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VIEWPOINT

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Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change

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Abstract

1. Atlantic salmon populations have declined in recent decades. Many of the threats to the species during its freshwater and coastal residency periods are known, and management approaches are available to mitigate them. The global scale of climate change and altered ocean ecosystems make these threats more difficult to address.
2. Managers need to be aware that promoting strong, healthy, and resilient wild populations migrating from rivers is the optimal approach currently to reduce the impacts of changing ecosystems and low marine survival. We argue that a fundamental strategy should be to ensure that the highest number of wild smolts in the best condition leave from rivers and coastal areas to the ocean. There is great scope for water quality, river regulation, migration barriers, and physical river habitat improvements.
3. Maintenance of genetic integrity and diversity of wild populations by eliminating interbreeding with escaped farmed salmon, eliminating poorly planned stocking, and reducing impacts that reduce population sizes to dangerously low levels will support the ability of Atlantic salmon to adapt to changing environments. Reducing the impacts from aquaculture and other human activities in coastal areas can greatly increase marine survival in affected areas.
4. As most of the threats to wild salmon are the result of human activities, a focus on human dimensions and improved communication, from scientific and management perspectives, needs to be increasingly emphasized. When political and social will are coupled with adequate resources, managers often have the tools to mitigate many of the threats to wild salmon.

KEYWORDS
aquaculture, catchment management, climate change, conservation evaluation, fish, habitat management, hydropower, ocean, river

1 | INTRODUCTION

The Atlantic salmon (*Salmo salar*) is native to European and North American catchments draining to the temperate and subarctic regions of the North Atlantic Ocean, Barents Sea, and Baltic Sea (Thorstad et al., 2011). It is one of the best studied and culturally valuable fish species in the northern hemisphere. Historically it has supported commercial, sustenance, and recreational fisheries throughout its range and is still a highly prized fish among anglers while also being used by indigenous peoples for food, social and ceremonial purposes. The value of the Atlantic salmon for biodiversity conservation is recognized through the formation of the inter-governmental North Atlantic Salmon Conservation Organization (NASCO) in 1983, which enables seven Parties (six countries and the European Union) that represent all countries in the North Atlantic producing wild Atlantic salmon to co-operate in its conservation. In addition, the Atlantic salmon is listed in Annexes II and V of the European Union Habitats Directive as a species of European importance (Council of the European Communities, 1992). Annex II lists species for which special areas of conservation should be designated by Member States, and Annex V lists species whose exploitation is subject to management measures. In the USA and parts of Canada, Atlantic salmon is listed as endangered under the US Endangered Species Act and Canada's Species at Risk Act.

The Atlantic salmon has a complex and diverse array of life histories. Most forms are anadromous with a juvenile phase in fresh water, followed by a migration of 1 to several years in the ocean for feeding and growth, and a return migration to fresh water for spawning (Klemetsen et al., 2003; Thorstad et al., 2011). Individual salmon return to spawn in their home river, and often even to the same part of the river where they were hatched. This has enabled the formation of genetically distinct populations, adapted to the local conditions among and within catchments (Garcia de Leaniz et al., 2007). As a result, guidelines agreed within NASCO state that management targets for the species should be set for each river, and that all stocks should be maintained above their conservation limits (NASCO, 1998). Conservation limits are defined as the stock level, in terms of number of spawners, that will achieve long-term average maximum sustainable yield (International Council for the Exploration of the Sea (ICES), 2020). Conservation limits can be developed at the tributary or river level, or at the level of a stock complex.

The Atlantic salmon has declined in large parts of its distribution during the last few decades, which has reduced or eliminated harvestable surpluses for fisheries, and in many extreme cases has severely reduced population abundance or resulted in extirpations (NASCO, 2019; ICES, 2020; Norwegian Scientific Advisory Committee for Atlantic Salmon Management, 2020). Human activities in catchments and near-coastal areas are generally well known and have directly contributed to population extirpations or declines. Among the many threats are impacts of hydropower production, other migration barriers (e.g. weirs and culverts), habitat alterations in rivers, multiple stressors from Atlantic salmon farming (e.g. escaped farmed domestic salmon, sea lice and transfer of other disease pathogens), invasive species, pollution, fisheries, and reduced water quality (Forseth et al., 2017; ICES, 2020). Some of these threats act at regional or larger scales. When political and social will are coupled with adequate resources, managers often have the knowledge and tools to mitigate many of the threats to wild salmon.

