Winter Ecology of Salmonids in Boreal Streams Under Climate Change

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Abstract Winter represents a challenging season for animals in boreal streams and is a period with low temperatures, extremely low levels of primary production, low metabolic rates of ectotherms, and little light. Yet, stabile ice cover provides shelter for salmonids residing in rivers. Despite low light levels in winter, stream salmonids are mainly nocturnal, which protects them from diurnally active predators. Climate change adds unpredictability, increases frequency of winter floods, and can reduce the time that salmonid embryos need to develop until hatching and emergence. These changes can increase natural winter mortality and cause recruitment failures in populations that already are under severe pressure from environmental changes and fishing. We identify a need to better monitor egg and fry survival to predict the effects of changing temperature and environmental stressors such as loading of organic material or flow regulation. Availability of microhabitats for sheltering during winter is crucial and should be considered in restoration efforts focused on recovering threatened salmonid populations. The importance of habitat quality will increase in an unpredictable environment, and both management attention and

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research on the early life-history phases of salmonids are needed to understand how climate change-induced environmental changes affect fish through winter processes.

Keywords Brown trout · Egg survival · Environmental change · Hydropower · Ice · Parr · Winter

1 Introduction

Winter in temperate and boreal regions is a challenging season for many animals. Some animals go to great lengths to avoid winter conditions completely, for example, by seasonal migration or by entering an inactive mode such as torpor or hibernation. Many aquatic animals, like salmonid fishes, do however remain active throughout winter but exhibit adaptive behavioral and physiological acclimatization, such as decreased foraging activity and metabolism (Storey and Storey 1989; Bull et al. 1996; Huusko et al. 2007; Marchand 2014). Yet, our knowledge of aquatic ecosystems in winter remains very limited compared to terrestrial ecosystems or to aquatic ecosystems in other seasons. Logistical constrains explain some of the scarcity of studies in salmonid winter ecology: streams and rivers are challenging to access and work in during winter. Winter has been considered a survival bottleneck for stream salmonids (i.e., both species that live their entire life in streams and certain life stages of migratory salmonids that live in streams), even though relatively little is known about the winter ecology of these species (Cunjak 1996; Reynolds 1997; Huusko et al. 2007; Carlson et al. 2008; Brown et al. 2011; Watz et al. 2015). Winter survival in riverine conditions is crucial, not only for resident populations but also for migratory salmonids; both for the juvenile life stages and for spawned adults that stay in running waters before returning to feeding areas the coming spring. The life cycles of autumn-spawning salmonids such as Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and Arctic charr (*Salvelinus alpinus*) also require that eggs survive and develop within the streambed substrate throughout winter. Winter conditions can thus be crucial for the recruitment of these species.

In this chapter, we will review the winter ecology of stream salmonids. We explore the conditions salmonids experience during winter and synthesize research on how they cope with the winter environment. This chapter also discusses how ongoing global warming changes winter conditions, and how this may affect salmonid populations. Finally, we will present some field examples of the winter ecology of brown trout in one of the northernmost countries in Europe, Finland. In these examples, we will report results from field surveys on the survival of brown trout eggs and juveniles throughout winter.

2 The Winter Environment

2.1 How Do We Define Winter?

Although the concept of winter may appear obvious, a definition may prove useful when we discuss winter from an ecological perspective. For most of us, winter in temperate and boreal regions is the season with freezing or near-freezing temperatures, accompanied by snow, ice, and short days. One could also argue that winter describes such seasonal conditions that induce consistent adaptive responses by animals and plants. In-stream salmonid ecology, there is a definition of winter that is partially linked to life history: winter is the period that starts from egg deposition by autumn-spawning salmonids and ends at ice break. Within this life-history context, spring starts from the commencement of smolt migration, or reproduction of spring-spawning riverine fishes (Cunjak 1996; Cunjak et al. 1998). These definitions encompass an extensive period of the year in boreal environments.

Although defining winter from spawning to ice break gives us a temporal definition of winter, it still is important to bear in mind that winter conditions vary considerably geographically. For example, many salmonids occur in northern and southern Europe, and in northern and southern (North) America. Winter conditions differ considerably within these regions and presumably so do fish populations that inhabit different latitudes. For example, in a study conducted in Norway, loss of energy stores during winter was measured in 13 Atlantic salmon populations along a latitudinal gradient (Finstad et al. 2010). Surprisingly, this study showed that energy depletion was lower in the northern than in the southern populations. Salmon from the northern populations also exhibited higher foraging activity when energy reserves decreased compared to salmon from the southern populations. Similarly, winter energy loss was positively correlated to latitude of population origin when no surface ice was present (Finstad and Forseth 2006). Hence, salmonid populations appear to show some counter-gradient variation, but adaptive differences along environmental gradients are yet generally poorly studied in salmonids. Similarly to counter-gradient variation, Jordan's rule (McDowall 2008) describes a direct ecogeographical relationship between latitude and intraspecific meristic characteristics, such as the number of fin rays, vertebrae, or scales. Whether this rule holds for salmonids remains to be studied. An array of local and latitudinal factors is likely to affect adaptive differences, which makes it challenging to determine the source of intraspecific variation without controlled experiments (McDowall 2008; Jonsson and Jonsson 2011; Morris et al. 2017).

2.2 Winter Conditions and Ice Formation

Short days, subfreezing temperatures, snow, and ice cover characterize winter (Hurst 2007; Huusko et al. 2007; McNamara and Houston 2008; Marchand 2014). In the northern hemisphere, 60% of all river systems develop ice, which affects discharge, water levels, hydraulics, habitat complexity, and light availability (Stickler et al. 2010; Brown et al. 2011). Ice conditions can affect salmonids both positively and negatively. For example, surface ice cover has positive effects on fish growth and survival (Prowse 2001; Finstad et al. 2004b; Huusko et al. 2007; Linnansaari et al. 2008; Brown et al. 2011; Hedger et al. 2013; Watz et al. 2015), presumably as ice cover provides protection against aerial and terrestrial predators, something we will explore in detail later in this chapter.

In late autumn, decreased air temperatures and reduced solar radiation induce cooling of water and ice formation begins. Surface ice first forms in slow-moving stream sections where thermal stratification of water layers may occur, for example close to streambanks (Fig. 1). Bridging of ice starts at the streambanks and on surface stones, and eventually the entire surface is covered by ice (Huusko et al. 2007; Hicks 2009; Marchand 2014). Ice-free pockets in an otherwise ice covered stream develop in areas where the water temperature does not reach freezing or the water velocity does not allow formation of surface ice. Ice cover may, therefore, not form in areas with groundwater input, substantial ground heat, or in areas with turbulence such as rapids that produce friction heat (Power et al. 1999). Large slow-flowing rivers often experience stable ice cover throughout winter, whereas small high gradient streams often have unstable ice formation where ice tends to form and break up throughout winter. In spring, the surface ice melts as solar radiation and temperatures increase, and spring floods mechanically break the remaining ice.

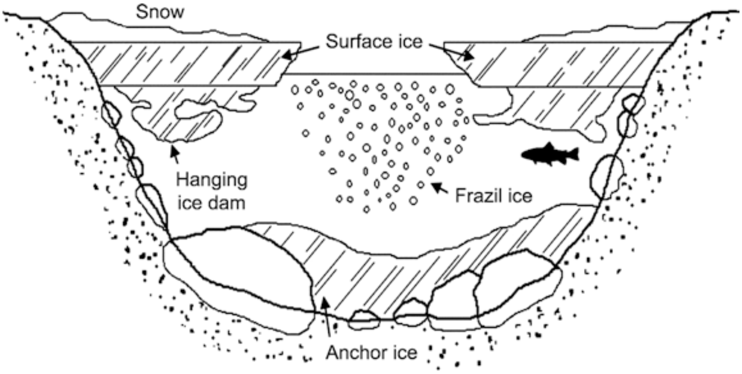


Fig. 1 Conceptual cross-section of a stream in winter. Surface ice forms in low-velocity areas close to the streambanks, and may eventually grow to cover the entire stream width. At high velocities and in turbulent water, temperatures may be <0°C, leading to formation of frazil ice platelets in the water. Frazil ice may attach to the streambed or to instream structures and form anchor ice. When frazil ice adheres to surface ice, the same process forms hanging ice dams

In streams with high flow and turbulence, stratification of water layers is inhibited and sub-zero temperatures can occur without freezing. Under these conditions, small disk-shaped platelets of ice, called frazil ice, are formed (Figure 1). Energy released during the formation of frazil ice, as water goes from a liquid to a solid state, inhibits further cooling, and the water temperature remains at approximately 0 °C. Frazil ice aggregates at instream structures such as rocks, stream wood, or surface ice, where it accretes and forms ice masses called anchor ice. Anchor ice may fully cover instream structures and in some cases even the entire streambed, which has major impact on the physical appearance of the instream environment. Aggregation of frazil ice not only occurs on structures located on the streambed, but it can also accrete to surface ice and form hanging ice sheets in slow-flowing areas. If frazil ice accumulates close to the water surface, ice cover can form and continue upstream as more ice aggregates (Hicks 2009; Marchand 2014). Anchor ice and hanging ice dams thus change the physical structure of fluvial ecosystems in winter, and also affect hydraulic properties such as depth and flow (Prowse and Gridley 1993; Brown et al. 2000; Kerr et al. 2002; Huusko et al. 2007). In addition to surface ice, anchor ice also has a substantial impact on the winter ecology of stream salmonids. How anchor ice affects salmonids will be explored in the forthcoming section on habitat choice in this chapter.

3 Salmonid Winter Ecology

3.1 Metabolism, Growth, and Survival

Salmonids experience the same challenges of low temperatures, predation, and diminished habitat availability during winter as most other animals. Compared to terrestrial winter-active animals such as mammals and birds, however, fish are poikilotherms. Poikilothermy means that animals cannot regulate their body temperature, except behaviorally. Hence, the body temperature of salmonids follows the ambient environment, which leads to reduced metabolic scope in winter. Physiological performance of poikilotherms is often constrained at low temperatures, with repercussions on behavioral activity, growth, and survival (Elliott 1994; Graham et al.1996; Johnston and Temple 2002; Guderley 2004; Jonsson and Jonsson 2011; Watz and Piccolo 2011; Watz et al. 2012; Huusko et al. 2013). Growth of stream salmonids is usually low in winter (Cunjak and Power 1986; Bradford et al. 2001; Härkönen et al. 2021), and there are even reports that juvenile salmonids can shrink (also in length) under harsh winter conditions due to catabolism of their own tissues (Huusko et al. 2011).

