Life in the ice lane: a review of the ecology of salmonids during winter

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ABSTRACT: The main objective of this presentation is 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 1996). 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 1996, Heggenes 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.

Ice regimes	Small, steep rivers	Large rivers	Regulated rivers
Freeze up	Border and skim ice formation	Border ice	Border ice Dynamic ice formation
	Dynamic Freeze-up	Ice cover formation	Reduced ice growth
Main winter	Extended dynamic freeze-up	Stable ice cover	Repeated ice break-ups
	Anchor ice dams	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

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 (Nicieza & 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 cms^{-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, Gowan 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, Erkinaro 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, Nykänen 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 (Nykänen 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 (Tschaplinski & 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, Tschaplinski & 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 sympatry 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.

REFERENCES

Alfredsen, K. & Tesaker, E. 2002. Winter habitat assessment strategies and incorporation of winter habitat in the Norwegian habitat assessment tools. *Hydrolog. Process.* 16: 927-936.

Amundsen, P.A., Gabler, H.M., & Riise, L.S. 2001. Intraspecific food resource partitioning in Atlantic salmon *Salmo salar* parr in a subarctic river. *Aquatic Living Resources* 14: 257-65.

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M., & Milner, N.J. 2003. Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* 62: 143-170.

Bradford, M.J. & Higgins, P.S. 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile chinook salmon *Oncorhynchus tshawytscha* and steelhead trout *Oncorhynchus mykiss*. *Can. J. Fish. Aquat. Sci.* 58: 365-374.

Bramblet, R.G., Bryant, M.D., Wright, B.E. & White, R.G. 2002. Seasonal use of small tributary and main-stem habitats by juvenile steelhead, cohon salmon, and Dolly Varden in a southeastern Alaska drainage basin. *Trans. Am. Fish. Soc.* 131: 498-506.

Brown, R.S. 1999. Fall and early winter movements of cutthroat trout, *Oncorhynchus clarki*, in relation to water temperature and ice conditions in Dutch Creek, Alberta. *Environ. Biol. Fish.* 55: 359-368.

Brown, R.S. & Mackay, W.C. 1995. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. *Trans. Am. Fish. Soc.* 124: 873-885.

Brown, R.S., Power, G. & Beltaos, S. 2001. Winter movements and habitat use of riverine brown trout, white sucker and common carp in relation to flooding and ice break-up. *J. Fish Biol.* 59: 1126-1141.

Brown, R.S., Power, G., Beltaos, S. & Beddow, T.A. 2000. Effects of hanging ice dams on winter movements and swimming activity of fish. *J. Fish Biol.* 57: 1150-1159.

Bustard, D.R. & Narver, D.W. 1975. Aspects of the winter ecology of juvenile coho salmon *Oncorhynchus kisutch* and steelhead trout *Salmo gairdneri*. *J. Fish. Res. Board Can.* 32: 667-680.

Carlson, S.M. & Letcher, B.H. 2003. Variation in brook and brown trout survival within and among seasons, species, and age classes. *J. Fish Biol.* 63: 780-794.

Chisholm, I.M., Hubert, W.A. & Wesche, T.A. 1987. Winter stream conditions and use of habitat by brook trout in high-elevation Wyoming streams. *Trans. Am. Fish. Soc.* 116: 176-184.

Cunjak, R.A. 1988. Physiological consequences of overwintering in streams: The cost of acclimitization? *Can. J. Fish. Aquat. Sci.* 45: 443-452.

Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. *Can. J. Fish. Aquat. Sci.* 53 (Suppl. 1): 267-282.

Cunjak, R.A. & Power, G. 1986. Winter habitat utilization by stream resident brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*. *Can. J. Fish. Aquat. Sci.* 43: 1970-1981.

Cunjak, R.A. & Power, G. 1987a. Cover use by stream-resident trout in winter: a field experiment. *N. Am. J. Fish. Manage.* 7: 539-544.

Cunjak, R.A. & Power, G. 1987b. The feeding and energetics of stream resident trout in winter. *J. Fish Biol.* 31: 493-511.

Cunjak, R.A. & Randall, R.G. 1993. In-stream movements of young Atlantic salmon *Salmo salar* during winter and early spring. In Gibson, R. J. & Cutting, R. E. (eds), *Production of juvenile Atlantic salmon, Salmo salar, in natural waters. Can. Spec. Publ. Fish. Aquat. Sci.* 118: 43-51.

Cunjak, R.A. & Therrien, J. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. *Fisheries Manag. Ecol.* 5: 29-223.

Cunjak, R.A., Curry, R.A. & Power, G. 1987. Seasonal energy budget of brook trout in streams: Implications of a possible deficit in early winter. *Trans. Am. Fish. Soc.* 116: 817-828.

