

## DOES ICE MATTER? SITE FIDELITY AND MOVEMENTS BY ATLANTIC SALMON (*Salmo salar* L.) PARR DURING WINTER IN A SUBSTRATE ENHANCED RIVER REACH

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### ABSTRACT

In-stream habitat enhancement is a common remedial action in rivers where degradation/lack of suitable fish habitat can be diagnosed. However, post-project monitoring to assess the response of the biota to modification is rare particularly during winter. We conducted *in situ* monitoring during the winters of 2004–2006 in the regulated Dalåa River, central Norway, in order to determine if winter habitat requirements of Atlantic salmon (*Salmo salar* L.) parr were realized in an enhanced (substrate and mesohabitat modification) reach. In total, 140 parr were marked with passive integrated transponder (PIT) tags and the fish were followed by carrying out active tracking surveys under variable ice conditions throughout the winter. Highest emigration (44%) occurred before ice formation started. Emigration was reduced after ice formed and was largely offset by parr re-entering the enhanced area. Dispersal into the non-enhanced, small substrate control area was observed only when the study reach was ice covered, and no parr were subsequently encountered in the control section after ice had melted. In the enhanced area, declining water temperature and surface ice conditions did not affect the spatial distribution of the resident salmon parr at the studied scale. Areas with ‘solid’ anchor ice precluded access for salmon parr whilst areas with ‘patchy’ anchor were used throughout the winter. Our results indicate that surface ice creates conditions that allow salmon parr to use stream habitats that otherwise provide only a limited amount of in-stream cover. Ice processes should be taken into consideration when habitat enhancement projects are carried out and subsequently assessed for effectiveness. Copyright © 2008 John Wiley & Sons, Ltd.

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### INTRODUCTION

Atlantic salmon (*Salmo salar* L.) stocks have experienced an overall decline in recruitment for the past few decades in many rivers draining into the North Atlantic. Thus, many populations are realizing reduced reproductive capacity (ICES, 2007). An increasing public interest to restore salmon stocks to a sustainable level has resulted in the expansion of freshwater habitat improvement work (referred as restoration, rehabilitation and/or habitat enhancement; e.g. Yrjänä *et al.*, 2002; Pretty *et al.*, 2003). Enhancements are also carried out in many regulated rivers as obligatory mitigation to compensate for habitat loss. The success of improvement projects is typically evaluated using electrofishing surveys (e.g. Arnekleiv *et al.*, 2002; Glen, 2002) and/or with other measures to monitor the whole ecosystem response (e.g. Muotka and Laasonen, 2002; O’Grady *et al.*, 2002). Typically such accountability is done during open-water conditions (i.e. spring, summer and/or autumn). However, the winter habitats of stream salmonids have been shown to differ from those used during warm water conditions (Heggenes and Dokk, 2001; Mäki-Petäys *et al.*, 2004) possibly due to the need to find refugia from predation or ice (Heggenes *et al.*, 1993; Valdimarsson and Metcalfe, 1998). In particular, a shift into deep, low velocity habitats is often

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reported in association with the use of coarse substrate material (Saunders and Gee, 1964; Heggenes and Dokk, 2001; Mäki-Petäys *et al.*, 2004). Furthermore, the formation of both sub-surface ice (i.e. frazil and anchor ice; *sensu* Prowse, 1994) and partial surface ice has been shown to affect the habitat use of stream salmonids and thus change their spatial distribution (Brown, 1999; Whalen *et al.*, 1999). Typically, the changes caused by sub-surface ice are described in a negative context where fish are precluded from their pre-ice habitats due to altered physical conditions and are forced to move to new locations by necessity rather than by choice (Brown and Mackay, 1995; Whalen *et al.*, 1999; Stickler *et al.*, 2007). By contrast, information on the spatial distribution and habitat requirements of stream salmonids under full surface ice cover is scarce (Huusko *et al.*, 2007).

If the habitat requirements differ between the ice-affected period and open water conditions, we suggest that there might be consequences when evaluating the success of habitat improvement projects during one season alone. To ensure that suitable habitat is provided throughout the year, adequate monitoring is necessary during all seasons. The main limitation of such an approach has been the lack of suitable monitoring methods after ice cover has formed. Fortunately, suitable methods now exist that enable effective winter habitat monitoring. For example, Carlson and Quinn (2005) examined the effectiveness of in-stream habitat structures (V-weirs) under ice by using video surveillance. Recent improvements in passive integrated transponder (PIT) technology have also proven valuable to effectively monitor fish behaviour and habitat selection even under severe winter conditions (Roussel *et al.*, 2004; Linnansaari *et al.*, 2007).

In the present study we followed individually tagged Atlantic salmon parr throughout autumn and winter in the river Dalåa, Norway, where a habitat enhancement project had previously been carried out. Our first objective was to evaluate if winter site fidelity of salmon parr was higher in a manipulated river reach with heterogeneous substrate composition relative to an unmanipulated (control) reach, and to determine the timing of possible emigration. Our second objective was to examine the spatial distribution of salmon parr during winter in relation to water temperature and ice; specifically we investigated (1) if there would be emigration in the autumn from sections dominated by fast velocity habitats into sections dominated by slow velocity habitats, (2) if the salmon parr would be precluded from the areas with anchor ice deposition and (3) if the build-up, presence or break-up of surface ice would explain movements between different habitat types.

## MATERIALS AND METHODS

### *River Dalåa habitat enhancement project*

The study was carried out in the river Dalåa (situated in Meråker, 100 km east of Trondheim, central Norway, 63°23'31"N; 11°47'24"E), a fourth-order tributary to the river Stjørdalselva (Figure 1A). The Dalåa River system has been subject to streamflow regulation associated with hydroelectric power generation since 1994, which has reduced the mean annual discharge by 87%. In general, the winter discharge regime has been altered from pre-regulation flows of 0.5–2.0 to 0.2–0.44 m<sup>3</sup> s<sup>-1</sup> after regulation (Arnekleiv *et al.*, 2002). Brown trout (*Salmo trutta* L.) is the only native fish species in the river Dalåa. Atlantic salmon can only ascend 57 km to Meråker where the Nustadfoss dam restricts wild salmon access upstream (Figure 1A). Despite the discharge regulation, the river is used as nursery and rearing habitat for stocked Atlantic salmon as a formal compensation. The annual stocking of salmon takes place in August/September using adipose fin-clipped age 0+ salmon of river Stjørdalselva strain (i.e. using first generation progeny of indigenous wild adults). In the study area (see below), 0+ salmon were stocked to a density of 2.5–3.0 individuals m<sup>-2</sup>.