In the ocean, management actions for salmon have focused historically on controlling and reducing all fisheries to sustainable levels and eliminating fisheries where sustainable harvesting is not possible. However, a recently recognized and ill-defined compounding threat to Atlantic salmon is the multiple effects of climate change on the aquatic environments and ecological functioning of salmon. Multiple stressors are already having a major impact on Atlantic salmon productivity as evidenced by reduced survival during its marine migration (ICES, 2020; Olmos et al., 2020). Marine survival may even decline further as the effects of climate change become more pronounced. Climate change is also likely to have adverse impacts on the freshwater environment of salmon, as temperatures warm and precipitation patterns change. Consequently, mitigation and conservation actions based solely on controlling harvests will not be sufficient to reverse declines in Atlantic salmon populations.

So how can managers conserve, protect and enhance wild Atlantic salmon populations at local, regional, and international levels in the face of these overwhelming challenges? The aim of this article is to give an overview of current stressors on Atlantic salmon populations, including those brought by climate change and altered ocean ecosystems, discuss the challenges faced in addressing them, and provide our vision of how local, regional, national, and international managers can best use available scientific knowledge to address these challenges. There is debate at present in the conservation community about what the best focus should be to address the restoration of Atlantic salmon. We present here the case for concentrating on fresh water and the nearshore coastal zone.

2 | THE FRESHWATER PHASE OF THE ATLANTIC SALMON

Anadromous Atlantic salmon spawn in rivers from September to February (Thorstad et al., 2011). During spawning, the females dig and deposit their eggs in one or more redds in the gravel. The eggs hatch in the following spring. The juveniles (parr) remain in fresh water for 1–8 years, before they migrate to sea for feeding. When they migrate to the sea for the first time, they are termed smolts; these are only 10–20 cm long, so the bulk of growth occurs in the sea.

River-specific productivity is largely determined by water discharge and the quality, quantity, and distribution of suitable spawning and shelter habitat for the juveniles (Finstad et al., 2007; Finstad et al., 2010; Foldvik et al., 2017); hence, these are key factors to be considered in stream restoration and habitat classification. Habitat quality and quantity can be reduced by human activities such as water regulation, channelization, flood control, intensive agriculture, forestry, gravel extraction, and other activities causing substrate removal or sedimentation. In addition, hydropower projects can alter the extent of wetted area and thermal regimes in rivers, which in turn may alter fish physiology, growth, and timing of important life history events such as hatching, emergence, smoltification, and smolt migration (McCormick et al., 1998; Finstad, Armstrong & Nislow, 2011; Enders & Boisclair, 2016; Harvey et al., 2020). Hydropower dams, weirs, and other migration barriers can affect the distribution both of juveniles and adult spawners in the river, and severely increase the mortality of downstream migrants (McCormick et al., 1998; Thorstad et al., 2012). There are also a host of damaging impacts associated with acid precipitation and a wide range of other freshwater contaminants derived from intensive agriculture, industry, and other human activities, which also affect Atlantic salmon in their freshwater phase (Rosseland & Kroglund, 2011).

3 | THE MARINE PHASE OF THE ATLANTIC SALMON

The marine feeding areas of Atlantic salmon cover large swathes of the North Atlantic Ocean, and marine survival rates have been shown to vary across time and space, declining considerably over the last 3 decades (ICES, 2020). Marine mortality rates have a large influence on the number of adult salmon returning to spawn (Nieland, Sheehan & Saunders, 2015). The lack of evidence for compensatory mortality in the marine environment (Milner et al., 2003; Einum & Nislow, 2011) means that increasing the number of smolts migrating to the ocean will not affect the marine survival of that cohort. Hence, any increase in the smolt output from a river is assumed to translate directly into an increase in the number of returning adults, assuming other factors influencing natural mortality in the ocean remain constant. It is hypothesized that early marine phase Atlantic salmon experience higher mortality rates than later phase migrants, but, for multi-sea-winter stocks, mortality during the second year can also be high (Chaput, 2012).

It is important to note that marine survival rates, from the point when salmon smolts leave the rivers until they return, are influenced by the condition and quality of the smolts when they leave fresh water (Russell et al., 2012), by human activities in coastal areas such as aquaculture (Thorstad et al., 2015), and by climate and other ecosystem changes in the sea (Beaugrand & Reid, 2012; Mills et al., 2013). Hence, there are human activities other than harvest controls that can be altered to help reduce marine mortality, indirectly by increasing freshwater survival to increase the number of smolts that reach the sea, and directly by reducing marine mortality caused by human activities in the coastal areas. Other natural resource managers and government sectors need to be engaged in salmon management to minimize the impact of human activities in rivers and coastal areas. However, mitigating marine mortality arising from climate and ecosystem stressors remains, for now, an intractable problem owing to the incomplete understanding of the marine phase of the salmon, the size of the habitat, and the complexity of the changing ecosystem.

