Atlantic salmon (Salmo salar) in winter: 'The season of parr discontent'?

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Atlantic salmon (*Salmo salar*) in winter: "the season of parr discontent[1]"?[2]

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Abstract: Winter is a dynamic period. Effects of the winter regime on northern streams and rivers is extremely variable and characterized by dramatic alterations in physical habitat to which Atlantic salmon (*Salmo salar*) must acclimate and adapt to survive. In this paper, we synthesize recent advances in the biological and hydrologic/geomorphic disciplines, with specific reference to Atlantic salmon overwintering in the freshwater portions of those running waters subject to freezing water temperatures. The specific requirements and adaptations for surviving winter at the three distinct life-stages in freshwater (egg, parr, kelt) are identified in relation to the characteristics of three biophysical phases: early winter (temperature decline and freeze-up), midwinter (ice growth and habitat reduction), and the break-up/warming phase. In a case study of Catamaran Brook (New Brunswick), a hydro-ecological analysis was used to explain interannual variability in juvenile abundance, especially for young-of-the-year salmon. A strong relation was found between winter discharge and interstage survival (egg to 0+, 0+ to 1+, 1+ to 2+) in 5 of 6 years. That is, juvenile salmon abundance in summer was highest following winters with high streamflow, presumably a function of habitat availability, especially beneath ice cover. However, the lowest measured egg-0+ survival (9.2%) was related to an atypical midwinter, dynamic ice break-up triggered by a rain-on-snow event that resulted in severe scouring of the stream-bed and redds. Thus, interannual variability in Atlantic salmon parr abundance from 1990 to 1996 was largely explained by density-independent (environmental) constraints to winter survival. The complexity of stream processes during winter underscores the need for interdisciplinary research to quantify biological change.

Résumé : L'hiver est une période dynamique. Les effets du régime hivernal sur les cours d'eau du Nord sont extrêmement variables et caractérisés par des altérations marquées de l'habitat auquel le saumon de l'Atlantique doit s'acclimater et s'adapter pour survivre. Dans cet article, nous faisons une synthèse des progrès récents en biologie et en hydrologie et géomorphologie, en traitant particulièrement du saumon atlantique qui hiverne dans les eaux douces de ces cours d'eau dont les températures approchent du point de congélation en hiver. Les exigences et les adaptations spécifiques pour la survie hivernale des trois stades dulcicoles distincts (oeuf, tacon, charognard) sont établies en rapport avec les caractéristiques de trois phases biophysiques : début de l'hiver (chute de la température et englacement), mi-hiver (croissance de la glace et réduction de l'habitat) et la phase de dégel et de réchauffement. Dans une étude de cas portant sur le ruisseau Catamaran (Nouveau-Brunswick), on a eu recours à une analyse hydro-écologique pour expliquer la variabilité interannuelle de l'abondance des juvéniles, particulièrement chez les jeunes saumons de l'année. On a observé une forte relation entre le débit hivernal et la survie interstades (oeuf à 0+, 0+ à 1+, 1+ à 2+) dans 5 années sur 6. Ainsi, l'abondance des saumons juvéniles en été était grande après les hivers caractérisés par des débits élevés, probablement parce que l'habitat disponible était plus important, particulièrement sous le couvert de glace. Cependant, on a observé le plus faible taux de survie du stade d'oeuf à l'âge 0+ (9,2 %) après un mi-hiver atypique caractérisé par une débâcle dynamique causée par la pluie, qui s'est soldée par un affouillement marqué du lit du cours d'eau et des nids de fraye. Ainsi, la variabilité interannuelle de l'abondance des tacons de saumon atlantique de 1990 à 1996 était largement tributaire de contraintes indépendantes de la densité (environnementales) pesant sur la survie hivernale. La complexité des processus fluviaux durant l'hiver fait qu'il est nécessaire de mener des recherches interdisciplinaires pour quantifier le changement biologique.

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Introduction

In the north temperate and subarctic latitudes which encompass the range of most Atlantic salmon, *Salmo salar* L., winter conditions last between 4 and 8 months, depending on geographical location. Freezing water temperatures, variable ice dynamics, snow accumulation, reduced solar radiation and photoperiod, pH depression, anoxia, ice surges, mechanical break-up events, flooding, and extremely low river flows are some of the characteristic physico-chemical conditions of the winter environment which confront coldwater species such as Atlantic salmon. In order to survive, stream fishes respond with a variety of tactics (Cunjak 1996) such as altering diel activity patterns, shifting microhabitats, moving variable distances to wintering areas, physiologically adapting to changing temperature and feeding regimes, and reducing energy expenditure to conserve depleted energy stores until replenishment in spring.

Much has been done in the past 15 years to elucidate the various physical processes occurring in winter in ice-covered rivers and to describe the dynamic nature of this season (e.g., Ashton 1986; Gray and Prowse 1993; Beltaos 1995). Similarly, many basic biological questions pertaining to overwintering by stream biota have been addressed (Ultsch 1989; Irons et al. 1993; Power et al. 1993; Cunjak 1996). However, an integrated treatment of physical winter conditions and concomitant ecological responses has generally been lacking (but see reviews by Prowse and Gridley 1993; Prowse 1994; Scrimgeour et al. 1994). The present paper synthesizes specific recent advances in the biological and hydrologic/geomorphic disciplines with respect to winter conditions in Atlantic salmon rivers. Given the unique habitat requirements and sensitivities inherent to the three freshwater stages of Atlantic salmon in winter (i.e., eggs, parr, and kelt), their biological responses were treated separately within distinct biophysical winter periods with an emphasis on implications for survival.

Winter, as referred to in this paper, is defined as that period immediately following egg deposition by Atlantic salmon (and coincident with a decline in water temperature) and extending until the loss of all surface ice (often accompanied by a major spate and snowmelt) or the commencement of smolt emigration. This biological definition is specific for the present subject (*S. salar*) and has been modified from one suggested by Cunjak (1996). The running waters reviewed in this paper are those subject to near freezing temperatures (<1°C) and, typically, ice-formation for some portion of the winter. Although some Atlantic salmon are known to rear in estuaries (Cunjak 1992; Kazakov et al. 1992) and lakes (Chadwick and Green 1985; Hutchings 1986; Kazakov et al. 1992; Erkinaro et al. 1995), this paper will limit its focus to lotic freshwater environments.

The paper has two objectives: first, to establish the concept of winter as a dynamic period (spatially and temporally) by identifying environmental conditions inherent to Atlantic salmon rivers in winter, and the specific requirements and adaptations for surviving winter at the egg, parr, and kelt stages. The second objective was to demonstrate the value of hydro-ecological analysis to explain density-independent (environmental) constraints to winter survival for a population of Atlantic salmon; this was accomplished by way of a case study.

Bio-physical phases of winter

Often thought of as a period of relative calm and inactivity, the winter regime of northern streams and rivers is actually a very dynamic period characterized by dramatic changes in physical habitat to which Atlantic salmon must acclimate and adapt. Many of the changes are due to the distinctive hydrologic regimes of cold regions that owe much of their uniqueness to the accumulation and ablation of snow and ice (Prowse 1990, 1994).

Although many processes are temporally interdependent, for ease of discussion, winter has been subdivided into three basic periods: early winter, midwinter, and break-up (often, but not exclusively a late winter event). Subsections review the major physical conditions that characterize each period, describe the varied biological conditions unique for distinct life-stages of Atlantic salmon, and discuss the implications of the most important biophysical relationships using specific examples from the literature.

Early winter

The early winter period in most northern rivers is characterized by general declines in solar input, air and water temperatures, and discharge — albeit with some intraseasonal variability introduced by, for example, late-autumn rainfall-runoff events. It can also be broken into two distinct phases: (*a*) the period immediately following spawning during which water temperatures decline from approximately 5°C to 0°C and (*b*) the subsequent period of first ice formation.

Cooling, water level decline, and photoperiod reduction

The hydrology of streams and rivers in cold regions is governed by a number of unique processes that control the timing, duration, and magnitude of flow and water levels. Consequently, hydrographs differ significantly from those characteristic of temperate climates (Prowse 1994). As winter approaches, less water is delivered by surface runoff to the main channel because of the accumulation of precipitation as snow. With the loss of flow originating from surface runoff, a steady recession begins in flow and water levels; the rate of decline being tempered primarily by additions of flow from groundwater and surface water bodies (e.g., ponds and lakes). Accompanying the decline in flow is a reduction in available fish habitat due to the drying of ephemeral low-order streams and the drying of margins of higher order streams.

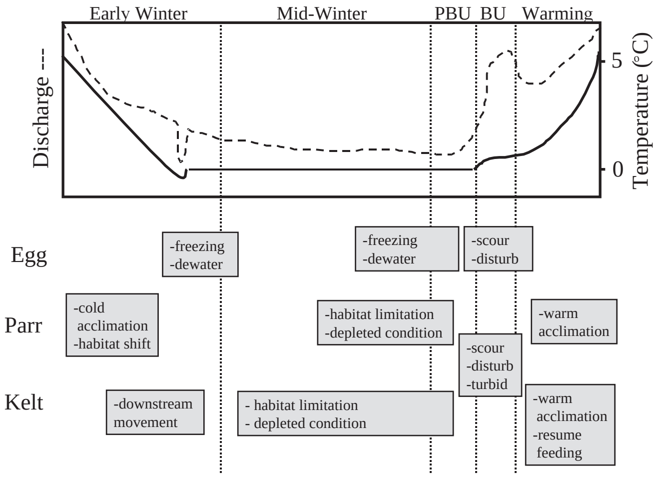
The specific hydraulic conditions and substrate chosen by Atlantic salmon for spawning (Peterson 1978; Fleming 1996), in combination with the immobility of eggs, results in eggs having the most restrictive winter niche of all life-stages. The coarse (gravel/cobble) composition of the redds and their general occurrence in midstream locations at the downstream end (tail) of pools and runs has the advantage of providing a continuous recharge flow of water and oxygen to the eggs within the substrate. These hydraulic conditions are in marked contrast to those experienced in the redds of another common salmonid of eastern North America, the brook trout (*Salvelinus fontinalis*), which prefer to spawn in areas of “winter-warm” groundwater discharge (Curry and Noakes 1995), close to stream margins, and often with little regard for substrate particle size (e.g., Fraser 1982). The midstream location of salmon redds may be particularly adaptive because, as discharge and river stage decline (and border ice formation is subsequently initiated), streamflow becomes concentrated in the deeper portion of the channel (often midstream), thereby ensuring water delivery to eggs.

