Review

Impact of climate change on salmonid smolt ecology

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Abstract: The migratory life history of anadromous salmonids requires successful migration between nursery, feeding and spawning habitats. Smoltification is the major transformation anadromous salmonids undergo before migration to feeding areas and prepares juvenile fish for downstream migration and entry to seawater. We reviewed the effects of climate change on smolt ecology from growth of juveniles in freshwater to early post-smolts in sea. Shift in the suitable thermal conditions by climate change is causing Atlantic salmon to expand their range northwards, while in the southern edge of their distribution populations struggle with high temperatures and occasional droughts. Climatic conditions, particularly warmer temperatures, are affecting growth during freshwater phase in the river. Better growth in the northern latitudes leads to earlier smoltification. Thermal refuges, the areas of cooler water in the river, are especially important for salmonids impacted by climate change. Restoring and maintaining connectivity and suitable diverse mosaic habitat in rivers are important for survival and growth throughout the range. The start of the smolt migration has shifted earlier as a response to increasing water temperatures, which has led to concerns of mismatch with optimal conditions for post-smolts in the sea decreasing their survival. A wide smolt window allowing all migrating phenotypes from early to late migrant's safe access to sea is important in changing environmental conditions. This is true also for regulated rivers, where flow regulation practices cause selection pressures on migrating salmonid phenotypes. Life history in freshwater affects also marine survival, and there is a need for better collaboration across life stages and habitats among researchers and managers to boost the smolt production in rivers.

Keywords: Climate change; salmonids; Salmo; rivers; freshwater; migration

1. Introduction

Anadromous and potamodromous salmonids migrate from their natal river to a feeding environment before returning for reproduction [1-3]. Migration enables fish to exploit many temporally productive and spatially discrete habitats with various fitness benefits (e.g., growth, reproduction, predator avoidance) [4]. Migratory life history requires unrestricted migration routes between nursery, feeding and spawning habitats [5]. During each life stage salmonids utilize the habitat that is advantageous for them, thus the migration between habitats clearly has adaptive value for the individuals [6]. Nursery and feeding habitats differ in environmental characteristics, and migrations precede adaptive physiological transformations and changes in the phenotype and behavior to be better suited in the new environment.

Smoltification is the major transformation that anadromous salmonids undergo before migration to feeding areas. Smolting prepares fish for downstream migration and entry to seawater. Atlantic salmon *Salmo salar* juveniles can stay in their natal river habitat for growth for 1–8 years before migrating [7,8]. Of the Pacific salmon, pink salmon *Oncorhynchus gorbuscha* and chum salmon *Oncorhynchus keta* can move almost directly after the emergence at fry-stage into sea water, while the others (masu salmon *Oncorhynchus masou, O. tshawytscha, O. nerka* and steelhead (rainbow) trout *Oncorhynchus mykiss* spend one or more years in fresh water before migrating to sea for feeding [7]. When smolting the phenotype of fish changes: coloration of smolts becomes silvery and body more streamlined [2]. This together with darkened fins, dark back and white abdomen helps fish to hide better in the pelagic environment [5]. Behavioral changes include loss of rheotaxis, and juveniles become more pelagic. Also, their tendency to group increases [9]. Several physiological changes take place, for example, increased salinity tolerance, increased metabolism, and the olfactory imprinting [10]. Environmental cues, photoperiod, temperature, and water flow, regulate physiological changes and initiate migration [2,5]. Smolting and seawater tolerance seem to develop for lake migrating populations also [11, but see 12], obviously due to genetic connections [13], although individuals spend their whole life cycle in freshwater.

Both Atlantic and Pacific salmon populations have been in decline throughout their range [13-15]. To turn this trend around, it is important to understand the role of different environmental and anthropogenic factors behind the decline [16]. Numerous effects have been found to influence the decline, and with the complex life history of migrating salmonids, the reasons for declines are obviously multiple and hard to unravel [17, 18]. Anthropogenic activities have a long history of altering salmonid populations, thus also smolt development and smolt migration. Smolting as life stage is often more sensitive compared to other life stages [2]. Smolt development, behavior and survival during migration may be adversely affected by several anthropogenic activities, such as hydropower, land use, pollution, fish farming and parasites, like the sea lice *Lepeophtheirus salmonis* [2,5]. Climate change changes the environmental cues and interacts with the other anthropogenic pressures to affect smolting and smolt migration.