Despite river invertebrate abundance and biomass being highest during winter (Hynes 1970; Lillehammer et al. 1989; Haapala and Muotka 1998; Chi et al. 2017), energy depletion can be a major cause of winter mortality (Finstad et al. 2004a; Hurst 2007). This means that if fish stay inactive and save energy during winter, their chances of survival may increase (Cunjak 1988; Berg and Bremset 1998; Simpkins et al. 2003; Biro et al. 2004; Finstad et al. 2004a; Finstad et al. 2010; Hansen and Rahel 2015). As for fish in general (Garvey et al. 2004), body size plays a major role in overwinter survival of salmonids. Small fish experience higher rates of winter mortality, particularly predation, than large fish. This pattern has been reported for several salmonids including Atlantic salmon, brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchys mykiss*), and coho salmon (*O. kisutch*) (Quinn and Peterson 1996; Meyer and Griffith 1997a, b; Johnston et al. 2005). Nevertheless, there are also studies that have not found a relationship between fish size and overwinter survival (Bradford et al. 2001; Lund et al. 2003; Johnston et al. 2005). This could be related to inter-annual growth differences, if mortality is non-linear with respect to size. If fish attain a critical threshold size, mortality is reduced disproportionally (Lund et al. 2003; Huusko et al. 2007). However, even inverse relationships between salmonid size and winter survival have been reported (Carlson and Letcher 2003; Hedger et al. 2013). In a study of Atlantic salmon parr, it was not body size, but the size of energy stores that determined overwinter survival (Finstad et al. 2004a). This suggests conditions experienced during the previous summer could indirectly affect overwinter survival by regulating the energy reserves accumulated over the summer. However, limited food intake during fall did not impact overwinter survival in the study of Näslund et al. (2017). In either case, depleted energy reserves result in behavioral changes, such as increased foraging and reduced activity, and energetic status during winter determines the foraging intensity that is necessary for fish to survive (Bull et al. 1996). Hence, salmonid overwinter survival is determined by a combination of body size, energy reserves, and environmental challenges that occur both prior to winter and during winter.

While many have regarded winter as a period of high mortality for stream fishes, other studies have not found seasonal differences in mortality rates. For example, Scandinavian data on brown trout populations suggest that mortality during winter may not actually exceed mortality in other seasons (Carlson et al. 2008). This inconsistency among studies may be due to a high inter-annual variation in winter survival: when overwinter survival has been examined over several consecutive years, great inter-annual variation has been observed (Huusko et al. 2007). In fact, stable winter conditions in terms of ice cover and constant water flow seem to correspond to periods of low salmonid mortality (Huusko et al. 2007; Linnansaari and Cunjak 2010; Hedger et al. 2013; French et al. 2017). This in turn suggests that climate change-driven instability in winter conditions might increase winter mortality of salmonids. The direct mechanism explaining why stable surface ice cover may reduce overwinter mortality will be discussed in the forthcoming section on predator–prey interactions.

3.2 Habitat Choice

As for many other animals, a heterogeneous environment benefits growth and survival of stream salmonids (Mitro and Zale 2002). It creates opportunities both to find food and avoid predators. Surface ice, undercut banks, crevices within the substrate, stream wood, vegetation, beaver dams, or deeper stream sections such as pools are used as shelter by salmonids in winter (Heggenes et al. 1993; Mitro and Zale 2002; Johnson and Douglass 2009). To spend a considerable amount of time sheltering among instream structures appears to affect winter survival positively (Valdimarsson and Metcalfe 1998; Armstrong and Griffiths 2001; Mitro and Zale 2002; Coulombe-Pontbriand and Lapointe 2004; Finstad et al. 2007), as this both minimizes metabolic costs and results in reduced predation risk (Heggenes et al. 1993; Cunjak 1996; Huusko et al. 2007). In addition, if fish have access to different stream microhabitats in winter this seems to increase their chances of survival (Elso and Greenberg 2001). For example, Koljonen et al. (2012) found that brown trout that overwintered in channelized streams had smaller body mass and exhibited more competitive behavior than trout in streams with sheltering opportunities. In addition, Watz (2017) showed that stress levels of brown trout in winter were lower when fish had the opportunity to shelter among instream wood. Hence, one way for stream salmonids to increase overwinter survival is to use different microhabitats for finding food and avoiding predators. A heterogeneous instream environment thus provides these possibilities in winter.

Instream ice can shape the habitat available for fish in winter and alter flow regimes (Whalen et al. 1999). Formation of anchor ice can homogenize the streambed and reduce sheltering opportunities for fish, resulting in increased mortality (Maciolek and Needham 1952; Jakober et al. 1998; Linnansaari et al. 2008). Anchor ice formation can also lead to large fish aggregations as fish get stuck in between ice formations. Sometimes these aggregations consist of several different species (Jakober et al. 1998; Simpkins et al. 2003; Lindstrom and Hubert 2004). Anchor ice often exhibits a diel formation pattern, especially in northern regions, where ice formation occurs at night. The risk of fish becoming trapped in anchor ice could therefore be greater at night (Heggenes et al. 1993; Whalen et al. 1999). There are reports of fish trying to disperse in an attempt to avoid anchor ice (Brown and Mackay 1995; Jakober et al. 1998; Brown 1999). Patchy anchor ice has, however, been reported to provide a structurally complex habitat and may sometimes function as shelter for salmonids (Roussel et al. 2004; Linnansaari et al. 2008; Stickler et al. 2008). The impact of anchor ice on stream salmonid habitat choice and overwinter survival thus seems to vary considerably, depending on how anchor ice formation alters the instream environment.

In addition to the formation of ice, salmonids also react to ice breakup, which occurs both during mid-winter, e.g., when rain induces rapid snowmelt, or at the onset of spring (Lawford et al. 1995). Ice breakup has a major impact on the river winter environment and may remold river channels and affect substrate transport and riparian vegetation (Gatto 1994; Hicks 1994; Power et al. 1999). Stream fishes, both salmonids and other species, can move long distances when the river environment changes during ice breakup (Brown et al. 2001). A study of Atlantic salmon parr in Norway did, however, show that fish moved the least during ice breakup and significantly more during other ice-related events, such as the formation of anchor ice (Stickler et al. 2007). Cunjak et al. (1998) found that mid-winter ice breakup in Canada resulted in reduced survival of several early life stages of Atlantic salmon, especially the eggs. Some fishes seem to avoid ice breakup altogether, especially when it causes ice scouring, which has been proposed as the reason why rainbow trout overwinter in deeper river sections underneath rocks and rubble (Swales et al. 1986). Ice breakup can also lead to unfavorable conditions when flow regimes change. In extreme cases, both water storage caused by ice jams, and drawdowns when jams break, can lead to fish becoming stranded in dewatered reaches and side channels (Needham and Jones 1959).

Although heterogeneous environments provide sheltering opportunities for salmonids, interspecific competition still occurs. For example, brown trout and Atlantic salmon may compete for shelter in winter (Harwood et al. 2001, 2002), and the competition between these species is often size dependent. Dominance by larger individuals becomes more evident when size differences among fish increase, and at large size differences, dominance is usually established without physical interaction. High growth rate during previous seasons is therefore likely to have positive effects on overwinter survival, as large size helps fish defend resources through increased dominance (Orpwood et al. 2003).

3.3 Diel Activity and Foraging

Diel variation in prey availability, foraging efficiency, and predator exposure influence the behavior of stream salmonids, in general, but perhaps most so during winter (Metcalfe and Thorpe 1992; Bull et al. 1996; Metcalfe et al. 1999; Watz and Piccolo 2011). Stream fishes generally shift from day-active behavior to nocturnal activity at low temperatures (Rimmer and Paim 1990; Heggenes et al. 1993; Fraser et al. 1995; Bremset 2000; Watz et al. 2016). This can be exemplified by the changes that have been reported in diel behavior at the onset of winter in several salmonids, including brown trout (Griffith and Smith 1993; Heggenes et al. 1993; Filipsson et al. 2019), Atlantic salmon (Fraser et al. 1993, 1995), and European grayling (*Thymallus thymallus*) (Nykänen et al. 2004). Similar behavioral changes have also been observed in other stream fishes such as European minnow (*Phoxinus phoxinus*) (Metcalfe and Steele 2001) and galaxiids (David and Closs 2003). In general, during winter, stream fishes stop being active in daylight and instead are active in darkness, whether it be during nighttime or under ice at low temperatures (Heggenes et al. 1993; Fraser et al. 1995; Bremset 2000; Watz et al. 2016). Interestingly, low temperatures can relax intraspecific competition. Alanärä et al. (2001) studied competition between dominant and subordinate brown trout during different seasons and times of day. They showed that trout were temporally segregated when they foraged during summer, with dominant trout foraging at dusk and early night and subordinates in daylight. In winter, this pattern disappeared and all trout foraged during low light conditions regardless of their social status. Thus, the strength of intraspecific competition is reduced at low temperatures, likely as a result of slower metabolism and the reduced need to feed during winter.

At northern latitudes, salmonids experience winter temperatures that are suboptimal for physiological performance. Low temperatures impair locomotion, foraging efficiency, and reaction capabilities in encounters with competitors or predators (Webb 1978; Rimmer et al. 1984; Graham et al. 1996; Alanärä et al. 2001; Jonsson and Jonsson 2011; Watz and Piccolo, 2011; Watz et al. 2012). Performance in relation to predators may be weakened, especially against cold stenothermic (such as burbot, *Lota lota*) and endothermic (such as mustelids) predators. The drift-feeding rate of juvenile salmonids is positively correlated with water temperature in winter as observed empirically in brown trout, Atlantic salmon, and European grayling (Watz et al. 2014a, b). The reduced drift feeding at low temperatures results from reduced energy needs and impaired swimming and prey detection capabilities (Watz and Piccolo 2011). Prey density also seems to play a role in the drift-feeding behavior of juvenile salmonids, as reduced foraging times in cold water are most pronounced, likely due to satiation, when densities of drifting invertebrates are high (Watz et al. 2014a).

Brown trout, Atlantic salmon, and European grayling exhibit higher drift-feeding success in daylight than in darkness (Watz et al. 2014b). Therefore, it is surprising that these species are predominantly nocturnal in winter, when their foraging efficacy would be especially low due to both limited light and low temperature (Watz and Piccolo 2011; Watz et al. 2012; Watz et al. 2014a, b). However, stream fishes usually avoid being active in daylight if their energetic needs can be fulfilled at night, regardless of temperature (Orpwood et al. 2006). This pattern is often explained by the reduced risk of being preyed upon in darkness compared to in daylight. These and other aspects of predator avoidance will be discussed in the next section of this chapter.

3.4 Predator Avoidance

Predators directly impact prey populations by consumption, but also by inducing indirect physiological and behavioral responses that typically vary among individuals (Rehnberg and Schreck 1987; Lima and Dill 1990; Hawkins et al. 2004; McCauley et al. 2011; Vainikka et al. 2021). Predator intimidation affects habitat choice and explains lower foraging activity than expected based on bioenergetic considerations only (Greenberg et al. 1997; Vehanen and Hamari, 2004; Preisser et al. 2005; Orrock et al. 2013; Enefalk et al. 2017; Filipsson et al. 2019). Stream salmonids spend a substantial proportion of time sheltering to avoid predators in winter (Valdimarsson and Metcalfe 1998; Jonsson and Jonsson 2011; Enefalk et al. 2017; Filipsson et al. 2019), and diel activity patterns seem to result from behavioral trade-offs between food intake and predator exposure (Metcalfe et al. 1999). Many semi-aquatic mammals, such as otters (Lutridae) and mink (*Neovison vison*) (Gerell, 1967; Wise et al. 1981; Heggenes and Borgstrøm 1988), or birds, like herons, kingfishers, mergansers, and even certain owls may prey on stream salmonids in winter (Harvey and Nakamoto 2013). Fish are preferred winter prey by some terrestrial generalist predators because of the impaired predator detection and escape capabilities of fish at low temperatures. In addition, terrestrial prey such as reptiles, amphibians, and insects are generally unavailable in winter, which makes fish and river invertebrates the most abundant prey for many winter-active animals (Alexander 1979; Harvey and Nakamoto 2013; Marchand 2014).

