Movements and habitat use by PIT-tagged Atlantic salmon parr in early winter: the influence of anchor ice

JEAN-MARC ROUSSEL,* RICHARD A. CUNJAK,[†] ROBERT NEWBURY,[‡] DANIEL CAISSIE[§] AND ALEXANDER HARO[¶]
Institut National de la Recherche Agronomique, Laboratoire d'Ecologie Aquatique, UMR 985, Rennes cedex, France
[†]*Canadian Rivers Institute, University of New Brunswick, Fredericton, NB, Canada*
[‡]*Newbury Hydraulics, Okanagan Centre, BC, Canada*
[§]*Department of Fisheries and Oceans, Maritime regions, Science Branch, Moncton, NB, Canada*
[¶]*US Geological Survey, S.O. Conte Anadromous Fish Center, Turners Falls, MA, U.S.A.*

SUMMARY

1. Movements and habitat use by Atlantic salmon parr in Catamaran Brook, New Brunswick, were studied using Passive Integrated Transponder technology. The fish were tagged in the summer of 1999, and a portable reading system was used to collect data on individual positions within a riffle-pool sequence in the early winter of 1999. Two major freezing events occurred on November 11–12 (*Ice 1*) and November 18–19 (*Ice 2*) that generated significant accumulations of anchor ice in the riffle.
2. Individually tagged parr (fork length 8.4–12.6 cm, $n = 15$) were tracked from 8 to 24 November 1999. Over this period, emigration (40%) was higher from the pool than from the riffle. Of the nine parr that were consistently located, seven parr moved <5 m up- or downstream, and two parr moved more than 10 m (maximum 23 m). Parr moved significantly more by night than by day, and diel habitat shifts were more pronounced in the pool with some of the fish moving closer to the bank at night.
3. During *Ice 2*, there was relatively little movement by most of the parr in the riffle beneath anchor ice up to 10 cm in thickness. Water temperature was 0.16 °C above the freezing point beneath anchor ice, suggesting the existence of suitable habitats where salmon parr can avoid supercooling conditions and where they can have access to low velocity shelters. To our knowledge, these are the first data on habitat use by Atlantic salmon parr under anchor ice.

Keywords: anchor ice, heat budget, juvenile, mobility, *Salmo salar*

Introduction

Winter survival is a major factor affecting fish population dynamics in cold-region rivers (Power *et al.*, 1993; Cunjak, Prowse & Parrish, 1998; Bradford, Grout & Moodie, 2001; Annear *et al.*, 2002). When air temperature drops below 0 °C, surface ice usually starts to form along the river bank, and in fast-flowing open water (e.g. riffles, rapids), the water temperature can be depressed a few hundredths of degree below the freezing point (supercooling). Thus, frazil ice particles form in turbulent water and subsequently adhere to any submerged structures building up on bottom substrates to form anchor ice (Tsang 1982, *in* Beltaos *et al.*, 1993). Thick and widespread anchor ice formations can dramatically affect river habitats, covering 95–100% of the streambed of Atlantic salmon streams (Whalen, Parrish & Mather, 1999).

Coincident with a decline in water temperature, shifts in habitat use and daily activity pattern have been noticed for many taxa in northern temperate

Correspondence: Jean-Marc Roussel, Institut National de la Recherche Agronomique, Laboratoire d'Ecologie Aquatique, UMR 985, 65 rue de Saint-Brieuc, 35042 Rennes cedex, France. E-mail: roussel@roazhon.inra.fr

latitudes. Salmonids are usually found to use deeper and slower habitats as winter progresses (Cunjak & Power, 1986; Cunjak *et al.*, 1998; Muhlfeld, Bennett & Marotz, 2001; Hiscock *et al.*, 2002; Vehanen & Huusko, 2002), and they become increasingly nocturnal, sheltering in the substrate during the day and emerging to feed at night (Rimmer, Paim & Saunders, 1983; Cunjak, 1988; Fraser, Metcalfe & Thorpe, 1993; Heggenes *et al.*, 1993; Fraser *et al.*, 1995; Valdimarsson *et al.*, 1997). This tendency to seek shelter was first interpreted as a way to reduce energy expenditure in flowing waters (Rimmer, Paim & Saunders, 1984). Laboratory studies by Valdimarsson & Metcalfe (1998) recently demonstrated that fish preferred concealment to hydraulic shelter, and argued that the primary function of sheltering was to hide from diurnal predators.