Historically climatic variability has affected patterns of abundance in Atlantic salmon and Pacific salmon populations [19-22]. Recently human exploitation, and especially climate change effects, have taken a larger impact on the declining stocks [13,17]. Although estuarine and marine mortality has been found to be an important determinant of survival, marine mortality is dependent on factors acting in freshwater and during smolt migration [23]. Thorstad et al. [24] argue that the best fundamental strategy to mitigate the changing environmental conditions should be to ensure that the highest number of wild smolts in the best condition migrate from rivers and coastal areas to feeding areas. Several factors, like the timing of migration and smolt size, must be in balance with the marine conditions for the successful fulfilment of the life cycle [18,23, 25]. In addition to survival of smolts during migration and post-smolts during early arrival to sea, it is important to address the links between river habitat conditions and physiological requirements of salmonids during their juvenile life stages in freshwater habitats [26]. Climate change will continue to affect not only smolting and migration, but also instream habitats across all seasons [26].

In this paper we review climate change effects on 1) in-river habitat conditions preparatory for smolting, 2) smolting process, 3) smolt migration and 4) early post-smolt survival. Our focus is on *Salmo* spp., but when relevant we also refer to Pacific salmon (*Onchorhynchus* sp.).

2. Climate change and salmonids distribution

Human activities are estimated to have induced approximately 1.0°C of global warming above pre-industrial levels (from 1880 to 2017), with a likely range of 0.8°C to 1.2°C. Global warming is likely to reach 1.5°C at about 2030 if temperature continues to increase at the current rate [27]. For example, higher winter discharge, earlier snowmelt, and earlier onset of summer low flow periods are predicted throughout the range of Atlantic salmon [28,29].

Increasing global surface temperatures are very likely to lead to changes in precipitation and atmospheric moisture because of changes in atmospheric circulation, a more active hydrological cycle, and increases in the water-holding capacity throughout the atmosphere. Overall, global land precipitation has increased by about 2% since the beginning of the 20th century. There have been marked increases in precipitation in the latter part of the 20th century over northern Europe, however, with a general decrease southward to the Mediterranean. Dry wintertime conditions over southern Europe and the Mediterranean and wetter than normal conditions over many parts of northern Europe and Scandinavia [30] are linked to strong positive values of the North Atlantic Oscillation (NAO), with more anticyclonic conditions over southern Europe and stronger westerly winds over northern Europe [reviewed by 31].

Northern Eurasia (north of approximately 40°N) showed widespread and statistically significant increases in winter precipitation during 1921–2015, with values exceeding 1.2–1.6 mm mo^{-1} per decade west of the Ural Mountains and along the east coast, while southern Europe exhibits coherent yet weaker amplitude drying trends that attain statistical significance over the eastern Mediterranean. These precipitation trends occur in the context of changes in the largescale atmospheric circulation, with negative SLP (Sea Level Pressure) trends over northern Eurasia and positive SLP trends over the central North Atlantic extending into southwestern Europe [32].

The magnitude of climate change is considered to depend on the atmospheric load of the two most important greenhouse gases, carbon dioxide (CO_2) and methane (CH_4). The terrestrial biosphere plays an important role in the global carbon balance. In boreal zones, forests and peatlands are an essential part of the global carbon cycle. Recent temperature increases have been associated with increasing forest fire activity in Canada since about 1970 and exceptionally warm summer conditions in Russia during the 2010 fire season [reviewed by 33].

Atlantic salmon is distributed form northern Portugal (42°N) to River Kara in northern Russian in Europe [34], and West Atlantic salmon is distributed from Connecticut River to Ungava region of northern Quebec. Southern Atlantic salmon populations have declined dramatically and face the highest risk of extinction as global warming moves its thermal niche northwards [35]. Suitable thermal habitat for salmon is expected to extend northwards with the invasion of new spawning, nursery, and feeding areas north of the species' present distributional range but with the loss of the most southern populations [36-39]. Indeed, salmon are already responding to warmer temperatures by expanding their range northwards into the Arctic Ocean [40,41] and disappearing from the southern edge of their distribution area [7,42, 43, 39]. The stock complex of Atlantic salmon in Europe has experienced a multidecadal decline in recruitment, resulting in the lowest stock abundances observed since 1970. Atlantic salmon abundance and productivity show similar patterns of decline across six widespread regions of North America [44]. Abundance declined in late 1980s and early 1990s after which it remained stable at low levels. Climate-driven environmental factors, as changes in plankton communities and prey availability in warmer ocean temperature were linked to low productivity of North Atlantic salmon populations [44]. Landlocked European populations of salmonids are found in Norway, Sweden, Finland and Russian Karelia [45-48]. The landlocked stocks of salmon have declined throughout their whole distribution range [48, 49]. Brown trout (*Salmo trutta*) is native to Europe and Asia where anadromous populations are found from Portugal to the White Sea [7]. In future, the living conditions for trout will probably deteriorate in the southern part of the current distribution. In the northern part of their current distribution, global warming may improve feeding opportunities, growth and survival conditions [7]. According to Filipe et al. [50], brown trout distribution will become progressively and dramatically reduced in European watercourses in future. Their forecasts indicated that the greatest losses in suitable habitats will take place in the southern Europe.