As water level and air temperature decline, water temperature also steadily falls (Fig. 1) although this is not a continuous process and is often interrupted by reversals in atmospheric heat fluxes. In general, the larger the surface area to volume ratio, the more efficient a river is in exchanging heat with the atmosphere. Hence, given the same meteorological conditions, wide shallow streams cool most rapidly while deeper rivers are usually the last to freeze. Inputs of groundwater also become increasingly important to the thermal balance as less surface runoff is directed to the stream. In many systems, including Arctic regions, “warm” groundwater is the main source of water that sustains winter streamflow (Reynolds 1997) and, where of sufficient magnitude, can keep sections ice-free. For some species, groundwater provides the only known overwintering and (or) spawning zones (Craig and Poulin 1975; Brown et al. 1994). Unlike many stream salmonids, Atlantic salmon (both wintering parr and spawning adults) appear *not* to seek out undiluted groundwater discharge zones in early winter (Cunjak 1996).

Coincident with a decline in daily water temperature below 8–10°C, juvenile Atlantic salmon display an autumnal shift in microhabitat choice and behaviour, moving beneath suitably sized stones during the daylight hours (Gibson 1966; Smirnov et al. 1976; Rimmer et al. 1983, 1984; Cunjak 1988*a*; Heggenes and Saltveit 1990; Veselov and Shustov 1991; Fraser et al. 1993; Erkinaro et al. 1995). Unlike the situation during summer when they are strongly photopositive (but see Gries et al. 1997), young Atlantic salmon become exclusively photonegative in winter (Rimmer and Paim 1990), leaving their shelters only during the night (or at dawn/dusk) to feed (Cunjak 1988*a*; Heggenes et al. 1993; Fraser et al. 1993). The reduced buoyancy of salmon parr at water temperatures <8°C (Pinder and Eales 1969) may be a synchronous adaptation for this cryptic behaviour. Frequency of emergence and nocturnal foraging is unknown, especially in far northern regions that are subject to months of polar darkness. Probably, foraging activity is minimal at such low temperatures because of the reduced metabolic demand and the inability to hold position in moderate water velocities (Rimmer et al. 1985; Heggenes and Traaen 1988) although visual acuity is improved at low light levels in winter (Fraser et al. 1993). Veselov and Shustov (1991) have suggested that this inability to resist water currents and the reduced fright reaction of overwintering salmon parr may explain the winter hiding behaviour — i.e., a tactic to avoid predation and minimize energy expenditure (Cunjak 1996).

There are, however, exceptions to the above-noted generalizations. At the northern end of their distributional range, such as in subarctic rivers (e.g., Ungava, Labrador, northern Scandinavia, and Russia), some young Atlantic salmon remain day-active above the substrate until water temperatures decrease below approximately 5°C (Cunjak, unpublished data). Such a variation seems adaptive where the growing season is so short because of the cold climate (Jensen and Johnsen 1986). Even in more temperate latitude streams such as in New Brunswick, juvenile salmon (age 0+ and 1+) have been observed underwater holding stations above the substrate and feeding in midday, when water temperature was <4°C (Cunjak, unpublished data) in the autumn. These observations were coincident with the spawning period of adult Atlantic salmon in the stream and may have been a periodic response to the sudden availability of a high quality food (eggs) for consumption.

Fig. 1. Conceptual representation of biophysical phases of winter depicting generalized pattern of discharge and water temperature in relation to freshwater lifestages (egg, parr, and kelt) of Atlantic salmon in ice-covered rivers. PBU = pre-break up and BU = break up. Sizes and placement of boxes correspond to timing and duration of the described events. Abbreviations: scour = ice scour; disturb = disturbance; dewater = dewatering; turbid = elevated turbidity.



During the early winter, metabolic rates of fish decline because of changes in photoperiod (Evans 1984), as well as, temperature. Higgins and Talbot (1985), in studying Atlantic salmon growth in freshwater, found a greater linkage between growth and photoperiod than growth and water temperature. The presumed mechanism was that photoperiod altered the endogenous rhythm of appetite and growth (Villarreal et al. 1988). Seasonal changes in gut evacuation rates of salmon that occur as a result of a lower metabolic rate were suggested to be neural or hormonal and, therefore, are affected by photoperiod (Higgins and Talbot 1985). Photoperiod is a more reliable cue for impending seasonal changes and, thus, physiological acclimation rather than responding only to declining temperatures that are extremely variable (Wootton 1990).

Although salmonids remain “active” during winter (i.e., do not exhibit torpor, Crawshaw 1984), it is the reduced assimilation efficiency and slow gut evacuation rates at low winter temperatures, and not food resources, that appear to be the limiting factors to meeting the physiological demands of cold acclimation in early winter (Fry 1971; Cunjak et al. 1987; Cunjak 1988*b*). The reduced appetite or “anorexia” reported by Metcalfe and Thorpe (1992) for young-of-the-year (YOY) salmon in early winter was regulated by the nutritional state of the fish. Further, these authors found that this anorexia was most pronounced among smaller members of the age-class and suggested this to be a tactic to minimize energy expenditure as these fish would not smoltify the following spring. During this stressful transition time (cold acclimation, Fig. 1), salmonids lose the greatest amount of lipids (brook trout and brown trout, *Salmo trutta*: Cunjak 1988*b*; Atlantic salmon: Gardiner and Geddes 1980; Sutton 1994). A recent model (Bull et al. 1996) corroborated these findings and showed that appetite was regulated adaptively in accordance with long-term energy requirements rather than short-term needs.

Of particular relevance to the topic of winter nutrition is the energetic value of egg consumption by parr, and specifically for the winter survival of pre-smolts. Largely speculative at this point, the story is nevertheless intriguing. Eggs have a high lipid content and are easily digestible. Their availability in early winter when physiological demands (i.e., for cold acclimation, Cunjak 1988*b*) are high, would make egg consumption an adaptive trait particularly if winter survival is strongly related to the acquisition of a threshold energy level (Gardiner and Geddes 1980). The problem of insufficient reserves for overwintering is most critical for post-spawned male parr and is the basis for the theory of high winter mortality at this life-stage (Dalley et al. 1983; Myers 1984; Prévost et al. 1992). Yet, some spent parr do survive winter and can even complete smoltification, as evidenced by milt production among early smolt migrants in Canadian and New England streams (R. Saunders, Canada, personal communication; Whalen 1998) and in Europe (Jones 1959; Berglund 1992). It may be that winter survival by some pre-smolts (especially spent male parr) or "upper mode" parr (*sensu* Thorpe 1977) is partly dependent on the acquisition of energy reserves provided via egg consumption in early winter. The relevance of this topic to smolt physiology, winter survival and life history theory, is deserving of future research.

Nutritional insufficiencies and parasite loads can act as stressors that debilitate young salmon and may result in winter mortality. Pickering and Pottinger (1988) found winter mortality among YOY salmon to be greatest for the smallest fish and attributed this to chronic stress resulting from a nutritional deficiency as measured by body condition, blood cell counts and cortisol levels. A study (Cunjak and McGladdery 1991) on the effect of glochidial parasitism on the gills of overwintering juvenile Atlantic salmon in a Nova Scotian river showed that heavy parasite loads were contributing to the poorer body condition and smaller size in salmon parr. This glochidia–salmon relationship is not unique to North America but shows a holarctic distribution extending through the U.K., and Russia (Ziuganov et al. 1990). Recent observations (Table 1) of a marked increase in the number of leeches (Hirudinea) attached to the body and fins of wild Atlantic salmon parr in early winter may further stress these fishes at this critical period of the year. It is interesting that the incidence of leeches is most prevalent in Atlantic salmon (Cunjak, unpublished data) and coincident with the time of year that the fish move beneath rock shelters, perhaps where they are more susceptible to attachment by the ectoparasites. The effect of leeches on winter survival is presently unknown but a related species of hirudinean has been identified as the vector of a hemoflagellate parasite in Pacific salmon (Bell and Margolis 1976).

Table 1. Frequency and incidence of leeches (*Piscicola punctata*) on the fins and body of Atlantic salmon parr collected from Catamaran Brook, 1993–1995.

Season	*N*	Parr with leeches (%)	Mean incidence per parr
Summer	3532	0	0
Early winter	2548	186 (7.3)	1.2
Spring	451	0	0

Note: *N* = number of parr examined.

Ice initiation and freeze-up

Once the water temperature reaches 0°C in a river, the first ice usually forms along the banks. Once the bank material is cooled below its threshold temperature, ice crystals will begin to nucleate and grow laterally across the surface into the main channel. Conditions are most suitable for this lateral growth where the flow is essentially laminar in the less turbulent reaches. Localised "border" ice growth may also occur well away from the shore around obstacles such as exposed boulders that create their own unique set of flow and thermal conditions.

