of these species in the river. *American Fisheries Society Monograph*, 9: 287–317.
- Ginbar, Y. 2009. Part III—Introduction. *Why Not Torture Terrorists?*, 65: 167–170.
- Goode, J.R., Buf, J.M., Tonina, D., Isaak, D.J., Thurow, R.F., Wenger, S., Nagel, D *et al.* 2013. Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins. *Hydrological*, 765: 750–765.
- Greene, C., and Pershing, A. 2007. Climate drives sea change. *Science*, 315: 1084–1085.
- Greene, C.H., Meyer-Gutbrod, E., Monger, B.C., McGarry, L.P., Pershing, A.J., Belkin, I.M., Fratantoni, P. S *et al.* 2013. Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. *Limnology and Oceanography*, 58: 803–816.
- Greene, C.H., Pershing, A.J., Cronin, T.M., and Ceci, N. 2008. Arctic climate change and its impacts on the ecology of the North Atlantic. *Ecology*, 89: 24–38.
- GrønkJær, P., Nielsen, K.V., Zoccarato, G., Meire, L., Rysgaard, S., and Hedeholm, R. B. 2019. Feeding ecology of capelin (*Mallotus villosus*) in a fjord impacted by glacial meltwater (Godthåbsfjord, greenland). *Polar Biology*, 42: 81–98.
- Haines, T. A. 1981. Acidic precipitation and its consequences for aquatic ecosystems: a review. *Transactions of the American Fisheries Society*, 110: 669–707.

- Harden Jones, F. R. 1968. Fish Migration. Edward Arnold Press, London.
- Hare, J.A., Morrison, W.E., Nelson, M.W., Stachura, M.M., Teeters, E.J., Griffis, R.B., Alexander, M. A *et al.* 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. *PLoS ONE*, 11: 1–30.
- Hawkes, J.P., Saunders, R., Vashon, A.D., and Cooperman, M. S. 2013. Assessing efficacy of non-lethal harassment of double-crested cormorants to improve Atlantic salmon smolt survival. *Northeastern Naturalist*, 20: 1–18.
- Hedger, R.D., Rikardsen, A.H., Strøm, J.F., Righton, D.A., Thorstad, E.B., and Næsje, T. F. 2017. Diving behaviour of atlantic salmon at sea: effects of light regimes and temperature stratification. *Marine Ecology Progress Series*, 574: 127–140.
- Hedger, R.D., Sundt-Hansen, L.E., Forseth, T., Ugedal, O., Diserud, O.H., Kvambekk, Å. S., and Finstad, A. G. 2013. Predicting climate change effects on subarctic-Arctic populations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 159–168.
- Henderson, M. E., Mills, K. E., Thomas, A. C., Pershing, A. J., and Nye, J. A. 2017. Effects of spring onset and summer duration on fish species distribution and biomass along the Northeast United States continental shelf. *Reviews in Fish Biology and Fisheries*, 27: 411–424.
- Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. *Rapports et procès-verbaux*, 20: 237.
- Hoar, W. S. 1976. Smolt transformation: evolution, behavior, and physiology. *Journal of the Fisheries Research Board of Canada*, 33: 1233–1252.
- Hodgkins, G.A., and Dudley, R. W. 2006. Changes in the timing of winter-spring streamflows in eastern North America, 1913–2002. *Geophysical Research Letters*, 33: 1–5.
- Hodgkins, G.A., and Dudley, R. W. 2011. Historical summer base flow and stormflow trends for New England rivers. *Water Resources Research*, 47: 1–16.
- Hodgson, E.E., Wilson, S.M., and Moore, J. W. 2020. Changing estuaries and impacts on juvenile salmon: a systematic review. *Global Change Biology*, 26: 1986–2001.
- Hubley, P.B., and Gibson, A. J. F. 2011. A model for estimating mortality of Atlantic salmon (*Salmo salar*) between spawning events. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 1635–1650.
- Hurrell, J.W., Kushnir, Y., and Ottersen, G. 2003. An overview of the North Atlantic oscillation. In *The North Atlantic Oscillation: Climatic Significance and Environmental Impact*, pp.1–35. American Geophysical Union, Washington D.C.
- Hutchings, J.A., and Jones, M. E. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 22–47. <http://www.nrcresearchpress.com/doi/10.1139/d98-004>.