3. In-river habitat conditions preparatory for smolting

Most important climate change -driven habitat changes that influence salmonid juveniles in rivers are changes in thermal and hydrological regimes [51-53]. These changes will affect how the juveniles use their physical habitat and affect growth and survival.

Water temperature has various effects on the biology of salmonids. Thermal optima allow salmon to maximize growth while temperatures above thermal optima can stress fish and finally lead to mortality [54,55]. Salmonids are cold water species; global warming will generally have a large impact on their success. On large-scale northern populations are being predicted to do better compared to southern populations under global warming [37, 56, 57], but even in the same river the effects on different populations can vary [55]. Some northern populations can have an increase in parr recruitment and smolt production [57]. However, also some Arctic salmonids are already experiencing warm (>21°C), physiologically challenging migratory river conditions [58], and an increase in river water temperatures has already been widely observed in several rivers [59-61]. In general, high latitude ecosystems are facing rapid warming, and cold-water fish will be eventually displaced by fish adapted to warmer water [62]. The range of temperatures in which fish survive or grow differs between development stages and salmonid species [for review see 7]. For Atlantic salmon, for example, eggs survive around 0-16°C, and alevins can develop normally up to 22°C [63]. Growth takes place in temperatures between 6°C and 22.5°C, maximum growth around 16°C, and upper lethal temperature is 29.5°C for parr depending on the acclimation period. With the warming of surface waters, the risk of local extinctions increases [64,65].

Smolt characteristics are in many ways dependent on the factors acting in freshwater [23, 66]. Temperature during the development in freshwater phase may have an impact on later behavior and life-history traits of salmonids. For example, incubation of eggs in higher temperatures have resulted in fry with reduced swimming performance or later returning adults [67, 68]. According to Thompson & Beauchamp [69] survival of steelhead trout in the marine environment can be driven by an overall higher growth rate set early in life freshwater, which results in a larger size at smolt migration. Climate induced instream thermal conditions affect parr size and age of emigration from the river [70]. For salmonid populations facing increased water temperatures, thermal heterogeneity in the river plays an important role in survival and growth [52, 71]. The density of juveniles in thermal refuges has been found to increase after high temperature effects [52]. Maintaining and restoring a diverse mixture of habitats and thermal refugia is important for salmonids impacted by climate change [72]. Thermal topology can also influence fish growth: fish in the least complex network grew faster and were ready to smolt earlier than fish in the more spatially complex temperature network [73]. Climate induced high-water temperatures can also interact with parr density: while on Chinook salmon at low parr density the effect of temperature on growth was positive, at high densities the relationship turned out to be negative [71].

Especially in the southern margins of the salmonid distribution ranges, the availability of suitable cold-water environments become more important as the temperatures rises [74]. The temporal variability of these cold refuges is high; the most stable ones typically are the groundwater seeps and cold-water tributaries [75]. For the cold-water species like salmonids, headwater streams may become more important structural and thermal refuges. In our experience, headwaters are in many cases less impacted by humans than the main streams. On the other hand, high-elevation streams, especially those above snowlines, can be especially vulnerable to climate change because they are likely to experience the greatest snow–rain transition [76]. Stream size is a limiting factor for some salmonid species, but for species like coho salmon differently sized streams can provide alternative rearing habitat [77]. For brown trout small streams are important spawning and nursery habitats [78,79]. Brown trout is well adapted and influenced by habitat variables associated with the size of small streams, especially with the flow variations [78, 80], and the population traits of anadromous brown trout from a small stream differ from those in larger rivers [68]. Conservation of headwater stream habitats maintains and increases the variability in habitats and life history of salmonids to mitigate the effects from climate change.

Seasonal flow is another key element impacted by climate change contributing largely to the habitat quality of salmonid juveniles [81]. Climate change has already profoundly altered the hydrological regimes of rivers. The intense changes for Atlantic salmon and brown trout include frequent periods with extreme weather, i.e., low and high flow events, precipitation falling as rain and less as snow, and decrease in ice-covered period [7, 82]. These changes can have a large negative impact on freshwater salmon instream habitat [76, 83]. Extremes in water flow can decrease recruitment and survival. Generally, the early life stages, i.e., the eggs, emerging alevins, fry and young juveniles, experience the highest mortalities [84,85]. High flow events during the emergence of fry from the gravel can cause flushing of fry to unsuitable habitats. The preferences for physical habitat parameters, like water velocity and depth, vary seasonally [86]. Climate change induced high or low flows causes variation in this suitable habitat for salmonid parr. Low flow conditions are often associated also with extended duration of high water temperatures [83]. The minimum levels of river flow have been found as regulators for parr survival, and hence for smolt production in Atlantic salmon and brown trout [57,80]. Stream hydrology is also predicted to change when winters get warmer, and increased fluctuations in winter discharge and temperatures and may lead to repeated ice formation and breakup [87-89]. As winters get warmer, it means less snow, more rain and higher winter discharges. These changes can negatively affect growth and survival of juvenile salmonids during winter [90]. The ability of the young salmonids to swim against strong currents is poor at low temperatures [7,91], and salmonid parr prefer relatively slow flow rates in winter [92]. Increased rain on snow with high flow can lead to in ice scouring of the streambed, which results in higher egg mortality [93]. The mortality of salmonids eggs and fry can become higher along climate change in northern rivers.