As a part of the compensation program for the hydropower generation, habitat enhancement project was carried out in two reaches of river Dalåa in 1993. The two selected reaches were considered to contribute very little to juvenile salmon production under the regulated discharge due to very low minimum flows, small substrate size and a general lack of in-stream cover. Thus, the objective of the habitat enhancement project was to modify these reaches into usable areas for juvenile Atlantic salmon production (Arnekleiv *et al.*, 2006). To accomplish the goal, physical alterations were carried out that included channel re-configuration to create different mesohabitats, and modification of the substrate material from small-sized, embedded gravel (<5 cm) to either blast-rock (5–20 cm) or cobble (10–30 cm). Since 1994, the success of the enhancement in each manipulated area has been annually

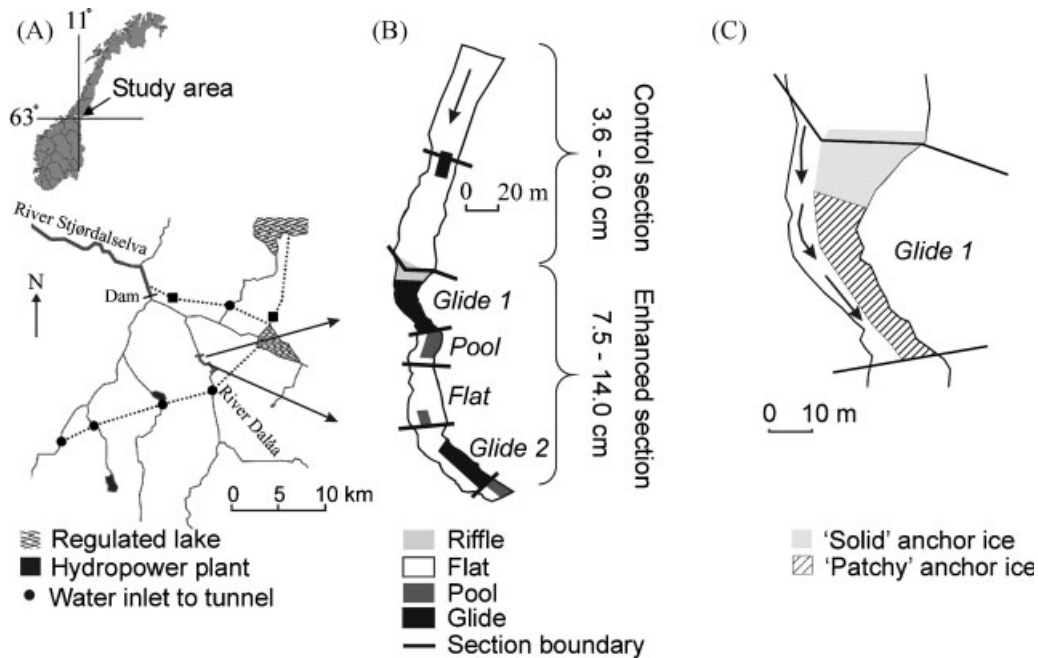


Figure 1. (A) Map of the river Dalåa system indicating the location of the Øyvollen reach in central Norway. The dam (Nustadfoss) restricts further upstream migration of adult salmon. (B) A schematic representation of the Øyvollen experimental reach and the location of control and enhanced study sections with different mesohabitats and the interquartile range of the substrate size in each section. The enhanced section is further divided into four sub-sections (italicized names) based on the descriptive mesohabitat in each section. Note that the section boundaries (cross-sectional lines) are for illustrative purposes only and are not barriers to fish movement. (C) An approximate representation of the ice formation processes in the Glide 1 section where the sub-surface ice production primarily occurred. Arrows refer to direction of streamflow

evaluated during open water conditions by measuring the relative increase in fish density in comparison to an adjacent (upstream), unmanipulated control reach (Arnekleiv *et al.*, unpublished work).

### Study area

To assess the effects of cold water temperature and ice on the suitability of the enhanced areas for juvenile salmon production, one of the enhanced reaches (Øyvollen, Figure 1B) was chosen for study. The site fidelity and spatial distribution of individually PIT-tagged salmon parr was studied over two winter seasons (2004–2005 and 2005–2006). Prior to the enhancement (1993), the reach was divided into two sections: an upstream control section where no manipulation was done (Control section, Figure 1B), and a downstream experimental section where the substrate size and stream configuration were altered (Enhanced section, Figure 1B). For the post-enhancement monitoring (i.e. long-term annual electrofishing surveys), the enhanced section was further divided into smaller (sub)sections based on their mesohabitat designation (Arnekleiv *et al.*, 2002). For consistency with the previous monitoring data, the same sections were used in the present study but the mesohabitats were determined using the classification system of Borsanyi *et al.* (2004) with some further modifications. Thus, all the habitats with broken surface pattern were termed as 'riffle'; the habitats with smooth surface pattern were termed as 'glide' (surface velocity  $>0.5 \text{ m s}^{-1}$ ), 'flat' (surface velocity  $<0.5 \text{ m s}^{-1}$ , depth  $<0.4 \text{ m}$ ) or 'pool' (surface velocity  $<0.5 \text{ m s}^{-1}$ , depth  $>0.4 \text{ m}$ ). The sections within the enhanced area were then named based on the mesohabitat that best characterized each subsection (from Glide 1 to Glide 2; Figure 1B). A general description of the microhabitat of the study sections is shown in Table I.

To confirm that the substrate size was different between the enhanced and control sections (11 years after the original manipulation), pebble counts were made along randomly assigned transects in the control ( $N=2$ ) and enhanced ( $N=6$ ) sections. The longest intermediate axis ( $B$ -axis) was measured from all the pebbles that were

Table I. Physical microhabitat features\* and the number of salmon parr PIT-tagged in different sections of the Øyvollen study reach in 2004 and 2005

	Depth (cm)	Velocity (cm s <sup>-1</sup> )	Embeddedness <sup>†</sup>	Parr tagged	
				2004	2005
Control	19 (10–35)	22 (0–36)	3.3 <sup>c</sup>	0	17
Glide 1	26 (10–38)	42 (35–65)	2.2 <sup>a</sup>	26 <sup>‡</sup>	26
Pool	40 (20–55)	21 (0–33)	3.3 <sup>c</sup>	0	8
Flat	25 (15–44)	24 (9–44)	2.9 <sup>b</sup>	0	14
Glide 2	30 (24–41)	32 (9–44)	2.8 <sup>b</sup>	24	25
<i>N</i> (total)				50	90

Values shown for depth and water velocity are averages of 8–12 measurements; bracketed values represent the range. Water velocity was measured at the  $0.6 \times$  depth. The index of average embeddedness of the sections was measured using the classification system of Eastman (2004). Numbers sharing the same superscript letter were not significantly different ( $p > 0.05$ ).