Cunjak, R.A., Prowse, T.D. & Parrish, D.L. 1998. Atlantic salmon *Salmo salar* in winter: "the season of parr discontent". *Can. J. Fish. Aquat. Sci.* 55 (Suppl. 1): 161-180.

Elliott, J.M. 1993. The pattern of natural mortality throughout the life cycle in contrasting populations of brown trout, Salmo trutta L. *Fish. Res.* 17, 123-136.

Elliott, J.M., Hurley, M.A. & Elliott, J.A. 1997. Variable effects of droughts on the density of sea-trout *Salmo trutta* populations over 30 years. *J. Appl. Ecol.* 34: 1229-1238.

Erkinaro, J. 1995. The age structure and distribution of Atlantic salmon parr, *Salmo salar* L., in small tributaries and main stems of the subarctic River Teno, northern Finland. *Ecol. Freshw. Fish* 4: 53-61.

Fausch, K.D. & Young, M.K. 1995. Evolutionary significant units and movement of resident stream fishes: a cautionary tale. *Amer. Fish. Soc. Symp.* 17: 360-370.

Finstad, A., Naesje, T.F. & Forseth, T. 2004a. Seasonal variation in the thermal performance of juvenile atlantic salmon Salmo salar. *Freshwater Biol.* 49: 1459-1467.

Finstad, A., Udedal, O., Forseth, T. & Naesje, T.F. 2004b. Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 61: 2358-2368.

Finstad, A., Forseth, T., Naesje, T.F. & Ugedal, U. 2004c. The importance of ice cover for energy turnover in juvenile Atlantic salmon. *J. Anim. Ecol.* 73: 959-966.

Fraser, N.H.C., Metcalfe, N.B. & Thorpe, J.E. 1993. Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proc. R. Soc. Lond. B* 252: 135-139.

Glova, G.J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon *Oncorhyn-*

chus kisutch and coastal cutthroat trout *Salmo clarki* in a laboratory stream. *Hydrobiologia* 131: 155-168.

Gowan, C. Young, M.K., Fausch, K.D. & Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? *Can. J. Fish. Aquat. Sci.* 51: 2626-2637.

Greenberg, L.A. & Giller, P. 2000. The potential of the flat-bed passive integrated transponder antennae for studing habitat use by stream fishes. *Ecol. Freshw. Fish* 9: 74-80.

Gregory, J.S. & Griffith, J.S. 1996. Winter concealment by subyearling rainbow trout: space size selection and reduced concealment under surface ice and in turbid water conditions. *Can. J. Zool.* 74: 451-455.

Griffith, J.S. & Smith, R.W. 1993. Use of winter concealment cover by juvenile cutthroat and brown trout in the South Fork of the Snake River, Idaho. *N. Am. J. Fish. Manage.* 13: 823-830.

Harper, D.D. & Farag, A.M. 2004. Winter habitat use by cutthroat trout in the Snake River near Jackson, Wyoming. *Trans. Am. Fish. Soc.* 133: 15-25.

Hartman, G.F. 1963. Observations on behavior of juvenile brown trout in a stream aquarium during winter and spring. *J. Fish. Res. Bd. Can*. 20: 769-787.

Harvey, B.C., Nakamoto, R.J. & White, J.L. 1999. Influence of large woody debris and a bankfull flood on movement of adult resident coastal cutthroat trout *Onchorynchus clarki* during fall and winter. *Can. J. Fish. Aquat. Sci.* 56: 2161-2166.

Harwood, A.J., Metcalfe, N., Griffiths, S.W. & Armstrong, J.D. 2002. Intra- and inter-specific competition for winter concealment habitat in juvenile salmonids. *Can. J. Fish. Aquat. Sci.* 59: 1515-1523.

Healy, B.D. & Lonzarich, D.G. 2000. Microhabitat use and behavior of overwintering juvenile coho salmon in a Lake Superior tributate. *Trans. Am. Fish. Soc.* 129: 866-872.

Heggenes, J. & Dokk, J.G. 2001. Contrasting temperatures, waterflows, and light: seasonal habitat selection by young Atlantic salmon and brown trout in a boreonemoral river. *Regul. River.* 17: 623-635.

Heggenes, J., Krog, O.M.W., Lindås, O.R., Dokk, J.G. & Bremnes, T. 1993. Homeostatic behaviour repsonses in a changing environment: brown trout *Salmo trutta* becomes nocturnal during winter. *J. Anim. Ecol.* 62: 295-308.

Holtby, L.B. 1988. Effects of logging on stream temperatures in Catamaran Creek, British Columbia, and associated impacts on coho salmon *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* 45: 502-515.