Poor ocean conditions leading to reduced survival in the marine phase lowers the resilience of salmon populations to other human impacts. For example, sea lice spread from salmon farms has been shown to reduce growth of wild salmon during the first months at sea. This synergistic effect is particularly strong in years when general ocean survival is low (Vollset, Barlaup & Friedland, 2019). Interaction effects like this underline the importance of reducing human impacts as a strategy to conserve salmon populations in the face of low marine survival and a changing climate.

An incomplete understanding of the causes of ocean mortality is one of the biggest problems faced in predicting the long-term future of Atlantic salmon and in forecasting abundances for management use. Marine mortality is difficult to monitor given the large expanse of the marine range of the species and because dead fish disappear, rendering marine mortality largely invisible. Marine mortality may also result from cross-over effects, where the impacts of a stressor applied in one environment do not emerge until the fish has entered the new environment. For instance, pollution in fresh water may result in mortality after the salmon smolts have entered the sea, and mortality from sea lice acquired in coastal areas may not occur before the sea lice have developed to adult stages and the post-smolts have entered the open ocean. Disentangling the various components that contribute to overall mortality is difficult. As an example, a common technique for estimating marine mortality is to compare the number of out-migrating smolts with the number of adult returns; however, this estimate may unintentionally contain a portion of freshwater and estuarine mortality (Flávio et al., 2020). Disentangling the contributing mortality components will allow a more accurate estimate of the mortality attributable to the marine environment (Stevens, Sheehan & Kocik, 2019). Moreover, when data are collected from returning fish (e.g. from scale samples of adult salmon after they have returned from the ocean), only the surviving fish are studied, which needs to be accounted for when interpreting results.

Predation by mammals and fishes can be one source of marine mortality (Strøm et al., 2019). With declining Atlantic salmon populations, mortality from predation seems to be increasingly in focus. However, conclusions on marine mortality based on studies of predation should be drawn with care. Predation is a natural phenomenon and just because it is documented, it does not mean that it is a driver of current salmon population declines. Also, simply showing that a post-smolt is eaten by a predator does not necessarily mean that the fish would have survived if it had not been preyed upon. Predation often preferentially occurs on individuals that have been weakened by other stressors, and even in the absence of predation these individuals may have eventually died (Thorstad et al., 2013). For instance, a post-smolt with a deadly infestation of sea lice is likely to be eaten by a predator before it dies from the sea lice. This fish would have eventually died from the lice infestation even in the absence of predators. Predation impacts are primarily of concern when predation rates in the ocean are increased above natural levels as a result of the variety of human-induced impacts, and when salmon populations are reduced because of other impacts and are close to critical lower limits.

In recent decades, reduced survival of Atlantic salmon during the feeding migration could be a cyclical phenomenon, and salmon productivity could increase again; however, human-induced climate change has been implicated as a cause. As temperatures continue to increase over the next century, the outlook for Atlantic salmon in the North Atlantic will result in significant challenges for managers to maintain all stocks above their conservation limits.

4 | ATLANTIC SALMON IN A CHANGING CLIMATE

4.1 | Climate alteration is changing ecosystems inhabited by salmon

Warming and its cascading effects in all ecosystems and habitats have put wild salmonids under pressure, which render them more vulnerable to other stressors. The greatest impacts experienced by Atlantic salmon are in the southern part of its range. At present, the northern populations have more scope for acclimatization, because temperature increases are not expected to force physiological status towards or beyond the species' upper thermal tolerance (Anttila et al., 2014).

Climate change is having a major impact on Atlantic salmon in fresh water and at sea, directly through changes in temperature, water flow, and other abiotic factors, and indirectly through ecosystem changes such as food availability and altered predator–prey dynamics. Under future climate scenarios, higher temperatures and increased hydrological variability are predicted to affect all components of freshwater systems (Schneider et al., 2013; Knouft & Ficklin, 2017). Precipitation is expected to increase in the Northern Hemisphere, with wet areas typically becoming wetter, but with increased variability such that the risk and intensity of floods and droughts will increase (Schneider et al., 2013). In northern Europe and North America, the climate is projected to have warmer, drier summers and milder, wetter winters with more precipitation falling as rain and less as snow, a decrease in ice-covered periods, and more frequent periods with extreme weather events (Intergovernmental Panel on Climate Change (IPCC), 2014; Hoegh-Guldberg et al., 2018; IPCC, 2018). Periods of extreme low water levels during summer and higher water temperatures must, therefore, be expected for many rivers. In addition, expected flash flooding events may lead to significant habitat damage and alteration of river beds. Marine ecosystems are also expected to continue to change. With rising ocean temperatures and acidity there will be concurrent shifts in circulation, stratification, nutrient input, and oxygen content, with potentially wide-ranging effects on ocean productivity, food web dynamics, and other ecosystem processes (Hoegh-Guldberg & Bruno, 2010; Doney et al., 2012).