During the early stages of freeze-up, all forms of border ice may provide overhead cover for stream salmonids in otherwise open stretches of stream (e.g., Maciolek and Needham 1952; Brown et al. 1994; Cunjak 1996). Parr may use ice cover when not occupying substrate shelters (Whalen 1998) whereas post-spawning salmon (kelts) have been observed resting beneath shelf ice (Cunjak, personal observations), which could serve the dual purpose of predator avoidance and energy conservation.

Although the entire channel width of some streams and small rivers may be covered by the gradual outward progression of border ice, especially under very cold meteorological conditions, increasing flow turbulence halts its lateral growth. In these turbulent areas, ice formation typically occurs by nucleation of small "frazil" particles (see Tsang 1982, typically 0.1 to 5 mm diameter) at a small degree of supercooling (~–0.1°C, see Fig. 1). Rapid secondary multiplication of additional frazil crystals can quickly result in high concentrations (e.g., as high as 10^6 m^{-3}; Gilfilian et al. 1972). While the crystals are in a supercooled or "active" state, they continue to grow and may adhere to one another or bond to other objects.

Under very cold winter conditions, frazil may be generated during the daytime but in general the formation follows a diurnal cycle characterized by rapid growth at night and a cessation during the day, due primarily to warming by solar radiation. Highly turbulent open-water reaches, such as found at riffles and rapids, create the best set of flow conditions for the generation of large amounts of frazil. Much of the frazil generated at such sites is subsequently deposited beneath ice cover in pools downstream. Where rapids remain open for protracted periods, large frazil accumulations known as “hanging dams” can virtually fill pools (Michel and Drouin 1981; Beltaos and Dean 1981) and lead to the main flow being channelled down to the pool bottom where frazil ice and high velocities can scour the substrate.

Recent radio-tagging studies of stream salmonids have related their movement to frazil ice. Brown and Mackay (1995) found cutthroat trout, *Oncorhynchus clarki*, avoided frazil deposition in pools in an Alberta river. Jakober et al. (1998) noted greatest winter movement by bull trout, *Salvelinus confluentus*, and cutthroat trout in those Montana streams where subsurface ice formation and supercooling were most common. Atlantic salmon kelts in the Miramichi River (Komadina-Douthwright et al. 1997), monitored over two winters, emigrated from tributary streams (<4th order) to main river channels immediately after spawning. These kelts quickly moved downstream (Fig. 1) to overwinter in backwater habitats, in the lee of islands or below the head of tide. In these areas, Komadina-Douthwright et al. (1997) speculated that ice, mainly frazil accumulation, would be reduced, and current velocities were low enough to ensure that energy expenditure was minimized. Main river pools, by contrast, were often choked with frazil ice reducing habitat suitability (Cunjak and Caissie 1994; Komadina-Douthwright et al. 1997).

In the more shallow turbulent reaches of a stream or river, active frazil ice and its associated supercooled water can be conveyed to the channel bottom where it can lead to the formation of “anchor” ice. Although such ice may adhere to almost any object, it most commonly bonds to aquatic vegetation, boulders, and even large areas of gravel and coarse sand. Given the right set of flow and weather conditions, anchor ice can spread and thicken over quite large portions of the channel bed. Calkins and Brockett (1988) and Whalen (1998) noted that 95–100% of the stream-bed of Atlantic salmon streams in New Hampshire and Vermont were blanketed with anchor ice prior to the formation of a continuous surface ice sheet. As long as conditions remain cold, anchor ice will only release when buoyancy is sufficient to lift the underlying bed material. Although such releases have frequently been cited as affecting the available invertebrate drift (e.g., Maciolek and Needham 1952; Miller and Stout 1989) the main ecological impact of anchor ice results from its effect on organisms within the bed material, particularly eggs and alevins. This can be either from a direct impact, such as through in situ freezing (Walsh and Calkins 1986) or indirectly through a restriction or elimination of flow (Fig. 1) and associated dissolved oxygen through the substrate (e.g., Calkins 1989; Power et al. 1993).

Earlier, we indicated that the location of salmon redds in midstream was adaptive in relation to flow hydraulics. The location of redds is not, however, without potential disadvantages given the unique physical conditions characteristic of early winter. Reiser and Wesche (1979) found eggs of brown trout buried 15 cm in the substrate to freeze despite 12–20 cm of water flowing over the redd in a Wyoming stream. This can likely be explained as intrusion of supercooled water into the interstitial spaces of the redd which subsequently froze as velocity was reduced. This form of subsurface ice would presumably be more deleterious to eggs (than frazil penetration) because of the denser nature of the ice. Such supercooled water penetration was noted in an Atlantic salmon stream in Vermont (Calkins 1989) but any effect on stream biota has yet to be confirmed.

Frazil ice crystals travelling with the flow continue to grow and agglomerate into larger flocs and become increasingly buoyant and less controlled by river turbulence (Tsang 1982). Eventually these crystals grow to sufficient size and concentration to arch across the river width, usually at some channel constriction often associated with encroaching border ice. Unless entrained by high flow velocities beneath this initial ice cover, subsequent incoming ice floes will begin to pack in and accumulate upstream forming a freeze-up ice cover. Formation of this initial, often very rough, ice cover can produce major changes to the flow regime as a result of the hydraulic storage of water (e.g., Gerard 1990; Prowse 1994; Gray and Prowse 1993). Consequently, upstream increases in water levels are often quite dramatic and have been cited as important in supplying water to aquatic habitats located along channel margins and in the floodplain (e.g., Paschke and Coleman 1986; Burn 1993). Concomitant with the increases in upstream water levels are the associated reductions in downstream discharge (Fig. 1). Although relatively short-lived, such ice-induced low-flow events can be lower than the more commonly recognized low-flow periods that occur in late winter as a result of minimal catchment runoff (Fig. 1). Periods of low flow have a number of important biological implications and many of these occur during the ice season when biological activity (and response) is slowed, or arrested, by low temperatures.

Midwinter

This period is typically characterized by declining water levels and stable near-freezing water temperatures (Fig. 1). In temperate-maritime regions, salmon rivers may develop only a partial ice cover or be intermittently ice covered during especially cold periods. In colder regions, however, a complete ice cover can develop and persist for several months. It is in these latter systems that ice becomes a dominant factor affecting the type and availability of stream habitat, including related factors such as light and oxygen levels and flow patterns.

Ice growth and habitat reduction

Once an ice cover has developed, water temperature remains close to 0°C (i.e., typically less than a few hundredths of a degree above freezing, Fig. 1). Any heat input by, for example, groundwater or radiative warming, is rapidly transferred by turbulent mixing to the overlying ice: the rougher the ice subsurface, the more rapid the heat transfer. Even though water temperatures may only be a fraction of a degree above freezing, the flow velocity can promote a rapid transfer of heat. Marsh and Prowse (1987), for example, found the water-to-ice heat transfer beneath a solid river ice cover to vary from approximately 10–30 $W\cdot m^{-2}$ with water temperatures of only 0.003–0.01°C. During midwinter, the magnitude of this water-to-ice hydrothermal flux is dwarfed by the large ice-to-atmospheric heat loss that promotes ice growth.

The growth of ice proceeds vertically downward into the water column. Growth rates can be accelerated by the presence of frazil deposited beneath the ice cover and retarded by the insulating effects of snow. With continued ice growth, an increasing portion of shallow water areas becomes frozen to the bed and the flow becomes increasingly concentrated in the deeper portions of the channel. Habitat reduction is further exaggerated by the deposition of frazil ice that tends to accumulate in low-velocity, marginal areas of the flow. The loss of river margin habitat may partly explain the redistribution and midstream concentration of salmon parr found sheltering beneath rocks during daytime in winter (Cunjak 1988*a*). In a section of a Vermont river, Whalen (1998) found that ice reduced the abundance of parr habitat such that the most commonly selected microhabitats represented <10% of those recorded when ice was absent.

Extensive frazil accumulations beneath ice cover can result in available habitat being largely restricted to the main flow channel and associated deep pools. Research by Calkins (1989) in New England salmon rivers found that ice could occupy 60–80% of the cross-sectional area of small to medium-order streams. Cunjak and Caissie (1994) found that 73–83% of the volume of a large (13 375 m^2) pool in the Miramichi River was occupied by frazil ice throughout the winter. Subsequent surveys in other main river pools in the Miramichi River found similar frazil accumulations (Komadina-Douthwright et al. 1997).

Such ice accumulation and associated habitat restictions may partly explain the winter movement patterns of fishes noted in recent years. Scruton et al. (1997) found landlocked Atlantic salmon kelts in a regulated Newfoundland river system moved considerable distances soon after spawning, and just prior to freeze-up, to subsequently overwinter in lakes. In the Miramichi River, radio-tagged Atlantic salmon kelts moved less in midwinter than early winter just prior to freeze-up (Table 2). Once a solid ice cover formed on the river, movements rarely exceeded 0.5 km per week (Komadina-Douthwright et al. 1997). An interesting finding was that most of the kelts (both years) moved to overwinter below the head of tide where presumably ice conditions and frazil accumulation would be reduced by tidal action. Longest winter movement was by those kelts which were farthest above head of tide (Table 2). Once in tidal water, kelts rarely returned upriver.

