Habitat use of Atlantic salmon *Salmo salar* parr in a dynamic winter environment: the influence of anchor-ice dams

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The effect of anchor-ice dams on the physical habitat and behavioural responses of Atlantic salmon *Salmo salar* parr in a small, steep stream was investigated. Anchor-ice dams formed periodically, leading to a dynamic winter environment as the study reach alternated between riffle and walk dominated habitat. Parr demonstrated large individual variation in habitat use, utilizing most of the wetted stream width, and were generally unaffected by diel changes in the mesohabitat composition. Furthermore, parr displayed high site fidelity in areas with low embedded substrata, and demonstrated few large movements between the three mesohabitat classes present: shallow riffle, walk and pool. Findings from this study question the importance of hydraulic variables such as water depth, flow velocity and dynamic ice formation as single habitat features for juvenile stream salmonids during winter and emphasize the importance of access to substratum cover. © 2008 The Authors

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Key words: anchor-ice formation; distribution; mesohabitat; passive integrated technology; *Salmo salar*; steep streams.

INTRODUCTION

The cold season in north-temperate regions may be a critical factor for stream fish populations (Hubbs & Trautman, 1935; Maciolek & Needham, 1952; Hunt, 1969; Cunjak *et al.*, 1998; Bradford & Higgins, 2001; Annear *et al.*, 2002; Finstad *et al.*, 2004). The effect of various winter conditions on stream fishes is still largely unknown, and much remains to be learned (Huusko *et al.*, 2007). Consequently,

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to improve the understanding of stream ecology dynamics during winter, multidisciplinary studies relating physical conditions and their impacts on lotic biota in natural environments are needed (Power *et al.*, 1988; Roussel *et al.*, 2004).

The ice regime in high gradient streams and stream reaches is controlled by dynamic ice formation (Barnes, 1906; Devik, 1944). Dynamic ice formation is characterized by the formation of tiny ice particles suspended in flow (termed frazil) and ice adhering to the bottom (termed anchor ice) in turbulent reaches when the water temperature drops below 0° C (referred to as supercooled water). In locations prone to anchor-ice formation, *e.g.* in locations with emergent boulders and narrow stream passages with high turbulence, anchor-ice dams may develop (Devik, 1944). Despite their common presence, little is known about their existence, their effect on the physical habitat and on fish distribution. The few qualitative studies conducted have shown that despite constant discharge, anchor-ice dams alter the in-stream flow conditions, both upstream and downstream of the dams (Barnes, 1906; Devik, 1944). The water level increases upstream of the dams (termed backwater effects), hence decreasing the flow velocity in these areas, while the opposite occurs below the ice dams. Therefore, riffle sections can be transformed into stepwise pool-riffle sections when anchor-ice dams form (Devik, 1944). As the dynamic ice formation displays a diel periodicity (Devik, 1944; Ashton, 1986), forming at night and disappearing during day, the ice dams cause a dynamic environment. For stream living fishes, these environments and their dynamics may pose a particular challenge as energy conservation during winter is crucial.

Environmental stochasticity affects population size and structure and is an important limiting factor for all living species (Lande, 1993). Hence, to understand critical factors that limit production of juvenile stream salmonid populations, physical habitat requirements have been intensively studied (Gibson, 1993; Cunjak, 1996; Heggenes, 1996; Armstrong *et al.*, 2003; Huusko *et al.*, 2007). Generally, water depth, mean flow velocity, substrata and cover have been used to describe valuable habitats for stream salmonids, largely during summer with low flow conditions (Bovee, 1982; DeGraaf & Bain, 1986; Morantz *et al.*, 1987; Heggenes & Saltveit, 1990; Heggenes *et al.*, 1991). In winter, however, attributes including ice formation have been given less attention. In some studies, interstitial spaces and coarse substrata have been suggested to be important factors for habitat choice during winter (Rimmer *et al.*, 1983; Heggenes *et al.*, 1993; Mäki-Petäys *et al.*, 1997). Heggenes (1996) observed that, for juvenile Atlantic salmon *Salmo salar* L. and brown trout *Salmo trutta* L., substrata shelter was most important during daytime. At night, flow velocity was the most important factor as the juveniles were in their foraging state and energy conservation is important. Hence, pools and back eddies can be important night habitat during winter. Also, stream-bank habitat has been suggested to be important during winter providing cover against homoeothermic predators and energy demanding water velocities (Cunjak, 1996; Mäki-Petäys *et al.*, 2004). Nevertheless, habitat studies are conventionally conducted under ice-free conditions and focus on the relationships between fish distribution and abiotic factors on a microhabitat scale (<10 m; Baker & Coon, 1997; Gries & Juanes, 1998; Lamouroux *et al.*, 1999; Alfredsen & Tesaker, 2002; Nagayama & Nakamura, 2007) or mesohabitat scale (10–100 m) (Borsányi *et al.*, 2004; Roussel *et al.*, 2004; Nagayama &