4.2 | Impacts on Atlantic salmon

Scientists are projecting that conditions that foster healthy Atlantic salmon populations will deteriorate, both in fresh water and at sea, as a result of the ecosystem changes brought about by climate heating. The vulnerability of salmon to a rapidly warming environment is a known concern but with some uncertainty as to how well the species will be able to adapt. Wild Atlantic salmon populations from rivers in Europe have displayed similar plasticity in physiology and acclimation capacities in response to acute warming despite their different acclimation history in the wild (Anttila et al., 2014). This indicates that these populations have the capacity to acclimatize to increasing water temperatures up to their upper lethal limit. Although Atlantic salmon have some capacity to respond and potentially adapt to variations in environmental conditions (Garcia de Leaniz et al., 2007), there are limits to these capacities, especially over short time periods. Further research is needed to understand the extent by which individual populations can adapt to increasing temperatures, especially as annual average temperatures approach, and in some cases exceed, lethal upper limits.

4.2.1 | Hydrology

The predicted changes to river hydrology are likely to influence the population dynamics of Atlantic salmon (Jonsson & Jonsson, 2009; Hedger et al., 2013; Sundt-Hansen et al., 2018). The average annual water flow in many regions is expected to increase, but the flow pattern will tend towards the extremes with high flows in the autumn and winter and very low flows during the summer. Therefore, the wetted habitat area available for juveniles will vary greatly during the course of the year. Future periods of low river flow and high temperatures during summers may, therefore, be a potential bottleneck for Atlantic salmon production and survival in some areas.

4.2.2 | Temperature

Migratory fishes are particularly vulnerable to warming environments as the transitions between habitats are finely tuned to specific environmental cues (Crozier et al., 2008). The success of these transition periods has consequences for subsequent survival. Salmon are ectotherms and, as such, water temperature directly controls their physiology and metabolism. During spawning, eggs are laid in the gravel, and the timing of hatching and the rate at which fry consume the nutrients from the yolk sack before emerging is controlled by water temperature (Crisp, 1981; Jensen, Johnsen & Saksgård, 1989). With increased water temperatures, this process will be more rapid, leading to earlier fry emergence and possibly to a disconnect between the timing of fry emergence and food availability. When temperatures increase, the growth of juvenile salmon in the river will generally increase, and the juveniles may reach smolt size earlier. Studies have shown that smolt age has decreased in the past decades, as water temperatures have increased (ICES, 2009; Russell et al., 2012).

Water temperatures in many rivers are expected to periodically exceed the upper thermal tolerance limit for salmonids, and during the summer many populations are already encountering water temperatures near or exceeding laboratory-derived lethal limits. Salmon, like other vertebrates, are most sensitive to high temperatures at the embryonic stage (16°C, Jonsson & Jonsson, 2009). For juvenile salmon in the river, growth is optimal from 16 to 20°C, and stops when the temperature approaches 23°C (Garside, 1973; Elliott, 1991; Jonsson & Jonsson, 2009). The incipient lethal temperature limit is estimated at 27.8°C and absolute mortality occurs at 33°C (Elliott, 1991; Jonsson & Jonsson, 2009). Although the lethal temperature for adult Atlantic salmon is expected to be lower than for juveniles (Breau, Cunjak & Peake, 2011), this information has not yet been published.

Warmer river temperatures earlier in spring appear to have influenced the timing of migration, with smolts migrating to the ocean earlier in the year (Otero et al., 2014). There is concern that the changed environmental conditions in the ocean are creating a mismatch between timing of smolt sea entry and favourable conditions at sea (Kennedy & Crozier, 2010; Hawkes, Sheehan & Stich, 2017).

Energy depletion at high temperatures before spawning has been shown to be greater in small than in large salmon, suggesting that smaller individuals may be more affected by high temperatures (Lennox et al., 2018). If so, long-term phenotypic change may be expected in salmon populations experiencing high temperatures. Exposure of female salmon to elevated water temperature prior to reproduction may also have detrimental effects on egg maturation, fertility, and survival (Pankhurst & King, 2010; Pankhurst et al., 2011).