Surface ice plays an important role in predator–prey dynamics in winter-time stream ecosystems, as it reduces predation risk, particularly from aerial predators (Huusko et al. 2007; Watz et al. 2013, 2015). Some semi-aquatic mammal predators, such as otters and mink, can forage under the ice. Nevertheless, otters usually exhibit a strong association with ice-free river sections or steeply banked shorelines where they can find access to the water underneath the ice (Melquist and Hornocker 1983; Marchand 2014). Salmonid activity during the day in winter can be positively correlated with surface ice thickness (Linnansaari and Cunjak 2013) and ice cover increases overwinter survival compared to ice-free conditions (Hedger et al. 2013). Exemplifying this, a population of rainbow trout occurring downstream of a dam decreased in size when reservoir water was released, preventing surface ice formation (Simpkins et al. 2000). In a field experiment, Watz et al. (2016) simulated ice cover by covering stream stretches with plastic sheets. Brown trout in uncovered stream stretches stayed closer to the streambanks during the day, often underneath undercut banks. Trout in covered stretches were, on the other hand, observed over the entire stream width. In addition, trout that spent the winter in plastic-covered stream stretches had higher growth rates than trout in areas without plastic sheeting.

Brown trout, Atlantic salmon, and Arctic charr show reduced metabolic rates under simulated ice cover (Finstad et al. 2004b; Helland et al. 2011). Several other studies also suggest that ice cover reduces stress levels, as indicated by body coloration (Watz et al. 2015), opercular beat rate (Millidine et al. 2008; Watz et al. 2013, 2015; Watz 2017), and cortisol levels (Watz 2017). In fact, high levels of stress hormones may directly influence overwinter survival, and artificially elevated cortisol levels correlate positively with winter mortality in brown trout (Midwood et al. 2015), which also exhibits a high expression of cortisol-related genes at low temperatures (Filipsson et al. 2020). In addition, studies have shown that bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarkii*) reduce the time they spend sheltering among instream structures when surface ice is present (Jakober et al. 1998) and that ice cover induces increased swimming activity, foraging intensity, and territoriality in juvenile salmonids (Watz et al. 2013, 2015). As most winter-active terrestrial piscivores such as otters, mink, and birds are visual predators, it is reasonable to assume that stream salmonids exhibit reduced vigilance and stress levels when ice cover is present, as it reduces the predation risk from these animals. Surface ice thus plays a major role in the winter ecology of stream salmonids (Finstad et al. 2007; Huusko et al. 2007; Watz et al. 2016), with bearing on several aspects of their ecology such as diel patterns, activity, habitat choice, and foraging behavior. Reduced surface ice cover, both temporally and spatially, is likely to become more evident in the near future as a result of warming winters. This change to the winter environment is thus likely to have negative effects on the overwinter survival of stream salmonids.

Stream salmonids are not only subjected to aerial and terrestrial predators in winter. There are other threats in the instream environment as well, from which surface ice provides little protection. Piscivorous fish also prey on stream salmonids in winter, and examples of piscivorous fishes in boreal regions include burbot (Tolonen et al. 1999; Kahilainen and Lehtonen 2003), northern pike (*Esox lucius*) (Hyvärinen and Vehanen 2004; Vehanen and Hamari 2004), and various salmonids (Hawkins et al. 2004). In an aquarium experiment, Enefalk et al. (2017) studied the shelter use of juvenile brown trout in winter at different times during the day and in the presence and absence of burbot. More brown trout sheltered among stream wood and within the streambed in daylight than in darkness. Trout sheltered less in the streambed, especially in daylight, when stream wood was available. Trout also avoided sheltering in the streambed in the presence of burbot. Likewise, Filipsson et al. (2019) showed that trout sheltered more under overhead cover in the presence of burbot when the amount of light increased, presumably to avoid terrestrial predators. At night and dawn, trout sheltered less than in daylight, but then instead spatially avoided the burbot. Hence, predator threat from piscivorous fish during winter may be most pronounced in darkness, when neither juvenile salmonids nor piscivorous fish are under strong predation pressure from mammals or birds.

4 Egg Survival and Embryonic Development

Not only do juvenile and adult salmonids inhabit streams in winter but these fishes also have overwintering eggs. Winter-time egg development is a crucial life stage for many salmonids and egg survival can form a significant population regulation bottleneck. Species like Atlantic salmon and brown trout spawn during the fall, deposit their eggs in the stream substrate, and their eggs hatch during late winter or in spring, depending on spawning time and river temperature from fertilization to late winter (Figure 2). The emergence of fry from the substrate occurs in spring or early summer. Many species of Pacific salmonids (such as coho, Chinook *Oncorhynchys tshawytscha*, sockeye *O. nerka,* chum, *O. keta*, and pink *O. gorbuscha* salmon) and chars (such as Arctic char and brook trout) also spawn in running waters during summer or fall and have eggs that hatch during the winter or early spring. Winter conditions can thus have a major impact on salmonid egg development, survival, and the time of emergence (Johnston 2006; Lavery and Cunjak 2019). Lavery and Cunjak (2019) found that several abiotic factors, such as water temperature, water level, dissolved oxygen, ice conditions, and substrate characteristics predicted the egg survival of Atlantic salmon. For instance, in gravel beds with low hyporheic quality and therefore low concentration of dissolved oxygen, Atlantic

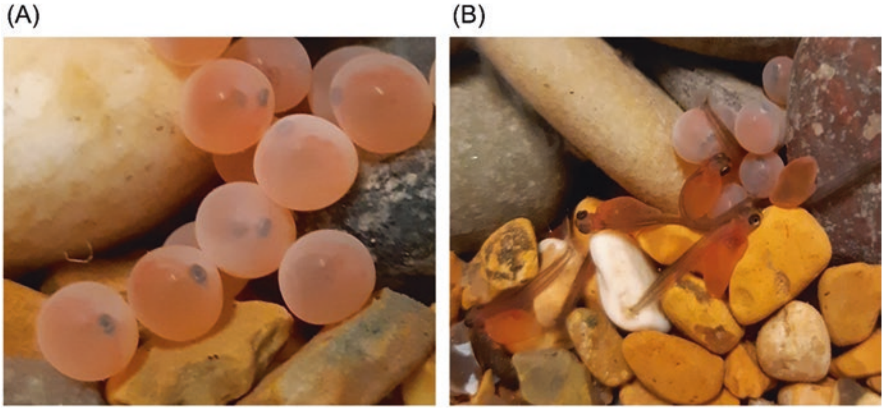


Fig. 2 Brown trout eggs at the eyed stage (A), and newly hatched yolk-sac fry (B) reared in captivity in artificial redds. Trout in the photos originate from the River Klarälven, Sweden, where developing eggs usually reach the eyed stage around the turn of the year and hatch in March–April. Photos: Karl Filipsson

salmon eggs suffer reduced egg survival (Malcolm et al. 2003, 2004, 2005). Lavery and Cunjak (2019) also found that interactions between different environmental factors likely play a major role in egg development, a conclusion drawn from other studies as well. For example, hatching success of Chinook salmon was reduced under hypoxic conditions, but even more so when in combination with warm water (Del Rio et al. 2019). Reduced oxygen concentration in hyporheic water often results from the upwelling of groundwater, causing egg mortality (Malcolm et al. 2004; Youngson et al. 2004; Bowerman et al. 2014), but it is unclear how groundwater–surface water interactions change if winter flow increases in rivers by repeated snow smelting. In ditched forests and peatlands, winter thaws may increase runoff of organic material, which in turn accumulates in bottom substrates, consumes oxygen when decomposing, and hinders water flow through interstitial spaces among gravel particles (Laine et al. 2001).

Temperature has the most important influence on salmonid embryogenesis (Hamor and Garside 1976; Tang et al. 1987; Elliott and Hurley 1998; Ojanguren and Braña 2003; Cingi et al. 2010; Janhunen et al. 2010), which is the case for ectothermic animals in general. Embryonic survival and development are highest at population-specific thermal optima and therefore reduced both at higher and lower temperatures (Ojanguren and Braña 2003; Réalis-Doyelle et al. 2016). Within the species-specific natural thermal range, time to hatching is shorter at higher temperatures. Lower temperatures throughout incubation seem to result in fewer deformities and reduced mortality (Ojanguren and Braña, 2003; Jeuthe et al. 2016; Lee et al. 2016). Temperatures approximately 5–10 °C above natural winter temperatures may result in suppressed development and increased mortality. Strengths of these effects and what thermal range a given species tolerates do, however, vary between species and populations (Janhunen et al. 2010; Lahnsteiner 2012; Réalis-Doyelle et al. 2016). Similarly, temperatures 5–10 °C above natural temperatures at the time of spawning have negative effects on gamete quality and gametogenesis of brown trout, e.g., sperm motility and enzymatic activity, thus affecting survival prior to the commencement of embryogenesis (Lahnsteiner 2012; Lahnsteiner and Mansour 2012). It is thus likely that warming winters can negatively impact the recruitment of autumn-spawning salmonids.

Embryonic temperature has been shown to affect gene expression associated with immunity and stress in brown trout (Meier et al. 2014). Gene expression responses influenced by thermal conditions during embryogenesis have also been found in Atlantic salmon, where salmon embryos subjected to heat shocks exhibited vertebral deformities in subsequent developmental stages. These deformities were related to the reduced expression of two genes that are involved in the proliferation and specification of skeletal cells (Wargelius et al. 2005). In contrast, incubation of lake whitefish (*Coregonus clupeaformis*) eggs at different temperatures exhibited deleterious responses at constant elevated temperatures but not during heat shocks (Lee et al. 2016).

Many animals prey on salmonid eggs, which results in extensive egg mortality during fall and winter. Several fishes and aquatic invertebrates such as cyprinids, cottids, and crayfishes consume salmonid eggs (Ellrott et al. 2007; Johnson et al. 2009; Palm et al. 2009; Findlay et al. 2015). In addition, salmonid eggs can be an important food source for both juvenile and adult salmonids (Johnson and Ringler 1979; Cunjak et al. 1986; Cunjak and Therrien 1998; Gende et al. 2002; Ruff et al. 2011), with reports of salmonid eggs constituting over 90% of the diet of juvenile salmonids during fall (Johnson and Ringler 1979). Hence, predation on salmonid eggs can be considerable and is likely to have major impacts on recruitment dynamics. Atlantic salmon parr feed readily on salmonid eggs in winter, and as eggs are of high caloric content this could possibly increase the likelihood of winter survival if lipid reserves of fish are low (Cunjak and Therrien 1998; Cunjak et al. 1998). As mentioned earlier, predators induce multiple sublethal anti-predator responses (Stoks et al. 2006; McCauley et al. 2011). Conditioning to predator cues during embryogenesis can affect fish after hatching. Rainbow trout juveniles conditioned to northern pike odors during embryogenesis, in combination with conspecific or heterospecific alarm cues, exhibited anti-predator behaviors in the presence of pike (Horn et al. 2019), whereas juvenile rainbow trout not subjected to predator cues as embryos did not react to the presence of pike. Direct embryonic responses to predator presence such as elevated heart rate have also been observed in a few teleost species (Oulton et al. 2013; Atherton and McCormick 2015), but have not been reported for salmonids.

