RIVER RESEARCH AND APPLICATIONS
River. Res. Applic. **23**: 469–491 (2007)

LIFE IN THE ICE LANE: THE WINTER ECOLOGY OF STREAM SALMONIDS

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ABSTRACT

Despite the common view that conditions in winter strongly influence survival and population size of fish, the ecology of salmonids has not been as extensively studied in winter as in other seasons. In this paper, we review the latest studies on salmonid winter survival, habitat use, movement and biotic interactions as they relate to the prevailing physical and habitat conditions in rivers and streams. The majority of research conducted on the winter ecology of salmonids has been carried out in small rivers and streams, where temperatures are above zero and where there is no ice. Investigations in large rivers, regulated and dredged rivers, and under conditions of different ice formations are almost totally lacking, presumably related to sampling difficulties with these systems. The studies-at-hand indicate that a multitude of physical and biological factors affect the survival, behavior, and habitat use of salmonids in winter. The general concept that winter functions as a critical period for the survival of young salmonids is not well supported by the literature. Instead, overwinter survival of juvenile fish appears to be context-dependent, related to specific habitat characteristics and ice regimes of streams. In general, over wintering salmonids prefer sheltered, low velocity microhabitats, are mainly nocturnal, and interact relatively little with conspecifics or interspecifics. Specific descriptions of microhabitat preferences of salmonids are difficult to make due to highly disparate results from the literature. We suggest that future research should be directed towards (1) being able to predict the dynamics of freezing and ice processes at different scales, especially at the local scale, (2) studying fish behavior, habitat use and preference under partial and full ice cover, (3) evaluating the impacts of man-induced environmental modifications (e. g. flow regulation, land-use activities) on the ecology of salmonids in winter, and (4) identifying methods to model and assess winter habitat conditions for salmonids. Copyright © 2007 John Wiley & Sons, Ltd.

KEY WORDS: biotic interactions; habitat use; ice conditions; stream salmonids; survival; winter

Received 18 December 2006; Accepted 21 December 2006

INTRODUCTION

In boreal areas, winter conditions prevail for a substantial portion of the year. At this time, natural streams are generally associated with low water temperatures, various ice phenomena, low discharge rates, short day length and low heat radiation (Prowse, 2001). Ice processes undoubtedly have a major influence on the ecology of animals living in boreal streams through their effect on the timing, duration, and magnitude of flow and water levels. In environments where marked seasonal environmental changes occur, adaptive changes in behaviour and activity of animals are expected (Chapman, 1966). Conditions taxing energy reserves require that animals make appropriate behavioural decisions to ensure survival.

Despite the general belief that conditions in winter strongly influence survival and population size of fish, the overwintering ecology of salmonids, and other fishes as well, has not been extensively studied (Hubbs and Trautman, 1935; Cunjak, 1996; Reynolds, 1997). This is presumably a consequence of the difficulty associated with sampling during winter. Much previous work conducted in winter has been carried out at water temperatures above

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freezing and without the presence of ice. Thus, we know little about the behaviour of fish in relation to ice (Robertson *et al*., 2003; Roussel *et al*., 2004), and little experimental work has been conducted on the impact of different ice conditions on fish (but see Finstad *et al*., 2004a). However, technological developments are improving our ability to study fish in icy conditions (Greenberg and Giller, 2000; Alfredsen and Tesaker, 2002; Robertson *et al*., 2004). Knowledge on how different types of ice affect the ecology of fish might have consequences for how we manage fishes and their habitats in boreal rivers.

The main objective of the present paper is to summarize the latest information about the survival, habitat use, movement and biotic interactions of salmonids as it relates to the prevailing physical conditions in rivers and streams during winter. Such information should be of use to both ecologists and resource managers who have interests in identifying where bottlenecks in fish production lie and in effective management of boreal streams. The bottleneck, as used in this article, is a critical period during which the density of a salmonid population is reduced through emigration and/or mortality, due to either density-dependent or density-independent processes. As we are summarizing the relevant literature on the winter ecology of salmonids, basic knowledge of the life cycles, life stages, and the general migration patterns of salmonids is needed as background information and can be found in Milner *et al*. (2003) and Klemetsen *et al*. (2003). In this review, we focus on the behaviour and ecology of riverine stages of overwintering salmonids, which include sea-run, lake-run and resident individuals (Figure 1). However, because of the close linkage between physical habitat and fish ecology, both physical and biological elements are discussed. We consider winter as a period with ice formation and low water temperature, reaching freezing or near-freezing water temperatures.

THE ICE LANE: WINTER CONDITIONS IN STREAMS

In boreal regions, different forms of ice are important to consider when characterizing environmental winter conditions in lotic systems (Figure 2). Characteristics of the physical habitat in rivers depend on numerous variables; the most important of which are related to stream flow distribution, morphology, cover, temperature and water quality (Berg, 1994; Cunjak, 1996; Reynolds, 1997; Tesaker, 1998; Alfredsen and Tesaker, 2002). Moreover,

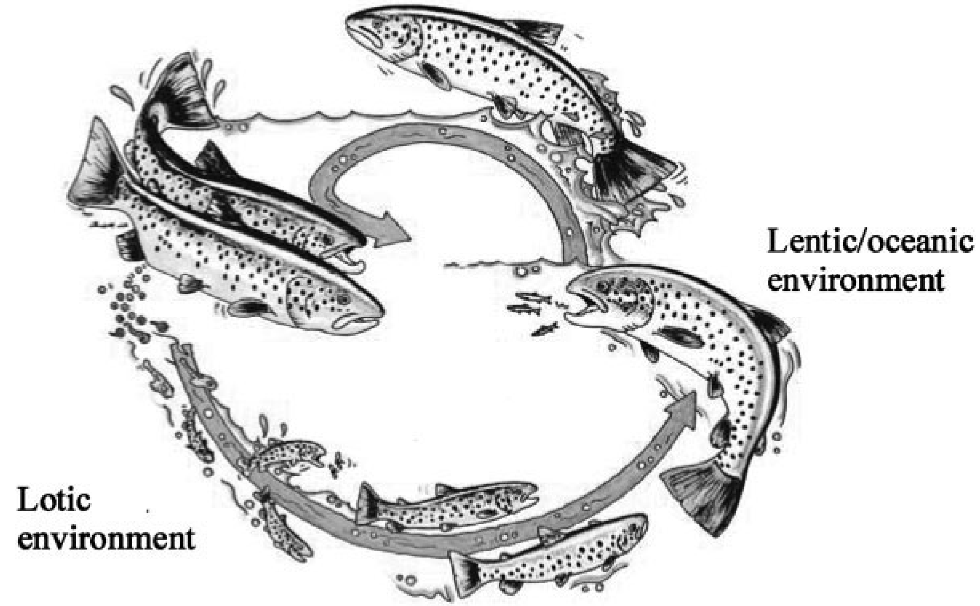

Figure 1. A general view of the life cycle of a salmonid fish. Individuals of sea- or lake-run populations migrate out of their natal rivers to mature in oceanic/lentic environments, and finally return to lotic environments to spawn. Stream resident populations spend their entire life in lotic environments

DOI: 10.1002/rra

Figure 2. Different forms of ice characterize the environmental conditions in boreal rivers in winter. Photo Morten Stickler

the formation and presence of ice will influence these variables. As proposed by Prowse and Gridley (1993), wintertime can be divided into three main periods: early winter (freeze-up), mid-winter (stable conditions) and late winter (ice break-up). In addition, ice regimes can be characterized according to river characteristics (Table I). Ice production in small, steep rivers can be dynamic, both melting and freezing throughout the entire winter, whereas ice conditions in large rivers are generally more stable. Anthropogenic impacts may also alter ice regimes. Hydropower production, particularly in high-head systems, alters both the discharge and the water temperature, with repeated ice break-ups and increased ice production as a result. In some rivers dredging is used to prevent ice jamming, which has repercussions for both the substrate composition and the flow distribution in the reach.