Under extreme ice conditions and reduced habitat availability, young salmon would be required to move to more suitable overwintering areas. In so doing, they might expend critical energy reserves. In northern rivers such as the Varzuga River (Kola Peninsula, Russia), it is possible that extensive freezing of the smaller tributary streams may limit accessibility in winter by stream fishes. This may partly explain the relatively greater biomass and productivity found in the main Varzuga River compared with the tributaries (Kazakov et al. 1992). By contrast, in the River Teno in Finland, tributary streams provide the most suitable winter habitat (coarse substrate and warmer water) for parr and may explain the movement of parr ≥1+ into these streams from the main river (Erkinaro 1995). In several ice-covered, eastern Canadian rivers, Cunjak and Randall (1993) found that winter movement by juvenile Atlantic salmon was significant, and site fidelity appeared to be related to the availability of suitable winter habitat. In relatively stable, cobble-bottomed stream sites, 19–30% of the original (early winter) population was recaptured compared with only 2% in a stream site where suitable winter habitat was scarce and where anchor ice formation was extensive.

As discharge declines during the ice growth period, the ice cover periodically fails along bank support zones (Billfalk 1981) and falls to the level of the new, lowered water surface. This does not tend to occur on streams where the narrowness of the channel or the positioning of numerous large boulders permits the cover to remain intact and suspended at or near the original freeze-up level. The air cavities beneath these suspended covers have a unique microclimate, insulated from the extremes of cold winter air temperatures yet warmed by the penetration of solar radiation. The biological significance of these air-gaps is yet to be studied although fish-eating mammals such as mink (Calkins et al. 1989) and emerging stoneflies (Pugsley and Hynes 1986) use such habitats in winter.

In addition to reduction in habitat *availability* (Fig. 1), another form of habitat change in winter is reduction in *suitability*. Once an ice cover blankets the water surface, gaseous exchange with the atmosphere is eliminated and photosynthesis is slowed. As winter progresses, dissolved oxygen levels typically fall because of an increase in the proportion of groundwater to streamflow and because of oxygen consumption by various biochemical processes (respiration and decomposition) within the water column and sediment. The latter is enhanced by an increase in the residence time (relative to open-water conditions) because of the decline in velocity induced by a surface ice cover. Anoxic (or very low dissolved oxygen) conditions in rivers beneath ice cover have been documented from geographically distant regions (e.g., Hynes 1970; Ranjie and Huimin 1987; Ultsch 1989) but appear to be most prevalent in higher latitudes (Schreier et al. 1980; Bendock 1981) where ice cover persists for longer periods. Winter depressions in dissolved oxygen can be exaggerated by anoxic groundwater intrusions and can reach concentrations which are lethal to young salmonids and eggs (Bustard 1986; Adams and Cannon 1987; Lacroix 1985). Schmidt et al. (1989) reported on an extreme situation of depleted oxygen (1.1 $mg \cdot L^{-1}$) in the Sagavanirktok River delta, Alaska, which resulted in mortality for fish (mainly round whitefish, *Prosopium cylindraceum*) that were crowded in the pool because of restrictive ice conditions and low streamflow. To date, there have been no published accounts of winter anoxia beneath an ice-cover in Atlantic salmon rivers. In Catamaran Brook, sub-ice oxygen concentrations were measured frequently over one winter in inundated main-channel beaver ponds but dissolved oxygen remained above 79% saturation (Komadina-Douthwright 1994).

Winter duration, fish condition, and body size

Lipid levels at the onset of winter have been linked to survival of many young-of-year fishes (e.g., brook trout: Toneys and Coble 1980; largemouth bass, *Micropterus salmoides*: Sullivan 1986; Ludsin and DeVries 1997; smallmouth bass, *Micropterus dolomieui*: Oliver et al. 1979; yellow perch, *Perca flavescens*: Toneys and Coble 1980; Sullivan 1986). In a comparison of lipid storage and use, Sullivan (1986) found that largemouth bass stored lipids in viscera and muscle whereas yellow perch stored fat mostly

Table 2. Timing of winter movement and average distance (km) travelled by wild, radio-tagged Atlantic salmon kelts in three pools in the Northwest Miramichi River where fish were originally tagged and released following spawning (1993–1994 and 1994–1995).

	Miner's Pool	Big Hole (1993–1994)	Big Hole (1994–1995)	Craig Pool
Early winter	–26.8	–6.1	–7.8	–4.6
Mid-winter	–5.5	–3.6	+0.5	–0.8

Note: Negative numbers represent net downstream movement; positive values, net upstream movement. Pools are arranged according to distance from head-of-tide with Miner's Bridge Pool being most upriver site.

in viscera and gonads, which explained why yellow perch must feed all winter and were more prone to starvation. Bass, because they do not feed, are more sensitive to long winters (Sullivan 1986). Atlantic salmon parr may adopt an intermediate mode of using lipids. That is, they continue to feed to some degree (Riddell and Leggett 1981; Cunjak 1988*a*) like yellow perch, but salmon also reduce their activity, similar to the mode of energy conservation noted for bass. Such an intermediate mode of limited feeding and activity adopted by salmon may be the most prudent approach to survival in the demanding winter environment of running waters (Fig. 1).

Another aspect of winter survival is the notion of size-selective mortality in fishes in relation to lipid use and energy efficiency. This factor is most pertinent to fish in their first year of life. In age-0 largemouth bass, lipids regulated size-related winter mortality directly because earlier-hatched bass grew faster, switched to eating fish earlier, and stored more lipids in the fall (Ludsin and DeVries 1997). Survival was greater for larger yellow perch than smaller ones and was thought to be related to loss of fat stores because survivors had higher fat contents than those that died (Toneys and Coble 1980). Hunt (1969) determined that there was a positive relation between size and winter survival in brook trout to which he suggested the probable mechanism was energetic efficiency at low temperatures. In Atlantic salmon, larger fish have greater fat stores (Metcalfe and Thorpe 1992). In a hatchery study, Lindroth (1965) found that the largest YOY salmon suffered the least mortality over winter, which he related to size position within a year class and not absolute size *per se*, a contention supported by the work of Reimers (1963) and by the threshold concept expressed by Toneys and Coble (1980).

Cunjak and Randall (1993) speculated that large body size may affect winter survival as a result of a competitive advantage over smaller conspecifics that are subsequently displaced from limited winter habitats. They found that by late winter, the mean size of resident YOY salmon was consistently larger than that of immigrant YOY within similar habitat types of three Canadian streams. Experiments with some salmonid species have shown that those individuals introduced to a new location experience higher mortality rates than resident fish (Noakes 1978), perhaps because of risk associated with moving to unfamiliar areas (Dolloff 1987). The concept of competition for limited winter habitat suggests a potential for aggressive interaction as was recently quantified by Gregory and Griffith (1996) for YOY rainbow trout (*Oncorhynchus mykiss*). They found that larger individuals successfully displaced smaller YOY and were more aggressive near dawn when fish were seeking daytime concealment cover. Atlantic salmon parr, which also seek daytime concealment cover in winter, may experience similar competition.

Atlantic salmon have complex life histories (see Hutchings 1998, this issue) in which size-selective winter mortality and lipid levels are likely also affected by parr maturation. Between summer and autumn, individually marked mature parr in Vermont grew approximately half as fast as immature parr (Whalen 1998). By February, lipid levels were lower for mature parr than immature parr (S. McCormick, personal communication). Males (which were mostly mature) had lower lipids than females in November, and in April (Sutton 1994). The acknowledged high rate of mortality among mature male Atlantic salmon parr in winter (Mitans 1973) has been attributed to insufficient energy reserves having been accumulated after spawning and particularly if attempting to smolt the following spring (Dalley et al. 1983). This phenomenon led Myers et al. (1986) to suggest a size threshold of 70–72 mm below which male Atlantic salmon cannot mature and subsequently overwinter. Winter duration was also found to be a contributing factor to the incidence of maturity among 1+ Atlantic salmon males from a Newfoundland river (Prévost et al. 1992) probably because of the consequent reduction in growing opportunities necessary to achieve maturation (see Berglund 1992).

For Atlantic salmon kelts, post-spawning survival is generally highest in northern latitude streams of North America and Europe (Fleming 1996) where winters are cold. Mortality of male and female kelts in a river in France was found to occur within 2 weeks following spawning (Baglinière et al. 1990, 1991). This rapid mortality may be related to a combination of relatively warm water temperatures (7–10°C) necessitating a higher metabolic rate (and demand) and a weakened condition exacerbated by spawning lesions and subsequent infection by *Saprolegnia* fungi such as are common in southern European salmon rivers (J.-L. Baglinière, France, personal communication). In the River Dee in Scotland, previous-spawners represented only 9.7% of returning large salmon for 1992–1994 (Anonymous 1996) suggesting a low level of kelt survival relative to Canada (Table 3). Similar low percentages of previous spawners for rivers in the U.K. were noted by Jones (1959).

Some of the between-river variation in the percentages of repeat-spawners (Table 3) may be attributable to the nature of the riverine environment where post-spawned salmon must overwinter. Among the Newfoundland rivers, Pinware River had the lowest representation of previous spawners in samples of large salmon (>63 cm); it is the most northerly

Table 3. Percentage representation by repeat-spawners in the spawning population of multi-sea-year (large) Atlantic salmon in rivers of Newfoundland (NF), Labrador (LB)) and New Brunswick (NB).