- ICES. 2016. Report of the Working Group on North Atlantic Salmon (WGNAS). ICES Expert Group Reports (until 2018), Copenhagen. <https://doi.org/10.17895/ices.pub.19284557.v1>.
- ICES. 2017. Report of the Workshop on Potential Impacts of Climate Change on Atlantic Salmon Stock Dynamics (WKCCISAL). 39: 90. Copenhagen, Denmark. 27–28 March 2017, ICES CM 2017/ACOM:20.
- ICES. 2020. Working Group on North Atlantic Salmon (WGNAS). 358 pp. <http://doi.org/10.17895/ices.pub.5973%0AEditors>.
- Ireland, L. C. 1998. MP736: maine's forest area, 1600–1995: a review of available estimates. University of Maine: College of Natural Sciences, Forestry and Agriculture Maine Agricultural and Forest Experiment Station Miscellaneous Publication 736.
- Ji, R., Edwards, M., MacKas, D.L., Runge, J.A., and Thomas, A. C. 2010. Marine plankton phenology and life history in a changing climate: current research and future directions. *Journal of Plankton Research*, 32: 1355–1368.
- Jonsson, B., and Jonsson, N. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 2369–2383.
- Jonsson, B., and Jonsson, N. 2018. Egg incubation temperature affects the timing of the Atlantic salmon *Salmo salar* homing migration. *The Journal of Fish Biology*, 93: 1016–1020.
- Jonsson, B., Jonsson, N., and Hansen, L. P. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? *Behavioral Ecology and Sociobiology*, 26: 225–230.
- Juanes, F., Gephard, S., and Beland, K. F. 2004. Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 2392–2400.
- Kaushal, S.S., Likens, G.E., Jaworski, N.A., Pace, M.L., Sides, A.M., Seekell, D., Belt, K. T *et al.* 2010. Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment*, 8: 461–466.
- King, H.R., Pankhurst, N.W., Watts, M., and Pankhurst, P. M. 2003. Effect of elevated summer temperatures on gonadal steroid production, vitellogenesis and egg quality in female Atlantic salmon. *Journal of Fish Biology*, 63: 153–167.
- Kircheis, D., and Liebich, T. 2007. Habitat requirements and management considerations for Atlantic salmon (*Salmo salar*) in the Gulf of Maine Distinct Population Segment (GOM DPS). National Marine Fisheries Service, Protected Resources Division: Orono, Maine.
- Klavans, J.M., Clement, A.C., Cane, M.A., and Murphy, L. N. 2022. The evolving role of external forcing in North Atlantic SST variability over the last millennium. *Journal of Climate*, 35: 2741–2754.
- Kleisner, K.M., Fogarty, M.J., Mcgee, S., Barnett, A., Fratantoni, P., Greene, J., Hare, J. A *et al.* 2016. The effects of sub-regional climate velocity on the distribution and spatial extent of marine species assemblages. *PLoS ONE*, 11. <http://doi.org/10.1371/journal.pone.0149220>.
- Kleisner, K.M., Fogarty, M.J., McGee, S., Hare, J.A., Moret, S., Perretti, C.T., and Saba, V. S. 2017. Marine species distribution shifts on the U.S. Northeast Continental Shelf under continued ocean warming. *Progress in Oceanography*, 153: 24–36.
- Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'Connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of Freshwater Fish*, 12: 1–59.
- Kocik, J.F., and Friedland, K. D. 2002. Salmons and Trouts: Order Salmoniformes. In *Bigelow and Schroeder's Fishes of the Gulf of Maine, Third*, pp. 170–181. Smithsonian Institution Press, Washington and London.
- Kocik, J.F., Hawkes, J.P., Sheehan, T.F., Music, P.A., and Beland, K. F. 2009. Assessing estuarine and coastal migration and survival of wild Atlantic salmon smolts from the narraguagus river, maine using ultrasonic telemetry. *American Fisheries Society Symposium*, 69: 293–310.
- Kurylyk, B. L., MacQuarrie, K. T., Linnansaari, T., Cunjak, R. A., and Curry, R. A. 2015. Preserving, augmenting, and creating cold-water thermal refugia in rivers: Concepts derived from research on the Miramichi River, New Brunswick (Canada). *Ecohydrology*, 8(6): 1095–1108.