Table I. Ice processes over the course of winter in three types of rivers

Ice regimes	River type Small, steep rivers	Large rivers	Regulated rivers
Freeze-up	Border and skim ice	Border and skim ice	Border ice
	Dynamic ice formation	Ice over formation	Dynamic ice formation
Main winter	Extended dynamic ice formation	Stable ice cover	Less surface ice
	Anchor ice dams	Dynamic ice formation in open riffles	Local ice runs
	Local ice runs		Increased dynamic ice formation
Ice break-up	Thermal ice break-up	Thermal ice break-up	Repeated mechanical ice break-ups throughout winter

DOI: 10.1002/rra

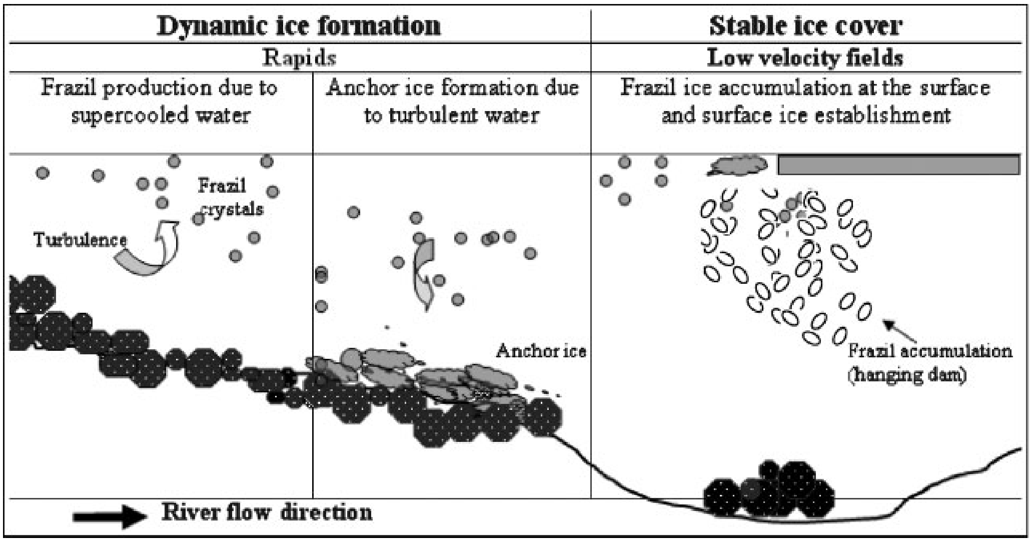

Figure 3. A schematic illustration of ice formation in rivers

Freeze-up

In late autumn, low air temperatures and negative energy balances cool the water until it reaches the freezing point and ice begins to form. At this time, border ice forms along the river margins and skim ice forms in low water velocity areas (Figure 3; Matousek, 1984). In large and/or low gradient rivers ice formation continues until ice completely covers the river (static formation of ice cover; Carstens, 1970). In small, steep rivers/river sections where rapids and riffles dominate, and in regulated rivers where flow varies, dynamic ice formation is expected (Carstens, 1970). Frazil ice is typically associated with these dynamic ice conditions (Figure 3) in turbulent areas when water temperatures in the surface layer or in the entire water drop below 0°C (i.e., super-cooled water). Frazil ice production begins with the formation of tiny, discoid- or needle-shaped ice particles in the water mass (Tsang, 1982). Normally, frazil production has a diurnal cycle: growth during night time when heat conduction is maximized and no growth during daytime due to increased short wave radiation from the sun. During conditions with severe cold, frazil ice has also been observed to form during daytime (Benson, 1955; Stickler and Alfredsen, 2005). The density of frazil crystals in water can be large, up to 10^6 particles m^{-3} (Gilfilian *et al*., 1973), and frazil may accumulate in large quantities, known as hanging dams, below the surface ice in areas with reduced water velocity, e.g. pools. In some cases, these hanging dams can extend down to the riverbed. Once a hanging dam is formed, it may often last until spring (Brown *et al*., 2000; Kylmänen *et al*., 2001).

In areas with sufficient turbulence and super-cooled water, frazil ice may be transported down to the riverbed, where it adheres and forms anchor ice (Figure 3; Ashton, 1986). Formation of anchor ice can also be triggered by direct underwater nucleation when super-cooled water is transported to the riverbed (Ashton, 1986). Naturally, both of these processes can operate at the same time (Tsang, 1982). Anchor ice typically consists of fluffy ice crystals that may form extensive, porous blankets of ice up to 50 cm thick (Benson, 1955; Power *et al*., 1999; Stickler and Alfredsen, 2005; Stickler *et al*., 2007). As with frazil ice, anchor ice often exhibits a diel pattern, with ice formation during night and no ice formation during the day, although anchor ice can be formed at any time in northern areas. During events with anchor ice formation, flow conditions may be substantially altered (Prowse and Gridley, 1993; Tesaker, 1994; Beltaos, 1995; Yamazaki and Hirayama, 1996; Kerr *et al*., 2002; Stickler *et al*., 2007). Anchor ice alters flow conditions by both artificially raising the riverbed (Prowse and Gridley, 1993) and by smoothing out irregularities on the river bottom (Arden and Wigle, 1972). Normally, anchor ice is found in highly turbulent, shallow rapids with rough substrates, but it can also occur in deep areas as noted by Ashton (1986), with observations of anchor ice at a depth of 6 m in the Niagara River, NY, USA, and 20 m in the Neva River, Russia.

DOI: 10.1002/rra

During freeze-up, some sections or areas in rivers may have relatively little ice or may even be ice-free. In regulated rivers, ice-free situations typically arise downstream of warm water release points. However, even in non-regulated rivers, there may be ice-free 'pockets', which are typically associated with groundwater, ground heat influxes from the river bed or friction heat through turbulent rapids (Power *et al*., 1999).

Main winter

During main winter, the lotic environment is influenced by local meteorology, topography and characteristics of the river. Main winter in large rivers, and in rivers with low gradient, is characterized by a stable, ice-covered state with ice-free openings in riffles. In contrast, small, steep rivers may undergo an extended period of dynamic ice formation before reaching stable winter conditions (Tesaker, 1994). Here surface ice formation is normally prevented by turbulent water flow. However, partial or full ice cover may develop from frazil ice accumulations, where frazil ice adheres to solid objects, clustering into large structures, or forms anchor ice dams (Tesaker, 1994; Stickler and Alfredsen, 2005). An anchor ice dam raises the water level, creating backwaters with reduced water velocities that may freeze over (Prowse and Gridley, 1993; Stickler and Alfredsen, 2005). The stability of an anchor ice dam is dependent on water pressure and temperature, where unstable dams may drain or break and cause local ice runs (Tesaker, 1994).

Due to man's high demand for electrical energy in winter, discharge is often higher in winter than in summer in regulated rivers. Moreover, ice conditions in regulated rivers are often highly variable due to artificially induced variation in flow and temperature. Such variation may prevent formation of stable ice covers and increase the degree of dynamic ice production. Furthermore, ice covers in regulated rivers are typically susceptible to breaking and thereby local ice runs and ice jams may occur even in mid-winter.

Ice break-up

Ice break-up is believed to be one of the most significant hydrological events of the year (Prowse, 1994; Prowse and Culp, 2004). The conditions that lead to ice break-up fall between two extremes, mechanical break-up and thermal break-up (Prowse and Gridley, 1993). Thermal break-up occurs as short wave radiation increases, thereby reducing ice thickness before the main spring runoff occurs. With increased water level, this weakened ice cover breaks-up and moves downstream without any significant effect on the river flood levels. In some cases, as in regulated rivers, ice may break up before the ice cover is thermally weakened. Here the potential for an abrupt break-up with ice jamming and ice-induced flooding increases. In both small and large rivers, an ice run can lead to considerable changes to the river bed due to increased scouring (caused both by the high water velocity and the transported ice) as well as to an increased sediment transport (Ashton, 1986; Prowse and Gridley, 1993; Beltaos, 1995; Cunjak *et al*., 1998; Prowse, 2001; Prowse and Culp, 2004). The potential damage in mechanical break-ups is higher than in thermally matured ice due to the nature of the break-up, and the occurrence of repeated ice break-ups over a winter period might exacerbate the physical damage. Water quality problems can also occur at this time as snow and ice melt (Prowse and Gridley, 1993; Prowse and Culp, 2004; Laudon *et al*., 2005). As reported by Cunjak *et al*. (1998) 'a stream can receive the entire winter chemical load of wet and dry atmospheric deposition within a few days' during the spring flood.