River	Province	Years of data	*N*	% repeat spawners
Western Arm Brook	NF	15	90	78.9
Torrent	NF	12	185	61.6
Harry's	NF	4	18	55.6
Humber	NF	14	496	51.4
Lomond	NF	10	53	22.6
Pinware	LB	13	329	9.7
Big Salmon	NB	3	230	85.2
Nepisiguit	NB	6	2110	53.7
Miramichi	NB	10	n/a	34.5
Restigouche	NB	6	1470	30.3
Buctouche	NB	2	114	21.8

Note: Sources: Mullins 1997; Mullins et al. 1997; C. Mullins, personal communication; Chaput et al. 1994; Ducharme 1969; Atkinson and Chaput 1995; Atkinson et al. 1997; Mowbray and Locke 1996; A. Locke, personal communication). *N* = total number of large salmon sampled for the period. n/a = no data available.

river in the list (in Labrador) and is a generally shallow river of high gradient. Western Arm Brook, a northern river of insular Newfoundland, is characterized by many lakes where kelts often overwinter (Lévesque et al. 1985; Scruton et al. 1997) and has a high percentage of repeat spawners which suggests good winter survival. Among the New Brunswick rivers, repeat-spawners are relatively scarce in the Buctouche River where the river is short, shallow, has little pool habitat, and which remains ice-covered for >4 months. The Humber, Nepisiguit, Miramichi, and Restigouche rivers are large rivers with complex river channels offering a variety of suitable overwintering habitats despite prolonged ice conditions. The Big Salmon River in southern New Brunswick is within the drainage of the Bay of Fundy, which significantly moderates the winter climate (i.e., minimal ice accumulation) and may partly explain the high survival of kelts in this system.

Break-up/warming

Most winters in temperate latitudes, are characterized by periodic melt periods. The more temperate the climate, the greater the probability that such warming will be of sufficient duration to initiate a break-up of the ice cover. In colder climates, midwinter break-ups are rare. Instead, ice break-up is usually confined to late winter (Fig. 1). Regardless of the seasonal timing, break-up of an ice cover is often the most significant hydrologic event of the year. From a "disturbance" perspective (*sensu* Sousa 1984, Resh et al. 1988), break-up has a much greater potential than open-water floods to reset the biotic template in both the channel and in adjacent floodplains (Gatto 1993; Scrimgeour et al. 1994; Prowse 1994; Prowse et al. 1996). This section reviews our current biophysical understanding of the significance of the melt and break-up phases, and is followed by a first-ever case study of the importance of interannual variations in break-up intensity on survival estimates of juvenile Atlantic salmon.

Snowmelt and pre-break-up

The late winter period on ice-covered systems begins with a sustained melt of the winter accumulation of snow and a related increase in river discharge (Fig. 1), velocity and water levels. Stream water quality may rapidly change during this period depending on the chemical composition of the ablating snowpack. In essence, a stream can receive the entire winter chemical load of wet and dry atmospheric deposition within a few days.

Snowmelt events have been shown to severely impact Atlantic salmon egg and alevin survival because of the undiluted nature of the low pH water entering streams (Haines 1981; Rosseland and Skogheim 1984; Lacroix 1985; Gunn 1986). In the case of southwestern Nova Scotia salmon streams where local geology offers little acid-neutralizing capacity, greatest pH depressions occurred in midwinter as a result of acidic rain that is more acidic than the snow (Watt et al. 1983). Recently hatched sac-fry (alevins) tend to be most sensitive to low pH (Daye and Garside 1979; Korman et al. 1994) and their arrival is, unfortunately, often coincident with snowmelt-mediated pH depressions (Gunn 1986). In Atlantic salmon rivers in Norway, it was the pre-smolt stage that was most sensitive to low pH snowmelt water (Rosseland and Skogheim 1984). In general, the situation for affected salmon rivers such as in southwestern Nova Scotia may be improving as atmospheric sulphate levels decline (Watt 1997).

Whereas midwinter was dominated by groundwater inputs (baseflow), the increase in surface melt reverses this situation and can even lead to a hydraulic displacement of groundwater through a reversal in flow directions. It has been shown, for example, that rising stage can lead to surface water penetrating deeper into substrate areas normally fed by groundwater inflow. Because there is generally a temperature difference between the two flows, such a flow reversal can have a direct thermal impact (cold shock) on biota inhabiting the substrate. Laboratory experiments with developing Atlantic salmon eggs noted slower growth and increased mortality for eggs and alevins exposed to sudden decreases in temperature (Peterson et al. 1977).

Although stream water temperatures remain very close to freezing during the melt period (Fig. 1), even minor changes (<0.1°C) in the temperature of rapidly flowing water can produce rapid thinning of the base of an ice cover. This, accompanied by changes in ice strength due to radiative heating (Ashton 1985; Prowse et al. 1990), hastens the onset of river ice break-up.

Break-up and disturbance

Break-up is commonly classified into two types based on associated hydrometeorological conditions: premature or dynamic, and over-mature or thermal. In the case of thermal break-up (which is common to lakes), streamflow increases tend to be small because of a shallow snowpack or protracted melt. This in turn permits the ice sheet to become extensively melted and structurally weakened before the ice is finally dislodged. Although some minor ice jamming may occur, increases in water level and physical disruption of the channel are minimal.

Quite a different set of conditions governs dynamic break-up. Such events are characterized by large and rapid spring runoff, especially when the melt process is assisted by substantial rainfall. So abrupt is such melt that the ice cover has little time to decay and, hence, offers maximum resistance to the downstream passage of the flood wave. Its subsequent downstream progression into more intact ice is typically characterized by a series of stalls and surges associated with the repetitive formation and release of thick ice jams (Beltaos 1995). Water stored behind these stalling ice jams often produces extensive flooding of the channel and adjacent floodplain. Notably, water levels produced by break-up events far exceed those possible under open-water conditions for equivalent discharge. Common ice-jamming sites include those where the channel planform obstructs ice movement, such as at river bends, meanders, and islands, and where the slope quickly decreases and the channel widens (e.g., at stream mouths entering larger ice-covered rivers and lakes). Ice-jam flooding, which rapidly increases the amount of available corridor and riparian habitat, is usually short-lived and is even more quickly reduced with the sudden drawdown of water associated with the subsequent release and downstream surge of the ice jam.

The surge of ice and water produced by the sudden rupture of an ice jam can have a significant impact on the downstream channel and banks. Again, the magnitude and velocity of such events can far exceed those occurring under natural open-water conditions. For example, break-up surge velocities in excess of 5 $m \cdot s^{-1}$ are not uncommon for dynamic break-ups (e.g., Doyle 1977; Gerard 1975; Prowse 1984; Ferrick et al. 1992). Such surges can be an important agent of erosional and depositional change, especially on alluvial rivers. In terms of bed-load transport, shear stresses associated with rapidly moving breakup fronts have been estimated to be able to move material as large as 0.2 m in diameter (Beltaos 1993). Under such high conditions of bed transport, it is likely that main channel habitats and associated biota would be severely disrupted. Just prior to, and during, ice break-up in the Northwest Miramichi River in 1995, radio-tagged salmon kelts were generally found near tributary mouths, point sources of groundwater (spring) discharge, and in backwater channels (Komadina-Douthwright et al. 1997). These sites (tributaries and back-channels) may provide refugia during the period of most dynamic break-up and related scour. Clifford (1969) suggested a similar tactic for leptophlebid mayfly nymphs, which he observed migrating into tributaries of an ice-covered Alberta stream in April, just before break-up.

Break-up fronts (moving transition zone between intact and fractured or fragmented ice) typically result from surges (river waves) produced by the dramatic failure of upstream ice jams (e.g., Beltaos and Krishnappen 1982; Henderson and Gerard 1981). In Atlantic salmon rivers in New England, Calkins et al. (1989) observed ice-push at break-up fronts of sufficient force to move 70 kg boulders and, therefore, capable of dislodging shelters (Fig. 1) and injuring fishes such as dace, cottids, and salmonids (eggs and parr), which typically overwinter within the substrate (Cunjak 1996). Commonly associated phenomena such as flooding and ice-jams can result in displacement and mass stranding of riverine species, which eventually suffocate as water levels recede.

Ice abrasion and high-velocity scour of the bank and channel substrate can also lead to very high suspended-sediment concentrations, as much as several times that for equivalent discharge under open-water conditions (Prowse 1993; Beltaos et al. 1994; Milburn and Prowse 1996). Subsequent resettling of this material can coat the bed and banks in a veneer of sediment. Accumulations of as much as 1 m deep have been observed at the edge of levees (Eardley 1938) but no published data are available about the thickness of in-channel coatings. The tenure of such sediment probably depends on the timing of breakup relative to subsequent spring increases in discharge.

Temperature increase and warm acclimation

Although temperatures beneath lake covers are known to climb to several degrees above freezing (Marsh and Prowse 1987), under-ice water temperatures in a river rarely climb above a few hundredths of a degree, except in cases of significant inflow of warm water from tributaries or groundwater, or in streams where an air gap may exist between the ice and water surface. Near-freezing temperatures are usually maintained because of the rapid heat transfer to the ice promoted by turbulent flow conditions (Fig. 1). At the time of break-up, however, very rapid changes can occur in water temperature. Changes are most pronounced in the case of dynamic break-ups because of the extensive open-water reach upstream of the main break-up front. Within this usually turbid zone, water is rapidly warmed by heat exchanges with the atmosphere (Prowse 1990). Measurements on large rivers have reported temperature increases of as much as 3 to 9°C (Parkinson 1982; Prowse and Marsh 1989) at the interface between open-water and the upstream edge of ice break-up. Smaller changes are expected on smaller rivers and streams where the biological implications are probably just as significant but, as yet, poorly understood. For example, substrate decomposition rates increase with water temperature in late winter and early spring with concomitant declines in dissolved oxygen and CO_2 (Peterson et al. 1982). Both variables can affect Atlantic salmon alevin survival, particularly where gravel permeability is reduced by fine sediment deposition (Peterson 1978), and where pH is low (Gunn 1986).

