

Winter behaviour of juvenile Atlantic salmon *Salmo salar* L. in experimental stream channels: effect of substratum size and full ice cover on spatial distribution and activity pattern

T. LINNANSAARI*†, R. A. CUNJAK* AND R. NEWBURY‡

*Canadian Rivers Institute and Department of Biology, University of New Brunswick, P. O. Bag Service 45111, Fredericton, NB, E3B 6E1 Canada and ‡Newbury Hydraulics, 11215 Maddock Avenue, Okanagan Centre, BC, V4V 2J7 Canada

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Activity and choice of areas offering different cover (substratum or surface ice) for juvenile Atlantic salmon *Salmo salar* were studied in experimental stream channels during winter. Channels were completely ice covered between December and March. During this period, the ice thickness increased from 50 to 300 mm after which 50% of the ice was experimentally removed and followed by c. 2.5-fold increase in discharge to simulate the effects of spring flood. Large substrata provided preferred habitats but areas with small substratum sizes were also used when full surface ice provided above-stream cover and the stream discharge was relatively low. The fish remained nocturnal throughout the study but the level of day activity significantly increased as the surface ice became thicker. Maximum movement distance during a 24 h period and homing-at-dawn behaviour remained at a constant level throughout the main winter, but significantly changed during the simulated spring flood (mean \pm s.e. maximum extent of movements within 24 h increased from 1.1 ± 0.1 to 3.0 ± 0.5 m; homing behaviour decreased from the highest level of 89.3 to 34.6% during spring flood). Overwinter survival was high (92.9%). Relative mass increase during the study ranged from -8.3 to 28.5%, and 84% of the juvenile Atlantic salmon gained mass. The highest rates of mass increase were associated with frequent movements between areas of different substratum size. The results indicate that during winter: (1) Atlantic salmon parr preferred large substratum cover compared with surface ice cover at the fish densities studied here, (2) juvenile Atlantic salmon were predominantly nocturnal but diurnal activity increased as surface ice became thicker and (3) increase in water discharge during spring altered the behaviour of juvenile Atlantic salmon and may have caused additional habitat shifts.

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INTRODUCTION

Winter conditions influence the metabolism of poikilothermic animals such that they have adopted a variety of mechanisms to survive during the cold period

†Author to whom correspondence should be addressed at present address: SINTEF Energy Research, Sem Sælunds vei, 7465 Trondheim, Norway. Tel.: +47 7359 7216; fax: +47 7359 3350; email: tommi.linnansaari@unb.ca

of the year (Ultsch, 1989). In running waters, many cyprinids enter a torpor-like state during the ice-affected period of the year whereas juvenile salmonids remain active even at freezing temperatures (Cunjak, 1996). Whilst remaining active, the behaviour of juvenile salmonids, including juvenile Atlantic salmon *Salmo salar* L., changes in autumn when water temperature falls below a population-specific threshold (typically below 5–10° C); namely, juvenile salmonids suppress their daytime activity and become largely nocturnal (Cunjak, 1988; Fraser *et al.*, 1993; Heggenes *et al.*, 1993). The adaptive function of this behaviour has been suggested to be avoidance of entrapment in ice during the night (Heggenes *et al.*, 1993), sheltering from the current to avoid displacement or to reduce energy expenditure (Rimmer & Paim, 1990; Heggenes *et al.*, 1993) or avoidance of predation by endothermic animals (Fraser *et al.*, 1993; Valdimarsson & Metcalfe, 1998). The relative risk of instantaneous mortality due to endotherm predation (typically by mink, *Mustela vison* Schreber or otter *Lutra lutra* L.) is increased during winter due to lowered swimming performance of juvenile salmonids (Rimmer *et al.*, 1985; Graham *et al.*, 1996) and the increased importance of fishes in mustelid diets (Gerell, 1967; Erlinge, 1969). Thus, the 'anti-predatory response' hypothesis has been considered to be the most plausible explanation for nocturnal behaviour during winter (Huusko *et al.*, 2007) although the hypothesis is still based on reasonable inference rather than experimental evidence (Reebs, 2002).

Due to the anti-predatory hypothesis mentioned above, the current understanding is that the optimal feeding period in winter is during the hours of darkness when survival is maximized rather than during the day when the feeding rate is maximized (Metcalf *et al.*, 1999). This diel pattern may change when full ice cover prevails because the predation risk by endotherms would be reduced or eliminated. Due to methodological constraints, fish behaviour has not been studied under full surface ice cover. In a recent study, however, Linnansaari *et al.* (2007) showed the suitability of portable passive integrated transponder (PIT)-antennae for accurately monitoring fish behaviour beneath ice.

The fact that juvenile salmonids suppress their daytime activity during cold-water temperatures leads also to specific requirements for overwintering habitat. Structures providing visual or overhead cover are of primary importance in determining suitable daytime habitats (Rimmer *et al.*, 1984; Mäki-Petäys *et al.*, 1997; Heggenes & Dokk, 2001). It remains unclear, however, how well surface ice meets the need for cover of juvenile salmonids (Gregory & Griffith, 1996). The results from both Cunjak & Power (1987) and Vehanen *et al.* (2000) suggest that submerged cover is preferred over above-water cover structures. If the winter cover choice is mainly an anti-predator tactic (Valdimarsson & Metcalfe, 1998), it is plausible that full surface ice alone would provide adequate cover for juvenile Atlantic salmon. Additionally, the cover preference might be different in early spring when the physical environment is further influenced by high discharge due to melting ice and snow. To examine the validity of the above-mentioned hypotheses, experimental channels with natural ice cover were constructed to determine if areas with small substratum size are used by Atlantic salmon parr under full surface ice. Also, the activity pattern of Atlantic salmon parr was followed to examine if the parr will increase their day activity under full ice cover and furthermore if the parr behaviour and habitat (substratum) choice will change in spring.