An earlier hypothesis proposed by Heggenes *et al.* (1993) was that the fish come out of their shelter at night to avoid becoming trapped in anchor ice that tends to form at night. However, Whalen *et al.* (1999) observed that although the behaviour and habitat use by juvenile Atlantic salmon were significantly affected by subsurface ice, some parr continued to persist in areas covered by anchor ice. Recent radio-tracking studies of large-bodied salmonids have related long distance movements of fish to frazil ice episodes in streams (e.g. Brown & Mackay, 1995; Komadina-Douthwright, Caissie & Cunjak, 1997; Jakober *et al.*, 1998; Simpkins, Hubert & Wesche, 2000). Part of the confusion about the nature of subsurface ice effects on fish behaviour in the wild may be that field investigations are technically challenging such that data on habitat use during supercooling and frazil ice events are scarce, especially for small-bodied fish.

To determine whether and how anchor ice influences Atlantic salmon parr behaviour, we used recent developments in Passive Integrated Transponder (PIT) technology applied to fine-scale studies of fish movements in shallow rivers (Roussel, Haro & Cunjak, 2000). To our knowledge, this is the first attempt at recording movements and habitat use by Atlantic salmon parr under anchor ice, specifically during its formation. It was hypothesised that fish would be more active in riffle to avoid habitat exclusion by anchor ice formation and, ultimately, that they would be forced to move to deeper habitat where anchor ice was largely absent.

Methods

The experiment was carried out in 1999 in Catamaran Brook (46°52′N, 66°06′W), a tributary of the Little Southwest Miramichi River (central New Brunswick, Canada). A thorough description of the brook and its biota can be found in Cunjak *et al.* (1993) and Cunjak (1995). The study site was located 0.5 km upstream from the confluence with the Little Southwest Miramichi River and consisted of a 72-m-long riffle-pool section. Aquatic habitat was assessed in late October 1999 based on 360 reference points evenly spaced on the section: water depth averaged 0.29 m (±0.09 SD, maximum depth 0.53 m) in riffle and 0.45 m (±0.19 SD, maximum depth 0.95 m) in pool. Mean water velocities were higher in riffle (0.41 m s^{-1} ±0.20 SD) than in pool (0.30 m s^{-1} ±0.16 SD), and substrate mainly consisted of gravel and cobble, with the occurrence of bedrock at the bottom and right side of the pool. Two temperature sensors (Model 107B, from Campbell Scientific Canada Corp., 1992; Edmonton, Alberta, Canada) were used to record water temperature on an hourly basis during anchor ice formation. They consisted of a Fenwal Electronic thermistor probe (Kidde-Fenwal, Ashland, MA, U.S.A.) with a reported absolute error of <0.2 °C for the range of −30 to +40 °C. The two sensors were calibrated against one another to determine relative accuracy; mean difference between sensors was 0.004 °C (maximum difference of 0.02 °C). The two sensors were installed mid-stream on the substrate next to a boulder (20–30 cm diameter), one in the riffle (20 cm water depth) and one in the pool (55 cm water depth).

The portable PIT-tag detector was constructed using a commercially available radio frequency identification system (TIRIS S-2000; Texas Instruments, Dallas, TX, U.S.A.). It consisted of a chest-mounted palmtop computer, a reader and 12 V battery enclosed in a backpack, and connected to the antenna (a 60-cm diameter coil) mounted on a 4 m pole. The detection range, i.e. the maximum distance between the horizontal plane created by the antenna and the transponder from which the transponder is detected, ranged from 70 to 100 cm depending on the orientation of the transponder. A thorough description and field test of the portable PIT tag detector can be found in Roussel *et al.* (2000). The PIT tags used were 23.1 mm long, 3.9 mm in diameter and weighed 0.6 g in the air (Texas Instruments). The study site was electrofished in early and

late summer (10–25 July 1999; 29–30 September 1999), using a backpack electrofisher (Smith-Root Canada, Merritt, BC, Canada; type 12, 500 V, 60 Hz). After being captured, Atlantic salmon parr were individually anaesthetised in a solution of 2-phenoxy ethanol (0.03%), weighed (nearest 0.1 g) and the fork length (FL) was measured (nearest mm). The transponders were surgically implanted into a fish's abdomen, and after recovery, fish were released back into the riffle or pool where they were captured. Details about surgical implantation are outlined in Roussel *et al.* (2000). During 1999, 46 parr were tagged in the summer, and 43 parr in the autumn (84 mm < FL < 126 mm). Implanted transponders represented 3.8–9.7% of the fish's body weight in the air.