Following the abrupt change in water temperature associated with the passage of the break-up front, direct atmospheric heating of the open water resumes. In general, increases in spring water temperatures tend to parallel those of air temperature but can exhibit increases when high turbidity associated with the break-up front enhances absorption of radiant energy in the water column (see Scrimgeour et al. 1994). The period of "warm-acclimation" is not as physiologically demanding as cold-acclimation (early winter) except that fish are starting from an already depleted condition having survived to late winter (Fig. 1). During the warming phase associated with break-up, parr that managed to survive the winter are faced with replenishing depleted lipids. The appetites of Atlantic salmon parr are geared to follow seasonal trajectories where lipids are lowest at the beginning of spring (Bull et al. 1996). Improved environmental conditions and feeding opportunities following late winter typically allow for a rapid increase in body lipids (Cunjak 1988*b*; Cunjak and Power 1987). In Newfoundland, lipids from Atlantic salmon rebounded from a winter low of ~ 6% in April to over 13% by June (Sutton 1994); in Vermont, the largest increase in lipids, on an annual basis, occurred in Atlantic salmon pre-smolts between February and April (S. McCormick, personal communication).

Warm-acclimation may be most difficult for kelts that are in poor condition by spring after fasting all winter, and mortality may occur at this time (Lévesque et al. 1985) as they try to resume feeding (Fig. 1). In a laboratory experiment to recondition Atlantic salmon kelts, Crim et al. (1992) found that kelts that failed to feed eventually lost weight and died, but only as water temperatures began rising. In general, however, winter survival in freshwater seems to be relatively high in most Canadian rivers based on the high percentage of repeat spawners among large Atlantic salmon in many populations (see Table 3 and earlier section). A mark-recapture experiment of post-spawned salmon in Western Arm Brook, Newfoundland, provides further evidence. At a counting fence in early spring for two consecutive winters, 37 and 47%, respectively, of kelts (marked as spawning adults the previous autumn) were recaptured (C. Mullins, Canada, personal communication). These survival estimates were minimum values as trap operation was dependent on water/ice conditions and likely missed the earliest emigrants (May). In fact, Chadwick et al. (1978) estimated winter survival of kelts in Western Arm Brook as high as 88% probably because of the abundant lacustrine habitat in this system where kelts prefer to overwinter (Lévesque et al. 1985; Scruton et al. 1997).

The availability of forage fishes following ice break-up has been suggested to be critical to the ultimate survival of kelts as they prepare to return to sea (Moore et al. 1995). In support, radio-tagged kelts in the Northwest Miramichi River showed a net upstream movement only 3 days after ice break-up (Table 4) and coincident with the start of the upstream migration of rainbow smelt, *Osmerus mordax* (Komadina-Douthwright et al. 1997), a favoured prey of salmon kelts. This was the first net upstream movement in several weeks by kelts.

Catamaran Brook case study — impact of variable winter conditions

The data collection and ongoing multidisciplinary research in the Catamaran Brook basin of New Brunswick (Cunjak 1995) lends itself to a detailed analysis of interannual variability in YOY Atlantic salmon abundance, and for deriving hydro-ecological explanations for the variability. Using counts of female spawners entering the brook and passing through the counting-fence each autumn (Hardie et al. 1998) and estimates of size-derived fecundity, egg deposition was calculated for each spawning cohort from 1990 to 1995 (Cunjak and Therrien 1996, 1998). These values were then related to annual estimates of YOY abundance in the brook (by electrofishing) approximately 1 month post-emergence (Cunjak, unpublished data). Electrofishing was conducted each summer, using barrier nets, by an experienced crew of 3–4 people in 26–32 sites. Estimates of population abundance were derived using a multiple sweep removal method. Corrections for "loss" of recently emerged fry from the brook via drift emigration in the first month of life were applied (Johnston 1997) in order to provide an estimate of the fry abundance in the brook immediately following emergence from redds (mid-June). Fry abundance was then compared with egg deposition (from previous November) to provide a measure of first winter survival.

Table 4. Distance moved (km) by 12 radio-tagged Atlantic salmon kelts in the Northwest Miramichi River between April 20 and April 25, 1995, the period of ice break-up in the river. Negative numbers represent net downstream movement; positive values are net upstream movement.

	Before (1 day)	Ice-out	After (3 days)
Average movement	–0.5	–0.7	+0.2
Maximum movement	–3.9	–1.6	+1.8

The number of salmon fry surviving winter to emergence in Catamaran Brook between 1991 and 1996 was poorly explained by egg deposition the previous autumn (r^2 = 0.001). Fry numbers resulting from the 1994 and 1995 spawning cohorts were similarly very low although they originated from markedly different egg depositions (Table 5). The low number of emergent fry from the 1994 cohort was readily explained by the low number of adult females (n = 27, compared with 84 females in 1995) that spawned in a restricted area as a consequence of unusually low water conditions that autumn (Fig. 2) and a beaver dam barrier to migration at river km 0.8 (Cunjak 1995). The poor winter survival of fry from the 1995 spawning cohort could not be so readily explained, as egg deposition was extremely high and water conditions (late October – early November) were sufficient that spawners were able to access >8 km of stream. The poor survival in 1995–1996 was especially problematic relative to the 1992 cohort that deposited a similar number of eggs (Table 5) under similarly moderate flow conditions in early winter (Fig. 2) but the 1992 cohort produced many more fry that survived to emergence (Table 5).

Density-dependent survival was unable to account for most of the variability in the data when egg density was regressed with survival to emergence (r^2 = 0.31). For most years, egg deposition was at moderate densities (3.1–7.0 eggs·m^{-2}, Table 5). These densities were within the range of suitable "target" egg depositions noted for Atlantic salmon (see reviews by Symons 1979; Kennedy and Crozier

Table 5. Annual estimates of egg deposition, egg density (no.·m^{-2}), emergent fry, and winter survival (egg to emergence) for Atlantic salmon in Catamaran Brook, 1990–1995.

Spawning year	Egg deposition	Egg density[a]	Emergent fry	% survival to emergence
1990	269 526	3.2	164 436	61
1991	375 562	4.5	93 665	24.9
1992	486 709	5.8	85 959	17.7
1993	265 806	3.1	143 190	53.9
1994	117 077	16.2	20 300	17.3
1995	504 490	7.0	46 384	9.2

[a] Density was calculated using the product of accessible river km for spawning and mean stream width (measured at summer low water levels). Separate values were calculated each year.

1993). In 1994, the year of highest egg density in Catamaran Brook (16.2 eggs·m^{-2}), winter survival was still 1.9 times greater than that in 1995 but similar to survival for the 1992 cohort when egg density was much less (Table 5).

Environmental factors have been suggested as affecting winter survival of salmonids, at various life-stages (e.g., Frenette et al. 1984; Seelbach 1987; Baglinière et al. 1993; Cunjak and Randall 1993; Power et al. 1993; Cunjak 1996; Meyer and Griffith 1997). Gibson and Myers (1988), in examining stock-recruitment data for six rivers in New Brunswick and Newfoundland, found a significant positive relationship between winter discharge and survival of underyearling salmon. For Atlantic salmon in Indian River, Newfoundland, Chadwick (1982) found annual egg-to-fry survival ranged between 22 and 67% and was significantly correlated with winter air temperature and stream discharge. Based on these relations, Chadwick suggested that low streamflow conditions in winter resulted in the freezing of redds. Power (1969) similarly suggested that egg mortality might occur from redd freezing in the salmon rivers of Ungava Bay. Such speculation is intriguing. As noted previously, however, the requisite physical conditions leading to eggs freezing within redds are very complex.

In Catamaran Brook, winter hydrographs (Fig. 2) were analysed to determine if streamflow conditions might explain egg to fry survival. When egg-fry survival was tested against mean winter discharge (Fig. 3A), a weak positive relation (r^2 = 0.173) was found. Unlike the trend for the first 5 winters where egg - fry survival clearly increased as winter streamflow increased, the high mean discharge in 1995–1996 was associated with the lowest survival. Residuals calculated for the regression analysis indicated that the winter of 1995–1996 was an outlier. Indeed, when that winter was excluded from the analysis, discharge explained >90% of the variability in the egg to fry survival, suggesting a strong relation between winter streamflow and egg survival (Fig. 3*a*).

What happened in the winter of 1995–1996 that could account for the extremely poor survival that year? As in 1992, the 1995 spawning cohort deposited about 500 000 eggs (Table 5) over >8 km of the brook. Mean winter discharge in 1995–1996 was high and very similar to that measured in 1990–1991 (Fig. 2) when the best egg survival was measured (Table 5). Air temperature records for the basin indicated a relatively mild winter (Fig. 2).

Catamaran Brook normally experiences a winter characterized by freeze-up in late November, an approximate 4-month period of ice growth, and a spring break-up in March-April (Fig. 2). In 2 of the 6 years shown, however, this typical trend was interrupted by midwinter break-ups: mid-December 1993 and late-January 1996. In both cases, peak discharge values of 6–7 m^3·s^{-1} were in the same range as those that typify the late-spring freshet (3–9 m^3·s^{-1}) but the physical severity of these midwinter events differed markedly. Although no direct, quantitative measures of physical disruption induced by these events were available, an indication of such was derived by comparing the controlling hydrometeorological conditions.

Two useful indices of break-up severity are pre-break-up ice strength (Prowse et al. 1990) and thickness, the latter especially as compared with the pre-break-up flow depth. The thicker an ice cover, the more likely it is to scour the banks and bed and, if of sufficient mechanical strength, to form ice jams. Although records of river-ice thickness are unavailable for the study site, it is possible to estimate pre-break-up values by using temperature-index models for ice growth (Michel 1971) and decay (Bilello 1980). Ice thickness (t_i) can be obtained from

$$t_i = \alpha D_f^{0.5}$$

where is α a coefficient varied to account for conditions of exposure, surface insulation, and subsurface heat flux (mm·°C$^{0.5}$·d$^{0.5}$), and D_f is the accumulated degree-days for mean air temperatures <0°C. Similarly, ice thickness reductions during the pre-break-up period (t_m) is estimated from

$$t_m = \beta D_b$$

where β is an empirical coefficient found by Bilello (1980) to range between 0.004 to 0.01 (m·°C^{-1}·d^{-1}) for northern (>60°N) rivers.