MATERIALS AND METHODS

CHANNEL SET-UP

The study was carried out in two experimental stream channels (channel 1 and channel 2) that were situated in South Esk, northern New Brunswick, Canada (46° 57' N; 65° 39' W). The channels were located inside a large tent that was constructed of white light-permeable polyethylene membrane so that the light conditions inside the building followed the natural diel rhythm and no artificial lighting was used. The channels measured 15 × 0.95 m. The uppermost 0.5 m was designated for a head pond from which the water was directed to the channels [Fig. 1(a)]. The lowermost 0.5 m was designated as an overflow area from which the water was directed out from the channels and thus was not accessible for the fish (Fig. 1). The area available for the fish was divided into two 7 m long segments with two substratum treatments (large and small substratum; 100–200 and 40–90 mm, respectively), in both channels [sections from UpSm to DnLg; Fig. 1(b)]. Each 7 m area was further divided into a 3 m riffle (3.3% gradient) and a 4 m pool [Fig. 1(a)]. The average depths and mean water velocities were measured through 25–48 holes that were made through the ice during the winter. After the measurement, these holes were filled with ice slush to allow them to re-freeze. The depths and velocities in the pools and riffles with the same substratum size were similar between the two channels (*t*-test, *P* > 0.05 for all tests) during both the stable winter period and simulated 'flood' conditions and the pooled data are shown Table I.

The fish were able to freely move between the sections and thus choose their preferred location (except for the time period between 11 to 30 November). The substratum treatments were arranged so that the large substrata were in the lowermost 7 m in channel 1 [DnLg; Fig. 1(b)] whereas large substrata were situated in the uppermost 7 m in channel 2 [UpLg; Fig. 1(b)]. The water intake to the stream channels was from the nearby Stewart Brook and both channels had a separate water intake. The discharge (*Q*) in channel 1

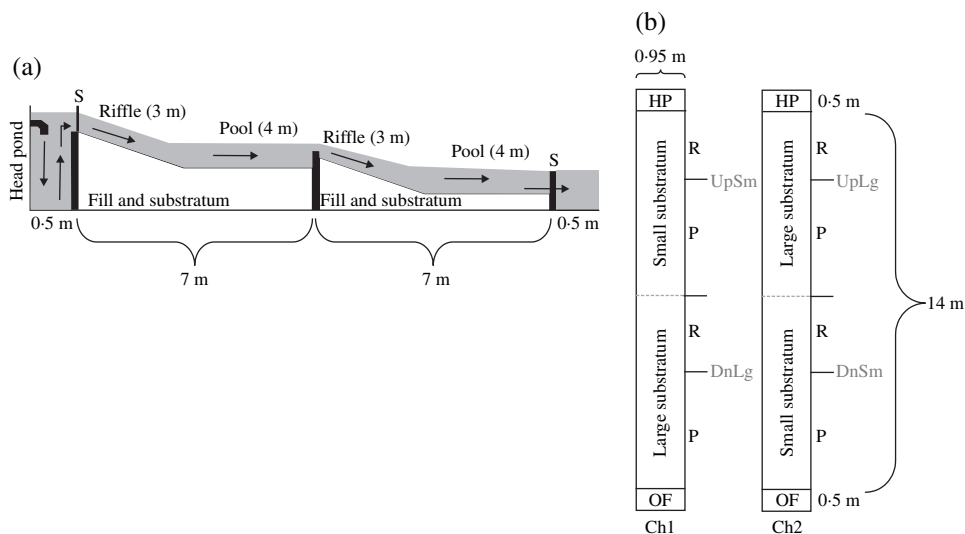


FIG. 1. A schematic representation of the experimental stream channels. (a) A generalized side-view of the channels. Grey colour represents water and the flow direction is indicated with → (S, screen to restrict fish movements) (b) A generalized top-view of the channels (channel 1 and channel 2) showing the location of sections UpSm, UpLg, DnSm and DnLg (HP, headpond area; OF, outflow area; P, pool; R, riffle). The dotted grey horizontal line represents the transition in the substratum size and thus was not a barrier for fish movements.

TABLE I. Physical microhabitat in different sections (see Fig. 1) of the stream channels during the 'winter' period (11 November to 5 April) and simulated flood (6 to 18 April). Values shown are means with their range in the parenthesis. Water velocity was measured at the $0.6 \times$ depth

	'Winter' period		Flood		Substratum (mm)
	Depth (mm)	Velocity (m s^{-1})	Depth (mm)	Velocity (m s^{-1})	
UpSm; DnSm, riffle	80 (60–100)	0.39 (0.28–0.45)	100 (40–190)	0.77 (0.24–1.00)	40–90
UpSm; DnSm, pool	150 (90–220)	0.10 (0.50–0.25)	190 (90–310)	0.28 (0.80–0.47)	40–90
UpLg; DnLg, riffle	100 (70–120)	0.33 (0.20–0.40)	130 (70–150)	0.55 (0.15–0.64)	100–200
UpLg; DnLg, pool	160 (70–210)	0.11 (0.70–0.26)	200 (150–300)	0.24 (0.15–0.36)	100–200

and channel 2 was 16.3 and 17.6 l s^{-1} , respectively, during the winter months (November to April). The stream water provided naturally occurring macroinvertebrate drift. No additional food was provided during the experiment. The benthic macroinvertebrate fauna was examined at the end of the study by analysing eight 0.3 m^2 substratum samples, which consisted mainly of larval Chironomidae and Simuliidae. Based on a sample of six parr, which were analysed for stomach contents at the end of the experiment, the larval Simuliidae were also the most common dietary item forming 67–95% of the stomach contents.