Four surveys were carried out in early winter 1999: first, before the first freezing event in the brook (8 November, *Pre-freeze*); following the first freezing event and after anchor ice had drifted out of the study section (12–14 November, *Post Ice 1*); during the second freezing event (18–19 November, *Ice 2*); and following the second freezing event (24 November, *Post Ice 2*). Multiple day and night records of fish position were performed to assess diel changes in habitat use and fish mobility during *Post Ice 1* (10 records) and *Ice 2* (four records). The tracking schedule was balanced to sample positions at different times of the day (morning, afternoon, early evening and late night). No sampling was carried out during twilight (i.e. 60 min before and after sunrise or sunset). When tracking, the operator waded the site in an upstream direction, moving the antenna just above the stream surface from bank to bank. The antenna was moved underwater only in the deepest habitats (>60 cm) to better detect fish close to the streambed. Once a fish was detected, its location in the channel was plotted relative to numbered flags that had previously been laid out along the stream bank, and by visually dividing the stream width into five strata. Occasionally, direct observations of fish detected in shallow habitats along the stream edge confirmed that the operator was able to locate the individual to within a square metre.

Each fish location was plotted into two-dimensional coordinate values y (metre transects along the stream length) and x (equidistant strata across the stream width). The x coordinate values were converted into metres according to width measured at 1 m increments along the edge. When multiple records of fish position (1, 2, 3…) were performed during *Post-freeze 1* and *Ice 2* surveys, the arithmetic mean position of each individual was calculated by averaging the x coordinate values of all points (x_1, x_2, x_3…) to obtain $\bar{x}$, and the y values (y_1, y_2, y_3…) to obtain $\bar{y}$. The arithmetic mean position ($\bar{x}$, $\bar{y}$) is the point from which the mean squared distance to all other points (x_1,y_1; x_2,y_2; x_3, y_3…) is minimal (Hayne, 1949; Lair, 1987). Thereafter, we calculated the radial distances (d_1, d_2, d_3…) between the arithmetic mean position ($\bar{x}$, $\bar{y}$) and every point in the distribution (x_1,y_1; x_2,y_2; x_3,y_3…) with the Pythagorean theorem. The arithmetic mean distance moved ($\bar{d}$) was calculated by averaging the radial distance values of all points (d_1, d_2, d_3…) to provided a measurement of fish dispersal around its arithmetic mean position. Then, the radial distance values (d_1, d_2, d_3…) of all individuals were grouped, and one-way ANOVA were carried out to test for differences in fish mobility between riffle and pool, and between day and night. Assumptions of normality and homogeneity of variance were tested using the Kolmogorov–Smirnow test (with Lilliefors probabilities) and Levene's test, respectively. When deviations were detected, non-parametric Mann–Whitney U-tests were performed. Statistical analyses were performed using SYSTAT 9 (SPSS Inc., 1996, Chicago, IL, U.S.A.) and considered to be significant at the $P = 0.05$ α level.

Results

Of the 15 PIT-tagged Atlantic salmon parr that were present in the experimental area before icing (*Pre-freeze*), nine fish were consistently tracked over the study period (Fig. 1); of these, seven moved less than 5 m up- or downstream, and two moved more than 10 m (maximum 23 m). An extended tracking survey was performed within 100 m directly upstream and downstream of the riffle-pool sequence on 24 November, but none of the missing individuals were found, suggesting that they had initiated long distance movements. Emigration was higher from the pool than from the riffle; the proportion of fish recorded in the riffle habitat increased from the *Pre-freeze* survey (33%) to the *Post Ice 2* survey (56%). Surface ice (up to 2 cm thick) developed on the edge at night on 11 November (*Ice 1*), and a thin anchor ice blanket partially covered the streambed of the riffle. As air temperatures rose in the morning of 12 November, anchor ice lifted off the substrate and floated out of

the brook whereas surface ice along the edges persisted for the next 3 days. After *Ice 1*, four parr left the pool and were not relocated during subsequent tracking, and one parr shifted from pool to riffle.