Interestingly, factors affecting egg survival and embryogenesis may not only affect fish during the egg phase, but also various traits later on in ontogeny (Jonsson and Jonsson 2014, 2019), as in the above-mentioned example on predator-conditioned rainbow trout. Not only perceived predation risk during embryogenesis, but also abiotic conditions may impact fish later in life. For example, brown trout reared under hypoxic conditions as eggs exhibited delayed emergence from the streambed when compared to trout from eggs reared under normal oxygen conditions. Hypoxia-reared trout also had reduced swimming activity in encounters with predators and suffered from higher predation mortality as a result (Roussel 2007). Thermal effects during embryogenesis also play a major role in the development of salmonid life-history traits. In Atlantic salmon, higher temperatures during embryogenesis resulted in accelerated growth, and earlier smoltification and sea migration (Jonsson et al. 2005; Finstad and Jonsson 2012; Burgerhout et al. 2017). Differences in growth were still evident in adult salmon, in which they also resulted in larger eggs and higher gonadal mass (Jonsson et al. 2014). Jonsson and Jonsson (2018) studied how embryonic temperature influenced migration behavior of Atlantic salmon. They found that salmon subjected to 3 °C warmer water as eggs returned to the Norwegian coast about 2 weeks later on average during their spawning migration compared to salmon from eggs incubated at natural winter temperatures. In brown trout, juveniles incubated at elevated temperatures as eggs had a lower metabolism than trout from eggs incubated at natural winter temperatures (Durtsche et al. 2021). For sockeye salmon, the swimming performance of the fry is reduced when they are reared at elevated temperatures as eggs (Burt et al. 2011). Temperature during the egg phase may thus have a major impact on the physiology, behavior, and life-history traits of salmonids post-hatching. Warmer winters and their impact on salmonid eggs, juveniles, and adults are likely to become even more evident in the near future as a result of ongoing climate change (IPCC 2021). In fact, the air temperature increase caused by climate change is especially pronounced during winter and at boreal latitudes, a topic we will revisit toward the end of this chapter.

4.1 Embryonic Development and Survival of Brown Trout: Case Studies from Finland

In this section, we present examples where development and survival of brown trout eggs have been quantified in the field in Finland. These examples cover the ecological aspects of egg development and overwinter survival, and some additional methodological and technical considerations.

The area of Finland (337,030 km^2) is representative of northern latitudes, as the country is situated between latitudes 60° and 70° N. Winter (here defined as when the mean air temperature remains below 0 °C) lasts for about 100 days in southern Finland and about 200 days in the north (Finnish Meteorological Institute 2021). Typically, winter begins in mid-October in northern Finland and during November in the rest of the country. Seasonally permanent snow cover is typically found two weeks after the start of the thermic winter, and snow cover is the deepest around mid-March, with an average of 60–90 cm of snow in eastern and northern Finland and 20–30 cm in southwestern Finland (Finnish Meteorological Institute 2021). The lakes and rivers typically freeze over in late November and early December. The coldest temperatures in winter are from −45 °C to −50 °C in Lapland and from −35 °C to −45 °C elsewhere in inland Finland (Finnish Meteorological Institute 2021).

In Finland, the timing of brown trout spawning depends on latitude (Seppovaara 1962; Saraniemi et al. 2008; Niva et al. 2013). The spawning period begins when water temperature is 8−12°C and ends when temperature is 0−2°C (Syrjänen, unpublished). The eggs incubate in well oxygenated gravel, and the alevins typically hatch in March–May in southern Finland and in May–June to the north, depending on the water temperatures (Fig. 3) (Louhi et al. 2008; Syrjänen et al. 2017; Louhi et al. 2010). Alevins emerge from gravel mainly in May in the south and in June in the north. Favorable conditions (i.e., good water quality and suitable water temperatures) in winter and during snowmelt freshets are essential for the development and survival of eggs, and also for parr in the river. Generally, the early life stages, i.e., the eggs, emerging alevins, fry, and young juveniles, experience the highest mortalities (Huusko et al. 2007). However, true estimates of survival in the field are difficult to obtain due to the difficulty of counting eggs without harming them and the harsh winter conditions with ice cover preventing access to spawning sites. In fact, most estimates of survival are based on apparent survival rates (Huusko

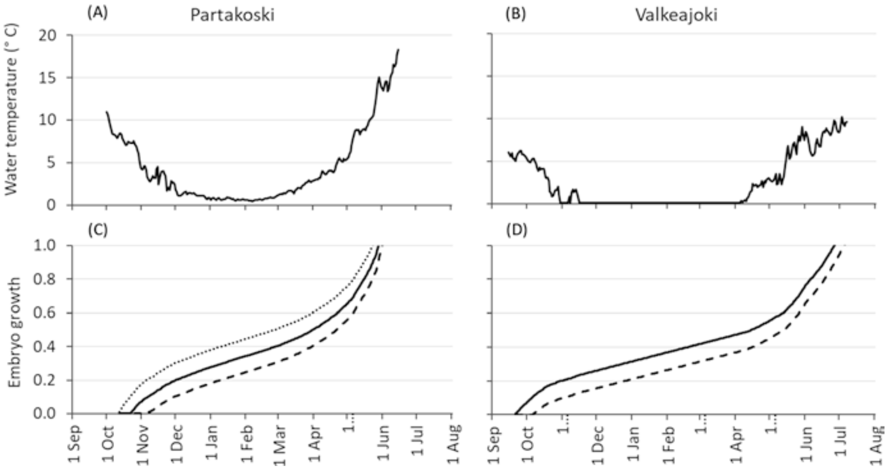


Fig. 3 River water temperature (**a**, **b**) and the progress of wild brown trout embryos (**c**, **d**) from fertilization to emergence in the Partakoski Rapids (61° 16.3’ N, 27° 42.0’ E) in southern Finland in 2017–2018, and the River Valkeajoki (67° 32.6’ N, 23° 54.5’ E) in northern Finland in 2019–2020. The fertilization period, that is the spawning period, was estimated with repeated redd counting in the study reaches and marking of new redds. The development of embryos was followed during the counting rounds when the earliest redds (dotted line), the highest number of redds (solid line), and the latest redds (dashed line), were found. The emergence day for alevins was estimated using the equation of Elliott and Hurley (1998), which reflects the consumption of yolk, or the growth of embryo, from fertilization to emergence. The average estimate (E_{50}, see Elliott and Hurley, 1998) was used, which reflects the day when half of the alevins from redds of each counting round had emerged. On the day of spawning and fertilization, the E_{50} was set to 0. Then, the daily development was calculated with the daily temperature value and added to the E_{50} of the day before. The yolk is absorbed, and emergence occurs the day when the cumulative sum reaches 1

et al. 2007), and few studies have actually compared survival rates of juveniles between winter and other seasons (Carlson and Letcher 2003; Carlson et al. 2008). Another difficulty in obtaining representative mortality estimates relates to the fact that most salmonids in southern Finland are of hatchery origin and known to display much reduced survival in the wild compared to native, wild populations (Syrjänen et al. 2017).

Mortality of embryos from fertilization to near hatching or to near emergence has often been studied in incubation chambers using hatchery-produced eggs deposited in natural streams (Syrjänen et al. 2017; Arola et al. 2019). The experimental design most often has included several plastic net cylinders filled with gravel, and 50 eggs in each cylinder. Cylinders have been placed in net baskets on the channel bottom of riffles in similar microenvironments where natural trout redds are situated. The survival of embryos has varied strongly between the studies and sites. Survival has been 85–98% in oligotrophic unregulated lake outlet rivers with stable channel substratum (Syrjänen et al. 2017), and 30–50% in forest streams that have ditched catchments and acidic water (Arola et al. 2019). The lowest documented survival levels, 0–10%, have been observed in streams with unstable substratum, i.e., sand that moves on the stream bottom and fills spaces between gravel particles and the eggs in the incubation cylinders (Arola et al. 2019), or streams situated downstream from peat mining sites (Laine et al. 2001).

Estimates of in situ growth of embryos have been performed in artificial incubation chambers by inspecting and lifting the chambers regularly throughout winter and spring (Syrjänen et al. 2008). Embryo development begins in autumn immediately after fertilization if water temperature is several degrees but slows gradually following a decrease in water temperature. In mid-winter, i.e., from December to February, development is very slow, as the water temperature is mainly 0–1 °C. In the spring, development accelerates again following a gradually rising temperature. The embryos mainly hatch from March to May, depending on degree days, latitude and distance to an upstream lake. In southern Finland, alevins in experiments have been estimated to emerge in late May and early June, but this may vary between years (Syrjänen et al. 2017).

A method to observe wild embryos in redds has been developed in recent years (Syrjänen, unpublished). In this method, the researcher systematically wades through the study riffles and inspects each redd encountered. This is done in November or December. The redds are verified by careful digging and visual confirmation of 2–3 eggs. The detected redds are marked on digital maps as well as with white-painted and numbered marker stones, in the field. The stone is placed precisely at the point where the eggs were found. The redds are visited again in April, May, or June, depending on the latitude and timing of freshets. Again, the redd is opened carefully, beginning from the marker stone so that 4–10 embryos are identified either in the gravel or are captured in a hand net positioned just downstream from the marker stone. If most or all of the exposed embryos are dead, the redd can be opened more to observe a larger number of embryos. Thus, the sample size per redd is often small, and only embryos situated nearest to the gravel surface are observed. There might be some differences in survival with redd depth, but this has not been studied. However, survival estimates with this method, as based on direct counting of live and dead eggs in spring, have been similar to egg incubation experiments conducted in natural rivers, as described earlier.

In most unregulated clearwater rivers and rapids, the average percentage of live embryos per redd (n = 5–30 in each case), hatched or unhatched, has been 85–100% of all observed embryos. In contrast, the proportion of live embryos has varied between 30 and 90% in riffle sections downstream of a hydroelectric power station. Observations have been made in two highly regulated Finnish rivers, in Ämmäkoski (in the city of Varkaus), Leppävirta watercourse and in Laurinvirta (in the city of Kontiolahti), Pielisjoki, both situated in the Vuoksi watershed, eastern Finland as well as in a regulated river with stable flow, i.e., Gullspångsälven, a tributary of Lake Vänern, Sweden. There may, of course, be other factors than fluctuating discharge affecting egg mortality in these regulated rapids, like the size of particles used in artificial gravel beds created when restoring the rapids or the amount of fine organic matter.