Hubbs, C.L. & Trautman, M.B. 1935. The need for investigating fish conditions in winter. *Trans. Am. Fish. Soc.* 65: 51-56.

Hunt, R.L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. *J. Fish. Res. Board Can.* 26: 1473-1483.

Jakober, M.J., McMahon, T.E., Thurow, R.F. & Clancy, C.G. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat in Montana headwater streams. *Trans. Am. Fish. Soc.* 127: 223-235.

Johnston, P., Bergeron, N.E. & Dodson, J.J. 2004. Diel activity patterns of juvenile Atlantic salmon in rivers with summer water temperature near the temperature-dependent suppression of diurnal activity. *J. Fish. Biol.* 65: 1305-1318.

Johnston, P., Bergeron, N.E. & Dodson, J.J. 2005. Assessment of winter size-selective mortality of young-of-year Atlantic salmon (*Salmo salar*) using otolith microstructure analysis. *Ecol. Freshwater Fish* (in press).

Lenormand, S., Dodson, J.J. & Ménard, A. 2004. Seasonal and ontogenetic patterns in the migration of anadromous brook charr *Salvelinus fontinalis*. *Can. J. Fish. Aquat. Sci.* 61: 54-67.

Letcher, B.H., Gries, G. & Juanes, F. 2002. Survival of stream-dwelling Atlantic salmon: effects of life history variation, season, and age. *Trans. Am. Fish. Soc.* 131: 838-854.

Lund, E., Olsen, M. & Vollestad, L.A. 2003. First-year survival of brown trout in three Norwegian streams. *J. Fish Biol.* 62: 323-340.

MacMahon, T.E. & Hartman, G.F. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* 46: 1551-1557.

Metcalfe, N.B. & Thorpe, J.E. 1992. Anorexia and defended energy levels in over-wintering juvenile salmon. *J. Anim. Ecol.* 61: 175-181.

Meyer, K.A. & Griffith, J.S. 1996. First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho. *Can. J. Zool.* 75: 59-63.

Meyer, K.A. & Griffith, J.S. 1997. Effects of cobble-boulder substrate configuration on winter residency of juvenile rainbow trout. *N. Am. J. Fish. Manage.* 17: 7-84.

Mitro, M.G. & Zale, A.V. 2002. Seasonal survival, movement, and habitat use of age-0 rainbow trout in the Henrys Fork of the Snake River, Idaho. *Trans. Am. Fish. Soc.* 131: 71-286.

Muhlfeld, C.C., Bennett, D.H. & Marotz, B. 2001. Fall and winter habitat use and movement by Columbia River red-band trout in a small stream in Montana. *N. Am. J. Fish. Manage.* 21: 170-177.

Mäki-Petäys, A., Muotka, T., Huusko, A., Tikkanen, P. & Kreivi, P 1997. Seasonal changes in habitat use and preference by juvenile brown trout, *Salmo trutta*, in a northern boreal river. *Can. J. Fish. Aquat. Sci.* 54: 520-530.

Mäki-Petäys, A., Vehanen, T. & Muotka, T. 2000. Microhabitat use by age-0 brown trout and grayling: seasonal responses to streambed restoration under different flows. *Trans. Am. Fish. Soc.* 129: 771-781.

Mäki-Petäys, A., Erkinaro, J., Niemelä, E., Huusko, A. & Muotka, T. 2004. Spatial distribution of juvenile Atlantic salmon *Salmo salar* in a subarctic river: size-specific changes in a strongly seasonal environment. *Can. J. Fish. Aquat. Sci.* 61: 2329-2338.

Needham, P.R., Moffett, J.W. & Slater, D.W. 1945. Fluctuations in wild brown trout populations in Convict Creek, California. *J. Wildlife Manage.* 9: 9-25.

Nichelson, T.E., Rodgers, J.D., Johnson, S.L. & Solazzi, M.F. 1992. Seasonal changes in habitat use by juvenile coho salmon *Oncorhynchus kisutch* in Oregon coastal streams. *Can. J. Fish. Aquat. Sci.* 49: 783-789.

Nicieza, A.G. & Metcalfe, N.B. 1997. Growth compensation in juvenile Atlantic salmon: responses to depressed temperature and food availability. *Ecology* 78: 2385-2400.

Nykänen, M., Huusko, A. & Mäki-Petäys, A. 2001. Seasonal changes in the habitat use and movements of adult European grayling in a large subarctic river. *J. Fish Biol.* 58: 506-519.

Nykänen, M., Huusko, A. & Lahti, M. 2004. Changes in movement, range and habitat preferences of adult grayling from late summer to early winter. *J. Fish Biol.* 64: 1386-1398.

Olsen, E. M. & Vollestad, L. A. 2001. Estimates of survival and stream-dwelling brown trout using mark-recaptures. *J. Fish Biol.* 59: 1622-1637.