\*Values of microhabitat variables were measured at the discharge of  $0.34 \text{ m}^3 \text{ s}^{-1}$ .

<sup>†</sup>1 = no embeddedness; 2 = low embeddedness; 3 = medium embeddedness.

<sup>‡</sup>Twenty-two fish were accidentally released into the section during a rapid increase in discharge during the night following the tagging. Thus, these fish were not randomly distributed into the site but instead, a bulk release occurred.

directly below a transect line extended between the stream banks and perpendicular to the flow. As expected, mean particle size was significantly larger in the enhanced section, but was similar among transects within each section (ANOVA,  $p < 0.001$ ; Tamhane's test,  $p < 0.001$  between the control and enhanced area,  $p > 0.99$  within both areas; Figure 2). In addition, substrate embeddedness was evaluated using the methods described in Eastman (2004) (Table I).

Surface ice formed across the entire study reach during both winters of the study. Sub-surface ice was produced prior to full surface ice conditions, but was largely restricted to the uppermost section of the enhanced area at the head of Glide 1 (Figure 1C). Specifically, as the freeze-up process was initiated, the areas to the left of midstream (looking downstream) in the Glide 1 were affected by anchor ice and consequently the stream flow was concentrated to the right side of the stream (Figure 1C). Anchor ice production/deposition was greatest at the head of Glide 1 section where a solid mass of anchor ice persisted even after surface ice had formed. By contrast, the middle and lowermost portions of Glide 1 were only temporarily affected by anchor ice and the ice deposition was patchy (Figure 1C) and unconsolidated.

### Fish collection and tagging

Atlantic salmon parr were captured by electrofishing (Norwegian Geomega FA3 backpack unit) on 27 September 2004 (water temperature  $5.8^\circ\text{C}$ ) and 31 August 2005 (water temperature  $11.5^\circ\text{C}$ ). The fish were individually

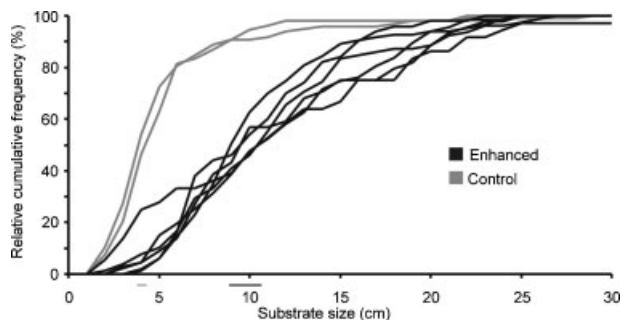


Figure 2. The relative (%) cumulative frequency distribution of substrate particles (longest intermediate axis) in the enhanced and control sections of the Øyvollen reach. The range of median particle sizes ( $d_{50}$ ) for transects in the two reaches is depicted below the x-axis

anaesthetized with clove oil (40 ppm, ethanol as carrier, Hoskonen and Pirhonen, 2004), measured (total length, mm) and weighed (0.1 g accuracy in 2004; 0.5 g accuracy in 2005). Maturity (i.e. percentage that were precocious males) was determined in September 2004 (44%), but could not be evaluated in 2005 because of the earlier tagging date (no reliable signs of maturity were obvious). As per the recommendations of Roussel *et al.* (2000), only salmon parr >84 mm (fork length,  $L_F$ ) were used for PIT-tagging; average weight and total length ( $\pm$ SD) of the tagged fish was  $14.1 \pm 4.5$  g and  $125 \pm 11$  mm, respectively, in 2004 ( $N=50$ ), and  $13.0 \pm 4.0$  g and  $114 \pm 13$  mm in 2005 ( $N=90$ ). After measuring, a 23 mm (0.6 g in air) Texas Instruments PIT-tag (RI-TRP-WRHP) was surgically inserted into the peritoneal cavity and the incision was closed with a single suture (Monosof black nylon, 6-0 taper, C-1 cutting needle). In addition to 23 mm tags, 50 salmon parr, all larger than 97 mm ( $L_F$ ), were tagged with a 32 mm PIT-tag (RI-TRP- WR2B; 0.8 g in air) in 2005. The tag represented  $4.6 \pm 1.2\%$  and  $6.0 \pm 1.4\%$  (mean  $\pm$  SD) of the body weight of fish in 2004 and 2005, respectively.

Tagged fish were allowed to recover overnight in substrate filled live-boxes situated in same sections of the stream where they were captured (Table I). In September 2004, a rapid increase in discharge during the night following the tagging caused an accidental bulk release of 22 of the 26 fish that had been captured in the Glide 1 site; the remaining four fish tagged in Glide 1 and all the 24 fish tagged in Glide 2 were evenly distributed to the corresponding sections the following day. In August 2005, all the fish ( $N=90$ ) were released to their original home sections 4.5 h after the tagging (Table I).

### Fish tracking

The daytime distribution of parr was determined by active tracking using a Texas Instruments Series 2000 portable antenna system (Roussel *et al.*, 2000; with modifications after Linnansaari *et al.*, 2007) on six occasions in 2004–2005 and on five occasions in 2005–2006 (Table II). The streambed was scanned for tags from bank to bank by proceeding in an upstream direction. During the months of extensive ice cover and snow accumulation, excess snow was removed, prior to scanning, to facilitate the detection of tags (detection distance  $\sim$ 70 and  $\sim$ 80 cm for 23- and 32 mm tags, respectively, when oriented with their cylindrical axis parallel to the plane of the antenna coil inductor loop). When a tagged fish was found, the 'blind-spot method' was used to determine the exact fish location (accuracy  $10.9 \pm 1.4$  cm; mean  $\pm$  SE; Linnansaari *et al.*, 2007). These locations were marked with a lead weight and a numbered float. After the tracking survey, exact fish positions ( $x$  and  $y$  coordinates) and the spatial distribution of ice were recorded with a total station (Leica TC307), except for one occasion (9 December 2004) when the ice distribution was reconstructed based on photographs (Table II).

Table II. Dates of active fish tracking surveys and the prevailing ice conditions (percentage of stream channel with ice) and water temperature in the Øyvollen reach of the Dalåa River during the winters of 2004/2005 and 2005/2006

Date	Ice conditions	Water temperature (°C)
4 November 2004	No ice	1.7
22 November 2004	100%	0.1
9 December 2004*	42% (71%) <sup>†</sup>	0.6
14 December 2004	31% (42%)	0.9
18 February 2005	100%	0.1
20 April 2005	No ice	1.5
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7 September 2005	No ice	12.5
2 November 2005	No ice	6.0
8 February 2006	95% (98%)	0.1
7 April 2006	100%	0.1
3 May 2006	No ice	3.0

Ice conditions for the control section are shown in parentheses if they were different from the enhanced section. The dashed horizontal line separates data for the two study winters.