The development rate of wild embryos can be high already in autumn, which has been seen in redds during November or December, as eyes of embryos can often be observed through the eggshell when the embryos are 10–15 mm long. In some extreme cases in southern Finland, some alevins have been observed already in December. These may represent offspring from fish that spawned very early in the season at water temperatures of 10–12 °C. It is also common that the embryos are not visible in autumn, and these eggs may represent fish spawning later in the season at water temperatures of 0–2 °C. Some observations in 2017–2019 have shown that the spawning period may occur later, based on observations made in the twentieth century (Syrjänen, unpublished).

There are some unpublished survival estimates of wild brown trout from fertilization to parr (first autumn values) from southern Finland (Figure 4). Egg density in the study areas was calculated by counting the number of trout redds and measuring the tail lengths of the observed redds and estimating the lengths of female spawners (Crisp and Carling 1989; Elliott 1995; Syrjänen et al. 2014). The density of 0-year-old parr was estimated by electrofishing in the standard sampling areas located inside the redd counting areas, and the density estimates were corrected and calculated with catchability values estimated in the same rivers. The range in survival from egg to parr was large, i.e., 0–21% between years in three riffle sections in the River Rutajoki (n_{years} = 17–21), two sections in the River Arvaja (n_{years} = 11–12), and two sections in the River Saajoki (n_{years} = 4), all small rivers discharging to Lake Päijänne (Figure 4). The average density of 0-year-old trout parr was 1–23 ind./100 m^2 between the study reaches in the rivers, estimated by catchability, indicating incomplete parr production compared to the potential of riffles as parr habitats. One main reason for this is the lack of lake migrating females because of high fishing mortality in lakes (Syrjänen and Valkeajärvi 2010). Unfortunately, no estimate of winter survival of wild embryos exists for these rivers, but in incubation experiments, survival of hatchery eggs from fertilization to May was high (Syrjänen et al. 2008). Mortality is probably high during emergence and the period immediately after (Cattanéo et al. 2002; Lobón-Cerviá 2004). Possible factors affecting

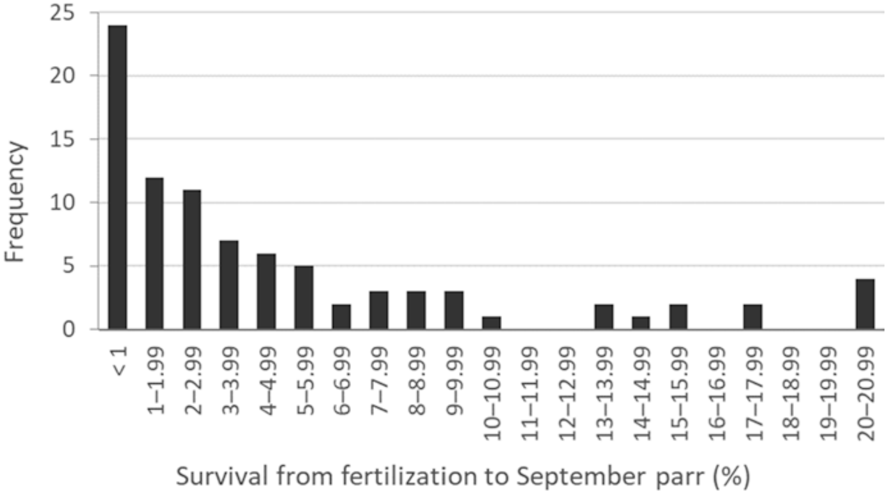


Fig. 4 Apparent survival estimates of brown trout from fertilization to parr (the following autumn) from Rivers Rutajoki (three riffle sections, 17–21 years in each section), Arvaja (two riffle sections, 11–12 years), and Saajoki (two riffle sections, 4 years) in southern Finland. Total number of observation years = 88

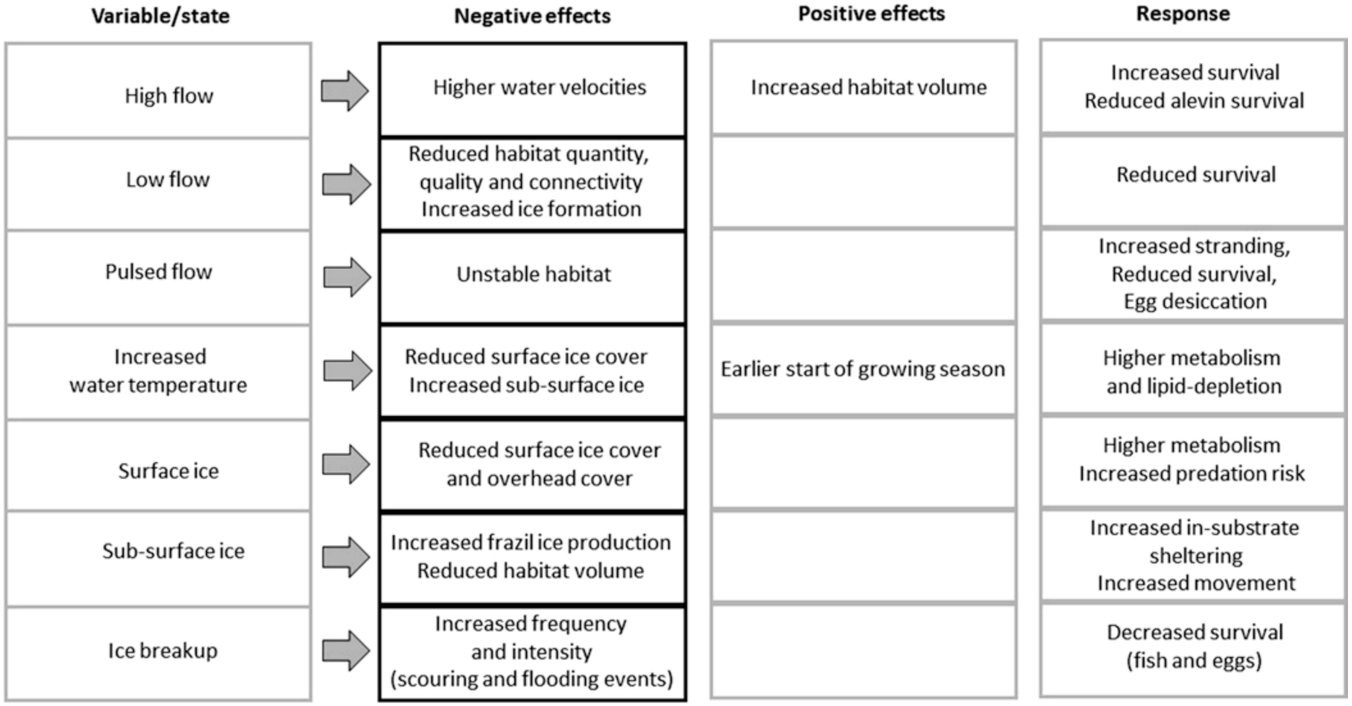
annual variation in egg-to-parr survival could be water temperature, river discharge, and fish predation during the emergence period. Unfortunately, during and just after emergence, survival estimates from nature are rare. Young parr are small and difficult to observe, so the density is difficult to estimate reliably at that point of the life cycle.

5 Regulated Rivers in Winter

Hydropower is a renewable energy source with substantial societal benefits, but it also has severe impacts on the riverine biota, particularly migratory fish (Soininen et al. 2019). The question that historically has attracted the most attention is the impact hydropower stations and dams have on fish migration and how to minimize this impact (Banks 1969). Dams and hydropower stations change the habitat and block movement to and from the natural spawning and feeding grounds for both upstream and downstream migrating fish, and therefore both technical and nature-like bypasses have been developed to facilitate migration of fish at hydropower stations (Clay 1995; Larinier and Marmulla 2004). Environmental impacts are likely to be complex in systems extensively regulated for hydropower, altering biodiversity and even life histories of the impacted species (Gillespie et al. 2015; Poff and Zimmerman 2010; White et al. 2017). The regulation system and operational strategy are the main drivers behind hydrological changes. Regulation systems can typically be divided into (1) high-head systems and (2) low-head or run-of-the river systems (Heggenes et al. 2018). High-head systems have high-elevation reservoirs and long transfer tunnels to the power station with bypass reaches receiving reduced residual or stable environmental flows. Empirical knowledge on the effects of short- and long-term regulation of flow and changes in water temperature on salmonid performance, survival, and production is relatively limited (Heggenes et al. 2018, 2021).

Winter river ice formation in naturally flowing rivers can be divided into (1) the dynamic period "freeze-up" in early winter with sub-surface ice, (2) more stable "mid-winter" with surface ice, and (3) the ecologically challenging "ice breakup" in late winter with potential mechanical ice runs and scouring (Turcotte and Morse 2013). The duration of these periods varies depending on prevailing climate. Flow regulation in hydropower production modifies these conditions, particularly in reaches downstream of power station outlets. This is caused by increased flow, higher water temperatures, reduced surface ice formation and increased sub-surface ice formation, and in bypass reaches by decreased flow and enhanced freezing. The stable mid-winter ice periods may be replaced by repeated unstable transition periods (i.e., repeated freeze-ups and breakups) or ice may become completely absent (Stickler and Alfredsen 2009; Gebre et al. 2013; Prowse et al. 2011; Weber et al. 2013). To this end, the environment downstream of hydropower stations in winter looks much like the changes forecasted by climate warming (Heino et al. 2016). In high-head hydropower regulation with large storage capacity and thermal stratification in the reservoirs, downstream effects from the power stations are stronger than in low-head systems. The latter may have small or no major impacts on downstream ice conditions and water temperature due to usually limited water storage capacity (Olden and Naiman 2010; Dickson et al. 2012). Systems with hydropeaking (pulsed flow regimes) are characterized by rapidly changing high and low flows, depending on down-ramping rate, ramping amplitude, and timing of pulses, creating unstable habitat conditions. In rivers with hydropeaking, flow changes typically match the demands in electricity consumption with high flows during day and low flows during night. Hydropeaking can have negative effects on salmonid populations, for example, by reducing overwinter survival, and has many ecologically harmful effects on river ecosystems (Puffer et al. 2015; Smokorowski 2022; Batalla et al. 2021).