Historically, research on climate effects on salmon in fresh water has focused on factors such as the changes in water temperature and flow, whereas research in the marine phase has examined temperature correlations with growth. Marine ecosystems have altered in response to climate change, which has influenced the food supply for Atlantic salmon in the marine phase (Beaugrand & Reid, 2012; Mills et al., 2013; Renkawitz et al., 2015). The spatial distribution of food and high-productivity areas will probably change, which may affect the ocean migration routes, distributions and marine survival of Atlantic salmon.

4.2.3 | Management options in freshwater

Changes in river hydrology, river temperatures and the marine environment due to climate change will radically alter the various habitats and environments on which Atlantic salmon rely. Some practical management options more directly related to the altered hydrology and water temperatures in the rivers are discussed here.

In freshwater areas where salmon encounter high water temperatures, suitable cold-water refuges can sometimes be found (Jackson et al., 2018; Jackson et al., 2020). The spatial heterogeneity of water temperatures in streams provides potential relief during warm water conditions if the animals can move to these cooler refugia. Atlantic salmon, as other salmonids, are known to thermoregulate behaviourally to maintain a body temperature close to optimal levels (Breau, Cunjak & Bremset, 2007) to minimize energetic costs associated with high temperature (Breau, Cunjak & Peake, 2011). Managers should prioritize promoting, protecting, and restoring cold-water refuges and habitat heterogeneity as it provides a range of thermal conditions for fish to select from based on their specific requirements. Managers should also prioritize maintaining and improving access to cold-water refuges, often located in headwater reaches, as these areas may be the most climate-resilient habitats within a catchment. This can be particularly challenging for salmon populations in rivers where there are problems with connectivity. It is expected that access to cold-water refuges will become increasingly important as more rivers experience extreme temperature events. A better understanding of habitat characteristics forming optimal cool water refuges is warranted if managers are to create artificial refuges. Removing dams, weirs, and other migration barriers, or constructing and improving road crossings and fishways to facilitate free movement of fish will improve river connectivity and access to cold-water refugia and the varied habitats that salmon need to survive. Removal of barriers also often facilitates increased production of salmon juveniles, by creating rearing habitats with faster flow.

The protection and restoration of native riparian shading and healthy forest cover are tangible local management actions that could mitigate some of the adverse effects of climate change. Riparian edges lower the water temperature of streams (Broadmeadow et al., 2011) and help to maintain cool water temperatures in thermal refuges (Breau, Cunjak & Bremset, 2007), as well as restoring access to the higher reaches, which are typically colder. Healthy forest cover composed of biodiverse native vegetation will also support a high abundance of good quality prey for salmon juveniles. Healthy forests throughout river catchments reduce problems related to flash flooding. These measures improve the overall river habitat for the benefit of all aquatic organisms, including salmon. This is particularly important for the southern populations that are already experiencing critically elevated water temperatures.

Hydropower production and other types of river regulation often have severe impacts on Atlantic salmon populations. In some instances, however, particularly when water is obtained from reservoirs, managers can try to ensure that the regulation scheme is adapted to counteract the impacts of climate change by applying water release strategies to avoid periods of extreme low flows and high water temperatures. Release of water from reservoirs also has the potential to regulate water temperatures, as taking water from various depths within the reservoir can influence the water temperature of downstream river stretches.

Catch-and-release fisheries have become common in many Atlantic salmon rivers as the populations have declined. There are differences among countries, regions and rivers in how catch-and-release angling is viewed and used by managers. Where catch-and-release is practised, it is important to recognize that the adverse impacts and mortality of released fish increase at high water temperatures (Lennox et al., 2017; Van Leeuwen et al., 2020), and to prohibit catch-and-release angling when water temperatures exceed temperature thresholds. Where the fishing regulations are based on mandatory release of all fish or some groups of fish (e.g. females, large fish), this may imply that all angling for Atlantic salmon is stopped above these temperatures. One option is to establish river-specific environmental thresholds (i.e. water temperature, flow and oxygen level) at which closures of recreational Atlantic salmon fisheries should occur (Breau & Caissie, 2012). A strategy that is used in New Brunswick, Canada, is to close identified ‘cold water pools’ to angling when water temperatures increase above 20°C for two consecutive days. This is to protect salmon when they congregate in the cold-water areas. Enforcement might be increased, if necessary, in cold-water refugia to discourage poaching when fish congregate in these areas. Better education of anglers on the relationship between water temperature and mortality, and appropriate catch-and-release techniques, might also be important measures.

4.3 | Other stressors caused by human activities reduce resilience to climate effects

As the ecosystems and habitats of Atlantic salmon change because of the effects of altered climate, there are cascading effects and negative feedback loops that are only now being identified. Some human activities will amplify the stress caused by climate change and reduce the resilience of salmon and their ability to adapt to changing environments. Known stressors of high concern in relation to climate alteration, and possible management options linked to are described in 4.3.1–4.3.6.