Fourteen individuals were relocated 10 times from 12 November at 16:00 hours to 14 November at 19:00 hours (*Post Ice 1*, Fig. 2). The arithmetic mean distance moved ($\bar{x}$) varied from 0 m (negligible or undetectable movement) to 2.5 m depending on the individual fish. On average, the arithmetic mean distance moved was 0.68 m during daytime and significantly increased to 1.15 m at night (ANOVA, $n = 140$, $F = 7.64$, $P = 0.006$). The arithmetic mean distance moved in riffle and pool were not signifi-

cantly different during daytime (riffle = 0.72 m; pool = 0.66 m; Mann-Whitney, $n = 70$, $P = 0.318$) or at night (riffle = 1.01 m; pool = 1.23 m; Mann-Whitney, $n = 70$, $P = 0.421$). The distance between day and night arithmetic mean positions ranged from 0 to 5.5 m depending on the individual fish (Fig. 2). The diel habitat shift was more obvious in the pool, where four individuals used positions close to the stream edge at night.

Water temperature reached the freezing point on 18 November at 17:00 hours (*Ice 2*). The average air temperature dropped to a minimum of −13.8 °C at 07:00 hours (Fig. 3); anchor ice formed on the substrate in the riffle and completely covered it (up to 10 cm thick). A slight increase in surface water temperature was recorded near the substrate, reaching +0.16 °C above the freezing point. As air temperature increased during the day of 19 November, water temperature progressively returned to the
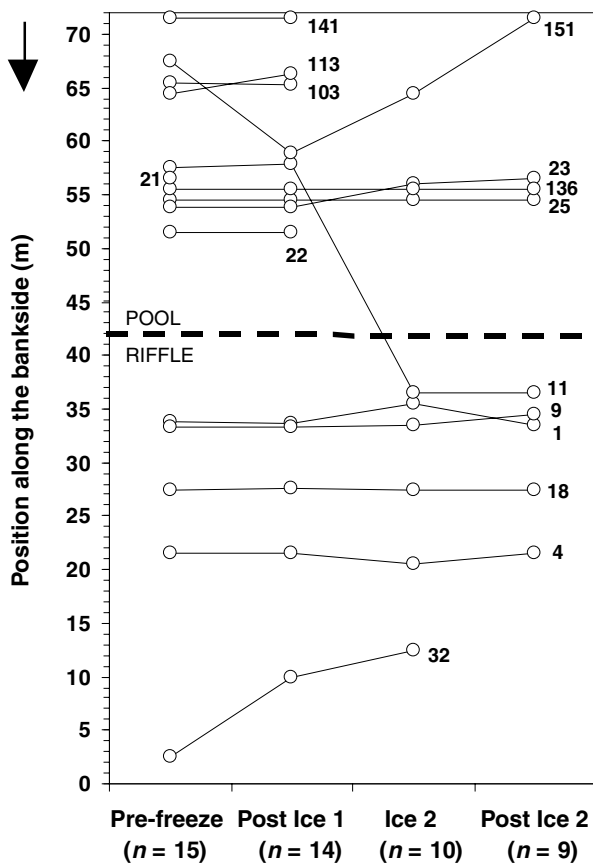