Fish may suffer or benefit from winter flow regimes modified by hydropower, as regulation directly modifies stream habitat and thereby fish behavior, survival, and production, thus resulting in a variety of biological responses (Heggenes et al. 2018, 2021). In winter, the impacts are mainly related to higher downstream water temperatures and flows, or reduced water flow in bypass reaches, and associated changes in ice (Fig. 5). Flow and ice directly affect spatial habitat conditions for fish, and thereby fish behavior and activity, but temperature also directly affects fish metabolism (Shuter et al. 2012; Heggenes et al. 2018, 2021). Higher flows in winter may increase rearing and/or resting habitat, which may potentially benefit fish survival (Forseth and Harby 2014). Low flows may increase ice formation, reduce and fragment available habitat, and may reduce egg and fish survival. Sudden drawdowns of flow during daytime may result in fish stranding as the fish are less inclined to move



Variable/state	Negative effects	Positive effects	Response
High flow	Higher water velocities	Increased habitat volume	Increased survival Reduced alevin survival
Low flow	Reduced habitat quantity, quality and connectivity Increased ice formation		Reduced survival
Pulsed flow	Unstable habitat		Increased stranding, Reduced survival, Egg desiccation
Increased water temperature	Reduced surface ice cover Increased sub-surface ice	Earlier start of growing season	Higher metabolism and lipid-depletion
Surface ice	Reduced surface ice cover and overhead cover		Higher metabolism Increased predation risk
Sub-surface ice	Increased frazil ice production Reduced habitat volume		Increased in-substrate sheltering Increased movement
Ice breakup	Increased frequency and intensity (scouring and flooding events)		Decreased survival (fish and eggs)

Fig. 5 Impacts of winter flow regulation for hydropower on river habitat and potential salmonid responses (adapted from Heggenes et al. 2018)

and seek shelter during the day (Saltveit et al. 2001; Halleraker et al. 2003). To this end, Halleraker et al. (2003) recommended dewatering in darkness at all times of year to reduce stranding of salmonids, and to use slow ramping rates <10 cm h^{-1} (i.e., the rate of change of water level). If flow during the spawning season is higher than the minimum maintained flow during winter, dewatering and mortality of eggs are often unavoidable (see the section "Embryonic development and survival of brown trout—case studies from Finland" in this chapter). Forseth and Harby (2014) summarized that a reduction of over 30 cm in water level from the spawning period average to the lowest weekly average during winter potentially causes a moderate to severe bottleneck for egg survival, although this is dependent on the occurrence and distribution of spawning areas. Casas-Mulet et al. (2015) reported about 20% lower survival of Atlantic salmon eggs in the top layers of gravel beds in the dewatered areas. However, deeper in the gravel beds, due to surface water and groundwater interactions, egg survival was comparable to permanently wet areas. Embryo development is linked to water temperature, with warmer temperatures shortening incubation time and advancing alevin emergence, which leads to a potential mismatch in the emergence time and food availability for the fry (Shuter et al. 2012; Myers et al. 2017). The impact of altered case-specific temperature regimes on embryo development and the timing of initial feeding ("swim-up") can be estimated using, e.g., the model of Crisp (1988) or Elliott and Hurley (1998).

6 Winter Ecology and Climate Change

6.1 Warming Winters

Global climate change is likely the most widespread anthropogenic threat to the environment and to biodiversity. During the last century, the global mean temperature has increased by ~1 °C, with the most accelerated temperature increase after 1970 (Hansen et al. 2010; IPCC 2021). Importantly, the temperature increase varies geographically, where mean air temperatures at northern latitudes are increasing more than twice as fast as the mean global temperature increase. In the last decades, an air temperature increase of 2–3 °C has been reported in the Arctic and boreal regions, with the largest increases in winter and spring (Brown 2000; Marchand 2014; IPCC 2021). This has resulted in warmer winters with more precipitation, whether it be snow or rain, or extremely variable, both spatially and temporally (Magnuson et al. 2000; Smol et al. 2005; Jonsson and Jonsson 2009; Callaghan et al. 2011; Walsh et al. 2011; Kang et al. 2016).

Warming of the climate leads to the loss of snow and ice cover, especially at the southernmost limits where snow covered winters occur. A lack of snow cover results in reduced albedo and causes a feedback loop that accelerates warming. Albedo is a measure of how much solar radiation that is reflected from a given surface. Dark surfaces such as water and soil have low albedo and thus absorb a high proportion of solar radiation. White surfaces such as snow and ice reflect solar radiation and instead have high albedo. Thus, snow and ice, with their high albedo, have the potential to suppress air temperatures by as much as 4−8 °C. The lack of snow and ice therefore results in higher winter temperatures (Leathers and Robinson 1993; Choi et al. 2010; Marchand 2014). Climate change can thus accelerate thawing of permafrost in the Arctic. This subsequently releases methane from soil and water, which accelerates the greenhouse effect through a positive feedback loop (Christensen et al. 2004; Kort et al. 2012). Loss of albedo results in spatial and temporal asymmetries of climate change and will likely lead to even warmer winters during the coming decades. For example, snow cover duration in Scandinavia is projected to decrease by 30−40% by 2050 (Callaghan et al. 2011).

Stream hydrology is also predicted to change when winters get warmer. Fluctuations both in winter temperatures and discharge may lead to repeated ice formation and breakup throughout winter (Magnuson et al. 2000; Döll and Zhang 2010; Pörtner and Peck 2010; Tisseuil et al. 2012; Schneider et al. 2013; van Vliet et al. 2013a, b). In the northern hemisphere, later freezing and earlier breakup dates for stream and lake ice have been recorded throughout the twentieth century (Magnuson et al. 2000). As mentioned previously in this chapter, loss of surface ice cover can negatively affect the growth and survival of overwintering stream salmonids (Härkönen et al. 2021). Conditions can be further exacerbated in regulated rivers due to fluctuations in discharge and water temperature, resulting in longer periods without ice cover or repeated ice formation and breakup throughout winter (Simpkins et al. 2000; Ugedal et al. 2008; Gebre et al. 2013; Nafziger et al. 2017; Heggenes et al. 2018, 2021).

6.2 Winter Ecology of Salmonids Under Climate Change

In the last decades, climate change effects on salmonids have received considerable attention. With this in mind, we will only present research that has examined how climate change directly affects the winter ecology of stream salmonids. Therefore, subjects such as phenological mismatches that often are discussed in relation to the ecology of anadromous salmonids during other seasons (Pörtner and Peck 2010; Donnelly et al. 2011; Bell et al. 2017; Myers et al. 2017) will not be our focus.

Climate change is projected to alter the structure and dynamics of fish communities (Buisson et al. 2008; Williams et al. 2009; Linnansaari and Cunjak 2012; Shuter et al. 2012; Wobus et al. 2015), which leads to major changes in freshwater ecosystems (Smol et al. 2005; Woodward et al. 2010; Shuter et al. 2012, Heino et al. 2016). This includes thermal effects on aspects of fish ecology during the entire life cycle, including reproduction, embryonic development, migration, invasive species resistance, species distributions, and trophic dynamics (Stenseth et al. 2002; Jonsson and Jonsson 2009; Wedekind and Küng 2010; Brodersen et al. 2011; Cahill et al. 2012; Bhat et al. 2014; Morita et al. 2014; Chown et al. 2015; Trigal and Degerman 2015, Heggenes et al. 2021). Taking embryonic development as an example, the development and survival of salmonid embryos depend heavily on abiotic conditions throughout winter. Higher winter temperatures expedite embryogenesis, with the possible effects on embryo condition and development as mentioned in the section about egg survival and embryonic development in this chapter. Warmer winters also mean less snow and with that, more rain (IPCC 2021). Cunjak et al. (1998) found that high egg mortality of Atlantic salmon was caused by rain on snow, as it resulted in ice scouring of the streambed, including the salmon spawning redds. Highest mortality occurred during a mid-winter thaw and breakup, when high discharge was confined to the river channel, constrained by frozen ice and snow banks. Hence, mortality of salmonids eggs and fry is likely to be higher as winter temperatures increase in northern rivers. Warming winters may also affect spawners and may in many cases lead to later spawning. This seems especially likely considering that these reproductive traits are under strong selection pressure (Hendry and Day 2005; Carlson and Seamons 2008). Energy consumption is likely to increase in spawners when temperatures rise, and there are studies on salmonids that show how spawning survival is reduced when energetic costs are high (Jonsson et al. 1997).

Thermal effects on biotic interactions are also likely to be a consequence of the changing climate and may in many cases have more pronounced ecological repercussions than the direct impact of elevated temperatures. One example would be the aforementioned consequences of reduced surface ice coverage on salmonid mortality during winter, where less ice makes fish vulnerable to aerial and terrestrial predators. Indirect effects on biotic interactions not only include predator–prey interactions, but also interspecific competition. Arctic char exhibits both greater foraging efficiency and growth in winter compared to sympatric brown trout (Helland et al. 2011). In a study of 190 Norwegian lakes, ice cover duration correlated negatively with brown trout biomass, but only in lakes where trout occurred in sympatry with char. Ice cover duration did not affect brown trout biomass in lakes without other fishes. Similarly, a high abundance of Arctic char was associated with low trout population growth only when ice cover was present. This suggests that elevated temperatures and loss of surface ice cover will benefit brown trout at the cost of Arctic char (Helland et al. 2011; Ulvan et al. 2012). In fact, some anadromous Arctic char populations that live in sympatry with Atlantic salmon in northern Norway have decreased in size, possibly as salmon are enjoying a competitive benefit over char by their better resistance to climate warming in this region. Interestingly, a positive correlation between growth and summer temperatures was found for both salmon and char, but salmon had higher growth rates (Svenning et al. 2016).

Different species also have different thermal optima for physiological processes (e.g., locomotion and reproduction). These interspecific differences may lead to thermal asymmetries in biotic interactions, such as those between predator and prey. In studies of predator–prey interactions between northern pike and brown trout, water temperature has been a major predictor of the outcome of the interaction. Öhlund et al. (2015) found a threshold temperature of 11 °C, under which the attack success of pike was significantly reduced compared to the ability of brown trout to avoid the pike. Above 11 °C, the performance of pike and brown trout was approximately equal and other factors were likely to influence the outcome of the predator–prey interaction. Interestingly, the results of this experimental study are consistent with field observations from small lakes in northern Scandinavia, where pike and brown trout occur in sympatry in cold water lakes but not in warm water ones (Hein et al. 2013).

In addition to the direct effects of warmer winters, warmer summers may also affect overwintering salmonids. Periods with extremely high summer water temperatures result in reduced availability of preferred thermal habitats or absence of suitable riverine habitats altogether, with consequences for the balance between anabolism and catabolism, foraging opportunities and growth. This could consequently result in reduced growth and fecundity, and decreased accumulation of fat reserves. As size and energy stores can be crucial for the survival of juvenile salmonids in winter (Finstad et al. 2004a), this could negatively affect salmonid populations as the climate gets warmer. High summer stream temperatures may also affect spawning (Mantua et al. 2010; Warren et al. 2012). A study on brook trout in eastern North America showed that high summer temperatures delayed spawning and also correlated with a lower number of spawning redds. This particular population of lake-spawning brook trout spawns in areas with discharging groundwater that has relatively constant winter temperatures, which results in consistent times for egg incubation. Hence, delayed spawning could cause delayed fry emergence and possible mismatches with the occurrence of suitable food for salmonid fry (Warren et al. 2012). This highlights how the temperatures that salmonids experience during summer could influence both recruitment success and overwintering survival at mobile life stages.

7 Brown Trout and Warming Winters: Examples from Finland

Here, we present case studies of brown trout survival during winter from Finland. We compare apparent survival of brown trout during winter to other seasons, and use data on egg and fry survival to model the impact of climate change on the survival of brown trout.