Power, G., Brown, R. S. & Imhof, G. 1999. Groundwater and fish - insights from northern North America. *Hydrolog. Process.* 13: 401-422.

Prowse, T. D. & Gridley, N. C. 1993. *Environmental aspects of river ice*. NHRI Science Raport No. 5.

Quinn, T.P. & Peterson, N.P. 1996. The influence of habitat complexity and fish size on over-winter survival and growth of individually marked juvenile coho salmon *On-*

corhynchus kisutch in Big Beef Creek, Washington. *Can. J. Fish. Aquat. Sci.* 53:1555-1564.
Reiter, P. & Huokuna, M. 1995. Ice problems in river engineering: a numerical model to study remedial measures. *Hydropower and Dams* 95: 58-62.
Rimmer, D.M., Saunders, R.L. & Paim, U. 1983. Autumnal habitat shift of juvenile Atlantic salmon *Salmo salar* in a small river. *Can. J. Fish. Aquat. Sci*. 40: 471-480.
Robertson, M.J., Clarke, K.D., Scruton, D.A. & Brown, J.A. 2003. Interhabitat and instream movements of large Atlantic salmon parr in a Newfoundland watershed in winter. *J. Fish Biol.* 63: 1208-1218.
Robertson, M.J., Pennell, C.J., Scruton, D.A., Robertson, G.J. & Brown, J.A. 2004. Effect of increased flow on the behaviour of Atlantic salmon parr in winter. *J. Fish Biol.* 65: 1070-1079.
Roussel, J.-M., Cunjak, R.A., Newbury, R., Caissie, D. & Haro, A. 2004. Movements and habitat use by PIT-tagged Atlantic salmon parr in early winter: the influence of anchor ice. *Freshwat. Biol.* 49: 1026-1035.
Saltveit, S.J., Halleraker, J.H., Arnekleiv, J.V. & Harby, A. 2001. Field experiments on stranding in juvenile Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* during rapid flow decreases caused by hydropeaking. *Regul. River.* 17: 609-622.
Simpkins, D.G. & Hubert, W.A. 2000. Drifting invertebrates, stomach contents, and body conditions of juvenile rainbow trout from fall through winter in a Wyoming tailwater. *Trans. Am. Fish. Soc.* 129: 1187-1195.
Simpkins, D.G., Hubert, W.A. & Wesche, T.A. 2000. Effects of fall-to-winter changes in habitat and frazil ice on the movements and habitat use of juvenile rainbow trout in a Wyoming tailwater. *Trans. Am. Fish. Soc.* 129: 101-118.
Smith, R.W. & Griffith, J.S. 1994. Survival of rainbow trout during their first winter in the Henry’s Fork of the snake River, Idaho. *Trans. Am. Fish. Soc.* 123: 747-756.
Swales, S., Lauzier, R.B. & Levings, C.D. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. *Can. J. Zool.* 64: 1506-1514.
Swales, S. & Levings, C.D. 1989. Role of off-channel ponds in the life cycle of coho salmon *Oncorhynchus kisutch* and other juvenile salmonids in the Coldwater River, British Columbia. *Can. J. Fish. Aquat. Sci.* 46: 232-242.
Tesaker, E. 1998. Mitigation of ice effects of the habitat in regulated and natural rivers. In Shen, H.T. (ed), *Proceedings of the 14th international symposium on ice*: 161-167. Potsdam/New york/USA.
Tschaplinski, P.J. & Harman, G.F. 1983. Winter distribution juvenile coho salmon *Oncorhynchus kisutch* before and after logging in Carantion Creek, British Columbia, and some implications for overwintering survival. *Can. J. Fish. Aquat. Sci.* 40: 452-4761.
Vehanen, T., Mäki-Petäys, A., Aspi, J. & Muotka, T. 1999. Intercohort competition causes spatial segregation in brown trout in artificial streams. *J. Fish Biol.* 55: 35-46.
West, R.L., Smith, M.W., Barber, W.E., Reynolds, J.B. & Hop, H. 1992. Autumn migration and overwintering of Arctic grayling in coastal streams of the Arctic National Wildlife Refuge, Alaska. *Trans. Am. Fish. Soc.* 121: 709-715.
Whalen, K.G. & Parrish, D.L. 1999. Nocturnal habitat use of Atlantic salmon parr in winter. *Can. J. Fish. Aquat. Sci.* 56: 543-1550.
Wootton, R.J. 1990 *Ecology of teleost fishes*. London: Chapman and Hall.
Young, M.K. 1998. Absence of autumnal changes in habitat use and location of adult Colorado River cutthroat trout in a small stream. *Trans. Am. Fish. Soc.* 127: 147-151.