Water temperature and flow variation, the two important aspects of climate change, are interacting with anthropogenic activities, such as the land-use in the catchment, to affect the fish community in rivers [94]. Anthropogenic activities have for a long time altered migratory fish by closing pathways and creating challenging migration conditions for smolts. Climate change can further strengthen these human caused effects. Climate change will intensify extreme precipitation and flood events over all climate regions [95], but difference at regional scale can be high [96]. Increased precipitation intensity enhances suspended solid and nutrient loadings in rivers especially in human altered catchments [97]. Increased rainfall with land use (i.e., forestry, agriculture) will intensify brownification of surface waters due to increased loading of dissolved organic carbon from the catchments [98,99]. This widespread phenomenon especially in boreal region will deteriorate habitat quality of salmonid juveniles habituated to good freshwater quality. Reduced freshwater habitat connectivity can decrease growth of juveniles and may have deleterious impacts on later marine life stages [100]. Flow regulation typically creates flow and temperature conditions for fish species that prefer warm- and slow-water habitats and can thus favor invasive species. Physically challenging migratory conditions caused by flow regulation together with large diurnal temperature fluctuations can restrict migration of salmonids by limiting their ability to recover from fatiguing exercise [58]. Rapid temperature raise also has negative effect on the osmoregulatory performance of the Atlantic salmon smolts [101]. Consequently, catchment scale conservation, including flow and connectivity restoration, is an important management priority to maintain and improve juvenile salmonid production, and thus smolt production. Conservating headwater stream habitats maintains and increases the variability in habitats and life history of salmonids to mitigate the effects from climate change.

4. Smolting

In salmonids, genetic diversity together with developmental flexibility leads numerous pathways to residency, migration or maturation [102] and, especially among Pacific salmon, there are also other phenotypes than smolts outmigrating rivers [103,104]. Anadromous salmonid juveniles transform from parr to smolts to prepare for downstream migration and entry to seawater. Physiological and behavioral changes take place in the spring when juvenile salmonids undergo smolting. Smolting and smolt migration are considered as a critical life-history stages essential for survival [5]. While still in fresh water, fish undergo a preparatory smolting process involving morphological changes as they become silvery and streamlined [2], (**Figure 1**). Behavioral changes include decrease in rheotactic and optomotor sensitivities and fishes station holding abilities decrease [9]. Photoperiod and temperature regulate physiological changes through their impact on the neuroendocrine system [2]. Thus, because the photoperiod remains the same at the same date and site each year, temperature will be critical in determining responses to future climate change. Within the same river system distance to the sea does not seem to play a role: populations closer or further from the sea smoltify the same time [105,106]. Water flow, and its variability as another major environmental factor, can act more as a timer, for example, to initiate migration [2,7].

Figure 1. When smolting Atlantic salmon smolts become silvery and body streamlined (Photo: Ville Vähä).

Smoltification varies depending on several factors like temperature, latitude, age and size, growth rate, and a combination of these factors. Hence, climate change with raising water temperatures obviously has a substantial impact on the smoltification process. Size and growth potential affect the timing of migration, and also survival of smolts [25,107-110]. Smolt age depends on growth rate: fast-growing parr smoltify younger and smaller than slow-growing parr [111]. Warmer river temperatures increase growth of parr and increase the share of fish smolting at earlier age [70]. Temperature naturally correlates with latitude and is a strong predictor of migration timing in Atlantic salmon [112].

The migration decisions, whether to smoltify or not, are decided between internal and external factors [110,113]. The important external factors are the growth rate and the energetic status of individual fish [5]. Differences in smolting rate between naturally anadromous and more resident populations have an inherited component [113]. High growth rate in late summer and early autumn the year before migration predicts smoltification [5].

Growth and energetics do not solely depend on temperature, but also on other factors, like the food availability. For example, it appears that that smolting may be switched off by poor nutritional conditions preceding smoltification [113,114]. Better growth conditions caused by river temperature rise can increase the proportion of sexually mature male parr, which have lower probability to migrate [115].