OVERWINTER SURVIVAL OF SALMONIDS

Mortality rates are not constant across the different life stages of salmonids. Instead, the early life stages, particularly the eggs and young juveniles, are believed to incur the highest mortalities. Successful incubation depends on numerous chemical, physical, and hydraulic factors within and outside the gravel (Chapman, 1988; Rubin, 1998). The rate of interstitial water flow in the bed material influences the pH, the presence of various toxic materials, sedimentation and dissolved oxygen concentrations, all of which can negatively affect egg survival. The movement of gravel beds in association with ice formation, ice break-ups, and high flows may also negatively impact eggs, by washing them out, by subjecting them to mechanical abrasion, or by decreasing wetted area and

DOI: 10.1002/rra

thereby exposing the eggs to desiccation or freezing. As egg survival is not the main focus of this review, we refer you to Crisp (2000) for more information.

Winter survival of the young, post-egg life stages of salmonids is believed to be low. True estimates of survival in the field are, however, difficult to measure accurately (Vetter, 1988) as changes in population size due to emigration and immigration are not usually taken into account. Thus, most estimates of survival are actually measures of apparent survival rates. Furthermore, published estimates of overwinter survival are not applicable for all types of streams as most studies have been conducted in small streams (Table II), largely due to difficulties associated with sampling large rivers in winter. Nevertheless, studies show that survival rates of fish during winter vary considerably, not only between rivers and over the winter season, but also between years (Table II). The annual variation in survival rates for salmonids in their first winter has been shown to be substantial, for brown trout *Salmo trutta* (15–84%), brook trout *Salvelinus fontinalis* (35–73%), Atlantic salmon *Salmo salar* (43–75%) and coho salmon, *Oncorhynchus kisutch* (16–84%) in studies spanning up to 17 consecutive years (Needham *et al*., 1945; Hunt, 1969; Holtby, 1988; Cunjak and Randall, 1993).

Amazingly few studies have actually compared survival rates in winter with other seasons, which is necessary if one is going to make any general conclusions about winter functioning as a bottleneck for survival. Recent studies indicate that there may not be any general seasonal bottleneck. Instead, survival rates are low in different seasons in different studies, sometimes in connection with episodic events such as floods and droughts (Elliott, 1993; Smith and Griffith, 1994; Elliott *et al*., 1997; Cunjak and Therrien, 1998; Olsen and Vollestad, 2001; Letcher *et al*., 2002; Carlson and Letcher, 2003; Lund *et al*., 2003). Studies have suggested that salmonid survival may be lowest in spring (Elliott, 1993), in autumn and early summer (Carlson and Letcher, 2003), in winter (Letcher *et al*., 2002) or that survival does not differ appreciably between seasons (Olsen and Vollestad, 2001; Lund *et al*., 2003). These studies indicate that there may be a complexity of physical and biological factors affecting the survival of fish. In some rivers the set of prevailing conditions in winter, such as severity and duration of the cold season, together with quality and suitability of habitats, may act as a bottleneck to survival, whereas in other rivers conditions during other seasons may be more limiting.

Winter survival varies not only between years, but also during the course of winter. In some streams survival is lowest in late winter (Reimers, 1963), whereas in others survival is reported to be lowest in early winter (Smith and Griffith, 1994). It may well be that acclimatization costs associated with rapidly changing temperatures both in early and late winter may contribute to high mortalities during these periods (Carlson and Letcher, 2003). A substantial decrease in condition of fish in early winter indicates a stressful period for fish (Mason, 1976; Gardiner and Geddes, 1980; Cunjak *et al*., 1987). Cunjak and Power (1987a), and Cunjak *et al*. (1987) observed that the high acclimatization costs in early winter limited the extent to which brook trout and brown trout were able to endure long winters. Nevertheless, the mere fact that acclimatization costs are high does not necessarily mean that mortality will be high (Olsen and Vollestad, 2001; Lund *et al*., 2003). Survival rate may remain relatively constant throughout the winter (Egglishaw and Shackley, 1977; Elliott, 1993; Elso and Greenberg, 2001). Finstad *et al*. (2004a) simulated conditions of complete ice cover, as is often in mid-winter, and found that Atlantic salmon parr had lower metabolic costs under simulated ice cover than when exposed to simulated ice-free conditions. More stable conditions presumably occur during periods of ice cover than during periods without ice cover and this may partly explain why survival was generally high or stable in mid-winter. Moreover, the results of the study by Finstad *et al*. (2004a) underscore the potential effect that ice regime may have for mortality rates of salmonids in different types of rivers over winter (Table I).

Winter mortality occurs due to predation, accidents and depletion of energy reserves, often in combination with harsh physical conditions. The actual causes of mortality are rarely identified, but Needham *et al*. (1945) and Maciolek and Needham (1952) reported accidental mortality associated with subsurface ice and collapse of overhanging snow banks. In general, survival in winter has been related to body size at the onset of winter, especially in lentic waters (Toneys and Coble, 1980; Garvey *et al*., 1998; Schindler, 1999). Small fish, with low absolute energy stores and relatively high metabolic rates (Paloheimo and Dickie, 1966), would be expected to have high mortality rates during winter when energy stores are metabolized (Gardiner and Geddes, 1980; Cunjak *et al*., 1987; Pickering and Pottinger, 1988). This idea is supported by numerous studies, which have reported positive relationships between size and winter survival for young-of-the-year brook trout, rainbow trout (*Oncorhynchus mykiss*), coho salmon and Atlantic salmon (Hunt, 1969; Quinn and Peterson, 1996; Meyer and Griffith, 1996, 1997;

Table II. Apparent overwinter survival estimates for salmonids in small streams

Species	Stream	Age	Measure	Values	Authors
Natural environment					
Brown trout	Convict Creek, California, USA.	0+	Survival (%,(range))	15–84	Needham *et al*. (1945)
	Convict Creek, California, USA.	1+	Survival (% (range))	10–52	Needham *et al*. (1945)
	Gjesa, south-east Norway	0+	Survival probability (average)	0.29	Lund *et al*. (2003)
	Ulvåa, south-east Norway	0+	Survival probability (average)	0.02	Lund *et al*. (2003)
	Osa, south-east Norway	0+	Survival probability (average)	0.91	Lund *et al*. (2003)
	5 streams, south-east Norway	1+	Monthly survival probability (range)	0.90–0.95	Olsen and Voellestad (2001)
	Black Brows Beck, England	0+	*Daily mortality rate (%day*$^{-1}$*(average))*	*0.32*	Elliott (1993)
	Black Brows Beck, England	1+	*Daily mortality rate (%day*$^{-1}$*(average))*	*0.17*	Elliott (1993)
	Wilfin Beck, England	0+	*Daily mortality rate (%day*$^{-1}$*(average))*	*0.22*	Elliott (1993)
	Wilfin Beck, England	1+	*Daily mortality rate (%day*$^{-1}$*(average))*	*0.14*	Elliott (1993)
	Bisballe Bak, Denmark	0+	*Daily mortality rate (%day*$^{-1}$*(range))*	*0.23-–0.54*	Mortensen (1977)
	Shelligan Burn, Scotland	0+	*Daily mortality rate (%day*$^{-1}$*(average))*	*0.43*	Egglishaw and Shackley (1977)
	West Brook, Massachusetts, USA.	0+	Survival probability (% (95% confidence limits))	0.55–0.71	Carlson and Letcher (2003)
	West Brook, Massachusetts, USA.	1+	Survival probability (% (95% confidence limits))	0.34–0.66	Carlson and Letcher (2003)
Atlantic salmon	Shelligan Burn, Scotland	0+	*Daily mortality rate (%day*$^{-1}$*(average))*	*0.55*	Egglishav and Shackley (1977)
	River Oir, France	0+	Survival (%,(range))	25–64	Bagliniére *et al*. (1993)
	River Oir, France	1+	Survival (%,(average))	32	Bagliniére *et al*. (1993)
	River Scorff, France	1+	Survival (%,(average))	80	Bagliniére and Campigneulle (1986)
	3 streams, eastern Canada	0+	Survival (%,(range))	43–75	Cunjak and Randall (1993)
	West Brook, Massachusetts, USA.	0+	Survival (%,(average))	56	Letcher *et al*. (2002)
	West Brook, Massachusetts, USA.	1+	Survival (%,(average))	46	Letcher *et al*. (2002)
	The West River, Vermont, USA.	0+	Survival (%,(average))	42	McMenemy (1995)
	The West River, Vermont, USA.	1+	Survival (%,(average))	43	McMenemy (1995)
Coho salmon	2 streams, Wisconsin, USA.	0+	Survival (%,(average))	46	Ford and Lonzaric (2000)
	Dick Creek, British Columbia, Canada	0+	Survival (%,(average))	35	Bustard and Narver (1975)
	Big Beef Creek, Washington, USA.	0+	Survival (%,(range))	25–46	Quinn and Peterson (1996)
	2 streams in Alaska, 2 streams in Washington, 4 streams in Oregon, USA.	0+	Survival (%,(range))	26–86	Murphy *et al*. (1984)
	Carnation Creek, British Columbia, Canada	0+	Survival (%,(range))	16–84	Holtby (1988)
Rainbow trout	Henry's Fork, Idaho, USA.	0+	Survival (%,(range))	0–23	Mitro and Zale (2002)
Brook trout	Lawrence Creek, Wisconsin, USA.	0+	Survival (%,(range))	35–73	Hunt (1969)
	Lawrence Creek, Wisconsin, USA.	1+	Survival (%,(range))	25–57	Hunt (1969)
	West Brook, Massachusetts, USA.	0+	Survival probability (% (95% confidence limits))	0.55–0.71	Carlson and Letcher (2003)
	West Brook, Massachusetts, USA.	1+	Survival probability (% (95% confidence limits))	0.34–0.66	Carlson and Letcher (2003)
Closed environment					
Brook trout	Cages in Henry' Fork, Idaho, U.S.A	0+	Survival (%,(average))	60	Meyer and Griffith (1996)
Brown trout	Stream enclosures, Sweden	0+	Survival (%,(average))	73	Elso and Greenberg (2001)
Rainbow trout	Cages in Henry' Fork, Idaho, U.S.A	0+	Survival (%,(average))	87	Meyer and Griffith (1996)
	Cages in Henry' Fork, Idaho, U.S.A	0+	Survival (%,(range))	63–100	Smith and Griffith (1994)
Atlantic salmon	Fish hatchery, Sweden	0+	Survival (%,(range))	94–98	Lindroth (1964)

