ABSTRACT: The main objective of this presentation is to describe the results of a review article that we have been writing. In this review, we have summarized 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 the 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. We mostly focus on behavioral and ecological aspects of overwintering fish, but because of the close linkage between physical habitat and fish ecology, both physical and biological elements are discussed.

1 INTRODUCTION

Winter conditions in boreal streams are generally associated with low water temperatures, various ice phenomena, low discharge rates as well as decreased sunlight and heat radiation (Prowse & Gridley 1993). 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. Despite the general belief that conditions in winter strongly influence survival and population size of fish, the ecology of fish has not been as extensively studied in winter as in other seasons (Hubbs & Trautman 1935, Cunjak et al. 1998). This is presumably a consequence of the difficulty associated with sampling in winter. Much previous work conducted in winter has been carried out at water temperatures above freezing without ice cover. Thus we know little about the behaviour of fish under 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 (e.g. Greenberg & Giller 2000, Alfredsen & Tesaker 2002, Robertson et al. 2004), and as a consequence, new insights will likely follow (e.g. Roussel et al. 2004, Johnston et al. 2004, 2005). Information on how ice affects the ecology of fish should have consequences for how we manage fishes in boreal rivers.

The main objective of the this article is to summarize the latest information about survival, habitat use, movement and biotic interactions in salmonids as it relates to the prevailing physical conditions in rivers and streams during the winter. Here we consider winter as a period with ice formation and low water temperature, reaching freezing or near-freezing water temperatures by mid-winter.

2 PHYSICAL CONDITIONS OF THE LOTIC ENVIRONMENT

Physical river habitat conditions depend on various variables, the most important of which are related to stream flow distribution, morphology, cover, temperature and water quality (Cunjak et al. 1993, Tesaker 1998, Alfredsen & Tesaker 2002). During winter, different types of ice form in sub-arctic streams (e.g. anchor ice, frazil ice, surface ice), which in turn affect these physical habitat conditions. As proposed by Prowse and Gridley (1993) and Cunjak et al. (1998), winter time 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 based on river type (Table 1). Ice formation in small, steep rivers is dynamic, in some cases changing throughout the entire river, whereas ice conditions in larger rivers are generally more stable. Anthropogenic impacts may also alter the ice regime. Hydropower production, particularly in high-head systems, can result in altered discharge regimes
and the release of warm water into rivers. In regulated rivers, the ice regime is characterized by repeated ice break-ups and increased ice production. In some cases rivers have been dredged to prevent ice jamming, and this will alter both substrate composition and flow conditions in the reach.

Table 1. Ice processes categorized by seasonal and river characteristics.

<table>
<thead>
<tr>
<th>Ice regimes</th>
<th>Small, steep rivers</th>
<th>Large rivers</th>
<th>Regulated rivers</th>
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<tr>
<td>Freeze up</td>
<td>Border and skim ice formation</td>
<td>Border ice</td>
<td>Border ice Dynamic ice formation</td>
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<td>Dynamic Freeze-up</td>
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<td>Main winter</td>
<td>Stable ice cover</td>
<td>Repeated ice break-ups</td>
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<td>Anchor ice dams</td>
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<td>Ice break up</td>
<td>Thermal ice break-up</td>
<td>Thermal ice break-up</td>
<td>Repeated mechanical ice break-ups</td>
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3 FISH SURVIVAL

Winter is often recognized as a bottleneck for survival for lotic fish populations. The data-at-hand show that survival rates of fish and their eggs during winter vary considerably, not only between rivers and over the winter season, but also between years. For example, in studies spanning up to 17 consecutive years, the annual variation in survival rates 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%) (Needham et al. 1945, Hunt 1969, Holtby 1988, Cunjak & Randall 1993). Surprisingly, 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 & Griffith 1994, Elliott et al. 1997, Cunjak & Therrien 1998, Olsen & Voellestad 2001, Letcher et al. 2002, Lund et al. 2003, Carlson & Letcher 2003). Survival has been shown to be lowest in spring (Elliott 1993), in autumn and early summer (Carlson & Letcher 2003), in winter (Letcher et al. 2002) or to not differ appreciably between seasons (Olsen & Vollestad 2001, Lund et al. 2003). These results indicate that there may be a complexity of environmental 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 winter, together with quality and suitability of habitats, may act as the bottleneck to survival, whereas in other rivers prevailing conditions during other seasons may be more limiting.