Fig. 1 Temporal variations in parr location within the riffle-pool section at the onset of winter 1999, from 8 November (*Pre-freeze*) to 24 November (*Post Ice 2*). Numbers from 0 to 72 on the vertical axe refer to meters along the site; the black arrow shows the main flow direction. When fish location was recorded more than once during the survey (*Post Ice 1* and *Ice 2*), the arithmetic mean position is displayed on the graph (see text for details). For convenient readings, fish identification number is quoted close to its final position.
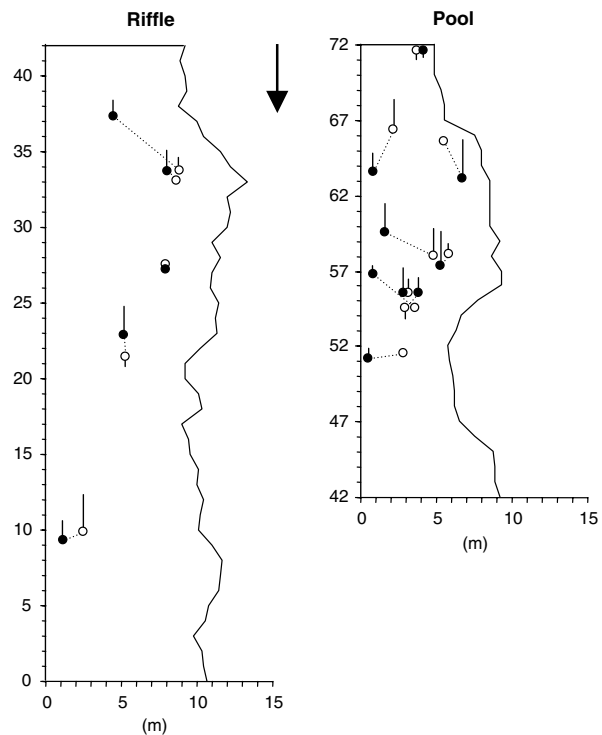
Fig. 2 Location of 14 Atlantic salmon parr in the riffle-pool section after the first freezing event (*Post Ice 1*). The right bank side is linearised for a more understandable display; numbers from 0 to 72 on the vertical axe refer to meters along the site. The arrow shows the main flow direction. For each individual, the arithmetic mean position during daytime (open circle) and at night (solid circle) are displayed, vertical bars indicate the arithmetic mean distance moved by the fish ($\bar{x}$, see text for details).
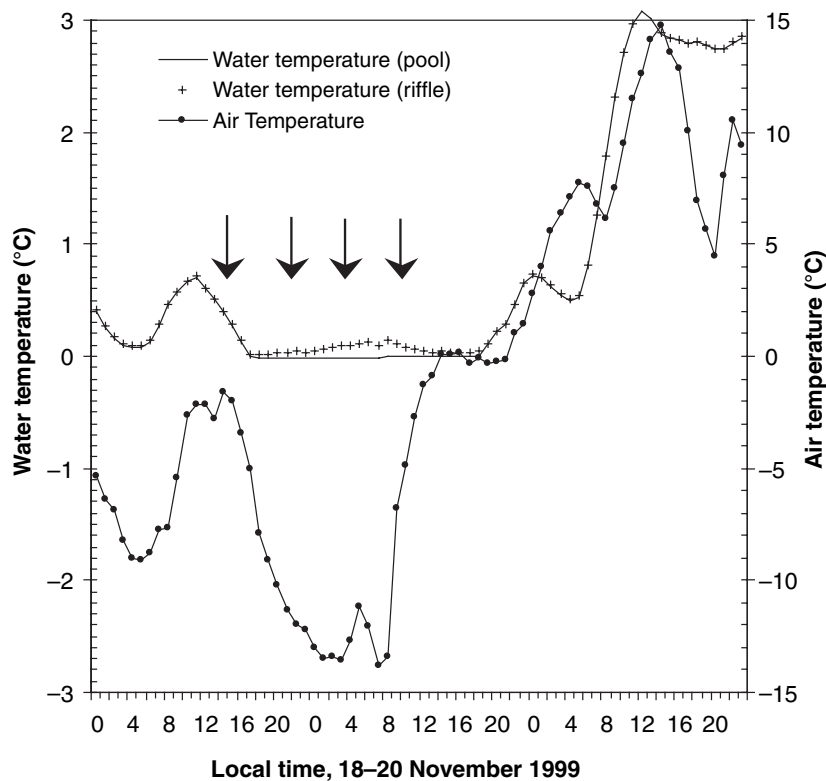
Fig. 3 Average water and air temperatures from 18 to 20 November 1999, during the second freezing event (*Ice 2*). Fish location was recorded within the riffle-pool section at 16:00, 23:00, 5:00 and 11:00 hours, local time (arrows).

freezing point in riffle and anchor ice lifted off the substrate. This slush ice floated downstream in the flow, eventually melting as water temperatures increased above 0 °C in both riffle and pool habitats after 18:00 hours.

In total, 10 PIT-tagged parr were relocated four times from 18 November at 16:00 hours (just prior to anchor ice formation) to 19 November at 11:00 hours. Of the six parr that were located in riffle, four parr were consistently detected in the same place ($\bar{x} = 0$). At 5:00 and 11:00 hours, all the fish in the riffle were detected beneath anchor ice up to 10 cm thick. Habitat used by salmon parr in the riffle was characterised as shallow (20–30 cm deep) with an abundance of small boulders and rubble (20–30 cm in diameter). Conversely, all the fish were mobile in the pool during *Ice 2*, and $\bar{x}$ varied from 0.4 to 3.2 m. Two parr were consistently detected in mid-channel in water 50–60 cm deep with large boulders on the bottom (>40 cm in diameter). No ice formation was observed in this part of the channel. Two other parr used both mid-channel and stream edges: at night, they were detected under the shelf ice along the edge in shallow microhabitats (<20 cm deep). Finally, nine of the 10

parr were re-located within the riffle-pool section on 24 November and survived to *Ice 2*.