Brown trout is native to Finland, with a distribution covering all of Eastern Fennoscandia (Kaukoranta et al. 1998). Throughout Finland, brown trout forms resident, mainly riverine populations, and migratory populations that feed in the sea (anadromous brown trout), large lakes (adfluvial brown trout), or larger riverine sections (potamodromous brown trout) (Huusko et al. 2018; Syrjänen et al. 2017; Rasmussen et al. 2019). Both resident and migratory individuals are found in sympatry in many systems. To compare apparent survival during winter with other seasons, we monitored the densities of brown trout juveniles for nine years (1999−2007) in six small forest streams (second-to-third order streams) with stable ice cover, situated in northeastern Finland (Figure 6). In a representative reach (~100 m long), containing several riffle-pool sequences, fish densities in each rapid were monitored

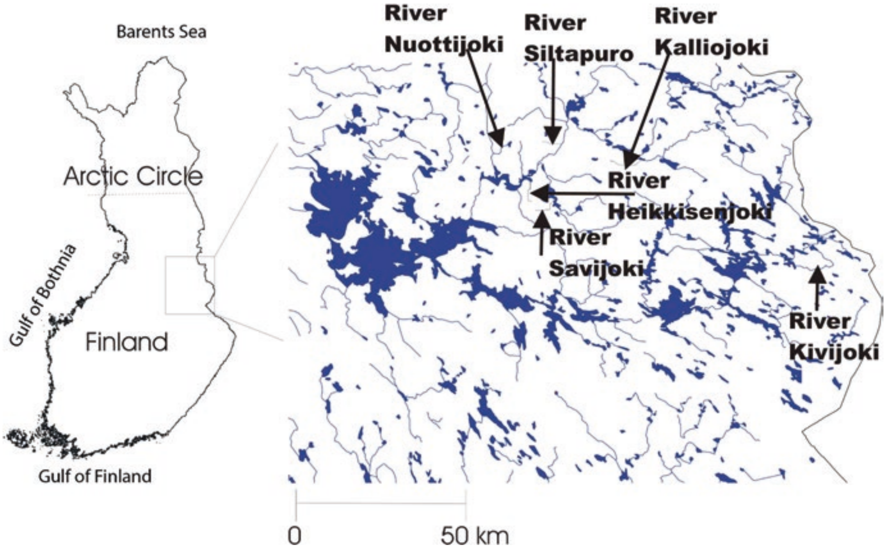


Fig. 6 Location of the six study streams

three times a year (June, August, October) using quantitative electrofishing (Vehanen et al. 2010; Louhi et al. 2016). The weight, length, and age (scale samples) of all fish caught were measured and fish densities were estimated by age group (Zippin 1956). Instantaneous daily loss rate (M_i, per day) was calculated for each period as $[\ln(N_{\mathrm{initial}}) - \ln(N_{\mathrm{final}})] \times (D_{\mathrm{final}} - D_{\mathrm{initial}})^{-1}$, where N is the density of parr observed, and D is the day of year. As the populations of brown trout in the study streams were very sparse in the beginning of the study, each study section was stocked with age-0 migratory brown trout (adipose fin clipped) at equal density (0.35 fish m^{-2}) every September, starting from 1998. The maximum summer water temperatures in the study rivers typically remained below 20 °C in July–August, and winter water temperatures were close to 0 °C.

Densities of stocked age-0+ brown trout declined substantially within one month following their release in September, indicating a high post-release natural mortality (Figure 7). The highest instant loss rates for hatchery trout were observed during this period (Figure 7). During October to June, i.e., the first winter, the densities declined noticeably, but instant daily loss rates were lower than in the fall. June to August had the highest survival for age-1+ and 2+ fish, but during August to October the loss rates increased again, with levels higher than winter (Figure 7).

In general, the densities of the age-0+ wild brown trout were low, and lower than the stocked fish of similar age (Figure 7). We assumed that the declines in densities of wild trout had already occurred before our first sampling in June, presumably during post-hatch stages in spring. The early life stages generally experience the highest mortalities (Huusko et al. 2007; Hayes et al. 2019). Thus, the instant loss rates for natural fish in our study were relatively low, and especially low during winter and summer (Figure 7). During autumn the loss rates, as

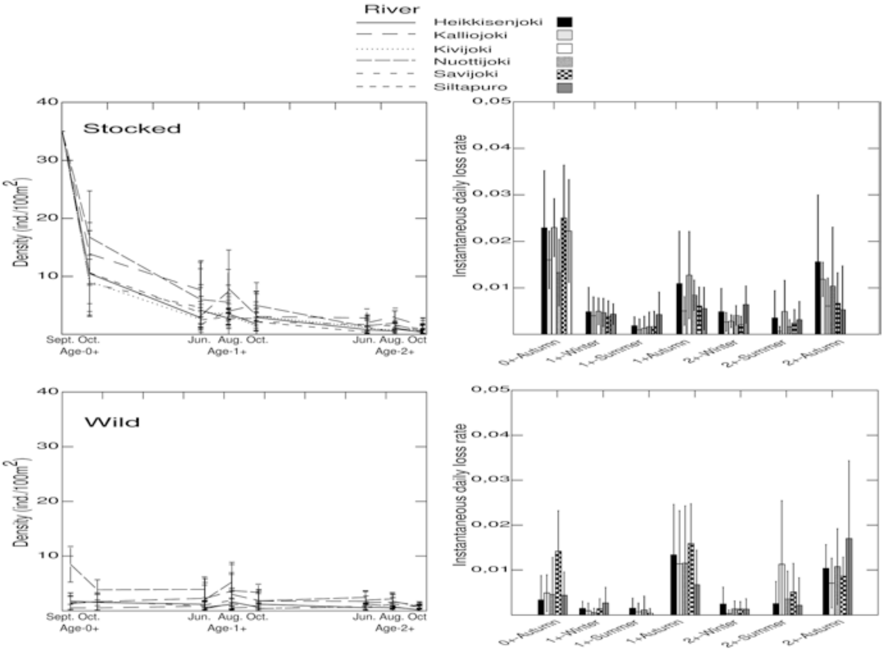


Fig. 7 Mean densities (mean ± SD, left panel) and instantaneous daily loss rates (mean ± SD, right panel) of brown trout in study streams. The upper panel shows the stocked fish (initial stocking density 35 ind./100 m^2), and the lower the wild brown trout

observed for stocked fish, increased. To conclude, our results from stocked and wild brown trout suggested that winter was not a period of especially high mortality in small streams under stable ice cover, when the duration of the period was considered.

We correlated the amount of precipitation (mm, sum) during September–October with the densities of 0+ natural wild fish (pooled from all rivers and over August and October samplings). There was a significant correlation between the September−October precipitation and the mean brown trout density of 0+-fish from the following year for the period 1999−2007 ($r = 0.74$, $p = 0.023$, $N = 9$) (Fig. 8). During a year with an exceptional drought, the brown trout year classes were at their lowest during the period monitored (Vehanen et al. 2010). Increased autumn stream flow due to precipitation increases potential spawning areas and can also support migrating spawning adults to reach these small streams (e.g., Kanno et al. 2014). We expect that this relationship between year class strength and autumn precipitation persisted, because winter water temperatures (Vehanen et al. 2010), and obviously also discharge conditions, remained constant under ice and snow cover. Winter conditions, such as water temperature, water level, and ice conditions, can have a large impact on salmonid egg survival (Kanno et al. 2016; Lavery and Cunjak 2019). Climate change is expected to shorten the

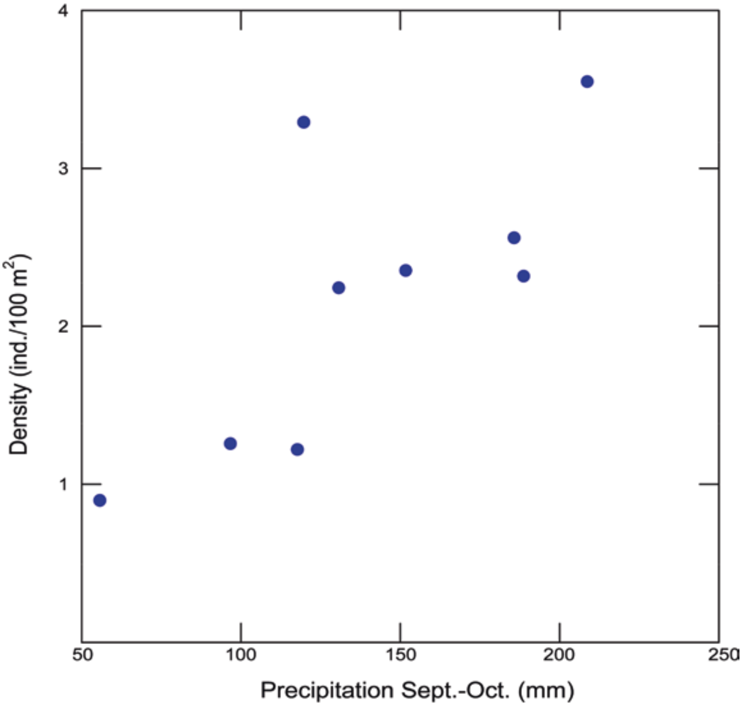


Fig. 8 Correlation between autumn precipitation (September-October, mm) and the mean density of natural wild brown trout populations in six study streams in Finland during study years 1999–2007

period of ice cover and increase winter rains, which can have a negative effect on egg survival in the future.

7.1 Modelling the Impacts of Climate Change

Factors such as increasingly frequent winter floods with potentially increased scouring (i.e., physical destruction of the eggs close to the gravel surface due to the erosion of the surface material), lack of surface ice cover and increasing runoff of fine sediments and organic material from terrestrial systems, caused by climate change, are all expected to decrease the survival of eggs, fry, and small parr (Montgomery et al. 1996; Cocchiglia et al. 2012; Gauthey et al. 2017; Junker et al. 2015). This may well be emphasized in dredged or poorly restored narrow river channels, and in dredged catchments. In some cold water locations, climate change might improve summer-time growth conditions for brown trout (optimum growth temperatures 15.4°C–19.1°C) (Forseth et al. 2009), but other effects, occurring via changes in egg and fry survival, might override the growth-related population-level effects. Thus, to quantify the population-level consequences of potential changes in winter-time survival of the developing eggs, we simulated an age-structured brown trout population model, parameterized for the Finnish–Russian River Oulanka system (see Syrjänen et al. 2017 for the model description) over a range of survival proportions from egg- to 1-year-old parr. Assuming constant mortality during other seasons, this parameter reflects changes in the winter-time survival of the developing eggs.

Through simulations with first-year survival varying from 1 to 30%, we showed that small changes in winter-time survival of eggs can have major population-level consequences (Figure 9a–c). In natural conditions, the critical egg-to-fry survival rate appears to be between 1 and 5%, while compensatory recruitment processes through Beverton-Holt type recruitment dampen potential effects at higher survival rates when the stock is close to the carrying capacity and the finite reproduction areas limit the total production of recruits (Figure 9a–c).