Numerous studies have reported positive relations between size and winter survival, with individuals under some minimum size in autumn being most prone to mortality (e.g. Hunt 1969, Quinn & Peterson 1996, Meyer & Griffith 1996, 1997, Johnston et al. 2005). However, some studies have reported the opposite, i.e. a negative relation between size and winter survival (e.g. Needham et al. 1945, Carlson & Letcher 2003) or no relationship whatsoever (e.g. Lund et al. 2003, Johnston et al. 2005). A recent study by Finstad et al. (2004b) presented evidence that YOY mortality may be linked to levels of energy stores at the onset of winter rather than body size per se. In summary, the main causes of mortality in winter are believed to be (1) depletion of energy reserves in combination with harsh physical conditions, (2) predation and (3) accidents. Thus, over-winter survival should be relatively high if fish have high energy stores in autumn, dwell in habitats with substantial cover, and perform low-risk activities to avoid predation (Cunjak et al. 1998, Finstad et al. 2004b, Johnston et al. 2005).

4 ACCLIMATION OF FISH TO WINTER

Ambient water temperature regulates the basal metabolism of poikilothermic animals such as salmonids. Thus, with dropping temperatures at the onset of winter, metabolic needs “gear down” and salmonids shift to an energetic “save” mode (e.g. Heggenes et al. 1993). Somatic growth ceases (Cunjak & Power 1987b, Cunjak 1988, Bradford & Higgins 2001) or decreases (Cunjak et al. 1987, Metcalfe & Thorpe 1992), even though nocturnal feeding continues throughout the winter (Cunjak & Power 1987, Cunjak et al. 1987, Cunjak 1988, Heggenes et al. 1993, Simpkins & Hubert 2000, Finstad et al. 2004c). Assimilation efficiency is low, however, and energetic deficiencies are common especially during the acclimatization period in early winter (Cunjak & Power 1987b, Cunjak et al. 1987). Deficiencies are not easily overcome during the course of winter and usually continue until water temperatures warm up again in spring (Nieieza & Metcalfe 1997).
5 MOVEMENTS AND HABITAT USE OF FISH – SEEKING FOR SHELTER

As water temperature decreases in autumn and it becomes unprofitable for fish to remain in energetically costly, fast-velocity sites, they shift to areas where they can conserve energy (Fausch & Young 1995, Cunjak 1996). This means that fish of all sizes occupy nearly the same kinds of local habitats in terms of velocity and substrate (e.g. Heggenes et al. 1993, Mäki-Petäys et al. 1997, Armstrong et al. 2003). In preferred winter sites the velocity is low, usually less than 10 cm s\(^{-1}\), and the substrate structure is diverse. Velocity and substrate seem to be the most important selection criteria in winter (Cunjak & Power 1986). Winter habitat use, especially for young salmonids, may resemble summer habitat use in terms of average global velocities for the habitats that they use, but fish in winter search for local microhabitats where nose velocities are close to zero. Depending on fish species and life stage, the shift from summer to winter habitats may thus involve movements ranging in length from some metres to over 100 kilometres (e.g. Rimmer et al. 1983, West et al. 1992, Gowen et al. 1994, Young 1998). The shift may occur within or between differing stream sites, sections or even between macrohabitats such as the main river and tributaries or a river and an estuary (e.g. Brown & Mackay 1995, Erkino 1995, Young 1998, Bramblet et al. 2002, Lenormand et al. 2004). Typically the shift occurs at water temperatures between 3 and 6°C (Jakober et al. 1998, Nyykänen et al. 2001, Bramblet et al. 2002), but temperatures of 10°C for Atlantic salmon (Fraser et al. 1993) and 10-14.5°C for adult European grayling (Nyykänen et al. 2004) have also been reported.