Discussion

This study offers a unique perspective of the pattern of individual movements of wild, Atlantic salmon parr at the onset of winter, particularly as it relates to ice processes in the stream. First, PIT-tagged fish that were consistently tracked over the freezing period (8–24 November) displayed restricted movements in the channel, only two fish moved more than 10 m up- or downstream. In the absence of ice in the channel (*Post Ice 1*) we found that parr mobility was slightly higher at night, confirming the nocturnal activity pattern already described for salmon in the wild (Rimmer *et al.*, 1983; Cunjak, 1988; Whalen & Parrish, 1999; Hiscock *et al.*, 2002) or under experimental conditions (Metcalfe, Fraser & Burns, 1999; Vehanen & Huusko, 2002). Fraser *et al.* (1993) observed that Atlantic salmon parr became increasingly nocturnal as water temperature dropped below 10 °C, seeking refuge by day and emerging to feed at night. Laboratory experiments by Valdimarsson & Metcalfe (1998)

suggested that the function of nocturnal behaviour during winter is most likely to hide from diurnally active (visual) predators. The mean arithmetic distances moved by the parr (calculated from repeated records of individual positions in the channel) in Catamaran Brook were short (<3 m), supporting the idea of limited movements by resident parr in early winter.

In contrast to the static behaviour of most parr in the study site, some individuals apparently initiated long-distance movements. Over the period of freezing temperatures (8–24 November), 40% of the parr disappeared and may have emigrated from the study site. Radio-tracking studies have related movements of salmonids to subsurface ice episodes in streams. Brown & Mackay (1995) noted that winter movements of adult cutthroat trout *Oncorhynchus clarki* were associated with frazil ice formation in high altitude rivers of Alberta. Jakober *et al.* (1998) and Simpkins *et al.* (2000) observed that the occurrence of frazil ice was associated with more frequent movements of distances longer than 1 km by bull trout *Salvelinus confluentus* and juvenile rainbow trout *Onchorhynchus mykiss* in high elevation streams of Montana and Wyoming. These results appear to be similar to our findings for Atlantic salmon in Catamaran Brook, where parr that disappeared during the freezing period were not found in the immediate vicinity (i.e. within 100 m directly downstream and upstream of the riffle pool sequence). Predation may also explain the fate of some of the unaccounted parr. One PIT-tag was found within 1 m of the pool bank on 24 November, and we suspect that the fish was eaten by a mink (*Mustella vison*). Predation by mink on Atlantic salmon parr in winter was also reported by Hiscock *et al.* (2002) who found that 2 of their 10 radio-transmitters had been transported up to 40 m away from a river in Newfoundland. Jakober *et al.* (1998) found three of the 24 transmitters that they implanted in bull and cutthroat trout in mink dens along the stream banks. Because we did not make an exhaustive search for transponders along the riverbanks, predation on parr may have biased our interpretation of parr emigration in early winter.

The heat budget for flowing water depends upon exchanges occurring at either air/water or substrate/water interfaces (Fig. 4). Heat transfer at the open water surface, including radiation, conduction, precipitation and evaporation, is the primary process
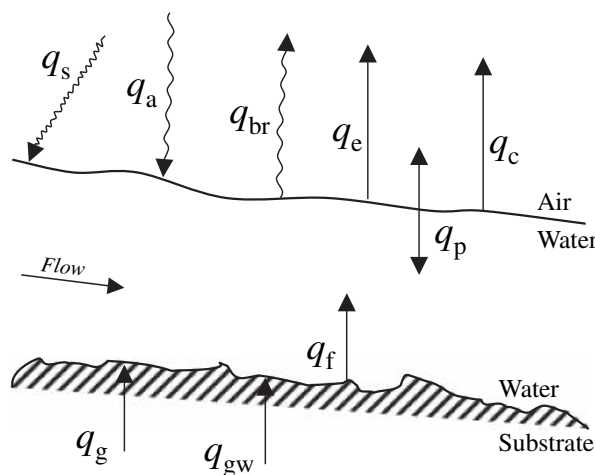