All streams have an average annual discharge below 5 m^3 s^{-1}, with the exception of Henry's Fork, Idaho, USA. (24 m^3 s^{-1}). Age: (0+) Fish in their first winter; (1+) in their later winters. Mortality measures reported instead of survival are given in *italics*.

DOI: 10.1002/rra

Johnston *et al*., 2005). In contrast, i.e. a negative relationship between size and winter survival was reported by Needham *et al*. (1945) and Carlson and Letcher (2003) (Table II), and no relationship whatsoever was found by Lund *et al*. (2003) and Johnston *et al*. (2005). Lund *et al*. (2003) suggested that the lack of size-dependent mortality might be related to differences in growth among years, i.e. the fish must reach some minimum size to ensure survival. This lends support to the idea of a threshold size, below which survival is size-dependent and above which it is not (Lindroth, 1964; Toneys and Coble, 1980). However, recently Finstad *et al*. (2004b) presented evidence that Atlantic salmon parr mortality was linked to levels of energy stores rather than body size *per se*. Finstad *et al*. (2004b) observed no changes in mean size of the fish or in the shape of the size distributions between successive sampling periods over the winter. Instead, there was a tendency for individuals with energy stores below a certain threshold level to disappear from the population, presumably because they died. Stochastic variation in winter duration and severity (Baglinière *et al*., 1993; Cunjak and Therrien, 1998; Bradford *et al*., 2001), combined with the previous summer's growth opportunities or possibilities to build up energy reserves, may thus provide a mechanistic explanation for the different relationships observed between size (or condition) and winter survival.

Predation seems to also be an important source of mortality in winter as survival in predator-free environments, such as fish hatcheries and closed experimental set-ups is generally higher than in natural open habitats (Lindroth, 1964; Smith and Griffith, 1994; Elso and Greenberg, 2001; Table II). Nevertheless, predation on salmonids has not been studied in any great detail in winter. Presumably predation by fish predators is low as poikilothermic predators are less active in cold water than in warm water (Egglishaw and Shackley, 1977), although predatory burbot (*Lota lota L.*) have been shown to be relatively active in winter (Pääkkönen, 2000). Predation by mammalian and avian predators is likely to be high, particularly in channels lacking ice cover. Garvey *et al*. (1998) and Garvey *et al*. (2004) hypothesized that predation might be important when winter temperatures are relatively warm and both the terrestrial and aquatic predators are active (as in southern systems). Further, predation may be important also when periods of autumn cooling and spring warming are long (as observed in mid-latitude systems), or when cold-active piscivores are abundant under the ice (as in northern systems).

Overwinter survival may not only depend on energy reserves and predation, but may also co-vary with environmental factors. Habitat characteristics may have a positive impact on survival, especially the availability of shelters, together with appropriate behavioural responses by fish, mitigating predation risk and decreasing the use of energy stores (Heggenes *et al*., 1993; Garvey *et al*., 1998; Whalen and Parrish, 1999; Armstrong and Griffiths, 2001; Bradford and Higgins, 2001; Coulombe-Pontbriand and Lapointe, 2004; Johnston *et al*., 2004). Mitro and Zale (2002) found support for this idea as overwinter survival was 18–23% greater in sections of a river characterized by complex bank habitat, high gradient, and large substrate than in sections with simple structure and few boulders (see also Coulombe-Pontbriand and Lapointe, 2004). Minimizing the risk of predation has been suggested to be one of the main reasons why juvenile salmonids become predominantly nocturnal at the onset of winter in channels with no ice cover (Fraser *et al*., 1993; Heggenes *et al*., 1993; Valdimarson and Metcalfe, 1998). Thus, to optimize overwinter survival, fish should have large energy stores in autumn, migrate to a habitat with substantial cover and perform low-risk activities.

PHYSIOLOGICAL ACCLIMATIONS OF SALMONIDS TO ENDURE LOW TEMPERATURE AND ICE

Rather than hibernate as many other poikilotherms (Ultsch, 1989), salmonids remain active in winter (in comparison to, e.g. many cyprinids; Cunjak (1996)), even at low or at near freezing water temperatures (Fletcher *et al*., 1988). Nevertheless, salmonid activity is constrained by the cold winter temperatures, which limit their swimming and acceleration abilities, making them susceptible to displacement and predation (Rimmer *et al*., 1985; McMahon and Hartman, 1989; Graham *et al*., 1996). From a physiological point-of-view, winter is a time of change and adaptation for fish, and a fish's primary concern is to minimize energy expenditures (Heggenes *et al*., 1993). Consequently, salmonids reduce movement, activity, aggression and feeding.

Even if activity is reduced, salmonids feed throughout the winter (Smirnov *et al*., 1976; Cunjak and Power, 1987a; Simpkins and Hubert, 2000), albeit with reduced appetite (Brett and Higgs, 1970; Metcalfe *et al*., 1986; Metcalfe and Thorpe, 1992) due to low metabolic costs in cold water. The composition of the diet, although not well studied, seems to reflect opportunistic feeding from both the drift and the benthos. Trichopterans, ephemeropterans and plecopterans have been found to comprise a large portion of the diet (Maciolek and Needham, 1952; Cunjak and Power, 1987a; Riehle and Griffith, 1993; Simpkins and Hubert, 2000; Lehane *et al*., 2001).

Wintertime growth of salmonids is usually negligible (Cunjak and Power, 1987a; Cunjak, 1988b; Bradford *et al*., 2001; Parrish *et al*., 2004). Nevertheless, life history strategy and habitat choice have been shown to affect the feeding activity of Atlantic salmon parr during winter (Valdimarsson *et al*., 1997; Valdimarsson and Metcalfe, 1999; Parrish *et al*., 2004), and thus differences in growth may arise between fish adopting different life-history strategies (Morgan *et al*., 2000). Specifically, large Atlantic salmon parr have been shown to continue to grow throughout the winter, smoltify and migrate to sea, whereas small salmon parr grow little, if at all, during winter (Metcalfe and Thorpe, 1992). Moreover, growth differences corresponded to differences in activity and aggression, with large fish being less active (presumably more efficient feeders) and more aggressive than small fish (Valdimarsson *et al*., 1997; Nicieza and Metcalfe, 1999; Valdimarsson and Metcalfe, 1999).