Simulations show that fishing at an annual instantaneous rate of 0.5 y^{-1} (i.e., 39% annual mortality) and a minimum size limit of 600 mm, gives a rapid increase in the population when the egg survival increases from 5% to approximately 10% (Figure 10a–c, see also Syrjänen et al. 2017). A fishing mortality rate of 0.5 y^{-1} but with a minimum size limit of 500 mm would require first-year survival of ~10% to sustain production (Figure 10d–f). In a scenario with historical brown trout fisheries management in Finland, i.e., with a fishing mortality rate of 1.0 y^{-1} (63%) and minimum size limit of 350 mm, the Oulanka brown trout population would likely become extinct even at first-year survival proportions up to 30% (Figure 10g–i). This result highlights the potential importance of ensuring low fishing pressure on populations under environmental stress during the first year of life. Thus, historical fishing regimes, rather than climate change, explain the poor historical trends of brown trout stocks in Finland.

The steep, nonlinear dependence of population metrics on first-year survival suggests that rather small environmentally driven changes in the survival of the early life stages of brown trout can have abrupt and detrimental effects at the population level if the winter time survival of eggs, alevins, and fry decreases due to environmental changes beyond the tipping point. Thus, this simple modelling exercise calls for better monitoring of egg and fry survival in natural waters under climate change. As we used rather conservative estimates of parr and smolt survival rates in the model (see Syrjänen et al. 2017 for the full parameter table), the absolute estimate of the critical 10% survival might be too pessimistic. Available data, for example, from the brooks of Gotland and rivers of the Pyrenean piedmont, suggest that this criterion is easily met in good quality spawning environments with egg-to-fry survival rates over 50% (Rubin and Glimsäter 1996; Dumas et al. 2007). Yet, the Finnish examples described in this chapter suggest that poor habitat quality may prevent recovery of many southern brown trout populations (see the previous section on embryonic development and survival of brown trout in this chapter).

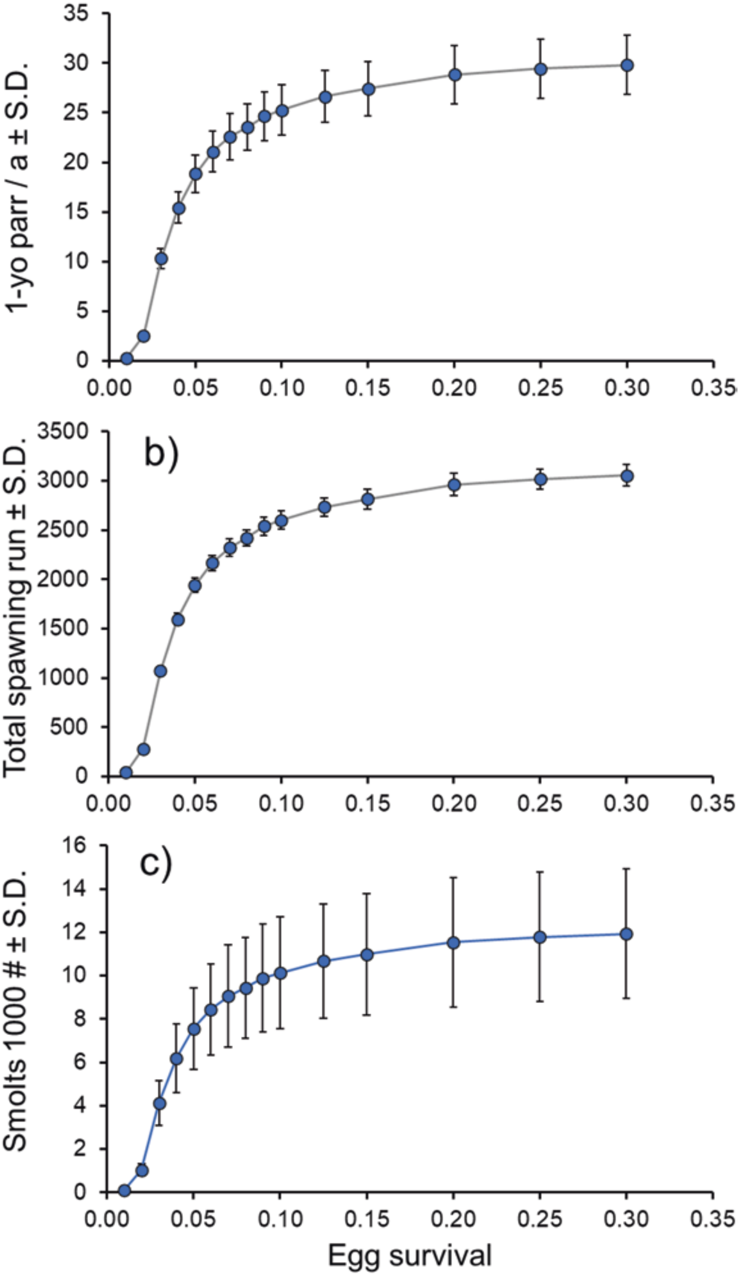


Fig. 9 The effect of varying egg survival on River Oulanka brown trout stocks as derived from the age-structured population models of Syrjänen et al. (2017). The standard deviation represents an average S.D. over ten model simulations

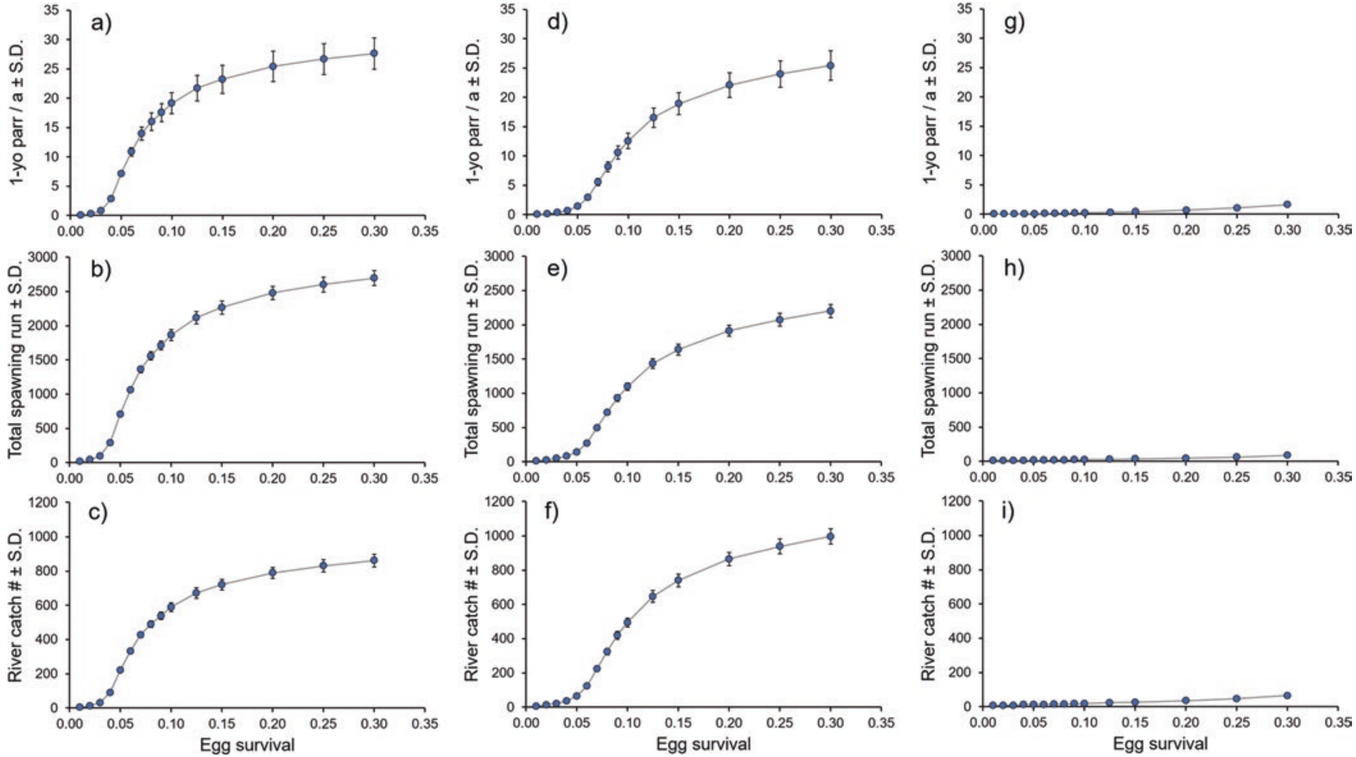


Fig. 10 The effect of varying egg survival on River Oulanka brown trout stocks under three different fishing scenarios (**a–c**): instantaneous fishing mortality rate $F = 0.5$/year, minimum size limit = 600 mm; (**d–f**): $F = 0.5$/year, minimum size limit = 500 mm; (**g–i**): $F = 1.0$/year, minimum size limit = 350 mm) as derived from the age-structured population model of Syrjänen et al. (2017). The standard deviation represents an average S.D. over ten model simulations

8 Concluding Remarks

In this chapter, we have reviewed the existing knowledge on the winter ecology of stream salmonids. We have presented the abiotic conditions that characterize winter in temperate and boreal regions and how salmonids are adapted to cope with them. The importance of abiotic conditions such as temperature, light, and ice (both surface ice and ice formations underwater) has been discussed in relation to survival, growth, and habitat choice. Not only juvenile and adult salmonids overwinter in running waters, but also the eggs. We have therefore also covered egg survival and embryonic development of salmonids and the impact of both abiotic and biotic conditions such as temperature and predation. Here, we also highlighted many of the issues we have discussed using examples from Finland. These examples demonstrate the contemporary importance of studies on egg survival and embryonic development of brown trout, and we have included both biological aspects and methodological considerations when surveying salmonid eggs in the field.

In addition to the natural stressors that shape the winter ecology of salmonids there are several human-induced threats that affect the survival and recruitment of salmonids. One such threat is the regulation of rivers for hydropower, which affects flow regimes, water temperature, and ice formation. The perhaps most evident threat to stream salmonids during winter, however, is the ongoing warming of the climate, which is especially pronounced at northern latitudes and during winter. Warmer winters are likely to directly affect metabolism and activity of overwintering fishes, as well as the timing of spawning and hatching of eggs. Warmer winters also result in several alterations to the physical winter environment, with the perhaps most obvious being the loss of surface ice, which makes stream salmonids susceptible to predation from mammals and birds. Changes in water temperature also lead to thermal asymmetries between species in biotic interactions, be it between predator and prey or competitors. Finally, this chapter presented an example from Finland, on how to estimate overwinter survival of brown trout. This example also included an exercise as how to model the potential impacts of climate change at the local scale.

Winter has long been the understudied season in salmonid ecology. It has often been considered as harsh and challenging and thus a contributor to fish mortality, although relatively few studies have explored whether this is actually the case. What we can conclude however is that winter conditions play a major role in the ecology of stream salmonids, with effects on adults, juveniles, and eggs. It, therefore, is of great importance that we understand how winter conditions affect these animals, and how changes in temperature, light, and ice impact their ecology. This knowledge is likely to be very important in light of ongoing climate change. We already observe major changes to the winter environment caused by climate warming, and these changes may have profound impacts on the ecology and recruitment of salmonids.

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