The above two equations were used with the daily air temperature data in Fig. 2 to determine values of pre-break-up ice thickness for the two midwinter events. A value of 14, characteristic of a *“sheltered small river with rapid flow”* (Michel 1971), was employed for α. β was set to 0.004, a value found by Prowse et al. (1989) to be applicable for the Nashwaak River, New Brunswick, which is within 100 km of the Catamaran Brook basin. Dates of freeze-up (beginning of ice growth) were determined from water-temperature records and field observations of ice conditions. In 1993, break-up was preceded by 17 days of ice growth resulting in a pre-break-up thickness of ~11 cm. Calculations of t_m were not included in this calculation recognizing that air temperatures were <–5°C on only 4 of the 17 “growth” days. The

Fig. 2. Winter hydrometeorological data collected in Catamaran Brook and its basin for the period, 1990–1996. Daily discharge as measured at the hydrometric gauge, river km 9.5; mean winter discharge (Q_{mean}) was measured for the period from 01 November (assumed date of egg deposition) to 31 March (the presumed last day of winter and start of snowmelt/runoff). Cumulative precipitation for snow is measured in water equivalents (mm); rain and snow were measured separately except for January–May 1994, when only total precipitation was recorded.

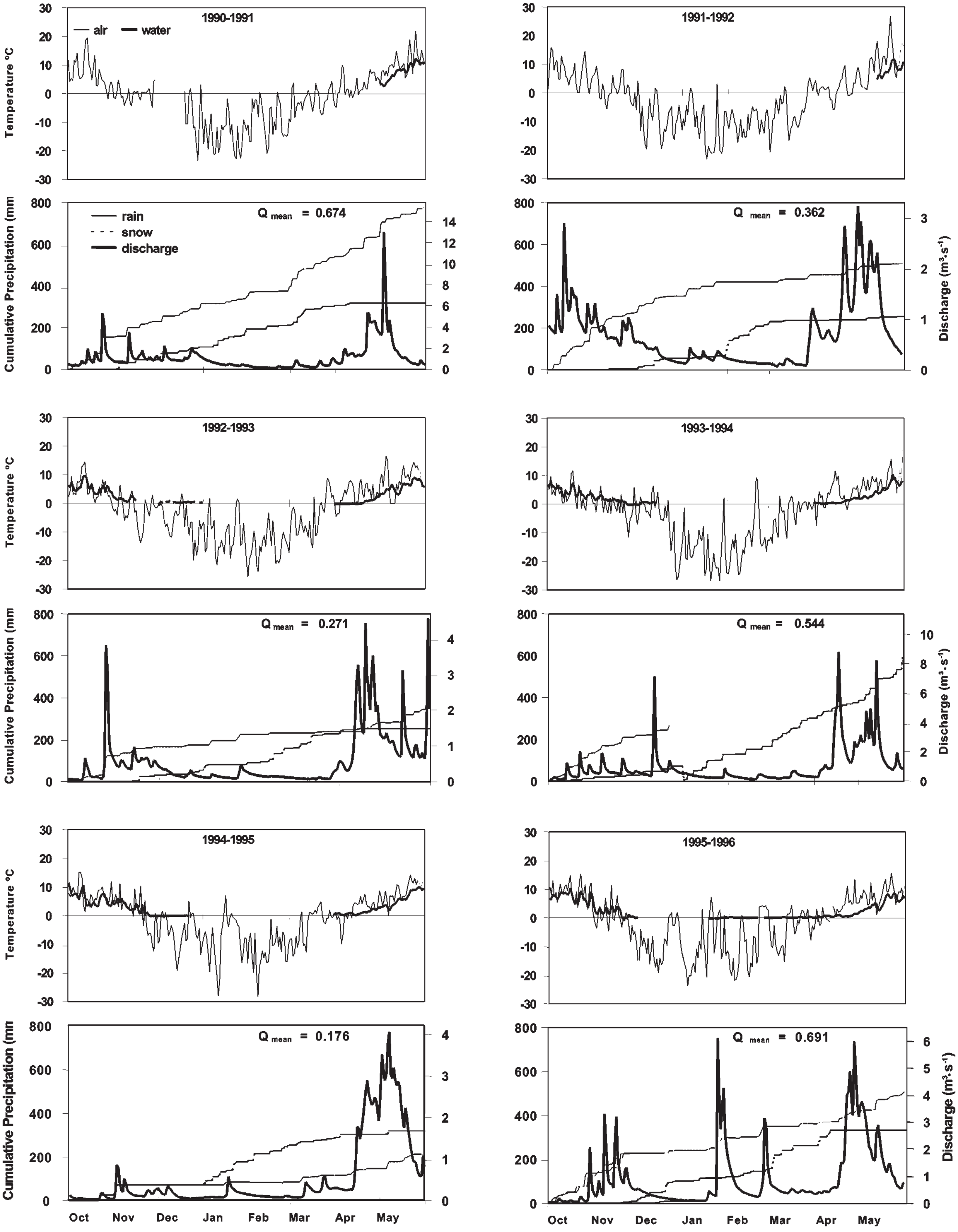
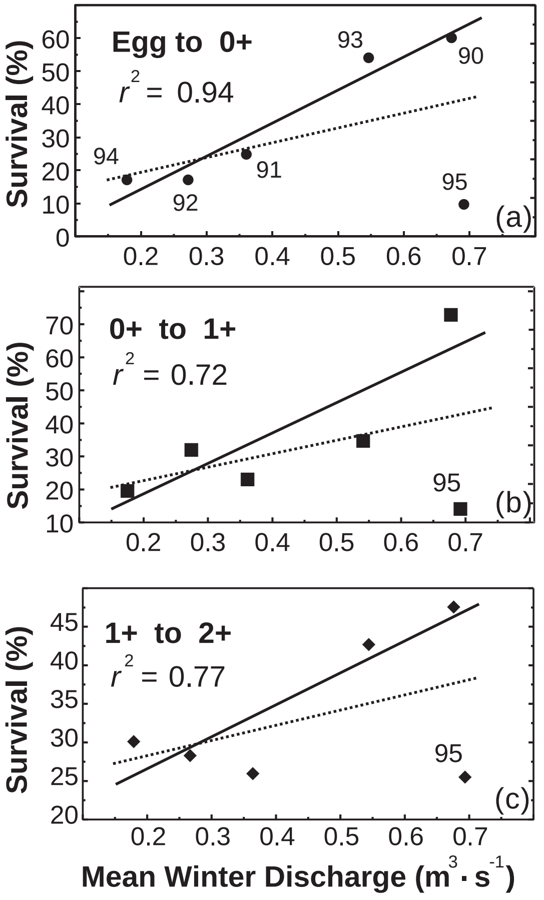


Fig. 3. Linear regression plots of mean winter discharge ($m^3 \cdot s^{-1}$) and survival of different stages of juvenile Atlantic salmon in Catamaran Brook 1990–1996. Solid line is regression excluding winter of 1995–1996; dashed line is regression using data for all six winters. Year values associated with points refer to the start of a particular winter (e.g., 95 refers to the 1995–1996 winter). (*a*) Egg to emergent fry survival (November–June); (*b*) Summer 0+ to summer 1+ survival (1 year interval); (*c*) Summer 1+ to summer 2+ survival (1-year interval). The r^2 values are calculated for regressions excluding the 1995–1996 winter.



potential over-prediction of ice thickness resulting from this, however, is assumed to be offset by increased rates of ice growth when the cover is relatively thin. That is, when <10 cm, t_i increases in direct proportion to D_f rather than its square root (Ashton 1986).

It is unlikely that the relatively thin ice cover of mid-December, 1993, equalling <20% of the flow depth at this time of early winter recession in flows, presented much of an obstacle to the flood wave produced by the rapid runoff. As such, it is unlikely that break-up ice jamming and associated ice scour caused much physical disruption of the channel. In essence, this event was similar to that of an open-water runoff event.

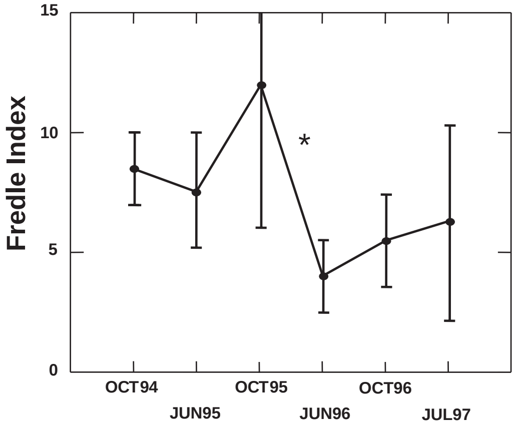
By contrast, the mid-January event of 1996 (Fig. 2) was characterized by a much larger, pre-break-up ice thickness of ~31 cm (t_i = 33 cm; t_m = 2 cm), a result of 55 days of potential ice growth between freeze-up and break-up on January 24, 1996. This large thickness developed, and gradually occupied most of the channel depth, as water levels declined to near-winter minima. One week prior to the increase in flows that immediately preceded break-up, flows were approximately 0.1 $m^3 \cdot s^{-1}$, only 20% of the flow at freeze-up. With this decline in flow and stage, and concomitant growth in ice, it is probable that the pre-break-up ice cover was freeze-bonded over a significant portion of the wetted perimeter (i.e., stream banks and protruding portions of the bed, such as large boulders) that existed at freeze-up.