Opaque, full surface ice cover formed across both channels during early December and the increase in ice thickness later during the study was produced by overflowing water from the head pond on top of the existing ice and allowing the water to freeze (details on ice thickness are given in Table II). After the initial freeze-up, a small air cap existed between the ice and water. Thus, the microhabitat conditions remained relatively stable during the ice covered period of the study. No anchor ice formation was observed as the radiation losses were limited by the enclosing structure and there was no snow on top of the ice.

FISH TAGGING AND TRACKING

The Atlantic salmon parr used in this experiment were captured in early November (Table II) from nearby Stewart Brook by electrofishing (Smith-Root LR-24) and thus were of wild origin. The juvenile fish ($n = 30$) were anaesthetized with clove oil (40 ppm, ethanol as carrier; Hoskonen & Pirhonen, 2004) after which they were measured (fork length, L_F , nearest mm), weighed (0.1 g precision) and checked for maturity. Only one fish was precocious and the effect of this was not considered further. An individually coded 23 mm Texas Instruments PIT-tag (RI-TRP-WRHP) was surgically inserted in the body cavity of fish (Roussel *et al.*, 2000) and the incision was closed with a suture (Monosof black nylon, 6-0 taper and C-1 cutting needle). Following the recommendations of Roussel *et al.* (2000), only Atlantic salmon parr >84 mm were used for PIT-tagging. The tag weighed 0.6 g in air and represented $5.4 \pm 1.3\%$ (mean \pm s.d.) of the fish wet mass. After a short recovery (1 h), 15 randomly chosen fish were evenly distributed in each stream channel by placing approximately one fish m^{-2} of the channel. Mean \pm s.d. wet mass and L_F of the tagged fish did not differ between the channels (t -test, $n_{\text{channel 1}}, n_{\text{channel 2}} = 15, 15$, $P > 0.05$ for both tests) and was 11.8 ± 3.0 g and 100 ± 8 mm, respectively, for the whole population.

The tracking of the fish was carried out using a portable one-person operated PIT-detector-antenna unit (Texas Instruments series 2000, Plano, TX, U.S.A.; Roussel *et al.*, 2000 with modifications following Linnansaari *et al.*, 2007). The operator scanned the wetted perimeter of the channels and upon tag encounter the fish identification code was recorded as well as the x and y co-ordinates using a grid marked into sides of the stream channels. The 'blind-spot' method was used for accurate fish positioning

TABLE II. Dates of physical alterations and tracking with prevailing physical conditions and water temperature in the stream channels. Each 24 h tracking occasion is individually named within these parentheses

Date	Event	Conditions	Water temperatures (° C)
11 November	Fish tagging	Open channel	4.0
30 November	Channel reconfiguration*	Open channel	3.0
14–15 December	24 h tracking (ICE 1)	5 cm ice thickness	0.2
13–14 January	24 h tracking (ICE 2)	15 cm ice thickness	0.2
4–5 March	24 h tracking (ICE 3)	30 cm ice thickness	0.2
8 March	Ice manipulation	50% no ice (0 cm); 50% 30 cm ice	0.2
19–20 March	24 h tracking (50/50)	50% no ice (0 cm); 50% 30 cm ice	0.2
6 April	Discharge increased to 'flood'	Open channel, increased discharge	0.9
14–15 April	24 h tracking (Flood)	Open channel, increased discharge	4.5
18 April	Fish recapture; end of experiment	Open channel, increased discharge	5.0

*Fish passage made possible between sections UpSm to DnLg and UpLg to DnSm (see Fig. 1).

(accuracy 10.9 ± 1.4 cm; Linnansaari *et al.*, 2007). As the channels were relatively shallow in comparison with the *c.* 70 cm detection distance of the antenna system and no emigration from the stream channels was possible, all the tags within the stream channels were detected on every tracking occasion. The bias in spatial distribution of fish due to fright response has been deemed negligible for juvenile Atlantic salmon during cold-water temperatures (Linnansaari & Cunjak, 2007; Linnansaari *et al.*, 2007).

The fish tracking took place repeatedly over a 24 h period on five occasions (Table II). During each 24 h tracking period, fish locations were determined approximately every 2 h, resulting in 10–12 trackings per occasion. The first three 24 h tracking events were carried out under full surface ice conditions (100% of the wetted width covered in ice) with increasing ice thickness from first to third tracking occasion (ICE 1–3; Table II). For the fourth tracking occasion (50/50; Table II), all the ice was manually removed from the lower sections [DnLg and DnSm; Fig. 1(b)] leaving only 50% of the channels ice covered (*i.e.* sections UpSm and UpLg). The tracking took place 11 days after ice manipulation (Table II). For the fifth 24 h tracking occasion (Flood; Table II), the discharge was increased 8 days before tracking in both channels to simulate spring flood conditions. The flow was increased to 45.3 and 43.2 l s⁻¹ in channels 1 and 2, respectively (a 2.8 and 2.5-fold increase). Clean-up of the downstream screens was carefully performed in preparation for the flood conditions. Two fish were lost as a result of this maintenance. This fish loss was due to experimental set-up and it is not considered in the survival calculation later in the article. The remaining fish were recaptured on 18 April by electrofishing and growth during experiment was determined as a relative rate of mass change,

$$\Delta w = 100(w_2 - w_1)w_1^{-1},$$

where w_1 and w_2 are the mass at tagging in autumn and recapture in spring, respectively (Ricker, 1975).