The low level of feeding observed in winter is not always sufficient to offset energetic needs and consequently a metabolic deficit may arise. This is especially the case in early winter, whereas later on, metabolic deficiencies are not as pronounced (Cunjak *et al*., 1987; Cunjak and Power, 1987a; Cunjak, 1988b). The fact that energetic intake is lower than energetic needs has been attributed to low assimilation efficiencies and low gastric evacuation rates during winter (Cunjak and Power, 1987a). Slow gastric evacuation rates in salmonids have been related to the occurrence of short photoperiods and cold water temperatures (Cunjak *et al*., 1987; Cunjak and Power, 1987a). Brett and Higgs (1970) suggested that digestion rates were the major factor limiting growth and consumption in fingerling sockeye salmon (*Oncorhynchus nerka* Walbaum).

Regardless of cause, if food intake does not meet energetic needs for standard/basal metabolism, fish have to catabolise their energy reserves, i.e. fats, proteins and glycogen. Fats are the primary energy reserve and thus are depleted whenever intake is not sufficient, whereas proteins and glycogen work as supplementary energy stores (Weatherley and Gill, 1987; Miglavs and Jobling, 1989). Indeed, the depletion of fat reserves has been widely observed in winter (Cunjak, 1988a; Metcalfe and Thorpe, 1992; Berg and Bremset, 1998; Hutchings *et al*., 1999; Finstad *et al*., 2004b), but evidence for protein catabolism during winter also exists (Berg and Bremset, 1998; Morgan *et al*., 2000). Cunjak and Power (1986a) and Cunjak *et al*. (1987) concluded the energy reserve depletion in early winter could not be replenished later, leaving fish in low condition until the arrival of spring. Further, while others observed that the fat content of Atlantic salmon and brown trout declined throughout the winter (Berg and Bremset, 1998; Finstad *et al*., 2004b), Cunjak (1988a) found an additional decline of lipids in conjunction with spring thaw. Other studies have presented contradictory findings. Hunt (1969) noted that fat increased from $<1\%$ to 3% of body composition from January to March in fingerling brook trout. In laboratory studies, juvenile Atlantic salmon increased their appetite in response to energy reserve depletion to regain lost fat (Metcalfe and Thorpe, 1992; Bull *et al*., 1996). In nature, however, it may not be possible to make this compensation due to limited food availability and high predation risk. Further, prevailing ice conditions have been observed to affect the energy balance of salmonids as Finstad *et al*. (2004a) observed that energy loss was slower in conditions of simulated ice-cover than in conditions simulating open areas.

Winter conditions induce many changes at the cellular and tissue levels (Jobling, 1994; Helfman *et al*., 1997). Changes in blood chemistry, including alterations in hormone and enzyme levels, have been shown to take place during winter (Pickering and Pottinger, 1988; Jobling, 1994; Helfman *et al*., 1997). Unsaturated fatty acids increase at the onset of winter (Jobling, 1994; Helfman *et al*., 1997), and the size of the heart and the liver may also increase during winter acclimatization (Helfman *et al*., 1997). Indeed, the heart of rainbow trout is better adapted to cold temperatures than the mammalian (rat) heart (Gillis *et al*., 1999). Pinder and Eales (1969) found that fish buoyancy was reduced in winter and may be an adaptation to life on or in the substrate. Even sensitivity to light seems to increase in winter, presumably to facilitate nocturnal feeding, as the ratio of retinal porphyropsin to rhodopsin increases (Tsin and Beatty, 1977).

Salmonids are not specially adapted to avoid freezing as polypeptides with antifreeze properties are absent in their plasma (King *et al*., 1989). The freezing temperature of the blood plasma of salmonids is between -0.7 and $-0.9^{\circ}C$ (Fletcher *et al*., 1988; King *et al*., 1989), so that *in situ* freezing of fish is rare unless trapped in ice. Brown *et al*. (2000) observed substantial reductions in plasma chloride, sodium and potassium levels and an increase in plasma glucose levels when juvenile rainbow trout experienced frazil and anchor ice conditions. For adult fish, a similar but non-significant pattern in blood plasma was observed. Further, the swimming activity and escape

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response of adult trout decreased during ice events (Brown *et al*., 2000). In addition, Tack (1938) and Brown *et al*. (1994) have speculated that frazil ice could directly affect the respiratory system of fishes by clogging the gills, causing suffocation.

HABITAT SHIFTS OF OVERWINTERING SALMONIDS

Winter usually influences the spatial distribution of salmonids in streams. As water temperature decreases in autumn fish shift to low velocity areas to conserve energy (Fausch and Young, 1995; Cunjak, 1996) and obtain shelter from endothermic predators and piscivores (Valdimarson and Metcalfe, 1998). Depending on the species and/or life stage, this may involve small-scale microhabitat shifts up to mesohabitat and macrohabitat movements, which may even involve leaving the stream if suitable habitats are not available (Bjornn 1971; Reynolds, 1997). Movements vary from few metres to 100 kilometres (Rimmer *et al*., 1983; West *et al*., 1992; Gowan *et al*., 1994; Young, 1998). Long-range movements are believed to have evolved in environments with predictable seasonality, and movement should be favoured if the fitness benefits of moving outweigh the costs of staying (energy loss, exposure to predators) (Fausch and Young, 1995; Begon *et al*., 2003). The autumnal shift from summer to overwintering habitats in fish is triggered by external stimuli or by its biological clock (Begon *et al*., 2003). The decision to make long distance movements is probably at least partly genetically determined, although the timing, duration and distance of migration are also influenced by learning (Linnér *et al*., 1990; Fausch and Young, 1995; Alerstam *et al*., 2003).

Typically fish migrate downstream in winter (Zacharchenko, 1973; Peterson, 1982; Jakober *et al*., 1998), but upstream movements are by no means uncommon (Brown and Mackay, 1995; Brown, 1999; Nykänen *et al*., 2001, 2004a). Large-scale autumnal movements from the main river upstream to tributaries and *vice versa* have been observed for juvenile salmonids (Erkinaro, 1995; Bramblet *et al*., 2002). Overwintering migrations from a river to a lake, from one river to another, and from an estuary to a stream have also been reported (Reynolds, 1997; Lenormand *et al*., 2004).

If the appropriate conditions are present within the summer area, no migration is necessary (Smirnov *et al*., 1976; Rimmer *et al*., 1983; Heggenes and Dokk, 2001). Shifts between river reaches within the main river, i.e. between summer positions in riffles and overwintering sites in lentic areas or in warm groundwater areas, are typical for adult salmonids (Cunjak and Power, 1986b; Brown and Mackay, 1995; Simpkins *et al*., 2000; Nykänen *et al*., 2001, 2004a, 2004b). If such a movement takes place, it generally occurs between August and November, depending on local conditions and population (Valdimarsson *et al*., 2000), and it usually coincides with the decline of water temperature below a certain temperature. Typically the shift occurs at water temperatures between 3 and 6°C (Hillman *et al*., 1987; Jakober *et al*., 1998; Nykänen *et al*., 2001; Bramblet *et al*., 2002), but other studies have reported shifts at temperatures of 10°C for Atlantic salmon (Fraser *et al*., 1993) and 10–14.5°C for adult European grayling *Thymallus thymallus* L. (Nykänen *et al*., 2004a). In addition to temperature, an increase in discharge (Peterson, 1982; Tschaplinski and Harman, 1983; Youngson *et al*., 1983), and possibly even changes in day length or prey availability are thought to play a role in the timing of autumnal habitat shifts. Even river type (Table I) may influence the timing of autumnal habitat shifts although this has never been examined.