How climate change will affect individual growth rates and energetics in salmonid populations will depend intimately on how it affects the ecological status of rivers, and particularly food availability. On a local scale controlling climate change drivers is not possible, therefore proactive measures are recommended against population declines [116]. These measures can include sustainable land use in the catchment and maintaining a diverse mosaic of habitats for salmonids [72,116]. Freshwater environment is especially vulnerable to climate change effects because it is already exposed to numerous anthropogenic pressures and water temperature and flow are highly climate-dependent [117,118]. Territorial salmonid parr also have limited capabilities to disperse as the environment changes.

Climate change can strengthen or weaken the effects of the anthropogenic activities on water quality important for smoltifying salmonids. Pollutants, acidity and sedimentation can adversely affect smolt development which can have negative consequences for their readiness for life at sea

[10,23]. Especially in northern temperate coastal regions, which will receive higher winter rainfall, phosphorus loading from land to streams is expected to increase, whereas a decline in warm temperate and arid climates is expected [119]. In the northern region increasing precipitation increases nutrient leaching especially from areas affected by human alteration: agriculture, forestry and other land uses [120]. For example, acid leaks from the catchment are expected to increase. Increased acidity has a large impact on the fish community, especially to acid sensitive salmonids [121]. Even short moderate exposure of acidity may require more than two weeks for the recovery of Atlantic salmon smolts [122]. Freshwater ecosystems are sensitive to anthropogenic flow regime alteration, which may cause temperature fluctuations. Close to its southernmost distribution, warming together with low flows threatens coho salmon in California, and environmental flow protections is needed to support Pacific salmon in a changing climate [123]. Rapid temperature shifts have negative impact on hypo-osmoregulatory capacities of Atlantic salmon smolts [124]. There is an interaction of salinity and elevated temperature on osmoregulatory performance of salmon smolts, and rapid temperature fluctuations above the threshold temperature (20 °C) have been found to cause osmoregulatory failure.

5. Smolt migrations

Smolts start their downstream migration during a "period of readiness", a smolt window when they are physiologically prepared to meet the conditions in their feeding area [2,125]. With the Atlantic salmon smolt, migration typically takes place during spring and early summer at length of 12–25 cm [126]. Temperature and flow are mostly mentioned environmental cues triggering the smolt migration. Migration times differ between years and rivers; temperature can be a good predictor for the timing [127-129]. Warmer temperatures result in earlier migrations [128]. Typically, a correlation between the onset of smolt emigration and the water temperature has been found [130]. Temperature experience, accumulated temperature, is the cue to initiate migration rather than any threshold temperature [128,131]. The initiation of the smolt migration was positively associated with freshwater temperatures up to about 10 °C and levelling off at higher values [18]. Another major environmental clue that plays an important role in initiating smolt migration is the river flow. During the smolt window increased water flow initiates smolt migration [126,130,132, 133], but high flows have been found also to influence the opposite way by depressing migration [128,130]. Depending on the conditions, the relative influence of water temperature and flow in initiating migration can differ across the years [134]. Other environmental cues, like the photoperiod, have been found to control the initiation of downstream migration [135], but temperature and flow are the key environmental factors to be considered in response to climate change.

When ready, smolts lose their willingness to maintain station in a flow and start migrating downstream with the help of the current. The speed of the current has an influence on the downstream travel time, but smolts actively swim, typically following the mainstream in the surface water layer [7,115,136]. Smolts predominantly migrate at night, but later in the migration period this may change [2,5,137]. Smolts migrate downstream in schools of varying sizes. Relatively little is known about the formation of these groups, some results indicate solitary movement from natal streams followed by schooling further downstream [138]. A genetic component is involved as smolts in Atlantic salmon migrate more in kin-structured groups than with the unrelated individuals [139]. Some environmental factors, like light and dark variation can influence schooling [140].

The timing of migrations has been adapted by evolution to avoid unfavorable conditions and arriving when environmental conditions are suitable for survival and growth [4]. Mismatched timing would lead to decreased fitness: depleted food sources and/or increased predation. As described above the environment has an effect on migration timing, but it is somewhat determined by also genetics [141,142]. The relative contribution of genetic differences remains uncertain [143]. Under climate induced environmental changes different migrating phenological traits may be especially important to the future fitness of the species [126]. It is obvious that Atlantic salmon migration timing is already responding to warming temperatures: the initiation of the smolt seaward migration has occurred approximately 2.5 days earlier per decade throughout the basin of the North Atlantic

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[18].Accordingly, the analysis of long time series (1978–2008) on the timing of smolt migration of Atlantic salmon in the River Bush, Northern Ireland, revealed that earlier emigration periods are evident across the time series [144]. Kastl et al. [123] found out that an increase from 10.2 to 12.8C in mean seasonal water temperature accelerated the migration window by three weeks in coho salmon living near its southern distribution range in California, USA.