DEFINITIONS AND STATISTICAL ANALYSIS

As fish positions were determined approximately every 2 h, an individual fish was defined as being active between successive tracking events n to $n + 1$, if its position had changed >0.3 m, which is the largest measured bias for detection accuracy for this antenna type (Linnansaari *et al.*, 2007). Movement was measured as the linear distance between the recorded fish positions and the maximum extent of movement within each 24 h tracking occasion was calculated as the greatest distance from the home stone. The home stone was defined as the initial daytime location of each parr at the start of 24 h tracking and the term is used throughout even though the parr could not be visually observed under the ice and the specific function of the home stone could not be determined. Homing, as used here, refers to behaviour where an individual fish returns exactly to the home stone after the hours of darkness. Further, the hours of darkness refer to a pooled time period of dusk, night and dawn and thus included the trackings when sunset and sunrise occurred (as distinguished from daylight).

Changes in the proportion of fish using different substrate sections between different tracking occasions was compared using log-likelihood ratio analysis and *post hoc* comparisons were carried out using a test analogous to the Tukey-test with angular transformed data (Zar, 1999). A Fisher exact test was used to test for differences in movement patterns between the two channels. To examine the differences in activity of juvenile Atlantic salmon between daylight and hours of darkness during each 24 h tracking occasion, the frequency of activity was calculated for each individual fish during day and night and this frequency was divided by the number of trackings carried out during the day and night, respectively (*i.e.* proportions of individual day and night activity were calculated). These proportions were compared within a tracking occasion using a Wilcoxon paired-sample test with a Bonferroni adjusted α -level. These proportions were further used when the level of day and night activity was compared between the tracking dates with a Friedman's test for non-parametric repeated-measures analysis of variance that was followed by Tukey-type *post hoc* tests. Because activity and homing were measured as dichotomous variables, Cochran's Q test was used whenever individual tracking occasions were compared (*e.g.* the activity levels between separate daylight tracking surveys within each 24 h period or comparisons between the first daylight tracking survey between the ICE1–ICE3 period). No between channel comparisons were carried out for activity and homing behaviour analysis and thus the analysis was carried out by pooling the data from the two channels. The differences between the maximum extent of movement between tracking periods were analysed using Friedman's test due to heteroscedasticity and non-normality of data that could not be removed by applying transformations. *Post hoc* tests were carried out using Tukey-type tests and pooled data from the two channels was used. Statistical analyses were performed with SPSS 14.0 software.

RESULTS

Winter survival of parr was similar between the two channels (Fisher exact test, $n = 28$, $P > 0.05$) and the pooled survival was 92.9%. One fish was removed from channel 1 during the first 2 weeks of the experiment by a mink that was observed inside the tent where the channels were situated. The water intake and outflow pipes were then blocked with a mesh and thus the possibility for predation was removed for the rest of the experiment. Another parr was determined to be dead in channel 1 during ICE2 tracking and occurred in an area that was frozen to the bottom.

DAYTIME FISH DISTRIBUTION AND COVER CHOICE

The tagged Atlantic salmon parr were first tracked on 30 November when it was noticed that they were constrained to the lowermost 7 m in both stream channels (Fig. 2) and were unable to move to the upper sections due to a visually obvious structural impediment in the section dividers. As a result, all the fish had established home territories in sections DnLg and DnSm (Fig. 2), regardless of the substratum size. The channel section dividers were subsequently