\*Exact coordinates for fish locations could not be recorded.

<sup>†</sup>Amount of ice based on photographic images instead of exact coordinates.

The shallow bathymetry and the general lack of overhanging vegetation, logjams and undercut banks allowed efficient tracking to be carried out in the study area. However, examination of the data suggested that some tagged parr had been missed due to human error wherein snow masked the actual edges of the stream. To take such incidences into account, we used an approach similar to Steingrímsson and Grant (2003), with some further constraints. Thus, if a parr was not found during tracking event  $N$ , but was observed on tracking events  $N - 1$  and  $N + 1$ , and the fish had remained within a square metre, the fish was assumed to have been in the study site but missed during the tracking event  $N$ ; such situations represented 5% of the data.

#### *Data analysis and statistical procedures*

Site fidelity was calculated separately for the enhancement and control sections. Tagged salmon parr that were not detected during the first tracking survey, and were not encountered during any subsequent trackings, were omitted from the site fidelity analysis. Site fidelity could not be calculated in the control section during the 2004–2005 season because no parr were tagged in the area. Immigrants were defined as parr that entered a section other than their original tagging section (i.e. moved from control to enhanced section or vice versa). In addition, parr that were absent from the study site but returned at a later tracking occasion were also considered immigrants when re-encountered. Within-site mortalities were documented during the last tracking occasion in spring when the substrate could be examined to ensure the fate of the tagged fish. The timing of the observed mortality was assigned to a tracking occasion after which no further movements were observed for each dead salmon parr. Since the level of within-site mortality was negligible (see Results Section), emigration is defined herein to represent all fish loss. Because the time interval between tracking surveys was not constant, the instantaneous daily loss rate was calculated as

$$L = \frac{-\ln(n_t - n_0)}{\Delta t}, \quad (1)$$

where  $n_0$  and  $n_t$  are the number of fish observed alive at the start and end of the period of interest, respectively, and  $\Delta t$  is the duration of the period in days (Ricker, 1975).

To determine if the condition of the parr or the burden of the tag weight contributed to the presence/absence of salmon parr by the spring, the mean condition factor ( $K$ ; Ricker, 1975) and tag-to-body weight ratio were compared between the parr that were found in spring and those that were absent (but were observed at least once during the study).

Movement was measured as the linear displacement distance between the daytime positions of each parr between two consecutive tracking occasions. Winter home ranges were calculated for the winter resident population (fish that were still present during the last tracking survey in spring) using the minimum convex polygon method of the Hawth's Analysis Tools extension for ArcMap 9.0 (Beyer, 2004). As the home ranges calculated using this method may include non-wetted areas in locations where the stream meanders, the areas of home range that were assumed on land were subtracted from the final home range.

Recognizing that the proportions (and the spatial distribution) of different mesohabitats change as a function of discharge fluctuation, the analysis of the spatial distribution of salmon parr within the study area was performed using predetermined 'home' sections (i.e. control section and Glide 1–Glide 2; Figure 1B). The changes in spatial distribution of parr were examined by calculating the frequency of occurrence of parr within these sections during each tracking survey. The similarity of these frequency distributions between different tracking surveys was compared using a Kolmogorov–Smirnov two-sample test.

The log-likelihood ratio test was used for all comparisons that included proportions (e.g. parr emigration between different subsections of enhanced area). However,  $2 \times 2$  tables were analysed using Fisher exact test (e.g. effects of maturity on emigration). If multiple comparisons were carried out following the log-likelihood test, the proportions were arcsine transformed as per recommendations by Zar (1999) and then Tukey-type *post hoc* comparisons were performed. The Mann–Whitney test was used where groups to be compared had similar (but non-normal) distributions and homogeneous variances (e.g. comparisons of condition factors and tag-to-body weight ratios between emigrant and resident fish, and overwinter displacement distances between the 2 years). The

likelihood of mature parr emigration relative to non-mature fish was quantified using odds-ratios; significance of the ratio was based on the Mantel–Haenszel statistic.

## RESULTS

### Site fidelity

During the first winter of the study (2004/2005), 26% of the tagged parr were never encountered over the course of the study. The majority (69%) of this loss occurred in the Glide 1 where there was an accidental bulk release of the tagged parr. Also, the proportion of precocious fish was higher in Glide 1 (53.8%) than in Glide 2 (33.3%). Indeed, there was a very strong association between parr maturity and their absence from the study area ( $p < 0.001$ ). The likelihood that a mature fish was absent from the study area was 13 times higher than that of immature parr ( $p = 0.002$ ). The effects of maturity could not be assessed during the second winter of the study (2005/2006) due to the earlier tagging date. However, the potential fish loss due to capturing and tagging was accounted for in 2005/2006 by carrying out an active tracking survey a week after the fish were released (based on the assumption that any capture/tagging effect was immediate). There was a significant difference in fidelity between the enhanced and control sections with relatively little (4%) emigration from the enhanced section compared with 41% emigration from the control section ( $p < 0.001$ ) before the first tracking. The number of tagged parr found in each section during the first tracking was then used as the initial population size for subsequent analysis (Figure 3).