- Kurylyk, B.L., MacQuarries, K. T. B., and Voss, C. I. 2014. Climate change impacts on the temperature and magnitude of groundwater discharge from shallow, unconfined aquifers. *Water Resources Research*, 50: 3253–3274.
- Letcher, B.H., Gries, G., and Juanes, F. 2002. Survival of stream-dwelling Atlantic salmon: effects of life history variation, season, and age. *Transactions of the American Fisheries Society*, 131: 838–854.
- Liebich, T., McCormick, S.D., Kircheis, D., Johnson, K., Regal, R., and Hrabik, T. 2011. Water chemistry and its effects on the physiology and survival of Atlantic salmon *salmo salar* smolts. *Journal of Fish Biology*, 79: 502–519.
- Limburg, K.E., and Waldman, J. R. 2009. Dramatic declines in North Atlantic diadromous fishes. *Bioscience*, 59: 955–965.
- Linnansaari, T., Alfreksen, K., Stickler, M., Arnekleiv, J.V., Harby, A., and Cunjak, R. A. 2009. Does ice matter? site fidelity and move-

- ments by Atlantic salmon (*Salmo salar* L.) parr during winter in a substrate enhanced river reach. *River Research and Applications*, 25: 773–787.
- Linnansaari, T., and Cunjak, R. A. 2013. Effects of ice on behaviour of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 70: 1488–1497.
- Lombard, P.J., Dudley, R.W., Collins, M.J., Saunders, R., and Atkinson, E. 2021. Model estimated baseflow for streams with endangered Atlantic salmon in Maine, USA. *USA. River Research and Applications*, 37: 1254–1264.
- Lynch, C., Seth, A., and Thibeault, J. 2016. Recent and projected annual cycles of temperature and precipitation in the Northeast United States from CMIP5. *Journal of Climate*, 29: 347–365.
- Magilligan, F.J., Graber, B.E., Nislow, K.H., Chipman, J.W., Sneddon, C.S., and Fox, C. A. 2016. River restoration by dam removal: enhancing connectivity at watershed scales. *Elementa*, 4: 1–14.
- Maynard, G.A., Izzo, L.K., and Zydlewski, J. D. 2018. Movement and mortality of Atlantic salmon kelts (*Salmo salar*) released into the Penobscot River, Maine. *Fishery Bulletin*, 116: 281–291.
- McCormick, S.D., Björnsson, B.T., Sheridan, M., Eilerlson, C., Carey, J.B., and O’dea, M. 1995. Increased daylength stimulates plasma growth hormone and gill Na<sup>+</sup>, K<sup>+</sup>-ATPase in Atlantic salmon (*Salmo salar*). *Journal of Comparative Physiology B*, 165: 245–254. Springer.
- McCormick, S.D., Cunjak, R.A., Dempson, B., O’Dea, M.F., and Carey, J. B. 1999. Temperature-related loss of smolt characteristics in Atlantic salmon (*Salmo salar*) in the wild. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1649–1658.
- McCormick, S.D., Hansen, L.P., Quinn, T.P., and Saunders, R. L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 77–92. <https://www.researchgate.net/publication/280800827>.
- McCormick, S.D., Keyes, A., Nislow, K.H., and Monette, M. Y. 2009b. Impacts of episodic acidification on in-stream survival and physiological impairment of Atlantic salmon (*Salmo salar*) smolts. *Canadian Journal of Fisheries and Aquatic Sciences*, 66: 394–403.
- McCormick, S.D., Lerner, D.T., Monette, M.Y., Nieves-Puigdoller, K., Kelly, J.T., and Björnsson, B. T. 2009a. Taking it with you when you go: how perturbations to the freshwater environment, including temperature, dams, and contaminants, affect marine survival of salmon. *American Fisheries Society Symposium*, 69: 195–214.
- McCormick, S.D., and Saunders, R. L. 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. *American Fisheries Society Symposium*, 1: 211–229.
- Menary, M.B., and Wood, R. A. 2018. An anatomy of the projected North Atlantic warming hole in CMIP5 models. *Climate Dynamics*, 50: 3063–3080.
- Menberg, K., Blum, P., Kurylyk, B.L., and Bayer, P. 2014. Observed groundwater temperature response to recent climate change. *Hydrology and Earth System Sciences*, 18: 4453–4466.