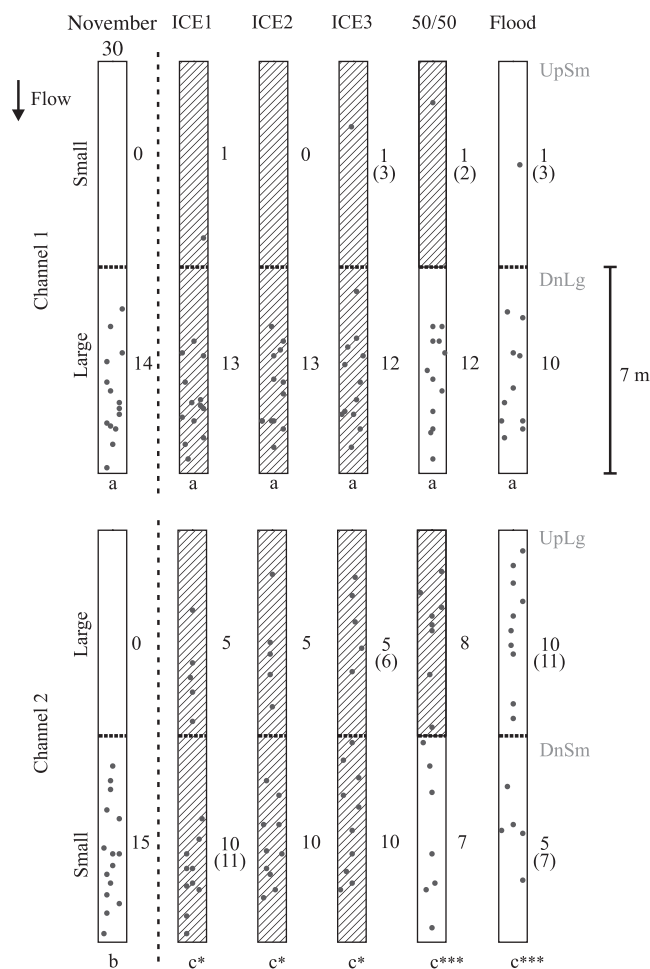


FIG. 2. The daytime distribution of Atlantic salmon parr (●) during the first daylight tracking at each occasion (see Table 1) (the number of fish remaining in each section is indicated on the right side of the channel for every tracking occasion; the number in parenthesis indicate the maximum number of fish observed in each section during the hours of darkness). UpSm–DnSm codes (grey colour; see Fig. 1) denote the channel sections used. Open areas represent no ice conditions; hatched areas represent ice. The dashed vertical line indicates the time when free passage between lower and upper sections of each channel was enabled. The substratum size in each section is indicated on the left side of the figure (small, 40–90 mm; large, 100–200 mm). The tracking occasions that share the same lowercase letter have statistically similar fish distribution between substratum sections (Tukey-type *post hoc* test; $P > 0.05$; * $P < 0.05$, *** $P < 0.001$). Note: head pond and overflow areas are not shown.

reconfigured on 30 November to allow fish passage between the sections with different substratum sizes.

Despite the improved passage opportunity to section UpSm, the daytime fish distribution remained practically unchanged in channel 1 throughout the study (log-likelihood ratio, d.f. = 5, $P > 0.05$) and the vast majority of Atlantic salmon parr remained in the large substratum section regardless of the ice conditions or increasing discharge (Fig. 2). The only fish that was found in the section with a small substratum during ICE1 tracking was confirmed as dead during the ICE2 tracking.

By contrast, the proportions of fish between different substratum sections significantly changed in channel 2 (log-likelihood ratio, d.f. = 5, $P < 0.001$; *post hoc* tests analogous to Tukey-test using arcsine transformed data; Fig. 2). A significant proportion (33%) of the fish had moved to the section with a large sized substratum (UpLg) before the ICE1 tracking (Fig. 2). The proportion of fish in different substratum sections remained stable throughout the period with full ice cover (ICE1–ICE3). Further, changes in spatial daytime distribution were observed when 50% of the surface ice was removed in channel 2 and more parr entered into the section UpLg (Fig. 2; 50/50 period). A similar response occurred also during the flood conditions (*i.e.* more parr entered into UpLg; Fig. 2). Due to the low sample size, the change in parr proportions between different sections during 50/50 and flood conditions were not significantly different in comparison to the ICE1–ICE3 periods (Tukey-type *post hoc* test, $n = 15$, $P > 0.05$; Fig. 2).

Since the parr daytime distribution was stable in channel 1 but changes occurred in channel 2, statistically significant differences between channels resulted. Whereas no difference in proportion of parr shifting between substratum sections was detected from ICE1 to ICE3 period (Fisher exact test, $n = 29$, $P > 0.05$), the difference between channels was considered significant during the 50/50 and flood occasions (Fisher exact test, $n = 28$, $P < 0.05$ for 50/50; Fisher exact test, $n = 26$, $P < 0.01$ for Flood). Thus, significantly more fish had shifted between substratum sections in channel 2 in comparison with channel 1 by the end of the experiment (Fig. 2).

It should be further noted, that temporary changes in the spatial distribution between substratum sections were observed during the hours of darkness as indicated in Fig. 2. Generally, the number of fish occasionally increased in the section UpSm in channel 1 during the hours of darkness whereas movements from section UpLg to DnSm and *vice versa* were seen in channel 2. The number of fish moving between different substratum sections during the hours of darkness was always low (Fig. 2), but interestingly, the same individuals were responsible for these movements between tracking periods. This movement pattern seemed to have consequences on the growth by the end of the experiment. Even though the majority (84%) of the parr gained mass during the experiment, the relative mass change was significantly better in both channels for individuals that made regular movements between the different substratum sections compared with those individuals that showed a more sedentary behaviour within any substratum section (channel 1, movers *v.* non-movers, $20.0 \pm 4.6\%$ *v.* $3.8 \pm 2.0\%$, mean \pm S.E., *t*-test, $n = 3$, 8, $P < 0.01$; channel 2, movers *v.* non-movers, $20.3 \pm 4.5\%$ *v.* $6.9 \pm 2.3\%$, mean \pm S.E., *t*-test, $n = 11$, 3, $P < 0.05$). Overall, the relative

mass change ranged from -8.3 to 28.5% from start to the end of the experiment but did not correlate with the initial fish L_F ($r^2 = 0.028$, $P > 0.05$) or initial mass ($r^2 = 0.12$, $P > 0.05$).

ACTIVITY

Atlantic salmon parr were more active during the hours of darkness than during daytime throughout the study (Fig. 3; Wilcoxon paired-sample test with Bonferroni adjusted- α , $n = 29$ for ICE1, $n = 28$ for ICE2, ICE3 and 50/50, $n = 26$ for Flood, $P < 0.001$ for all comparisons). Generally, the activity peaked at dusk and dawn, and remained at a high level during the night regardless of the date or the physical conditions in the channels. The level of daytime activity, however, increased as the surface ice became thicker (Fig. 3) and the mean daytime activity was significantly higher during ICE3 (*i.e.* 300 mm ice) in comparison with ICE1 (*i.e.* 50 mm ice) (Friedman's test, d.f. = 4, $n = 26$, $P < 0.01$; see Fig. 3 for *post hoc* tests). The increase in the mean day activity under full ice cover was attributed mainly to the fact that the level of activity was higher during the first daylight tracking than during any other tracking over the rest of the daylight hours (Fig. 4; Cochran's Q, d.f. = 2, 3, 4 and $n = 29$, 28, 28 for ICE1, 2, 3, respectively, $P < 0.01$ for ICE 1 and ICE3; $P = 0.05$ for ICE2). Further, there was an indication that the proportion of fish remaining active during the first daylight tracking was higher as the surface ice became thicker (Cochran's Q, d.f. = 2, $n = 28$, $P < 0.001$; see Fig. 4 for *post hoc* tests). The increase in mean day activity could not solely be attributed to increased activity level during the first daylight tracking as the activity level increased