During winter, most fish seem to be more or less active, although they rarely move far (Cunjak 1996, Jakober et al. 1998, Bradford et al. 2001, Muhlfeld et al. 2001). If long distance movements are made, they are usually related to unstable ice conditions, such as accumulation of frazil and anchor ice in preferred habitats (Brown 1999, Brown et al. 2000, Simpkins et al. 2000), or to high discharge events (Brown et al. 2001).

Availability of cover has been shown to influence the number of fish that overwinter in an area (Tschaplniski & Harman 1983, Meyer & 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 & Zale 2002). Small fish are probably better able to use crevices within the substratum, whereas large-bodied individuals may have to move into pools or other deep, slow velocity areas to find suitable shelters from ice and predators (McMahon & Hartman 1989, Cunjak 1996, Robertson et al. 2003). In addition to pools, other slow-velocity habitats, such as off-channel ponds (or alcoves), logjams, undercut banks, swamps, side channels, beaver ponds and tributaries have been identified as suitable overwintering areas for fishes (Bustard & Narver 1975, Tschaplniski & Hartman 1983, Swales et al. 1986, Chisholm et al 1987, Swales & Levings 1989, Nickelson et al. 1992, Cunjak 1996, Harper & Farag 2004). In some systems, areas influenced by groundwater provide the only refugia for overwintering (Power et al. 1999).

6 BIOTIC INTERACTIONS STILL IN OPERATION

Intra- or interspecific competition occurs either indirectly through competition for resources or directly through agonistic behaviour (Wootton 1990). Salmonids have been shown to be less aggressive in winter than in summer (Hartman 1963, McMahon & Hartman 1989, Heggenes et al. 1993, Whalen & Parrish 1999) and territorial behaviour may be less important at this time (Bustard & Narver 1975, Cunjak & Power 1987a, Griffith & Smith 1993).

Several authors have reported overlap in habitat use by juvenile salmonids during winter, suggesting the potential for interspecific competition (Glova 1986, Mäki-Petäys et al. 2000, 2004, Heggenes & Dokk 2001). Heggenes & Dokk (2001) found that niche overlap between juvenile salmon and brown trout is higher during the winter than in summer. Harwood et al. (2002) suggested that competition for food and resources may affect overwintering survival in salmonids as they found that Atlantic salmon became less nocturnal or occupied shallower water when in sympathy with brown trout than when alone.

There is also potential for intraspecific competition as different age classes of the same species have been reported to use similar habitats or food resources during winter (Mäki-Petäys et al. 1997, Whalen & Parrish 1999, Amundsen et al. 2001). The spatial niche of brown trout has been shown to be narrow during winter (Mäki-Petäys et al. 1997) and as a consequence different cohorts may use similar microhabitats. Large individuals have also been observed to dominate over their smaller conspecifics during winter (Gregory & Griffith 1996, Vehanen et al. 1999), even if levels of aggression are lower in winter than in summer (McMahon & Hartman 1989, Harwood et al. 2002).

7 MORE RESEARCH IS NEEDED

There is still much we do not know about the effects of winter conditions on the ecology of salmonids. Ice conditions, for example, are in many cases believed to have negative impacts on fish populations, particularly in regulated and dredged
rivers, and yet no studies have quantified winter survival or other effects on fish populations in regulated rivers (Saltveit et al. 2001). Attempts at modeling freeze-up and ice dynamics at local scales, such as individual rapids, have not been satisfying (Alfredsen & Tesaker 2002), although models devised for larger scales, such as river sections, have been successful (Reiter & Huokuna 1995). Predicting the formation and dynamics of frazil and anchor ice and their effects on the behavior and microhabitat selection of salmonids is largely unknown. Surprisingly, even basic habitat preference curves used in habitat-hydraulic modelling are almost totally lacking for young salmonids such as Atlantic salmon and brown trout (but see Mäki-Petäys et al. 1997, 2004, Armstrong et al. 2003). In summary, we believe 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 modifications on the ecology of salmonids in winter (e.g. flow regulation, land-use activities) and (4) identifying methods to model and assess winter habitat conditions for salmonids.

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