- Metcalfe, N.B., and Thorpe, J. E. 1990. Determinants of geographical variation in the age of seaward-migrating salmon, *Salmo salar*. *Journal of Animal Ecology*, 59: 135–145.
- Miller, A.S., Miller, T.J., Mills, K.E., and Sheehan, T. F. 2014. Retrospective analysis of Atlantic salmon (*Salmo salar*) marine growth and condition in the northwest Atlantic based on tag-recovery data. *Fisheries Oceanography*, 23: 103–115.
- Milliman, J.D., and Farnsworth, K. L. 2011. *River Discharge to the Coastal Ocean*. Cambridge University Press, Cambridge. <http://ebooks.cambridge.org/ref/id/CBO9780511781247> (last accessed 1 November 2021).
- Milliman, J.D., and Syvitski, J. P. M. 1992. Geomorphic/tectonic control of sediment discharge to the ocean: the importance of small mountainous rivers. *The Journal of Geology*, 100: 525–544.
- Mills, D. H. 1989. *Ecology and management of Atlantic salmon*. Chapman & Hall, London.
- Mills, K.E., Pershing, A.J., Sheehan, T. F., and Mountain, D. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, 19: 3046–3061.
- Mohseni, O., and Stefan, H. G. 1999. Stream temperature/air temperature relationship: a physical interpretation. *Journal of Hydrology*, 218: 128–141.
- Morrill, J.C., Bales, R.C., and Conklin, M. H. 2005. Estimating stream temperature from air temperature: implications for future water quality. *Journal of Environmental Engineering*, 131: 139–146.
- Murray, C.S., Wiley, D., and Baumann, H. 2019. High sensitivity of a keystone forage fish to elevated CO<sub>2</sub> and temperature. *Conservation Physiology*, 7: 1–12.
- Neto Gonçalves, A., Langan, A.J., and Palter, J. B. 2021. Changes in the Gulf Stream preceded rapid warming of the Northwest Atlantic Shelf. *Communications Earth & Environment*, 2: 1–10.
- NMFS, U. S. F. and W. S.. 2018. Recovery plan for the Gulf of Maine Distinct Population Segment of Atlantic salmon (*Salmo salar*). 74pp.
- NOAA Physical Sciences Laboratory. (n.d.). NOAA’s Climate Change Web Portal: CMIP5. <https://psl.noaa.gov/ipcc/ocn/> (last accessed 15 December 2020 ).
- Nye, J., Link, J., Hare, J., and Overholtz, W. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the northeast United States continental shelf. *Marine Ecology Progress Series*, 393: 111–129. <http://www.int-res.com/abstracts/meps/v393/p111-129/> (last accessed 4 June 2014).
- Otero, J., L’Abée-Lund, J.H., Castro-Santos, T., Leonardsson, K., Storvik, G.O., Jonsson, B., Dempson, B *et al.* 2013. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology*, 20: 61–75.
- Parsons, L.S., and Lear, W. H. 2001. Climate variability and marine ecosystem impacts: a North Atlantic perspective. *Progress in Oceanography*, 49: 167–188.
- Pershing, A.J., Head, E. H. J., Greene, C.H., and Jossi, J. W. 2010. Pattern and scale of variability among Northwest Atlantic Shelf plankton communities. *Journal of Plankton Research*, 32: 1661–1674.
- Pershing, A.J., and Stamieszkin, K. 2020. The North Atlantic ecosystem, from plankton to whales. *Annual Review of Marine Science*, 12: 339–359.
- Peyronnet, A., Friedland, K.D., Maoileidigh, N. Ó., Manning, M., and Poole, W. R. 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar* L. *Journal of Fish Biology*, 71: 684–700.
- Pilgrim, J.M., Fang, X., and Stefan, H. G. 1998. Stream temperature correlations with air temperatures. *Journal Of The American Water Resources Association*, 34: 1109–1121.
- Pitz, C. F. 2016. Predicted Impacts of Climate Change on Groundwater Resources of Washington State. <https://fortress.wa.gov/ecy/publications/documents/1603006.pdf> Last accessed: December 15, 2022 State of Washington, Department of Ecology
- Pörtner, H.O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Giuliani, A *et al.* 2001. Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research*, 21: 1975–1997.