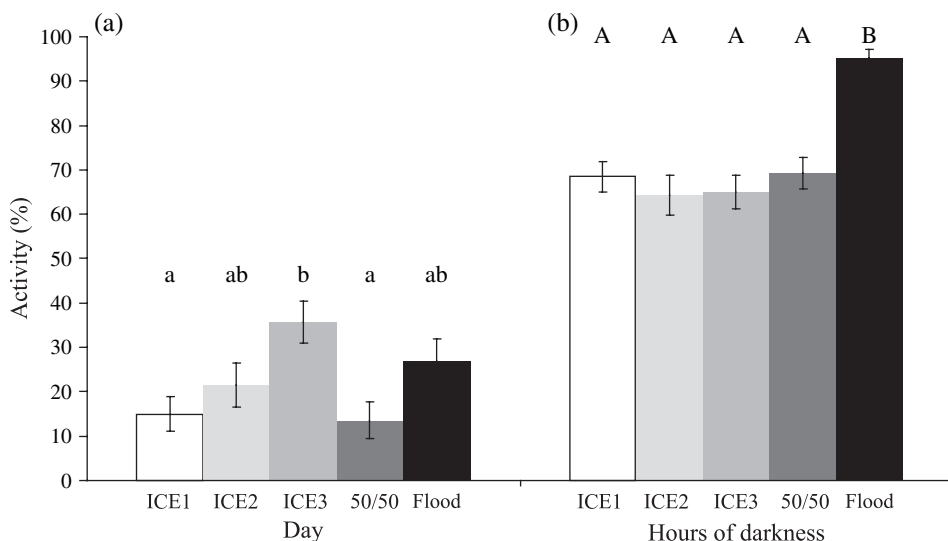


FIG. 3. Mean \pm s.e. activity of Atlantic salmon parr during (a) daylight and (b) hours of darkness on each 24 h tracking occasion (see Table II). Activity is measured as the proportion of the trackings each individual has been active. Means sharing the same letter [(a) lower case; (b) upper case] are not statistically different (*i.e.* $P > 0.05$; Tukey-type *post hoc* test).

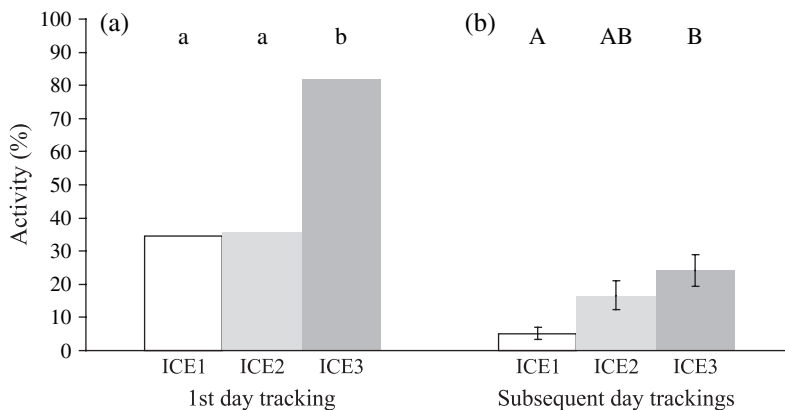


FIG. 4. The level of daytime activity during (a) the first daylight tracking and (b) subsequent daylight trackings (pooled data; mean \pm S.E.). Activity is measured as the proportion of the population that has been active between tracking n and $n+1$. Means sharing the same letter [(a) lowercase; (b) uppercase] are not statistically different (*i.e.* $P > 0.05$; Tukey-type *post hoc* test).

also during subsequent daylight trackings (Friedman's test, d.f. = 2, $n = 28$, $P < 0.01$; see Fig. 4 for *post hoc* tests). Furthermore, the day activity level was higher for the fish remaining under the ice cover (20.0%) in comparison with fish with no ice cover (8.9%) during the 50/50 tracking, but the difference was not statistically significant (Mann–Whitney U -test, $n_{\text{icefree, ice cover}} = 18, 10$, $P > 0.05$).

The level of activity during the hours of darkness did not differ significantly between the occasions from ICE1 to 50/50 (Friedman's test, d.f. = 4, $n = 26$, $P < 0.001$, *post hoc* tests between ICE1 to 50/50, $P > 0.05$; Fig. 3). The highest level of activity during the hours of darkness was observed during the flood tracking during which the activity level was significantly higher than during any other tracking occasion (Friedman's test, d.f. = 4, $n = 26$, $P < 0.001$, *post hoc* tests between flood and any of the other four trackings, $P < 0.05$; Fig. 3).

There was no significant relationship between the level of individual fish's activity and initial or final L_F or mass during any 24 h tracking occasion during day or hours of darkness (Spearman r_s ; range -0.37 to 0.25 , $P > 0.05$ for all correlations).