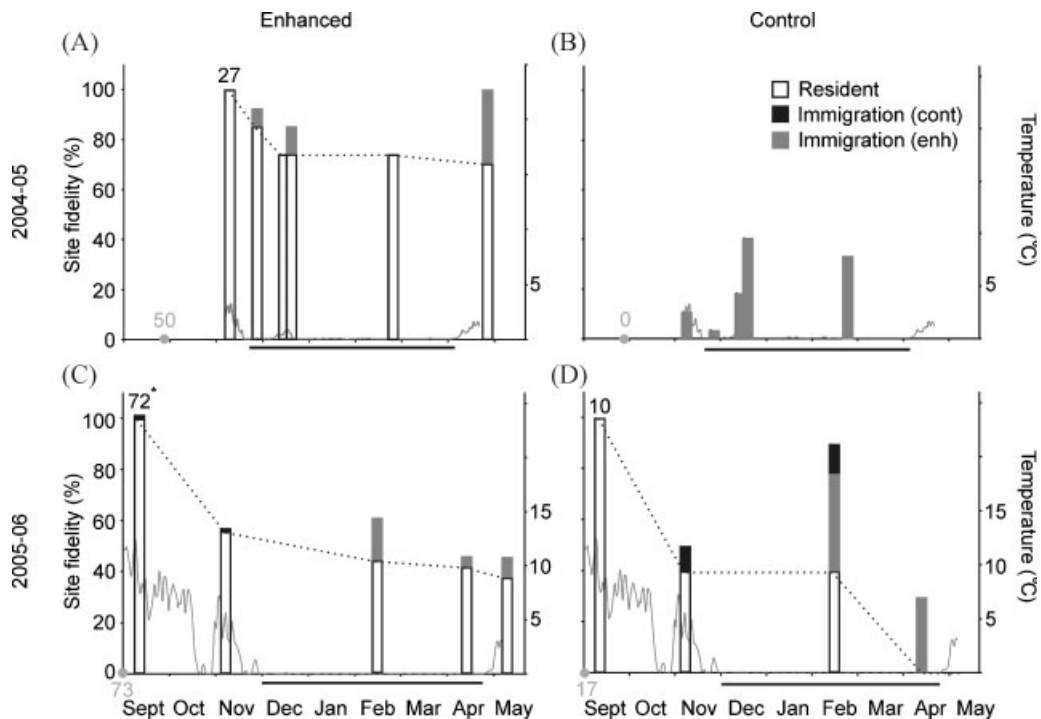


Figure 3. Percentage of tagged Atlantic salmon parr located in the enhanced (panels A and C) and control sections (panels B and D) of Øyvollen reach (primary y-axis) and the prevailing water temperature (grey line; secondary y-axis) during the two winters of study. The date and number of parr tagged are indicated in grey on the x-axis. The number of tagged salmon parr encountered during the first tracking survey in each section is shown immediately above the bar. The white bars connected by the dashed line represent the percentage of salmon parr that remained within their original tagging section (i.e. enhanced or control); grey and black bars represent immigration into section by parr originally tagged in the enhanced section and the control section, respectively. The period dominated by surface ice is depicted by the horizontal black line below the x-axis. In panel B, the proportion of immigrants is calculated based on the initial number of parr ( $N = 27$ ) from the enhanced section (panel A).\*

Two of the salmon parr found in September 2005 were tagged the previous year (2004)

Site fidelity prior to ice formation (between September and November) could be assessed only during the 2005/2006 because there were too few surveys the previous year (Table II). The highest emigration from the enhanced section (44.4%; instantaneous daily loss rate 0.010) occurred during this period coincident with a decline in water temperature (Figure 3C). However, a large portion (50%) of these fish returned at least periodically, to either the enhanced or the control section later in the winter (Figure 3C). Emigration was less pronounced during the ice-affected period of winter in the enhanced reach (Figure 3A and C). Within a winter season (November to early May), fish loss did not differ between tracking occasions in the enhanced section ( $p = 0.10$  in 2004–2005 and  $p = 0.35$  in 2005–2006) or between the two winters ( $p = 0.79$ ), and the combined fish loss during winter was 32.3%. The instantaneous daily loss rate was 0.002 during both winters. In addition, the fish loss in the enhanced section was offset by immigration of tagged individuals that were located in the control section or outside the study area during the first tracking survey. Therefore, the absolute number of PIT-tagged individuals was the same in November and April in 2004–2005 (i.e. 0% fish loss; Figure 3A) even though the composition of the tagged population was different. The number of parr decreased by 19.5% in 2005/2006 during the same time period (i.e. November–May; Figure 3C). Overall, emigration occurred from all the mesohabitats within the enhanced area during winter. The proportional fish loss over winter was similar between the Glides 1 and 2 during 2004–2005 (where the tagging occurred;  $p = 0.27$ ) and between all the areas within the enhanced section in 2005–2006 ( $p = 0.92$ ).

Similar to the enhanced section, there was an abrupt emigration of parr from the control section in 2005 as the water temperature declined but before ice formed (Figures 3D and 4). In contrast to the enhanced area, fish loss was total (100%) by spring in the control area such that no parr were remaining in the section during the tracking survey carried out after ice break-up (April 2005 and May 2006; Figure 3B and D). As a result, winter site fidelity was significantly lower in control area in comparison with the enhanced area ( $p < 0.001$ ).

Condition factor or tag-to-body weight ratio did not significantly differ between the parr that remained in the study reach in spring and those that had emigrated ( $p > 0.05$  for both variables and both seasons). The (actual) observed within-site mortality was low (2% of the tagged fish).

#### Changes in spatial distribution

In addition to the patterns of salmon parr emigration, the spatial distribution of the winter resident fish was examined in relation to prevailing physical conditions in the study reach. One of the anticipated changes was a

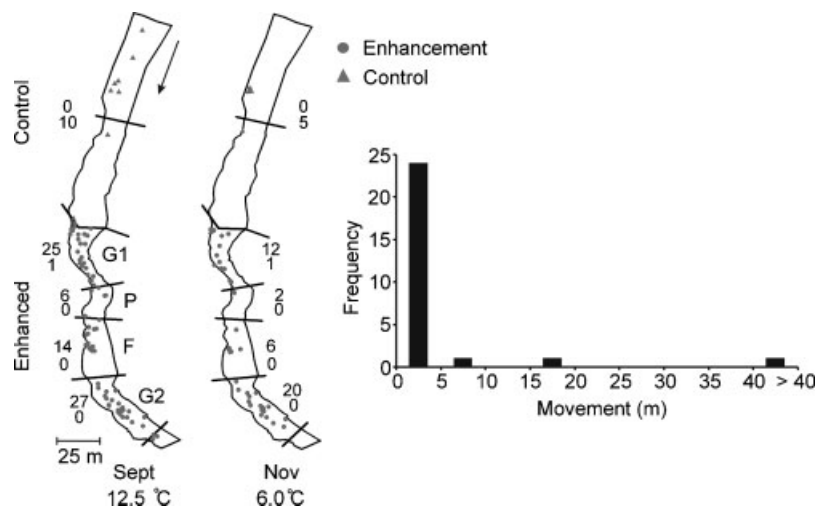


Figure 4. The spatial distribution of PIT-tagged Atlantic salmon parr in the control and enhanced sections of the study area during September and November of 2005 and the frequency distribution of the movement distances of the resident parr between the two consecutive trackings. The number of parr found in each sub-section is shown separately for the parr originally tagged in the enhanced (upper number) and control section (lower number). G1 = Glide 1, P = Pool, F = Flat and G2 = Glide 2. Arrow refers to direction of streamflow



potential shift into deep mesohabitats as the water temperature declined below 10°C, which could only be examined during the 2005–2006 season (September–November). Even though significant emigration occurred during this period (see above), the extent of movements by individual salmon parr residing within the study site was minimal (Figure 4; median displacement 1.1 m) and the spatial distribution for the resident (i.e. non-emigrant) fish remained unaltered ( $p = 1.0$ ; Figure 4). Therefore, instead of attracting salmon parr, there was a net emigration from the deepest (pool) section from September to November (Figure 4).