- Portner, H.O., and Farrell, A. P. 2008. Physiology and climate change. *Science*, 322: 690–692.
- Pörtner, H.O., and Knust, R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, 315: 95–97.
- Pörtner, H.O., and Peck, M. a. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of fish biology*, 77: 1745–1779. <http://www.ncbi.nlm.nih.gov/pubmed/21078088> (last accessed 12 July 2014).
- Reddin, D.G., Helbig, J., Thomas, A., Whitehouse, B.G., and Friedland, K. D. 2000. Distribution and migration of Atlantic salmon, *Salmo salar* L., in the sea. In *The Ocean Life of Atlantic Salmon: Environ-*

- mental and Biological Factors Influencing Survival, pp. 88–91. Ed. by D Mills. Fishing news books: Boston.
- Reddin, D.G., and Shearer, W. M. 1987. Sea-surface temperature and distribution of Atlantic salmon in the northwest Atlantic Ocean. *American Fisheries Society Symposium* 1: 262–275.
- Renkawitz, M.D., and Sheehan, T. F. 2011. Feeding ecology of early marine phase Atlantic salmon *Salmo salar* post-smolts. *Journal of Fish Biology*, 79: 356–373.
- Renkawitz, M.D., Sheehan, T.F., Dixon, H.J., and Nygaard, R. 2015. Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. *Marine Ecology Progress Series*, 538: 197–211.
- Rice, K.C., and Jastram, J. D. 2015. Rising air and stream-water temperatures in Chesapeake Bay region, USA. *Climatic Change*, 128: 127–138.
- Rieman, B.E., and Dunham, J. B. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. *Ecology of Freshwater Fish*, 9: 51–64.
- Saba, V.S., Griffies, S.M., Anderson, W.G., Winton, M., Alexander, M.A., Delworth, T.L., Hare, J. A *et al.* 2016. Enhanced warming of the Northwest Atlantic Ocean under climate change. *Journal of Geophysical Research: Oceans*, 120: 1–15.
- Saunders, R., Hachey, M.A., and Fay, C. W. 2006. Maine's diadromous fish community: past, present, and implications for Atlantic salmon recovery. *Fisheries*, 31: 537–547.
- Sciaccia, R., Straneo, F., Cenedese, C., and Heimbach, P. 2013. Seasonal variability of submarine melt rate and circulation in an East Greenland fjord. *Journal of Geophysical Research: Oceans*, 118: 2492–2506.
- Scott, A.P. 1990. Salmonids. *In* Reproductive seasonality in Teleosts: Environmental Influences, pp. 33–51. Ed. by A.D. Munro, A.P. Scott, and T.J. Lam. CRC Press, Boca Raton, FL.
- Sibly, R.M., and Atkinson, D. 1994. How rearing temperature affects optimal adult size in ectotherms. *Functional Ecology*, 8: 486–493.
- Smakhtin, V. U. 2001. Low flow hydrology: a review. *Journal of Hydrology*, 240: 147–186.
- Snyder, N.P., Castele, M.R., and Wright, J. R. 2009. Bedload entrainment in low-gradient paraglacial coastal rivers of Maine, U.S.A.: implications for habitat restoration. *Geomorphology*, 103: 430–446.
- Snyder, N.P., Nesheim, A.O., Wilkins, B.C., and Edmonds, D. A. 2013. Predicting grain size in gravel-bedded rivers using digital elevation models: application to three Maine watersheds. *Bulletin of the Geological Society of America*, 125: 148–163.
- Stabell, O. B. 1984. Homing and olfaction in salmonids: a critical review with special reference to the Atlantic salmon. *Biological Reviews*, 59: 333–388.
- Staudinger, M.D., Goyert, H., Suca, J.J., Coleman, K., Welch, L., Llopiz, J.K., Wiley, D *et al.* 2020. The role of sand lances (*Ammodytes* sp.) in the Northwest Atlantic ecosystem: a synthesis of current knowledge with implications for conservation and management. *Fish and Fisheries*: 522–556.
- Staudinger, M.D., Mills, K.E., Stamieszkin, K., Record, N.R., Hudak, C.A., Allyn, A., Diamond, A *et al.* 2019. It's about time: a synthesis of changing phenology in the Gulf of Maine ecosystem. *Fisheries Oceanography*: 532–566.