As for 1993, the 1996 midwinter break-up was initiated by a rain-on-snow event in which rapid development and prevailing meteorological conditions offered little opportunity for the ice sheet to thin or decrease in strength from radiation decay. Hence, it is believed that the thick ice cover that existed on January 24, 1996, would have offered considerable resistance to the downstream passage of the flood wave that peaked at a mean daily flow of 6.1 $m^3 \cdot s^{-1}$ on the day of break-up. The rapidly rising flow and water levels accompanying this flood would have lifted and dislodged the intact ice cover and, given its large relative thickness, would probably have caused severe scour of the bed and banks as it was driven downstream. In general, the hydro-meteorological conditions that characterized the 1996 midwinter event are most typical of dynamic break-up events which are known to produce severe ice jams and to cause maximum disturbance to the fluvial geomorphology of rivers (Scrimgeour and Prowse 1993; Scrimgeour et al. 1994) such as Catamaran Brook. Finally, the limited ice growth and snow accumulation (see Fig. 2) that followed the midwinter (January) 1996 event led to a late-winter *thermal* break-up — one that produced minimal disturbance of the stream channel.

Further support for substrate disturbance in Catamaran Brook during the winter of 1995–1996 was evidenced from Fredle Index (f_i) calculations (Fig. 4). This index was developed by Lotspeich and Everest (1981) to quantify streambed porosity and the reproductive potential of spawning gravel by relating particle sizes to a sorting coefficient, and has been directly linked to salmonid alevin survival. In the spring of 1996, a significant ($p < 0.05$) decrease in substrate quality was measured in the lower reach of Catamaran Brook (Fig. 4) in an area typically used for spawning. By 1997, sediment porosity had still not recovered to levels measured prior to the winter scour event of 1995–1996 (Fig. 4) despite stream discharge peaks of >7 $m^3 \cdot s^{-1}$ measured in the summer of 1996 and in the spring of 1997 (D. Caissie, unpublished data). These data indicate a severe disruption of the substrate and high infiltration of fines during the winter of 1995–1996.

Based on these analyses, we suggest that the combination of mild weather initiating runoff, and the rain-on-snow event of late-January 1996, initiated a mechanical (dynamic) break-up of a significant ice cover in Catamaran Brook. The subsequent increase in river stage and discharge and associated ice scour caused major bedload movement and substrate disturbance. Might the 1995–1996 egg mortality in Catamaran Brook have been due to low winter streamflow (as suggested for other winters), the effect of which was masked by the January break-up event and associated discharge peak? This scenario seems improbable. If the period of the discharge peak was removed from the calculations,

Fig. 4. Seasonal changes in spawning substrate quality in the lower reach of Catamaran Brook, NB as determined by Fredle index estimates (mean ± SD), 1994–1997. Each point is a composite of 2–3 substrate samples (to 20 cm depth) covering 1 m^2 from two spawning sites (see St. Hilaire et al. 1997 for full description of methodology). Asterisk indicates significant difference ($p < 0.05$) between two dates as determined by *a posteriori* Bonferroni test following ANOVA (Systat 1996).



mean winter discharge in 1995–1996 was 0.522 $m^3 \cdot s^{-1}$, still relatively high (Fig. 2) and still an obvious outlier to the discharge-survival regression (Fig. 3).

Interestingly, regression plots of interannual survival for age 0+ to 1+, and for 1+ to 2+ parr were also closely related to, and well explained by, mean winter discharge (Fig. 3*b*,*c*). These results suggest that parr, as well as eggs, were severely affected by low water levels and reduced habitat availability in winter and also by the midwinter break-up event of 1995–1996. This relationship was less expected as the data for parr deal with a 12-month interval and more potential variables (environmental and density-dependent) affecting survival.

The impact of winter discharge on survival, although realized among all life-stages, was particularly devastating on egg survival, perhaps a reflection of the immobility and restrictive niche of this life-stage. The implications for juvenile salmon population dynamics are significant because this stage is the set-point for determining the size of subsequent life-stages and, ultimately, smolt production. For example, the 1996 smolt output from Catamaran Brook (predominantly age-3) was well below average (Cunjak and Therrien 1998; Hardie et al. 1998). Although the number of age-3 pre-smolts (predominant smolt age-class) was certainly affected by the January 1996 break-up, that smolt cohort was the result of the 1992 egg deposition which,albeit high, realized poor egg-0+ survival (Table 5), as a consequence of the low winter discharge (Figs. 2, 3*a*) and reduced habitat availability beneath a very thick ice cover (estimated to be between 42 and 48 cm by the time of April 1993 break-up).

It is important to relate the significance of events, such as the winter 1995–1996 break-up, on salmon populations at various spatial and temporal scales. In the Catamaran Brook catchment, the impact of the midwinter break-up on juvenile salmon survival was similarly realized in three study reaches representing approximately 15 km of stream. The magnitude of the January 1996 event, in terms of discharge, was far less than the 1-in-25 year flood of May, 1991 (Fig. 2), *not* an ice-related flood. That flood had little impact on the salmon population as egg survival was the highest recorded (61.9%, Table 5), and parr abundance and densities in the summer of 1991 were among the highest estimated, in all reaches (Cunjak and Therrien 1996). In the larger branches of the Miramichi, specifically the Little Southwest Miramichi River into which Catamaran Brook drains, the midwinter 1995–1996 break-up had little apparent effect on juvenile salmon densities estimated by electrofishing in the late summer of 1996. D. Moore (Canada, unpublished data) found that parr densities actually increased in index sites relative to previous years. By contrast, a major, dynamic ice break-up in the main river branches of the Miramichi in April 1994 was believed to be responsible for the significant declines in YOY and parr densities in many index sites later that summer (D. Moore, unpublished data). No such break-up, or related impact to salmon survival, was found in Catamaran Brook in 1994; instead, egg and parr survival were quite high (Fig. 3, Table 5).

Summary

The foregoing demonstrates the dynamic physical nature of winter in northern streams and rivers. As was shown in the case study for Catamaran Brook, the effects of winter conditions, particularly discharge and break-up events, on survival of Atlantic salmon can be significant although the nature and magnitude of the impact is complex and dependent on a variety of interrelated factors. Such complexity is further evidence of the dynamic nature of the winter stream environment and of lotic ecosystems in general (e.g., Hynes 1975; Power et al. 1995).

The inherent complexity of stream processes, of which winter is but one important factor, serves to underscore the need for interdisciplinary research in order to understand biological change. Following are some suggestions for future research related to the winter biology and conservation of Atlantic salmon.

There is a need to conduct manipulative field experiments to address the linkages of lipid levels, fish size, and maturity on winter survival. For example, Hutchings (1994) suggested a relation for winter survival, lipids, and maturation costs for brook trout in a Newfoundland stream The enlightening experimental findings by researchers such as Pickering and Pottinger (1988), Metcalfe and Thorpe (1992), Bull et al. (1996), and Gregory and Griffith (1996) need to be field tested for their relevance to what is happening in salmon rivers in Europe and North America.

Can a link be made between “severity” of in-stream habitat, stream morphology, and spatial scale? Is it possible, for example, that at some point along small (first–third order) streams, channel width:depth ratios change to favour winter survival because of less streambed disturbance during spates, reduced probability of dynamic ice break-up, less anchor ice production because overhead canopy reduces radiant heat loss, and because of less freezing to stream bottom due to perching of sheets? By contrast, ice accumulation can be relatively more extensive in larger, wider rivers and disturbance is more likely than in headwaters and tributaries. Might these spatial differences in the probability of winter disturbance explain the apparent attempts by Atlantic salmon to spawn as far upstream as possible each year (e.g., Hay 1989; Cunjak, unpublished data)? Interdisciplinary research aimed at comparing egg and juvenile survival for varying stream orders relative to stream morphology and reach-specific hydrology could answer such questions.

Competition for space during winter has long been suggested as a major factor in population regulation in winter (Chapman 1966). Does competition for winter habitats affect juvenile Atlantic salmon populations in rivers? In North America and in Europe many stream species that coexist with Atlantic salmon share similar habitat preferences — i.e., access beneath cobble to boulder-sized substrates. These observations led Cunjak (1988*a*) and Heggenes et al. (1993) to speculate about potential competitors for winter space because habitat availability was more restricted than in summer. Recently, Gregory and Griffith (1996) have quantified aggressive behaviour among YOY salmonids as fish entered concealment habitat at water temperatures between 2 and 6°C in a laboratory setting. That the aggression was primarily initiated by the largest individuals and resulted in displacement of subordinate fishes might explain the smaller size of immigrant YOY Atlantic salmon compared with larger "resident" YOY that remained in the same stream habitat all winter (Cunjak and Randall 1993). Is this evidence of winter competition?

Coincident with the need for further research is the realization that different, and often innovative, approaches to field studies are needed to effectively study the winter behaviour of fishes (e.g., Emmett et al. 1992; Presnyakov and Borisenko 1993) and physical winter phenomena (e.g., Arcone and Delaney 1987). Indeed, the same rigorous environmental conditions to which fishes, such as the Atlantic salmon, have adapted for overwintering often preclude the use of traditional techniques for scientific study and partly explain the dearth of information on the topic. For example, physical habitat measurements associated with freeze-up and anchor ice formation, and the severity of ice break-up in rivers has made field studies logistically difficult during these periods. As a result, most of our knowledge about the effects of ice break-up and formation are based on post-impact assessments. Moreover, these are few in number and have primarily focused on physical impacts. Scientific monitoring around events of such (potential) magnitude and force may require specialized technology as well as different sampling regimens and study designs in order to account for the temporal variance in estimates of population abundance (e.g., Underwood 1991).

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