MOVEMENT AND HOMING

The mean maximum extent of diel movements was relatively short given the limited space available for the fish in the channels (range between the trackings from 1.1 ± 0.1 to 3.0 ± 0.5 m; mean \pm S.E.; Fig. 5) and did not differ between the channels (Mann–Whitney U -test, $n = 26$, $P > 0.05$ for all tracking occasions). Mean movements were stable during the ice-affected period of the study (ICE1 to 50/50) and did not statistically differ between tracking occasions (pooled data, Friedman's test, d.f. = 4, $n = 26$, $P < 0.001$; *post hoc* tests $P > 0.05$; Fig. 5). The extent of these movements was longer (*i.e.* 3.0 ± 0.5 m), however, during the flood tracking (pooled data, Friedman's test, d.f. = 4, $n = 26$,

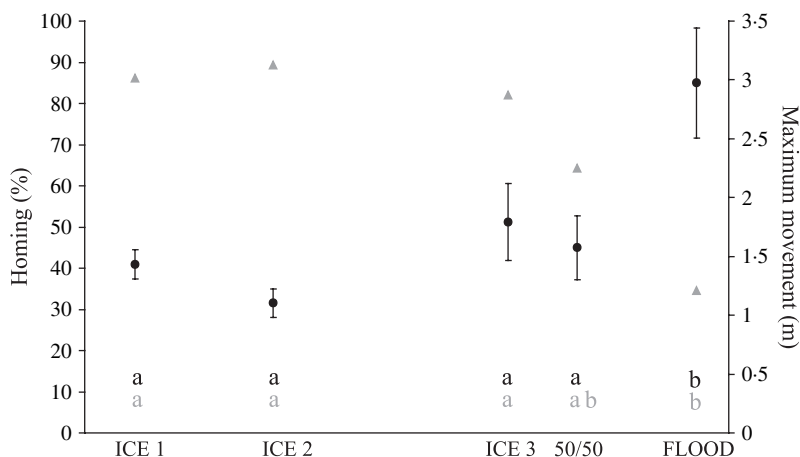


FIG. 5. Mean \pm S.E. maximum extent of movement (●) and the proportion of Atlantic salmon parr homing (▲) during each 24 h tracking occasion (see Table II) in the experimental channels. The x-axis is scaled to represent the time difference between the tracking occasions. Occasions sharing the same lower case letter are not significantly different (Tukey-type *post hoc* test, $P > 0.05$; $n = 26$ for all occasions in movement analysis, bold; $n = 29$ for ICE 1, $n = 28$ for ICE 2 to 50/50 and $n = 26$ for flood in the homing analysis, grey letters).

$P < 0.001$; all *post hoc* tests $P < 0.05$; Fig. 5). The increase in movement distance was not a result of involuntary downstream displacement of the fish as the maximum movement was directed upstream in 53.8% of the cases during the flood tracking.

As the activity pattern remained largely nocturnal throughout the study, fish were generally found immobile at their home stone during daylight, left the location at dusk and returned to this exact location again in the morning (*i.e.* homing). A high proportion of homing took place at dawn but homing was delayed with increasing amount of surface ice so that an increasing number of fish came back to home locations only by the time of second daylight tracking. The homing behaviour was particularly high during the ICE 1–3 events (82.1–89.3% of population) but the proportion of population homing decreased significantly towards the spring (lowest homing 34.6% during Flood, Cochran's Q , d.f. = 4, $P < 0.001$; see Fig. 5 for *post hoc* tests).

DISCUSSION

Surface ice and spring-like conditions altered the activity and cover choice of juvenile Atlantic salmon. Large substrata provided preferred habitat sections by the end of winter and early spring, as evidenced by the scarcity of movements away from the large substratum section in one channel but a significant shift into the area with large substrata in the other. These results corroborate prior research on juvenile salmonids wherein suitable winter habitat is often associated with the presence of large substrata (Rimmer *et al.*, 1984; Mäki-Petäys *et al.*, 1997; Heggenes & Dokk, 2001). It is very important, however, to note that the majority of the fish remained in the small substratum section

in channel 2 throughout the ice covered period of the winter. This fact provides an additional insight to former work that has demonstrated that habitats with small substrata are only used during the hours of darkness in winter (Heggenes *et al.*, 1993; Whalen & Parrish, 1999; Hiscock *et al.*, 2002). In the current study, the factors affecting the suitability of section DnSm as habitat were revealed by the timing of the additional shifts into section UpLg. Therefore, it appears that surface ice provided suitable winter cover for Atlantic salmon parr to the extent that they were willing to remain in the small substratum section. Also, the simulated flood indicated that, at a relatively high winter discharge, more Atlantic salmon parr sought shelter within large substrata. The latter point highlights the fact that substratum size plays another role than just providing cover from predators, *i.e.* large substrata serve also as shelter to avoid the physical forces and possible displacement (Rimmer *et al.*, 1984; Mäki-Petäys & Vehanen, 2000; Vehanen *et al.*, 2000). The notion is also supported by the fact that a significant proportion of fish shifted to section UpLg even though full ice cover was present and thus provided cover from predators anywhere in channel 2. Further, a negligible proportion of fish moved to section UpSm in channel 1 albeit the full ice cover would have provided a risk-free environment but no shelter from current.

The cover use pattern is also affected by the strong attachment to the home stone and the choice of location is not dynamic. Hence, this behaviour may confound the interpretation about true preference in this study since the fish movements were initially constrained due to the impediment between different substratum sections. If an Atlantic salmon parr remains in an area where no resource competition is apparent (*i.e.* abundance of cover and shelter locations and food in relation to fish density) and the physical conditions are suitable, parr have no reason to move and seek for areas that are even more suitable. Applied to the current experiment, it cannot be concluded if the parr preferred, *e.g.* the section DnSm to the UpLg in channel 2, since the extent of diel movements was too short for some parr to be aware of the large substratum section that was available after the impediments for movements were removed. It follows, that in cases where territorial fish are introduced to new areas, true habitat preference may be best studied after conditions that follow a disturbance that necessitates the exploration of the surrounding areas (*e.g.* in channel 2 after ice removal and Q increase).