Movement of fish in winter is typically minimal (Komadina-Douthwright *et al*., 1997; Jakober *et al*., 1998; Muhlfeld *et al*., 2001; Linnansaari *et al*., 2005). Nevertheless, winter movement patterns can be complex, with individual differences that are at least partly dependent on body size (Hiscock *et al*., 2002a). There may even be mobile and non-mobile individuals within the same fish population (Nakamura *et al*., 2002). If long distance movements are made, they are usually related to accumulation of frazil and anchor ice in preferred habitats (Brown *et al*., 2000; Simpkins *et al*., 2000; Lindström and Hubert, 2004), high discharge events (Brown *et al*., 2001) or level of maturation (Whalen *et al*., 1999; Robertson *et al*., 2003). Salmonids are typically more mobile in areas with unstable ice conditions than in areas with stable ice conditions (Jakober *et al*., 1998, Brown *et al*., 2000; Simpkins *et al*., 2000). Hiscock *et al*. (2002b) showed that movements mainly occurred during night but others have reported movements throughout the diel cycle in winter (Hiscock *et al*., 2002a; Robertson *et al*., 2004; Stickler *et al*., 2007). European grayling have been documented to migrate up to 1 km in a day from a pool to an open rapid to feed (Zacharchenko, 1973).

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The type of habitat shift depends on the species and size (and thus age). Small fish use crevices within the substratum, whereas large-bodied individuals may have to move into slow velocity areas, such as pools, to find suitable shelters from ice and predators (McMahon and Hartman, 1989; Heggenes *et al*., 1993; Hiscock *et al*., 2002b; Lindström and Hubert, 2004). In addition to pools, other slow-velocity mesohabitats, such as off-channel ponds (or alcoves), logjams, swamps, side channels, beaver ponds and tributaries have been described as suitable overwintering areas for salmonids (Tschaplinski and Harman, 1983; Swales *et al*., 1986; Swales and Levings, 1989; Nichelson *et al*., 1992; Harper and Farag, 2004). Backwater habitats have also been shown to be used by adult brown trout (Brown *et al*., 2001), and even by salmon kelts during ice break-up (Caissie *et al*., 1997; Komadina-Douthwright *et al*., 1997). Availability of cover has been shown to influence the number of fish that overwinter in an area (Tschaplinski and Harman, 1983; Meyer and Griffith, 1997; Harvey *et al*., 1999). Fish found in habitats with little structure in autumn have been observed to move into sites with more complex structure in winter (Mitro and Zale, 2002).

BEHAVIOR AND HABITAT USE OF SALMONIDS IN THE ICE LANE

Diel activity patterns

Activity of salmonids changes with season. Juvenile salmonids are typically active during both day and night in summer, but become largely nocturnal in winter (Eriksson, 1978; Cunjak, 1988b; Fraser *et al*., 1993, 1995; Heggenes *et al*., 1993; Bremset, 2000; Jakober *et al*., 2000; Heggenes and Dokk, 2001; Robertson *et al*., 2003), although large individuals (25–60 cm) may remain active during the day (Heggenes *et al*., 1993). Thus, nocturnal behaviour of juveniles in winter is largely due to suppressed daytime activity rather than an increase in nighttime activity (Cunjak, 1988b; Fraser *et al*., 1993, 1995). Nocturnal behaviour has been documented for Atlantic salmon (Fraser *et al*., 1993, 1995), chinook salmon *Oncorhynchus tschawytscha* Walbaum (Hillman *et al*., 1992), coho salmon (Hillman *et al*., 1992; Roni and Fayram, 2000), brown trout (Griffith and Smith, 1993; Heggenes *et al*., 1993), rainbow trout (Riehle and Griffith, 1993; Contor and Griffith, 1995), Arctic char (*Salvelinus alpinus* L. (Linnér *et al*., 1990), bull char *Salvelinus confluentus* Suckley (Jakober *et al*., 2000), and cutthroat trout *Oncorhynchus clarki* Richardson (Griffith and Smith, 1993; Jakober *et al*., 2000). However, it is important to note that most of the observations of nocturnal behaviour of salmonids in winter originate from streams and rivers and from experimental set ups without ice cover, and thus the pattern may be valid only for those systems.

Nocturnal activity in winter is believed to be controlled more by temperature than by day length (Rimmer *et al*., 1983; Fraser *et al*., 1993, 1995; Heggenes *et al*., 1993; Valdimarsson *et al*., 1997; Valdimarsson and Metcalfe, 2001). The temperature for when this seasonal change to nocturnal behaviour occurs has varied widely among studies, from 5 to 13°C (Hartman, 1965; Rimmer *et al*., 1983, 1984; Heggenes, 1988; Fraser *et al*., 1993; Riehle and Griffith, 1993; Bradford and Higgins, 2001), suggesting that there is no universal temperature for the switch in behaviour (Bremset, 2000). Moreover, nocturnal activity is not restricted to winter as it has been observed at water temperatures ranging from 2 to 20°C in both the fall and summer (Hillman *et al*., 1992; Fraser *et al*., 1995; Gries *et al*., 1997; Whalen and Parrish, 1999).

Several factors, both physical and biological in nature, may, however, interact with temperature, affecting the diel activity patterns of salmonids. Light intensity is one such factor as salmon have been shown to hide more at high light levels than at low light levels when temperature is low (Eriksson, 1978; Valdimarsson *et al*., 1997). Even social status (Alanärä and Brännäs, 1997; Bolliet *et al*., 2001; Harwood *et al*., 2001), life history strategy (Metcalfe *et al*., 1998), and age (Hiscock *et al*., 2002a; Johnston *et al*., 2004) have been shown to affect an individual's degree of nocturnality. Geographic variation in diel activity patterns has also been observed. Bradford and Higgins (2001) found that diel activity pattern varied with location within a river, and others have presented evidence for between river variation in response to temperature changes, suggesting that there may be local, genetically based adaptations (Valdimarsson *et al*., 2000). Further, Stickler *et al*. (2007) found no nocturnal behaviour in a Norwegian regulated river, which may reflect differences between river types (Table I). These results suggest that while temperature is an important factor affecting nocturnal behaviour in salmonids, other factors may modify this general seasonally based diel activity pattern (Reebs, 2002).

The adaptive function of the change to nocturnal behaviour in winter has been related to adverse physical conditions associated with ice formation. Ice conditions are relatively stable during daytime, whereas the risk of being trapped in anchor ice should be greater at night (Tsang, 1972; Heggenes *et al*., 1993; Whalen *et al*., 1999). Thus, leaving the river bottom before nightfall should reduce the risk of getting trapped by ice. Nevertheless, this explanation cannot be the sole reason for nocturnal activity in winter as the switch to nocturnality happens long before ice formation commences (Fraser *et al*., 1993), and fish have been observed to use anchor ice as a cover (Roussel *et al*., 2004).

Predation risk is a more likely explanation for the shift to nocturnality. Diurnal endothermic predators have been shown or implicated to impose a substantial predation risk for salmonids, especially in channels with no ice cover (Heggenes and Borgström, 1988; Fraser *et al*., 1993, 1995; Heggenes *et al*., 1993; Valdimarson and Metcalfe, 1998; Metcalfe *et al*., 1999; Hiscock *et al*., 2002a). The switch to nocturnality is believed to involve a cost to the fish as foraging efficiency of salmonids at night is much lower than during the day (Valdimarsson *et al*., 1997). The reduced efficiency is offset to some degree by the sometimes documented greater density of invertebrate drift at night (Valdimarsson *et al*., 1997, but see Heggenes *et al*., 1993), but the increase is probably too low to compensate for the reduced ability of salmonids to visually detect prey. Nevertheless, the low metabolic rates in cold water mean that food requirements are low, and the fish seem to obtain sufficient energy at night while benefiting from a low risk of predation (Fraser and Metcalfe, 1997; Valdimarson and Metcalfe, 1998).

Local habitat use

Diel changes in activity are also associated with changes in microhabitat use. During daytime, juvenile salmonids typically use coarse substrates, aquatic vegetation, large woody debris or in some cases deep, slow flowing waters as shelter (Heggenes *et al*., 1993; Bunnell *et al*., 1998; Muhlfeld *et al*., 2001; Muhlfeld *et al*., 2003). Some individuals have even been found to bury themselves within the substrate (Bonneau and Scarnecchia, 1998; Hiscock *et al*., 2002a). At night, the salmonids leave their shelters and enter the water column. The distance moved between daytime and nighttime microhabitats is generally short; e.g. in Atlantic salmon parr averaged small home ranges (<3 m) in winter (Roussel *et al*., 2004; Scruton *et al*., 2005). Furthermore, diel changes in habitat use lead to changes in the spatial distribution of fish. Salmonids have been shown to be more closely associated with stream edge rather than midstream habitats during night time than during daytime (Cunjak, 1988b; Whalen and Parrish, 1999; Whalen *et al*., 1999; Roussel *et al*., 2004). However, as the fish usually spend daytime in shelters, the spatial distribution of fish is dependent on the location of these shelters, and thus the relation to stream bank during daytime might be trivial.