4.3.1 | Escaped farmed salmon and sea lice

Farmed salmon are genetically different from their wild conspecifics and less adapted to the natural environment, particularly in a rapidly changing natural environment (Karlsson et al., 2016; Glover et al., 2017). Genetic introgression of escaped farmed salmon represents an existential threat to the viability of many wild salmon populations. For instance, in Norway there were indications of genetic introgression from escaped farmed salmon in the wild population in two-thirds of the screened rivers (150 of 225 rivers), of which 67 populations were severely affected (30% of the screened populations) (Diserud et al., 2019). Similar results have been demonstrated from eastern Canada (Wringe et al., 2018). Wild salmon populations suffer a loss of local adaptation when they interbreed with farmed salmon owing to the introgression of maladapted genotypes and life history traits (McGinnity et al., 2003; Bolstad et al., 2017). Genetic introgression of farmed salmon imposes an extra impediment to the natural process of adaptation and may reduce the ability of Atlantic salmon to adapt to rapid environmental changes. Beyond genetic introgression, sea lice from salmon farms can increase mortality substantially and reduce Atlantic salmon population sizes (Thorstad et al., 2015), which contribute to reducing population resilience to climate change.

There is a need to develop fish farm technologies and approaches for eliminating escapes, sea lice and other disease pathogens from farms that are influencing wild Atlantic salmon. This can be done by developing closed containment technologies for sea-based farms, using sterilized fish to avoid genetic introgression, and developing land-based technologies. Using sterilized fish will not by themselves solve all the problems related to escapes from farms, because farmed salmon also affect wild salmon through interference competition (Robertsen et al., 2019), and sterilized fish will not solve problems with sea lice and disease pathogens. Therefore, closed containment technologies in the sea or on land are needed. Beyond the technical challenges of conducting intensive and large-scale Atlantic salmon production on land, these operations require much space and potential conflicts may arise with other uses of these areas. Most salmon-producing countries have agreed, through NASCO, to the goals of eliminating escapes and the impacts of sea lice (NASCO, 2006), and there are several emerging technologies and approaches to address these issues; however, a lack of strong political will is preventing these goals from being realized.

4.3.2 | Habitat alteration

Atlantic salmon populations are sensitive to freshwater habitat loss and alteration from a range of human activities, including hydropower production, damming, intensive agriculture, river and flood control near towns and cities, transport, and forestry. Poorly executed land-use practices can result in reduced productive area, substrate quality and prey abundance, and can also have many other detrimental impacts on Atlantic salmon. Habitat alterations can interact with the effects of climate change through direct impacts on population size and indirect impacts through altered flow rates and thermal regimes. Any changes to salmon habitat that reduce population size or smolt quality have the potential to exacerbate changes caused by climate change and further erode population resilience.

Management options related to habitat alteration are diverse and often river specific. Examples of potential management actions to correct habitat alterations are removal of dams and other barriers, building and improving fish passes, liming to address low pH, substrate restoration, afforestation and forest tending, pollution control, repairing and replacing culverts, and creating settling ponds to capture sediment from agricultural lands. There is significant potential for improvements in many salmon rivers related to hydropower development and other habitat alterations that have yet to be explored and employed. Managers are encouraged to follow a process-based approach to river restoration aimed at addressing the root causes of habitat degradation in a sustainable manner (Beechie et al., 2010).

4.3.3 | Pathogen diseases

Elevated temperatures may increase the virulence of several disease pathogens in fishes (Marcogliese, 2001). Atlantic salmon will experience temperatures that are outside their optimal range, which may affect immunological and physiological functions necessary to combat diseases. Wild Atlantic salmon may be adversely affected by climate-induced effects of pathogens (Johnsen & Jensen, 2005; Sterud et al., 2007), both in their natural habitats and by pathogen transmission from salmon farms. Understanding and reducing the spread of pathogens from farms to wild fish is highly important. Preserving genetic diversity in wild populations is also essential so that they have the best chance of adapting to new and increased disease challenges as a result of projected climate warming and increased disease outbreaks in aquaculture farms (de Eyto et al., 2007; de Eyto et al., 2011).