Anchor ice formation did not lead to displacement of tagged salmon parr during the first winter of study (2004–2005) because no tagged parr were resident in the areas where the subsurface ice formed. During 2005–2006, a number of tagged salmon parr were already resident in the study section where anchor ice subsequently formed in December (Figure 5). When salmon parr distribution was re-examined in February 2006, no tagged parr were found in the section where a mass of solid anchor ice had formed that extended from the substrate to the surface (Figure 5). These parr relocated to the control section, beyond the study site, or to other areas in Glide 1 where no anchor ice formed. It was notable that salmon parr were able to reside throughout the winter in the section where patchy, unconsolidated anchor ice formed (Figure 5).

The effect of build-up of surface ice on redistribution of tagged parr was best examined in November 2004 when an exceptionally rapid, complete freeze-up of the study area occurred within four days (15–18 November). The spatial distribution of resident fish during the period of surface ice formation was largely unchanged ( $p = 0.26$ ; Figure 6A and B), and the vast majority of movements were <5 m (median displacement 2.8 m; Figure 6). In the longer term, the persistence of a surface ice cover facilitated the redistribution of tagged parr into the control section during both study winters. In 2004–2005, parr had started to immigrate into the control section already by early December (Figure 3B) but were only using areas beneath surface ice. The same pattern was apparent on 14 December when parr used surface (border) ice as overhead cover in the control section but not in the enhanced section (Figure 6C). An increasing number of tagged salmon parr were located in the control section in mid-winter during both study years when full surface ice was present (Figure 7A). The majority (85%) of the parr entering the control section originated from the Glide 1 site with the remainder originating from the Flat or Glide 2 sites. No other directed movement patterns were apparent in mid-winter within the study area. Thus, the majority of the resident parr remained within the sections where they were initially tagged and the overall change in the spatial distribution of parr between early and mid-winter was non-significant ( $p > 0.05$  for both years). Due to the immigration into the control section, there was a higher frequency of longer distance movements (median displacement 4.2 m; Figure 7) in comparison with the autumn and early winter. The majority (73%) of movements >10 m were associated with those parr entering the control section. This immigration continued until April 2006 when the study reach was still totally ice covered.

Ice break-up also affected the spatial distribution of salmon parr in the control section. Following the ice run and subsequent spring flood, no salmon parr were found in the control section during either of the study years (Figure 7B). Fish that had overwintered in the control section were either not detected or had returned to their initial

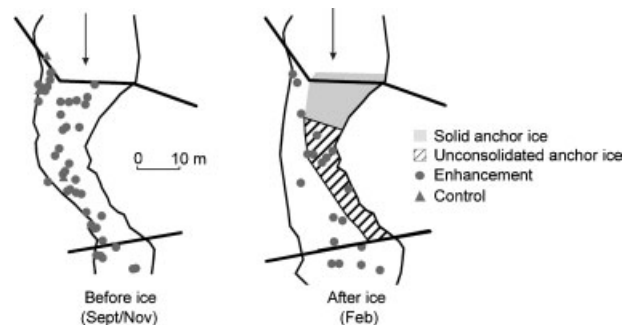


Figure 5. The spatial distribution of PIT-tagged Atlantic salmon parr in Glide 1 of the enhanced section of Øyvollen reach prior to (September/November) and after (February) subsurface ice formation in 2005/2006. Parr originally tagged in the enhanced and control section are distinguished by different symbols. The border between solid and unconsolidated (patchy) anchor ice is an approximation. Note, that the Glide 1 was almost completely covered with surface ice in February beneath which the anchor ice prevailed; for the ease of interpretation, surface ice is not shown in the figure. Arrows refer to direction of streamflow

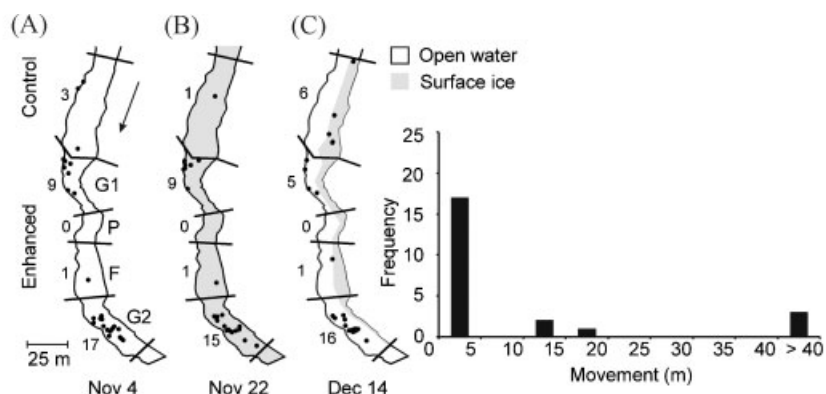


Figure 6. The spatial distribution of PIT-tagged Atlantic salmon parr in the control and enhanced sections of the study area (A) prior to ice formation (4 November), (B) with full surface ice cover (22 November) and (C) with partial ice cover (14 December) in 2004, and the frequency distribution of the movement distances of the resident salmon parr between the two November trackings in the study area. The number of tagged parr found in each sub-section is also shown. Arrow refers to direction of streamflow. Note that only the area consistently searched for tags is shown (i.e. uppermost areas of the control section are excluded). G1 = Glide 1, P = Pool, F = Flat and G2 = Glide 2

tagging section. In fact, all the movements >10 m between mid-winter and spring (Figure 7) were attributed to those parr returning from the control section to within three metres of their initial (autumn) location. Ice break-up did not significantly alter the spatial distribution of parr in the enhanced section such that parr distribution in spring was similar to the ice-covered period for both years ( $p > 0.05$ ).

Displacement over the winter (November to April/May) was similar between years ( $p = 0.29$ ) with a median displacement of 3.4 m ( $N = 55$ ). The majority (91%) of the winter resident salmon parr were found in the same sections where they were originally tagged. There was no overall direction in winter displacement (60% upstream and 40% downstream) nor was there a correlation between initial fish length and displacement distance ( $r_s = 0.001$ ,  $p = 0.99$ ). Median winter home range was estimated to be 14.1 m<sup>2</sup> (no difference between the years,  $p = 0.81$ ) with an interquartile range from 8.2 to 52.6 m<sup>2</sup>.