The hypothesis that parr would only be diurnally active when full surface ice prevails was not supported and the fish remained largely nocturnal throughout the winter and early spring period as previously described for juvenile salmonids (Cunjak, 1988; Fraser *et al.*, 1993). The current study was designed to determine the activity pattern under ice and the ultimate reasons for the observed pattern cannot be explicitly named based on the activity data collected in this study. One of the possibilities is that the juvenile Atlantic salmon will not increase their fitness (*i.e.* survival in this context) by becoming only diurnally active under surface ice. Atlantic salmon parr will fix the required energetic demand with temporally short foraging bouts if they feed during the day in winter (Fraser & Metcalfe, 1997). By investing more time they can similarly suffice the demand for energy during hours of darkness because the basal metabolism of Atlantic salmon parr is low during winter. Thus, both

behavioural strategies result in a satisfactory energy balance and it may follow that no increase in fitness is gained by shifting to diurnal activity in winter and no evolutionary selection towards the diurnal activity strategy has taken place. Another possibility explaining the continued nocturnal behaviour is that the instantaneous mortality rate due to predation remains, in fact, higher during daylight regardless of the full ice cover. Indeed, it is typical that while the vast majority of the stream is ice covered during winter, some sections remain open (due to groundwater influx or snow bridging and insulation; Cunjak, 1996; Hubert & Pru, 2000) and allow access points to water for endothermic predators. Further, lowering of water level leads to existence of an air-gap between the ice and water surface (Calkins & Brockett, 1988). Observations from small streams in Canada and Norway confirm that these sub-ice spaces are readily used by mink and otter (pers. obs.) as is also reported by Calkins (1993).

It should also be kept in mind that the mainly nocturnal pattern of activity of the present population may not be indicative of all populations. Local adaptations may influence the activity patterns that juvenile salmonids demonstrate (Valdimarsson *et al.*, 2000). Therefore, Atlantic salmon from river systems where ice cover usually is only partial or fluctuates between full and partial ice cover (as used in this study) may not be adapted to alter their activity pattern during full ice cover period whereas populations from high latitudes may demonstrate different tactics. Such population specific adaptations to ice cover have been documented for growth rate, food intake and energy loss (Finstad *et al.*, 2004; Finstad & Forseth, 2006).

Despite, the fact that the Atlantic salmon parr remained nocturnal throughout the study, the level of day activity was higher as the amount of ice increased. In particular, more activity was observed during the first tracking survey after dawn. This indicates that the role of surface ice was most important in lengthening the hours of darkness under ice. The results from this study demonstrate that while there still was enough light to suppress the day activity in general, the increased amount of ice probably reduced the amount of light so that it facilitates some activity even during the daytime and will therefore lengthen the time available for fish to use for feeding. Accumulation of snow on top of surface ice causes additional reduction of light in nature. This, in turn, may result in even higher activity level during the daylight. As winter has been shown to be energetically taxing for juvenile Atlantic salmon (Berg & Bremset, 1998; Cunjak *et al.*, 1998), the presence of surface ice will allow fish to better maintain a positive energy budget during winter. Finstad *et al.* (2004) came into similar conclusion based on energetical modelling work using simulated ice cover.

It is also notable that the activity level increased significantly during the flood tracking in spring. This is not surprising as the basal metabolism and therefore demand for energy of fish was probably elevated due to increasing amount of light (Wendelaar Bonga, 1993) and increase and fluctuation in water temperature. As the day activity still was suppressed, however, decreased time was available for fish to gain nutrition due to increasing day length, which further necessitated higher activity level during the night.

In addition to elevated activity level during the night, other changes also took place in parr behaviour in early spring. Whereas the level of homing

and mean maximum movement distances during the diel cycle showed that Atlantic salmon parr are very sedentary during winter, the movements were significantly longer during the flood tracking. This lends further support for increased demand for energy since the source of the most numerous dietary object found in the experimental channels (larval Simuliidae) is a patchily located resource (Zahar, 1951) and thus the longer movements were probably required in order to access more nutrition. Additionally, preparation for smolt migration might cause changes in behaviour and energetic needs. For example, the decrease in homing behaviour is a likely consequence of the smoltification process that causes fish to abandon sedentary behaviour. The increase of discharge in an unregulated natural stream in spring is typically larger than the 2.5 to 2.8-fold increase in the current study. Thus, the habitat suitability may be altered during high flows and the need to find locations with better shelter may also cause additional movements in nature in spring.

In summary, the results from this study showed that juvenile Atlantic salmon are able to use habitats with small and moderate substratum sizes if these areas are: (1) under full surface ice cover and if (2) stream discharge is relatively low. Large substrata, however, provide the preferred winter cover regardless of other physical conditions. If the home territory is initially situated within large substratum cover and no resource competition is apparent, high site fidelity can be expected regardless of ice conditions. Albeit the Atlantic salmon parr were primarily night active, daytime activity increased when surface ice was present. Furthermore, the homing behaviour and the extent of diel movements of Atlantic salmon parr were altered when spring-like conditions were simulated. These are the first results, as far as is known, to describe juvenile Atlantic salmon behaviour at the micro-scale under conditions of natural, full ice cover. As the sample size was low in the current study, more research with better replication is needed in naturally ice covered streams to improve understanding of the apparently complex mechanisms that regulate behaviour and habitat use of juvenile Atlantic salmon during winter.

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