4.3.4 | Artificial stocking of natural populations to augment abundance

Stocking is frequently used as an attempt to augment wild populations in response to declines. Although well intentioned, stocking often comes with a range of harmful consequences and may, overall, often be counterproductive (O'Sullivan et al., 2020). Such genetic consequences include reduction of effective population size and loss of genetic variation owing to a disproportionately large contribution of stocked individuals from a low number of broodfish; loss of local adaptation if using non-local broodfish; unintentional domestication selection in the hatchery; and epigenetic effects from being reared in the hatchery instead of in a natural river (Christie et al., 2012; Christie et al., 2016; Hagen et al., 2019). The consequences of poorly planned or inappropriate stocking will reduce the ability of Atlantic salmon to adapt to environmental change (McGinnity et al., 2003). Consideration should be given as to whether stocking is really needed to maintain a population. If a population is self-sustaining, or this goal can be reached through habitat improvements or other management actions, managers should consider these options before issuing permits for stocking. Stocking should be a last resort to preserve endangered populations, after other impacts on the populations have been tackled. If stocking is undertaken, proponents should have the obligation to monitor both its effectiveness and the consequences for wild salmon. General guidelines for stocking include the use only of local wild broodfish; stocking with the earliest possible life stages to minimize the risk of unintentional domestication selection and epigenetic effects; balancing the number of stocked fish with the number of broodfish and the number of naturally reproducing fish; avoiding using broodfish with genetic introgression from escaped farmed salmon; and ensuring that all hatchery-produced fish are traceable so that the effects of stocking can be evaluated (Karlsson et al., 2016; Hagen et al., 2019; Hagen et al., 2020).

4.3.5 | Selective fishing

Selective exploitation of early running fish or certain size groups may induce genetic and phenotypic changes in Atlantic salmon (Consuegra et al., 2005; Harvey et al., 2017), which in turn may reduce genetic variation and the ability of populations to adapt to climate change. Managers should, therefore, evaluate the risk of fishing imposing selective mortality in the different catchments. Potential problems caused by selective fishing can be counteracted by adjusting fishing regulations (timing, gears, etc.), and also by introducing mandatory catch-and-release of certain groups of fish or at certain times of the year.

4.3.6 | Invasive alien species

A range of introduced fishes and other organisms may affect Atlantic salmon as competitors, predators, vectors of new disease pathogens, or as plants that alter aquatic habitats. With increased temperatures, new species may invade rivers inhabited by Atlantic salmon, and some introduced species may increase in abundance. This may lead salmon to face additional competition for resources, increased predation, or other harmful ecological impacts. With the arrival of invasive species, the risks of exposure to new viruses, bacteria, protozoans, and multicellular parasites may also increase. A contemporary example of this stressor is the increased likelihood of the continued expansion and establishment of invasive pink salmon (*Oncorhynchus gorbuscha*) populations in rivers around the Atlantic Ocean (Sandlund et al., 2019; Hindar et al., 2020), given a warming ocean and other impacts of climate change.

Educational information on the damage that invasive organisms can do to native species, including salmon, should be a pillar of management actions to limit intentional releases. Once invasive species are present, they are cause for significant concern owing to the difficulty to control or eradicate them. However, if sufficient effort and resources are applied, progress can be made. For example, large or visible organisms such as invasive plants and fishes (e.g. rainbow trout and pink salmon) can be eliminated or reduced to a point where they pose significantly less threat by intensive fishing or harvesting. Elimination has also been possible for the small invasive parasite *Gyrodactylus salaris*, which nearly eradicated the Atlantic salmon in more than 50 rivers in Norway (Forseth et al., 2017). Eliminating the parasite from more than 40 of these rivers has cost 1 billion NOK, equivalent to about 110 million euros. This example shows that elimination or severe reduction of introduced organisms can sometimes be achieved, but it requires significant resources and political will for it to be accomplished. The education of the public and anglers on the adverse impacts of non-native fish on salmon should be done to limit intentional releases of fish in rivers. Resources and site- and species-specific knowledge are also needed to reduce potential harm to Atlantic salmon and other native species during mitigation.

5 | DISCUSSION

Global responses to reduce carbon emissions, which are beyond the scope of fisheries management, are needed to reduce planetary warming and its impacts. In the interim, we argue that managers must meet the challenges of maintaining and even increasing current wild Atlantic salmon populations by incorporating climate perspectives into decision making. This will demand a holistic view of salmon management and will require working across sectors, governments, and borders to effectively reduce human induced pressures on salmon.

5.1 | Ensuring strong, healthy, and resilient populations

At present, it is not possible to identify and implement direct management actions to counteract salmon declines resulting from climate and ecosystem alteration in the ocean. Given the challenges of managing threats in the ocean, an emphasis should be placed on freshwater ecosystems and salmon health during that period of their life cycle while also minimizing the undesirable impacts from salmon farming in coastal areas.