- Stephenson, D.B., Wanner, H., Brönnimann, S., and Luterbacher, J. 2003. The history of scientific research on the North Atlantic Oscillation. *Geophysical Monograph Series*, 134: 37–50.
- Stich, D.S., Zydlewski, G.B., Kocic, J.F., and Zydlewski, J. D. 2015b. Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. *Marine and Coastal Fisheries*, 7: 68–86.
- Stich, D.S., Zydlewski, G.B., and Zydlewski, J. D. 2015a. Physiological preparedness and performance of Atlantic salmon *Salmo salar* smolts in relation to behavioural salinity preferences and thresholds. *Journal of Fish Biology*, 88: 595–617.
- Straneo, F., Hamilton, G.S., Stearns, L.A., and Sutherland, D. A. 2016. Connecting the Greenland ice sheet and the ocean. *Oceanus*, 29: 22–33.
- Summers, J.K., Paul, J.F., and Robertson, A. 1995. Monitoring the ecological condition of estuaries in the United States. *Toxicological & Environmental Chemistry*, 49: 93–108. Taylor & Francis.
- Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *Journal du Conseil*, 18: 287–295.
- Tague, C., Farrell, I.M., Grant, G., Lewis, S., and Rey, S. 2007. Hydrogeologic controls on summer stream temperatures in the McKenzie River basin, Oregon. *Hydrogeological Processes*, 21: 3288–3300.
- Taranger, G.L., and Hansen, T. 1993. Ovulation and egg survival following exposure of Atlantic salmon, *Salmo salar* L., broodstock to different water temperatures. *Aquaculture and Fisheries Management*, 24: 151–156.
- Thibeault, J.M., and Seth, A. 2014. Changing climate extremes in the Northeast United States: observations and projections from CMIP5. *Climatic Change*, 127: 273–287.
- Thomas, A.C., Pershing, A.J., Friedland, K.D., Nye, J.A., Mills, K.E., Alexander, M.A., Record, N. R *et al.* 2017. Seasonal trends and phenology shifts in sea surface temperature on the North American northeastern continental shelf. *Elem Sci Anth*, 5: 48. <https://www.elementascience.org/article/10.1525/elementa.240/>.
- Thompson, J.R., Carpenter, D.N., Cogbill, C.V., and Foster, D. R. 2013. Four centuries of change in northeastern United States forests. *PLoS ONE*, 8:e72540.
- Thorstad, E.B., Whoriskey, F., Rikardsen, A.H., and Aarestrup, K. 2011. Aquatic nomads: the life and migrations of the Atlantic salmon. *In* Atlantic Salmon Ecology, pp. 1–32. Blackwell Publishing Ltd., Oxford.
- Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81: 500–542.
- Townsend, D.W., Pettigrew, N.R., Thomas, M.A., Neary, M.G., McGillicuddy, D.J., and O'Donnell, J. 2015. Water masses and nutrient sources to the Gulf of Maine. *Journal of Marine Research*, 73: 93–122.
- USASAC. 2021a. Annual Report of the U.S. Atlantic Salmon Assessment Committee, Report no. 33, 2020 Activities. <https://repository.library.noaa.gov/view/noaa/30915>. last accessed 15 December 2022.
- USASAC. 2021b. Annual Report of the U.S. Atlantic Salmon Assessment Committee, Report no. 33, 2020 Activities.
- Wilbur, N.M., O'Sullivan, A.M., MacQuarrie, K. T. B., Linnansaari, T., and Curry, R. A. 2020. Characterizing physical habitat preferences and thermal refuge occupancy of brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*) at high river temperatures. *River Research and Applications*, 36: 1–15.
- Wilkins, B.C., and Snyder, N. P. 2011. Geomorphic comparison of two Atlantic coastal rivers: toward an understanding of physical controls on Atlantic salmon habitat. *River Research and Applications*, 27: 135–156.
- Xu, H., Kim, H.-M., Nye, J.a., and Hameed, S. 2015. Impacts of the North Atlantic Oscillation on sea surface temperature on the Northeast US Continental Shelf. *Continental Shelf Research*, 105: 60–66. <http://linkinghub.elsevier.com/retrieve/pii/S0278434315001582>.

Handling editor: Jonathan Grabowski