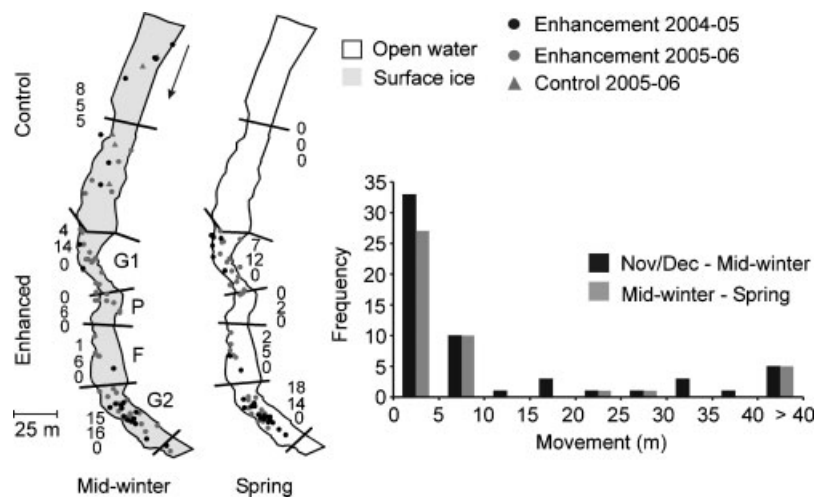


Figure 7. The spatial distribution of PIT-tagged Atlantic salmon parr in the control and enhanced sections of the study area during complete mid-winter surface ice cover (February) and in spring after ice break-up (April/May). The number of parr found in each sub-section is shown separately for the parr originally tagged in the enhanced (uppermost number for 2004/2005, middle number for 2005/2006) and control section (lowermost number for 2005/2006). Also, the frequency distribution of the inter-seasonal movement distances of the resident parr (data pooled for the 2 years) is shown. Arrow refers to direction of streamflow. G1 = Glide 1, P = Pool, F = Flat and G2 = Glide 2

## DISCUSSION

In this study the effects of declining water temperature and subsequent formation of ice on Atlantic salmon parr distribution was contrasted between two very different stream sections. The results indicated that the enhanced section with relatively large substrate sizes supported a juvenile salmon population at all times during the autumn, winter and early part of the spring regardless of the ice conditions. By contrast, the control section where only a limited amount of in-stream cover was present, failed to provide suitable parr habitat during all periods of the study.

The suitability of the control section as winter habitat for salmon parr was affected by the presence of surface ice. Most salmon parr emigrated from the control section between September and November and only a few individuals used the control section when the water temperature had declined close to 0°C but no ice had yet formed. Tracking surveys carried out in the control section approximately a month after ice had started to form showed that salmon parr started to immigrate to the site and were using the areas beneath border ice. By mid-winter, the entire control section was being used by salmon parr during both study years, and many of the immigrant parr were originally resident from outside the control section. Thus, surface ice seemed to play an important role by providing increased amount of overhead cover in the control section and thereby increased the amount of suitable habitat during winter.

Why did the salmon parr leave the enhanced section and enter the control area in winter? Most likely, the high density of juvenile salmon in the enhanced section contributed to the emigration. The majority of tagged parr that entered the control section during winter originated from the adjacent Glide 1 area where mean density in the autumn was 25 times greater in comparison with the control section during the 2005–2006 season (111.9 vs. 4.4 individuals 100 m<sup>-2</sup>; all age classes; Arnekleiv *et al.*, unpublished work; no density data available for 2004). In addition, solid anchor ice formation at the head of Glide 1 site further exacerbated the situation by precluding parr from using some portions of the enhanced section. Intra-specific competition for daytime refuges has been shown to be intense in winter and sharing of sheltering locations is uncommon (Harwood *et al.*, 2002). Therefore, it may have been profitable to migrate into the control area where only a few conspecifics were present and no resource competition (for shelters) was apparent. It has also been shown that shifting between sections with different substrate size in winter may benefit stream salmonids by allowing better growth (Linnansaari *et al.*, 2008) or survival (Elsø and Greenberg, 2001).

No tagged salmon parr were encountered in the control section in the spring tracking during either study year. Physical disturbance due to ice break-up and the subsequent increased discharge may have induced emigration from the control section where the small substrate did not provide any cover against the demanding conditions. Linnansaari *et al.* (2008) simulated spring-like conditions in an artificial stream channels and noted salmon parr moving from small substrate sections into large substrate sections when surface ice was removed and the discharge increased. It was interesting to note that the salmon parr that returned to the enhanced section were consistently relocated in very close proximity (even within <10 cm) to their initial home stone. Saunders and Gee (1964) and Cunjak and Randall (1993) observed similar homing behaviour by Atlantic salmon parr. It appears, therefore, that salmon parr have some spatial memory and can recognize their former territories even after being absent for months.

In comparison with the control section, the build-up, presence or break-up of surface ice did not cause significant changes in the winter spatial distribution of salmon parr within the enhanced section of the Dalåa River. Although ice-induced changes in spatial distribution of salmon parr have been observed elsewhere (Whalen *et al.*, 1999; Brown *et al.*, 2001), substrate seemed to provide sufficient shelter for salmon parr in the enhanced section such that the increased amount of overhead cover did not attract parr to change location within the enhanced section in winter and any adverse effect from ice break-up could be avoided in spring. Linnansaari *et al.* (2008) also observed that salmon parr were not attracted into ice-covered areas if they already were occupying areas with suitable substrate cover. Similarly, Cunjak and Power (1987a) reported preference for in-stream rather than overhead cover for brook trout, *Salvelinus fontinalis* (Mitchill), and brown trout during winter.

Small-scale distribution shifts in response to ice conditions were, however, noted even in the enhanced section. In particular, the response of salmon parr to sub-surface ice formation in the enhanced section was dependent on their specific location within the Glide 1. Solid anchor ice formed a dense mass at the head of Glide 1 where slope and water velocity were greatest and persisted beneath surface ice throughout the winter. As the water column essentially was solid ice from substrate to water surface, the salmon parr were unable to remain in, or re-enter, into this area. Hence, these parts of the Glide 1 became unavailable for salmon parr during winter. Avoidance of anchor

ice affected areas by stream salmonids has also been observed in other studies (Brown and Mackay, 1995; Jakober *et al.*, 1998; Stickler *et al.*, 2007). However, not all areas affected by anchor ice were unsuitable for salmon parr. Parr overwintered in the lowermost areas of Glide 1 where anchor ice formed soft, unconsolidated patches. Similarly, Roussel *et al.* (2004) and Linnansaari and Cunjak (unpublished work) have observed that Atlantic salmon parr are able to tolerate anchor ice when they can find shelter within the interstices of large substrates. Recent evidence from a concurrent study in Norway and Canada suggests that the physical nature of anchor ice differs depending on the formation processes and that different types of anchor ice may cause different responses in biota (Stickler *et al.*, unpublished work). Our results concur with this theory that suggests an avoidance/dispersal response by fishes occurs in zones where anchor ice forms through direct nucleation whereas (patchy) unconsolidated areas of sub-surface ice deposition do not cause emigration (Stickler *et al.*, unpublished work).