Velocity and depth. Juvenile and adult salmonids typically move into deep, low velocity microhabitats during late fall (Cunjak and Power, 1986b; Baltz *et al*., 1991; Simpkins *et al*., 2000; Heggenes and Dokk, 2001; Nykänen *et al*., 2004a, 2004b; Mäki-Petäys *et al*., 1997, 2004). In some cases, the slow focal velocity areas are situated in close proximity to high water velocity areas so that fish take advantage of high drift densities (Cunjak, 1988b; Simpkins *et al*., 2000). Of course, habitat use is influenced by availability and thus exceptions to the general trend occur (Heggenes *et al*., 1993; Mäki-Petäys *et al*., 1997). Several studies have reported use of shallow, fast velocity areas especially for juvenile Atlantic salmon (Rimmer *et al*., 1983; Cunjak, 1988b; Roussel *et al*., 2004).

The mean water column velocity and depth used by salmonids in winter varies from 0 to 60 cm s^{-1} and 0–400 cm, respectively, depending on habitat availability. Typical values of mean water column velocity and depth are <40 cm s^{-1} and 20–60 cm for juvenile *Salmo* spp. (Mäki-Petäys *et al*., 1997, 2004; Heggenes and Dokk, 2001), <30 cm s^{-1} and >40 cm for *Oncorhynchus* spp. (Baltz *et al*., 1991; Harper and Farag, 2004) and 20–80 cm s^{-1} and 150–400 cm for adult grayling (Nykänen *et al*., 2001, 2004a, 2004b), respectively.

Diel differences in microhabitat use reflect differences in daytime and nighttime activity. Focal velocity, which is close to 0 cm s^{-1} when fish shelter in substrate during the day, is greater at night when the fish move into the water column (Heggenes *et al*., 1993; Baxter and McPhail, 1997; Hiscock *et al*., 2002b; Muhlfeld *et al*., 2003). Habitat use by different age/size classes in a population is relatively more similar in winter than in summer (Baltz *et al*., 1991; Heggenes *et al*., 1993; Mäki-Petäys *et al*., 2004), even if differences have been reported for some populations (Cunjak and Power, 1986b; Harwood *et al*., 2001).

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Cover and substrate. One way juvenile salmonids minimize costs during daytime when they are not foraging is to hide in unembedded coarse substrates (Cunjak, 1988b, 1996; Griffith and Smith, 1993; Vehanen *et al*., 2000). A number of studies have shown, for example that juvenile Atlantic salmon and brown trout of all sizes use or prefer large substrate sizes (from large pebbles to boulders) in winter (Rimmer *et al*., 1984; Cunjak, 1988b; Elso and Greenberg, 2001; Heggenes and Dokk, 2001; Mäki-Petäys *et al*., 1997, 2004). Rimmer *et al*. (1984) and Cunjak (1988b) stated that the size of daytime sheltering rocks is often proportional to the size of the fish hiding under it. However, this might not always be the case as Heggenes *et al*. (1993) did not find any relationship between fish length and substrate particle size.

Salmonids are not necessarily restricted to areas with coarse substrate during daytime in winter. For example, rainbow trout have been shown to use a broad range of substrate particle sizes, with little preference towards certain substrate size classes (Baltz *et al*., 1991). Some salmonid species (e.g. Atlantic salmon and rainbow trout) have been observed to burrow in loose gravels rather than hide under coarse substrates (Erkinaro *et al*., 1994; Meyer and Griffith, 1997). European grayling, which has never been reported to hide under the substratum, and *Salvelinus* spp. have also been shown to dwell in sites with particles of small size (Chisholm *et al*., 1987; Nykänen *et al*., 2001, 2004a,b; Muhlfeld *et al*., 2003).

Salmonids, which actively feed at night in channels with no ice cover are not restricted to coarse substrates (Hiscock *et al*., 2002b). The majority of juvenile salmon may use silt, sand and gravel habitats during night, even when cobble and rubble substrates dominate (Whalen and Parrish, 1999). Similar observations have also been made for juvenile brown and steelhead trout (Heggenes *et al*., 1993). Moreover, salmonids have generally been shown to be on or close to the bottom at night (Heggenes *et al*., 1993; Whalen and Parrish, 1999; Heggenes and Dokk, 2001).

In addition to coarse substrate, salmonids have also been found hiding in or under large woody debris, aquatic vegetation, undercut banks, surface turbulence and ice (Baltz *et al*., 1991; Heggenes *et al*., 1993; Cunjak, 1996; Muhlfeld *et al*., 2001, 2003; Meyer and Gregory, 2000). Woody debris is a preferred source of cover for brook trout, cutthroat trout, brown trout and coho salmon, but may become unprofitable for fish during frazil ice events, forcing them to move into other areas (Brown *et al*., 1994; Cunjak, 1996; Quinn and Peterson, 1996). The complexity of woody debris structures may also influence preferences as shown for coho salmon (McMahon and Hartman, 1989). Emergent vegetation might also be expected to provide cover for juvenile salmonids during winter (Cunjak and Power, 1987b; McMahon and Hartman, 1989; Heggenes *et al*., 1993), but due to dieback, areas with emergent vegetation may not provide cover throughout the winter (Griffith and Smith, 1995; Simpkins *et al*., 2000; Mitro and Zale, 2002).

Role of water temperature and ice as habitat variables. Local areas of warm water, created by groundwater influxes or by release of warm reservoir water in regulated rivers, have been shown to attract fish during coldwater periods. Such behavior has been documented for brook trout (Cunjak and Power, 1986b) and cutthroat trout (Brown *et al*., 1994; Brown and Mackay, 1995). Even brown trout has been shown to position itself in the vicinity of warm groundwater (Cunjak, 1996). In some watersheds, groundwater-influenced areas might represent the only refugia from ice during winter and provide a place where all age classes may gather for overwintering (Craig and Poulin, 1975; Craig, 1978; Brown *et al*., 1994; Reynolds, 1997). This does not appear to be the case for all salmonids as Atlantic salmon parr have been shown to avoid spring sources (Cunjak, 1996).

Although microhabitat studies have not been carried out under full surface ice conditions, it has been shown that surface ice is used as overhead cover (Meyers *et al*., 1992; Young, 1995). Surface ice has also been shown to influence local density as densities of young-of-the-year rainbow trout were two times greater in enclosures with 50% surface ice than in enclosures with 10% surface ice (Meyer and Griffith, 1997). Surface ice also affects feeding as salmonids have been shown to feed less in areas lacking ice cover than in areas with full surface ice (Finstad *et al*., 2004a). There even seems to be a relationship between surface ice and use of coarse substrates during daytime. Gregory and Griffith (1996b) found that juvenile rainbow trout did not conceal themselves as often during daytime in coarse substrates under surface ice, presumably reflecting low risk of predation from endotherms in ice-covered areas (Valdimarson and Metcalfe, 1998). Border ice has also been shown to be used as overhead cover (Emmett *et al*., 1996; Stickler, 2003; Stickler *et al*., 2007), and it may also act as a refuge from unstable frazil/anchor ice formation in open areas (Brown *et al*., 1994; Brown and Mackay, 1995; Simpkins *et al*., 2000; Stickler, 2003; Stickler *et al*., 2007).