The earlier migration timing has given rise to growing concerns about smolts potentially missing the optimum environmental migration “window” [23]. Global warming affects also the receiving marine ecosystem by increasing surface sea water temperatures, and the results of this mismatch are difficult to predict. Climate change affects how and when species interact, potentially decoupling species interactions, and combining others, restructuring predator–prey interactions [145]. Some of these mismatches may lead to increased predation on smolts, or cause starvation, some may have no effect. Better understanding of how these interactions work is crucial to predict vulnerability to climate change effects.

Changed timing of smolt migration can lead to long-term changes to migratory phenotypes of salmonids [e.g., 4]. A wide migration window with diversity of phenotypes can act as a safeguard against uncertainty in resource availability, buffering the variability in predator pressure or thermal mismatch. Survival of phenotypes can depend on the seasonally fluctuating conditions, such as thermal or hydrological circumstances affecting food availability, either directly or indirectly [146]. For example, Sturrock et al. [104] found that relative proportions of migrating phenotypes that contributed to the spawning population differed between the wet and dry year in Chinook salmon. In California’s Chinook salmon the late migrating phenotype dominated, but other strategies played an important role in many years [72]. Kennedy and Crozier [144] observed that marine survival of one sea winter Atlantic salmon were strongly influenced by the run timing, and during the observation period later emigrating cohorts demonstrated increased survival. In lake migrating sockeye salmon entering Lake Washington juveniles migrating later in the season encountered higher zooplankton abundance and warmer water but the optimal date for lake entry ranged across years by up to a month [146]. These examples show that the success of migratory phenotypes varies with environmental conditions. Warming of waters may highlight the importance of rare phenotypes in responding to climate change [72]. Therefore, the loss of phenotypic diversity can have a large impact on population persistence in a warming climate (**Figure 2**).

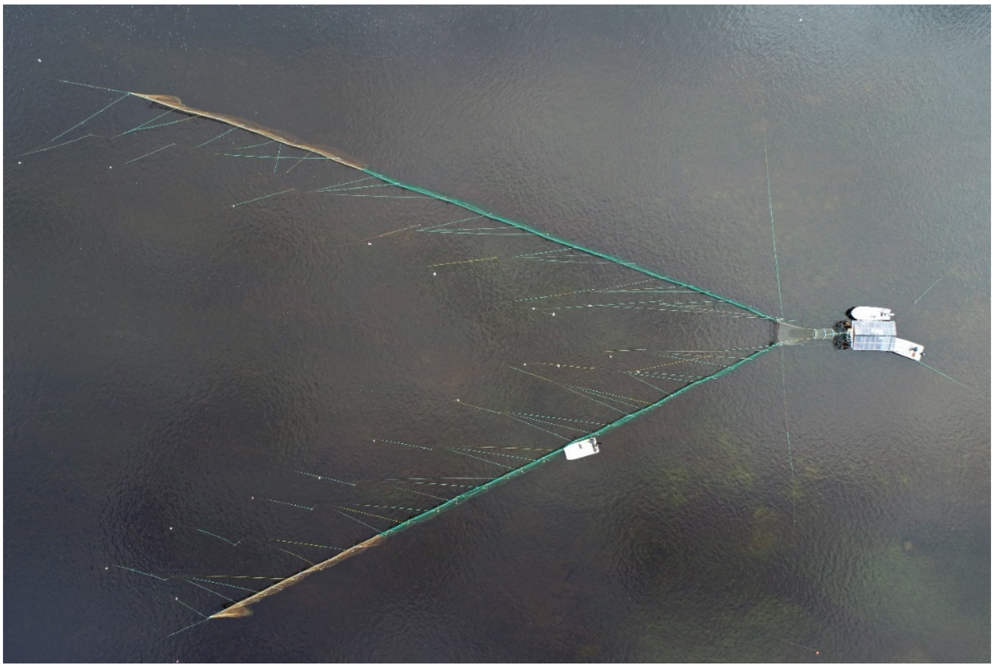

Figure 2. Smolt trap in the River Tornionjoki, Finland, to catch the downstream migrating smolts and monitor their annual numbers and condition (Photo: Ville Vähä).