One of the anticipated changes in the spatial distribution of salmon parr at the onset of winter was a mesohabitat shift from fast, shallow habitats (e.g. riffles, glides) to slow, deep areas (e.g. pools). Although commonly observed elsewhere (e.g. Baltz *et al.*, 1991; Mäki-Petäys *et al.*, 2004), the autumnal decline in temperature did not trigger such a directed movement by parr within the study area. The significantly higher embeddedness of the substrate material in the slow velocity mesohabitats may indicate its relative unsuitability. Access to unembedded interstices is often viewed as the most important habitat characteristic for stream dwelling juvenile salmonids during winter (Rimmer *et al.*, 1983; Cunjak, 1988a; Heggenes *et al.*, 1993). The abundance of such in-stream cover in the original locations of parr may have satisfied their winter habitat requirements such that no mesohabitat shift was necessary.

Overall, the winter resident population of Atlantic salmon parr showed very limited movements and had relatively small home ranges in the enhanced area. The median home range (14.1 m<sup>2</sup>) was comparable in size to a concurrent study carried out in similar winter conditions in Canada (Linnansaari and Cunjak, unpublished work; median home range 9.8 m<sup>2</sup>). These estimates, however, differ drastically from the highly variable and relatively frequent large-scale movements documented in other winter studies of juvenile Atlantic salmon (Hiscock *et al.*, 2002; Robertson *et al.*, 2003; Stickler *et al.*, 2007). The differences between these studies and the current work likely stem from the methodological differences (radio vs. PIT-telemetry) and the subsequent difference in the body size of the parr used for tagging (mean fork length 13–16 cm in above-cited studies vs. ~10 cm in our study). It should also be noted, that our ability to track the movements of salmon parr was limited to a relatively short segment of the stream. Thus, our estimates of home range are only representative for the non-emigrant population.

In addition to the winter resident population, a considerable part of the population disappeared from the study area during both study years. Predation was assumed to be negligible as there are no large piscivorous fish species capable of consuming salmon parr >90 mm and no avian predators were present during the study period. We also never observed mammalian predators, such as mink or otter, or their tracks in the study area. Finally, the detection of actual in-site mortality was low. Therefore, the observed salmon parr dispersal and subsequent re-encounters of many of the temporarily absent parr lead us to believe that the observed fish loss was mainly due to emigration. The greatest emigration occurred in autumn before the initiation of ice formation, and took place in both the enhanced and control sections. A large part of the emigration occurred following capture and tagging but before the first tracking survey. Previous research has shown that sampling methods like electrofishing may cause increased emigration (Nordwall, 1999; Young and Schmetterling, 2004). However, our observations suggest that the nature of the release of the tagged fish and habitat suitability in the release site may be more important than the method of capture for explaining the emigration in our study. The emigration of salmon parr was considerably higher in the Glide 1 section during the 2004–2005 season and was likely a consequence of the accidental bulk release of tagged parr coincident with high discharge conditions at the time. Typically tagged parr were individually released throughout a site; this was the method used in Glide 2 where emigration was much lower (31% vs. 69% of the initial emigration). Also, the release of salmon parr to the homogeneous small substrate (i.e. control section) triggered a larger initial emigration in comparison with the enhancement section in 2005–2006 even though the fish were returned to the original section of capture. However, as the tagged parr were not necessarily returned within their familiar range, it seems that it was more difficult to find familiar landmarks for orientation (Braithwaite and De Perera, 2006) in the small, homogeneous substrate section and consequently parr may have dispersed farther in search of suitable winter shelters. The need to find shelter within coarse substrate material was likely to further contribute to the increased emigration from the control section when the water temperature was approaching 0°C (Rimmer *et al.*, 1983).

Precocious maturity of salmon parr also had a strong (negative) effect on site fidelity. Similar observations have been made in numerous studies (Buck and Youngson, 1982; Whalen *et al.*, 1999; Linnansaari and Cunjak, unpublished work). Such an effect may have been exaggerated in the Øyvollen reach where no spawning opportunities were available. Furthermore, the physiological consequences of acclimatization to fluctuating (but rapidly declining) water temperatures have been shown to be very taxing on the energy reserves of stream salmonids (Cunjak *et al.*, 1987; Cunjak and Power, 1987b; Cunjak, 1988b). The emergence of such energetically demanding conditions has been observed to cause considerable fish loss (Riddell and Leggett, 1981; Smith and Griffith, 1994; Finstad *et al.*, 2004) and may have also contributed to the observed parr emigration in the Øyvollen reach in autumn.

Once the water temperature stabilized close to 0°C and a surface ice cover formed, emigration slowed considerably. A similar emigration pattern has been observed in Catamaran Brook, Canada, with negligible salmon parr emigration during the period with a surface ice cover (Linnansaari and Cunjak, unpublished work). The amount of winter emigration was similar between different subsections within the enhanced area. As the density of salmon parr significantly varied between these areas based on multi-year autumn/spring electrofishing surveys (Arnekleiv *et al.*, 2002, 2006), our data suggests that the winter emigration of salmon parr was not a density dependent process in the Øyvollen reach of the Dalåa River.

In summary, the results from this study showed that the substrate enhancement project carried out in the Øyvollen reach of the Dalåa River certainly improved habitat suitability and site fidelity for Atlantic salmon parr between autumn and spring. The manipulated area provided suitable winter shelter for juvenile Atlantic salmon whereas the unmanipulated control areas did not. Pool habitats in the enhanced area were not frequently used which emphasizes the role of large, unembedded substrate as an indicator of good quality winter habitat. However, habitats with small substrates can still be important for overwintering parr if surface ice is present to provide suitable cover. The period with a surface ice cover appears more stable in terms of site fidelity (even in the areas with suitable substrate cover) compared with the open channel (non-ice) period with similarly cold temperatures (i.e. late autumn–early winter). Finally, the influence of subsurface (anchor) ice on winter habitat suitability for salmon parr seems dependent on the specific ice processes contributing to its formation. Although the data were collected from a single enhanced stream reach in the current study which may limit the applicability of the results on a general level, our data suggest that ice processes should be considered in northern regions when habitat enhancement projects are planned and carried out.

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