Whilst streams covered with surface ice are regarded as stable environments for fish, streams with frazil and anchor ice are generally regarded as unstable, dynamic environments (Ashton, 1986). These unstable environments presumably have consequences for microhabitat use by salmonids. Cutthroat trout, for example moved away from preferred woody-debris areas in direct response to the formation of frazil and anchor ice (Brown *et al*., 1994; Brown and Mackay, 1995; Brown, 1999). Similarly, others have observed salmonids avoid anchor ice by moving to the bottom of deep pools or to shallow nearshore areas under shelf ice during frazil ice episodes (Jakober *et al*., 1998; Simpkins *et al*., 2000; Stickler, 2003; Stickler *et al*., 2007). Frazil ice may also indirectly affect habitat use by fish by altering water velocities and depth. In pools, hanging dams create high near-bed water velocities, forcing kelts to move into areas of pools with less frazil ice and low water velocities (Komadina-Douthwright *et al*., 1997). Brown trout move out of pools with hanging dams, but return when conditions are favourable (Brown *et al*., 2000).

Although environments with frazil and anchor ice are generally regarded as negative for fish, this is not always the case. For example Whalen and Parrish (1999) found Atlantic salmon parr resting on top of anchor ice, and parr have also been observed burrowing into anchor ice during daytime (Linnansaari, personal observation). In other studies, Linnansaari *et al*. (2005) and Stickler *et al*. (2007) found that salmonids did not necessarily avoid frazil and anchor ice in streams dominated by coarse substrates. In a recent study by Roussel *et al*. (2004), salmon parr used habitats covered by hanging 'collars' of anchor ice around boulders. Further, microtemperature under anchor ice where fish resided was slightly warmer than in nearby areas, and thus the fish could avoid freezing conditions by using the anchor ice (Roussel *et al*., 2004).

Biotic interactions

Interspecific competition occurs either indirectly through competition for resources or directly through agonistic behaviour (Wootton, 1990). Most of the literature on competition in salmonids is based on summer conditions, and during summer juvenile stream salmonids typically form dominance hierarchies, compete for resources, are aggressive and defend territories (Bachman, 1984; Hughes and Dill, 1990; Fausch, 1998; Heggenes *et al*., 1999; Young, 2001; Forseth *et al*., 2003). At low temperature, salmonids become less aggressive (Hartman, 1963; McMahon and Hartman, 1989; Heggenes *et al*., 1993; Whalen and Parrish, 1999; Vehanen and Huusko, 2002) and territorial behaviour diminishes or disappears (Cunjak and Power, 1987b; Hillman *et al*., 1987; Riehle and Griffith, 1993; Griffith and Smith, 1993). Reduction of territorial aggression may also result from limited availability of winter habitat (Cunjak, 1996; Whalen and Parrish, 1999). Anchor or frazil ice formation can force stream salmonids into restricted areas, resulting in large aggregations of fish (Brown and Mackay, 1995; Whalen *et al*., 1999; Brown *et al*., 2000). In addition to the temperature effect on aggression, fish are also less aggressive at low light levels (Fraser *et al*., 1993; Hill and Grossman, 1993; Vehanen *et al*., 2000; Vehanen and Huusko, 2002), which are typically associated with ice-covered streams.

Several authors have reported overlap in habitat use by juvenile salmonids during winter, suggesting potential for interspecific competition (Glova, 1986; Mäki-Petäys *et al*., 1997; Heggenes and Dokk, 2001). Heggenes and Dokk (2001) found that niche overlap between juvenile salmon and brown trout is higher during the winter than in summer. In this light, Harwood *et al*. (2001) found that Atlantic salmon became less nocturnal or occupied shallower water when in sympatry than in allopatry with brown trout, indicating that competition for food and resources may affect overwintering survival in salmonids. Hartman (1965) even suggested that vertical partitioning between steelhead and coho salmon in winter might reflect interspecific competition. It has also been shown that signal crayfish (*Pacifastacus leniusculus*) will outcompete juvenile salmon for use of shelters during winter (Griffiths *et al*., 2004).

There is also potential for intraspecific competition as different age classes of the same species have been reported to use similar habitat or food resources during winter (Mäki-Petäys *et al*., 1997; Whalen and Parrish, 1999; Amundsen *et al*., 2001). Large dominate smaller conspecifics during winter (Gregory and Griffith, 1996a; Vehanen *et al*., 2000), even at low levels of aggression (McMahon and Hartman, 1989; Healy and Lonzarich, 2000; Harwood *et al*., 2001). Intraspecific competition for shelters occurs in winter, especially when these refuges are limited in number (Armstrong and Griffiths, 2001; Harwood *et al*., 2001, 2002; Orpwood *et al*., 2004). Gregory and Griffith (1996b) reported that aggressive competition for shelters took place mainly at dawn as fish entered the shelters. Large individuals and prior resident fish seem to have an advantage in this context. Sharing of winter refuges is uncommon, but sometimes two or more fish have been found in the same shelter (Cunjak, 1988b; Vehanen *et al*., 2000; Harwood *et al*., 2002). This is especially true of fish reared at high densities in hatcheries and then released

DOI: 10.1002/rra

into streams (Burns *et al*., 1997; Armstrong and Griffiths, 2001; Griffiths and Armstrong, 2002). Such aggregations of fish may have costs in terms of increased exposure to predators or competition for local resources (Orpwood *et al*., 2004). Griffiths *et al*. (2003) demonstrated that juvenile Atlantic salmon avoid sharing winter refuges with their siblings.

CONCLUSIONS

The studies-at-hand indicate that there may be a multitude of factors, both physical and biological, that affect the survival, behaviour, and habitat use of salmonids in winter. This makes interpretation of observed patterns complicated and difficult to generalize. The fact that winter seems to function as a bottleneck for survival of young salmonids in some rivers but not in others suggests that survival may be highly context-dependent, related to the habitat characteristics and ice regimes of individual rivers.

In general, overwintering salmonids are mainly nocturnal, prefer sheltered, low velocity microhabitats, and interact relatively little with conspecifics or interspecifics. It is difficult to obtain a precise description of the microhabitat preferences of any given species as published results vary considerably between studies. Thus, even basic generalized winter habitat preference curves used in habitat-hydraulic modelling are almost totally lacking for young salmonids in winter (but see Mäki-Petäys *et al*., 1997, 2004; Armstrong *et al*., 2003). Experimental approaches, both field- and laboratory based, are sorely needed so that we may be able to define criteria that salmonids use when selecting microhabitats in different kinds of rivers in winter.

Attempts at modelling freeze-up and ice dynamics at local scales, such as individual rapids, have not yet been satisfying (Alfredsen and Tesaker, 2002), although models devised for larger scales, such as river reaches, have been more successful (Reiter and Huokuna, 1995). Predicting the formation and dynamics of frazil and anchor ice, and their effects on the behaviour and microhabitat selection of salmonids is largely unknown. Ice regimes are in many cases believed to have negative impacts on fish populations, particularly in regulated and dredged rivers (Saltveit *et al*., 2001; Dare *et al*., 2002; Scruton *et al*., 2005). However, there are not any studies that quantify overwinter survival of salmonid populations in these impacted rivers (Saltveit *et al*., 2001), nor are there any studies that convincingly show that ice limits survival.

Not surprisingly, the focus on winter-related issues in lotic fish research during the last decade or so has provided much new information about overwintering fish. Still, further work is needed so that we may be better able to manage boreal rivers and streams (Cunjak 1996; Huusko and Yrjänä, 1997; Alfredsen and Tesaker 2002; Barrineau *et al*., 2005). The majority of research conducted on the winter ecology of salmonids has been carried out in small rivers and streams, where the temperature remains a few degrees above zero and with no ice. Very little information exists on the behaviour of fish in relation to ice, and experimental research on the impact of different ice conditions on fish is almost completely lacking. Further, there is little information on overwinter survival in large rivers and in regulated rivers (Bradford, 1997; Saltveit *et al*., 2001). We suggest that future research should be directed towards (1) being able to predict the dynamics of freezing and ice processes at different scales, especially at the local scale, (2) studying fish behaviour, habitat use and preference under partial and full ice cover, (3) evaluating the effects of human impact (e.g. flow regulation, land-use activities) on the ecology of salmonids in winter, and (4) identifying methods to model and assess winter habitat conditions for salmonids.

ACKNOWLEDGEMENTS

The authors grateful to COST Action 626 (European Aquatic Modelling Network) for networking and allowing them to meet, thus making writing of this paper possible. The authors thank the late Petri Kreivi for his help in gathering and summarizing literature data in the early phase of writing this manuscript. L.A. Voellestad, D. Scruton and several anonymous reviewers are acknowledged for astute and constructive comments on the previous drafts of the manuscript.

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