Anthropogenic use of freshwaters, especially flow regulation with dam construction, has resulted in large population declines and loss of salmon life history diversity [147,148]. Anthropogenic pressures, including climate change, affect the selection pressures in migratory salmonids, also on migrating smolt phenotypes. Hence it would be difficult to consider potential evolutionary responses to climate change without considering other human effects. For example, migration route selection at hydropower plant intake has been found to be consistent with phenotypes, and those traits selecting turbines could potentially be eliminated from the population due to high mortality [149]. To secure the adaptive variability of smolts safe downstream passage should be ensured at hydrodams, either by physical structures or long enough spill time windows. A long spill time is needed to protect the earliest and latest phenotypes migrating [129]. Low flows are expected to become more frequent especially in the southern distribution area of salmonids, and during low flows even small weirs can cause significant delays in smolt migration impacts [150]. River regulation practices are affected by the climate induced changes in temperature and precipitation depending on the region, and they may also change election pressures affecting salmonid populations. The examples above postulate that improved flow management is needed under climate change to avoid further loss of phenotypic diversity in salmonids.

Survival during migration and patterns of mortality has the potential to yield important insights into population bottlenecks [151]. Smolts are vulnerable to predators during their downstream migration in the surface layer. In the southern River Minho (Spain/Portugal) and in the River Endrick (Scotland) the mortality of Atlantic salmon smolts by avian and piscine predators was high, demonstrating that the amount of smolts lost in the river is likely to have strong constraint to these populations [151,152]. High in-river mortalities during downstream migration have been found also in Pacific salmon [153]. Climate change may create conditions that allow successful spreading of predators including invasive species [154-156]. For example, increasing predator populations of cormorants, (*Phalacrocorax carbo sinensis*) and an invasive terrestrial predator in Europe, American mink (*Neovison vison*) can cause elevated predation pressure on smolts [157-159]. Further studies quantifying the impact of invasive species and climate change on smolt migration in more detail are needed for future management considerations.

6. Early post-smolt survival

Most mortality between smolt and adult stages is generally considered to take place during the first year of life at sea when survival, maturation, and migration trajectories are being defined [39,160-162]. The first year of salmon at sea, known as the post-smolt year, is characterized by variable rates of mortality [163]. Mortality has been often considered to be highest during the first few months at sea [164,165]. Young salmonids are sensitive to variable climatic factors and to food availability [166-168]. Reduced marine survival is widely accepted as an important contributor to the observed salmon population declines in recent decades [24,39,169,170]. Ocean climate variability during the first springtime months of juvenile salmon migration to sea seems to be central to the survival of North American stocks, whereas summer climate variation appears to be important to adult recruitment variation for European stocks [163]. In the Baltic Sea, marine survival estimates of salmon post-smolts were negatively correlated with temperature [171]. The anticipated warming due to global climate change will impose thermal conditions on salmon populations outside historical context and challenge the ability of many populations to persist [163].

Salmon post-smolt survival rates in the sea can be influenced by the condition and quality of the smolts when they leave fresh water [23]. In such an effect, the impacts of a stressor experienced in riverine environment do not emerge until the fish has entered the post-smolt phase in the sea [24]. Over recent decades, juvenile salmon in many rivers have grown faster but left freshwater at a younger age, resulting in smaller smolts and increased mortality at sea [23]. In the Gulf of St. Lawrence, northwest Atlantic, the survival of sea entering small smolts was found inferior to large smolts [172]. Smolt size can also influence the subsequent growth rate of Atlantic salmon at sea, with larger smolts showing slower growth [173].

Timing of salmon smolt seaward migration and size of the smolts must be in balance with the marine conditions for the successful fulfilment of the life cycle [18, 23, 174]. The smolt seaward migration should coincide with optimal thermal conditions at sea to maximize survival [2,39,175], but climate change has advanced the timing of salmon smolt migration and created mismatch with optimal conditions for post-smolt growth and survival [18,144,176]. Higher temperature increases in rivers compared to marine habitats increase the risk of resource mismatches and high early post-smolt mortality [168,177], potentially causing smolts to miss the optimum environmental migration "window" [23]. Throughout the basin of the North Atlantic, salmon smolts are initiating their seaward migration 2.5 days earlier per decade in response to the climate change [18]. Observations on brown trout in the River Imsa, Norway, suggest that increased water temperature will induce seaward migration in early spring when sea growth and survival are poor [168].

Warmer temperatures in the North Atlantic have modified oceanic conditions, reducing the growth and survival of salmon by decreasing marine feeding opportunities [39,162,178,179]. Spring plankton blooms and therefore the peak of higher trophic resources available for salmon may be advanced in the season and may occur in different places [180-182], thus potentially creating a mismatch between salmon smolt migration and available resources [170,183]. A climate-driven shift in zooplankton community composition towards more temperature tolerant species with limited nutritional content may be associated with decreased marine survival and growth of salmon smolts [167].