Fig. 4 Heat budget for flowing water in decreasing air temperature at the onset of winter. Heat is mainly gained by short-wave or solar radiation (q_s), long–wave atmospheric radiation (q_a), and lost by long-wave back radiation (q_{br}) and air/water conduction (q_c). In very shallow flows some of the back radiation component may be coming from the bed directly. Other heat transfers may also occur at the surface of open water because of evaporation/condensation (q_e) and precipitation (q_P). Principal heating sources at the streambed are fluid friction (q_f), geothermal conduction (q_g) and inflowing groundwater (q_{gw}). Modified from Newbury (1967).

by which the water temperature decreases in the autumn (Newbury, 1967). On a cold night in early winter when the difference between air temperature and open water temperature is the highest, the loss of heat to the atmosphere is the greatest because of back radiation (q_{br}) from the flow and from the bed, as well as by conduction (q_c) from the water surface (Fig. 4). The sum of the components of the heat budget may allow the bed and the flow in a shallow and open water area to reach temperatures slightly below freezing (supercooling), as low as $-0.1\ °C$ (Davar, Beltaos & Pratte, 1996). As long as the budget is negative enough to overcome the incoming heat (from inflowing sensible groundwater, frictional heating and geothermal conduction), ice can form on the bed (anchor ice) and within the water column (frazil). Frazil ice particles rapidly adhere to each other and to fixed ice boundaries leading to the formation of ice pans, hanging dams, or anchor ice on the bed where the flow is shallow. Anchor ice usually starts to grow in the shallowest part of the flow, for example on the top of larger rocks where supercooling is greatest, and rapidly spreads on the substrate of the riverbed. As soon as there is enough

of an increase in incoming atmospheric and/or solar radiation and/or a rise in air temperature during the day, the budget is not sufficiently negative to overcome the bed heating sources. Consequently, the ice melts at the bed/ice boundary, resulting in anchor ice detachment and downstream movement called 'slush ice'.

Two successive freezing events occurred from 8–24 November 1999 in Catamaran Brook that each generated accumulations of frazil ice in the river. It has been reported that ice crystals can plug the mouth and gills of fish (Tack 1938 in Power *et al.*, 1993; Carstens 1966 in Simpkins *et al.*, 2000), and Simpkins *et al.* (2000) observed an increase in radio-tagged fish mortality within 3 days of a frazil-ice episode. Simpkins *et al.* (2000) also reported that radio-tagged juvenile rainbow trout *Oncorhynchus mykiss* moved to shallow habitats near the shore under shelf ice and others moved to the bottom of deep pools when frazil ice was present. Whalen *et al.* (1999) made snorkeling surveys in the headwaters of the Connecticut River and observed that parr tended to avoid high velocity areas after ice had formed, instead preferring lateral positions along the ice boundary. These results are similar to our findings in Catamaran Brook where Atlantic salmon parr selected slow flowing habitats in the pool, under the shelf ice or in the deepest microhabitats in mid-channel during the second ice event (18–19 November).