Fisheries managers, other natural resource and environmental managers and conservation organizations need to promote strong, healthy, and resilient populations of local wild salmonids in rivers and coastal environments. A fundamental strategy to achieve this is to optimize species productivity by ensuring that the greatest number of wild smolts in the best condition enter the ocean. Migration barriers, loss of rearing and spawning habitat, changes in prey base, introduction of non-native species, and poor water quality have contributed to declines and loss of populations in large parts of the range of Atlantic salmon. Improving or maintaining habitat quality, connectivity, ecological functioning, and water quality are front-line defences to mitigate the compounding effects of altered freshwater ecosystems. There is great potential within the Atlantic salmon range for improvements related to water quality, river regulation, migration barriers, refuges (e.g. cold water), and physical river habitats, which can increase production of Atlantic salmon, and improve the quality of juveniles entering the ocean from rivers and coastal areas.

Population-specific conservation limits and management targets that are based on biological reference points have been developed to evaluate attainment of conservation goals (NASCO, 1998). Varying methods to establish conservation limits and assess compliance with these limits and management targets have been developed and used in different countries. Developing conservation limits based on maximizing smolt output from the rivers, and including sufficient levels of uncertainty in the models used to establish the conservation limits and evaluate whether they are attained, will help to ensure that fisheries are not a primary cause for population decline. Research is needed on current conservation limits and the methods used to produce them in order to evaluate whether they provide a robust metric that reflects genetically and demographically healthy populations in the long term.

Maintaining genetic integrity, diversity, and life history variation in Atlantic salmon populations is vital to maximize their ability to adapt to altered environments. Escaped farmed salmon, poorly planned stocking, and all impacts that reduce effective population sizes contribute to undermining the resilience of salmon populations and to their ability to adapt rapidly to climate change. Eliminating interbreeding with escaped farmed salmon, reserving stocking activities to preserve endangered populations after other damaging population impacts have been mitigated, ensuring that genetic integrity and variation is maintained in any stocking programmes, avoiding selective fishing that may alter the genetic variation of populations, and reducing or eliminating other activities that lower effective population sizes are strategies that will maintain the ability of salmon populations to adapt to climate change.

5.2 | Importance of the human dimension

Conservation action (or inaction) is largely an expression of societal values towards wild salmon and their environment. Although most large-scale commercial Atlantic salmon fisheries have been closed or greatly reduced, wild salmon continue to display significant cultural, social, and economic values through indigenous fisheries, recreational fisheries, and tourism. These values, and the people who hold them, are vital for generating and maintaining public, political, and financial support for conservation, protection, and wise management of the resource. Furthermore, much of the practical work of salmon conservation (e.g. habitat restoration) is led by anglers, indigenous communities, and community-based non-governmental organizations, often in partnership with various levels of government. The need for such shared stewardship and meaningful stakeholder engagement is increasingly recognized in government policy (see, e.g. Canada's Wild Atlantic Salmon Conservation Policy (Fisheries and Oceans Canada, 2018). Thus, policies and decisions that disconnect people from wild salmon, or cause them to feel alienated from conservation efforts, can be counter-productive to long-term conservation goals. As salmon populations decline, conservationists and managers are faced with the very real challenge of finding solutions that balance the need to maintain or enhance the value of wild salmon to society against the need to meet biological targets. Simple or obvious solutions – such as the complete closure of indigenous or angling fisheries – may sometimes be less optimal than innovative solutions that allow people to maintain some level of resource use while aiming to increase community stewardship and engagement in conservation efforts to address the root causes of population decline. Developing such solutions will require knowledge of and ability to work with a diverse range of stakeholders.

Most or all of the problems facing wild salmon result, directly or indirectly, from human activities. In many cases, existing scientific knowledge of these issues is sufficient to develop solutions, but the inability to implement such solutions in a timely and effective manner is often hampered by social–political–economic factors (Aas et al., 2018). These include conflict of interest, lack of consensus, mistrust of science and of other stakeholders, diversity of environmental values and ethics, ineffective governance, failure to consider alternative perspectives (e.g. indigenous perspectives), and difficulties in motivating governments, communities, and individuals to take appropriate action. These challenges lie in the realm of communications, education, community engagement, conflict resolution, consensus building, organizational behaviours, and agency culture. Conservationists and managers must, by necessity, expand their capacity to meet these non-biological challenges.

Thus, restoration and conservation of wild Atlantic salmon require attention to the human dimensions from the perspective both of science (i.e. understanding human values, attitudes, and behaviours) and management (i.e. applying a knowledge of human dimensions to develop and implement solutions). Managers, scientists, conservation organizations, and governments must recognize that people are a critical element and need to be deeply involved in the conservation process (Bennett et al., 2017), and that human dimensions must be integral in efforts to conserve, restore and enhance Atlantic salmon populations.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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