7. Conclusions

Atlantic salmon are already experiencing and responding to climate change induced warmer water temperatures at different scales. On a large scale there are signs of salmon expanding their range northwards, as expected due to suitable thermal habitat shift, while the southern populations are struggling more due to high temperatures and periodic droughts. While increased temperature can have positive effects on the production of northern populations, by increasing growth leading to earlier smoltification, there are also concerns of increased water quality problems by water brownification and eutrophication particularly from human impacted land areas by the effects from increased rain especially during winter. The risk of local extinction of salmon populations has increased especially in the southern edge of salmon distribution. Especially the low flow events, typically associated with high water temperatures, are the population bottlenecks. Mitigating the effects of climate change on a local scale to increase smolt production are flow management and precautionary efforts to maintain and improve the ecological status of rivers. These measures are land use planning and restoration on a catchment scale to diminish loading from the catchment and conservation and restoration of instream habitats.

Smolt characteristics are in many ways dependent on the factors acting in freshwater, and these characteristics affect the post-smolt survival in the feeding area (**Figure 3**). Thermal heterogeneity in the river has a significant role in survival and growth, and we should have better knowledge of the magnitude and location of cold-water refuges in streams. Mapping of these areas with the modern technology would help in conservation work. Maintaining diverse mosaic of habitats and connectivity through conservation and restoration is crucial to mitigate the climate change effects in rivers.

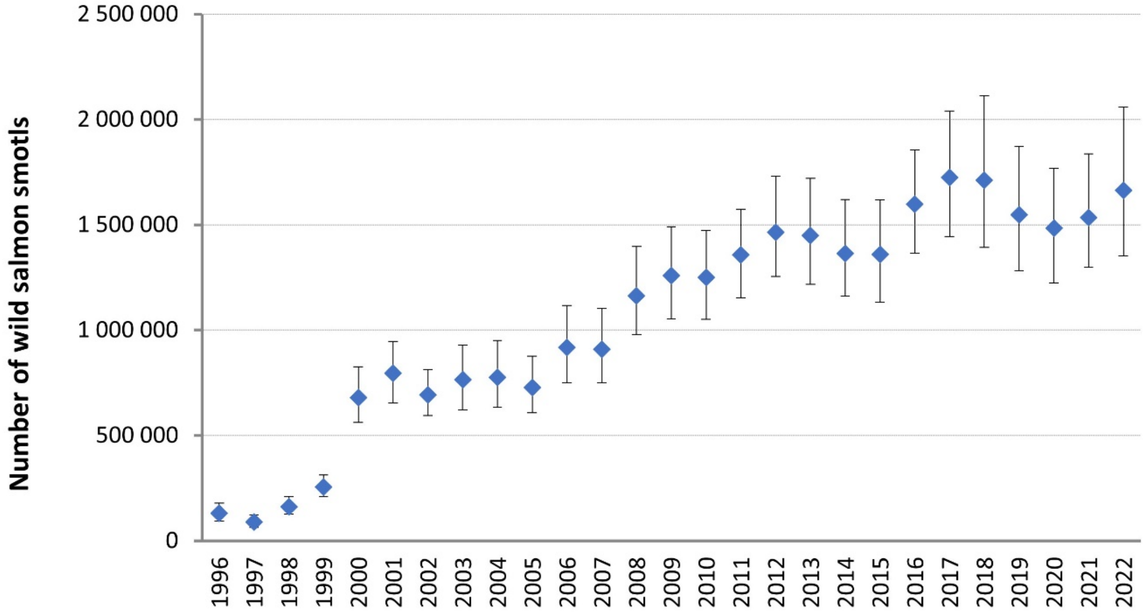

Figure 3. Towards a better future: After successful management actions in the Baltic Sea and in the river itself the annual amount of smolts migrating from the River Tornionjoki has increased substantially [184].

As a response to increasing temperatures an earlier migration timing of smolts is evident throughout the range of salmonids. This changes how and when species interact, and restructures also predator–prey interactions. To readjust to the changed, and still changing, conditions it is important to maintain as wide smolt-window as possible to allow all existing phenotypes, early or late migrants, to prevail. Under climate change different migrating phenological traits may be especially important to the future fitness of the species. This is especially important in regulated rivers where anthropogenic alteration of water flow creates not only increased mortality, but also artificial selection pressures on migrating smolts. This would mean, for example, longer spill water times or keeping the downstream routes open throughout the migration period.

Predation creates a substantial impact on migrating smolts and thus to the entire population. Climate change enhances the spreading of invasive species, including invasive predators, which can increase the total predation pressure on smolts. This emphasizes better control of invasive species, both prevention of their dispersal and better control of their populations.

Finally, we agree with earlier literature stating that there is urgent need for collaborations and research among scientists and managers across life cycle stages and ecosystems to address the research gaps [26], and that the basic strategy to protect salmonids against the effects of climate change should be to make sure that the maximum amount of wild smolts in the best condition leave from rivers [e.g., 23,24].

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