According to Annear *et al.* (2002), the use of slow, deep areas may reflect an apparent strategy to avoid supercooled flows. As anchor ice progresses, Power *et al.* (1993) suggested that fish can either shelter in low velocity microhabitats under shelf ice or they may be forced to emigrate from riffles. Brown (1999) observed that radio-tagged cutthroat trout moved in early winter when their habitat was occluded by anchor ice. Heggenes *et al.* (1993) performed underwater observations of brown trout under freezing temperatures in Norway and observed that fish came out of their shelter at night. They hypothesized that the fish were more active during darkness hours to avoid becoming trapped in anchor ice that tends to form at night. Although anchor ice completely blanketed the riffle in Catamaran Brook, the parr were not forced to move. They were detected in shallow microhabitats close to large stones and below 10 cm thick anchor ice. It is possible that the cover created by anchor ice may actually contribute a beneficial aspect for the fish (Fig. 5). When frazil crystals adhere to the top of larger stones in riffle, it creates an insulating layer that may reduce the heat loss from the bed. This is a plausible explanation for the water temperature increase recorded under anchor ice (Fig. 3). The two different bed heating sources, geothermal heat and groundwater flow (q_g and q_{gw} in Fig. 4), have recently been studied in Catamaran Brook (Alexander & Caissie, 2003; Caissie & Giberson, 2003), and Alexander *et al.* (2003) demonstrated the significance of the geothermal heat flux at the onset of winter. Such conditions, associated with low velocity pockets beneath large stones, may provide suitable habitats
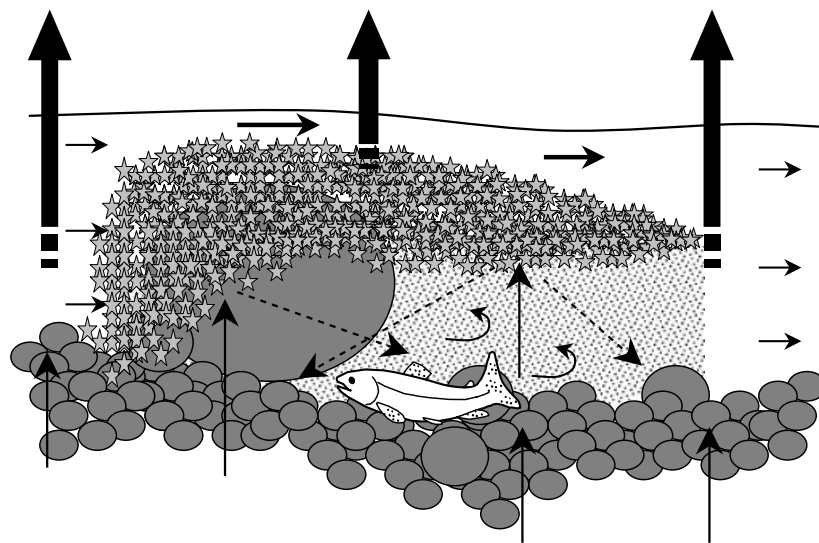

Fig. 5 Schematic drawing of microhabitat use by Atlantic salmon parr in riffle during the anchor ice event. The continuous loss of heat to the atmosphere (heavy vertical arrows) leads to generation of frazil ice particles (stars) that adhere to the top of larger rocks to form anchor ice. The cover created induces a low velocity pocket beneath the rock (curved arrows), and the heat flux at the substrate/water interface to the atmosphere (light vertical arrows) is reduced (dashed arrows). As a result, the water temperature slightly increases above the freezing point. Horizontal arrows indicate flow direction, heavy arrows for the swiftest velocities.

under anchor ice in early winter, where parr can avoid supercooling in turbulent reaches and therefore be protected against freezing.

The cyclic nature of anchor ice may also indirectly be advantageous to fish that do not leave the riffle at the onset of winter. The number of invertebrates in the drift can be significantly increased on mornings following anchor ice formation (Maciolek & Needham, 1952; Martin *et al.*, 2000). Some studies have presented evidence of winter-feeding by Atlantic salmon parr (Riddell & Leggett, 1981; Cunjak, 1988), and Maciolek & Needham (1952) observed trout feeding among floating frazil slush. Therefore, active parr in the riffle may have access to more drifting prey during the daytime when anchor ice releases. Metcalfe *et al.* (1999) showed, in experimental tanks, that when food is scarce at the onset of winter, brief daytime foraging bouts may have major impacts on individual growth rate. Daytime feeding activity of parr in frazil slush may have important physiological implications to offset the costs of maintenance metabolism in early winter, and this aspect should be investigated in future studies.

Results of this study on parr movements at the onset of winter were based on a small number of individually tagged fish from a single study site, and conclusions are certainly preliminary. In Catamaran Brook, we found evidence that anchor ice influences parr behaviour, but the extent of its effect is difficult to determine as investigations in the field are technically challenging. Insights from PIT technology support the theory that movements of fish at the onset of winter correspond to a general avoidance of supercooling conditions and habitat inclusion by ice (Heggenes *et al.*, 1993; Annear *et al.*, 2002), but it suggests that long distance movements may not be necessary as fish can find suitable microhabitat under the anchor ice in turbulent waters. Future projects that integrate fish movements across spatial and temporal scales will have to provide better analyses of behavioural patterns of habitat use by over wintering fish in streams. Protocols that combine recent advances in PIT and radio-telemetry methodologies should be helpful to this end. Finally, the PIT-tracking method may offer a unique opportunity to estimate the natural level of winter predation on parr by mammals (mink and otter), as the transponders can be easily detected in predator scat along the stream banks.

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