Nakamura, 2007). To understand seasonal variations in habitat selection by juveniles, studies in natural environments should also include ice conditions (Huusko *et al.*, 2007). In particular, investigations under dynamic winter conditions may increase the understanding of the importance of various habitat variables.

Based on the suggestion that distribution and behaviour of salmonids may be largely controlled by density-independent factors, rather than density-dependent factors in winter (Chapman, 1966; Heggenes *et al.*, 1993), stream salmonids should be sensitive to dynamic ice formation and potentially make habitat shifts according to in-stream changes. In this paper, data are presented on mesohabitat use of *S. salar* parr in a dynamic environment including dynamic ice formation, both on a periodic scale (periods with and without presence of ice dams) and on a diel periodicity (day and night). In-stream changes related to hydraulic heterogeneity, in terms of change in water depth, flow velocity and mesohabitat composition, were individually analysed to demonstrate the local, physical effects caused by anchor-ice dams. The main objective was to determine if significant changes in the mesohabitat composition caused by ice formation affected the distribution and habitat use of parr. Three specific questions were addressed: (1) how does formation of anchor-ice dams affect mesohabitat composition in a high gradient environment? (2) Do anchor-ice dams influence mesohabitat use by *S. salar* parr? (3) Do parr prefer stream-bank habitats in a dynamic winter environment? Finally, analyses of movement between and within mesohabitat classes and size of home ranges were included to investigate site fidelity and individual differences among parr. This study may be the first that attempts to investigate the effect of anchor-ice dams on habitat use of juvenile stream fishes.

MATERIALS AND METHODS

STUDY SITE

The study was conducted in Southwest Brook, a small, natural river located in Terra Nova National Park (48° 36′ N; 53° 58′ W) on the north-east coast of Newfoundland, Canada (Fig. 1). The river has a catchment area of 36·7 km^2 with an average winter discharge of 0·4 m^3 s^{-1}. The selected study reach was *c.* 200 m long with a mean wetted width of 10·0 m and a mean stream gradient of 1·8%, favouring dynamic ice formation. In ice-free conditions, the reach is riffle dominated (1881 m^2, 83% of wetted area) and has three small pools (total area: 101 m^2; 4%, maximal water depth: 0·4 m), one at the downstream end and two at the upstream end. Within 100 m in upstream and downstream direction, two larger pools (70 m^2, water depth <2 m) are present. Moreover, a walk section (296 m^2, 13%) is located in the mid-part of the study reach. Along the stream-banks a variety of canopy can be found, increasing the habitat complexity and potential stream-bank cover, with overhanging trees and undercut stream-bank. Also, large rocks (>1 m) are located along the stream-bank providing potential shelter in these areas. In-stream dominant and subdominant substrata are cobble and boulder, respectively. At the time of study, compaction of fine sediments (embeddedness) was minimal in both riffle (0–20%) and walk habitat (0–20%), while pool habitat had medium embeddedness (40–60%). Beside *S. salar*, which is the dominant species, brook charr *Salvelinus fontinalis* (Mitchell) and American eel *Anguilla rostrata* (Lesueur) are abundant within the study reach.
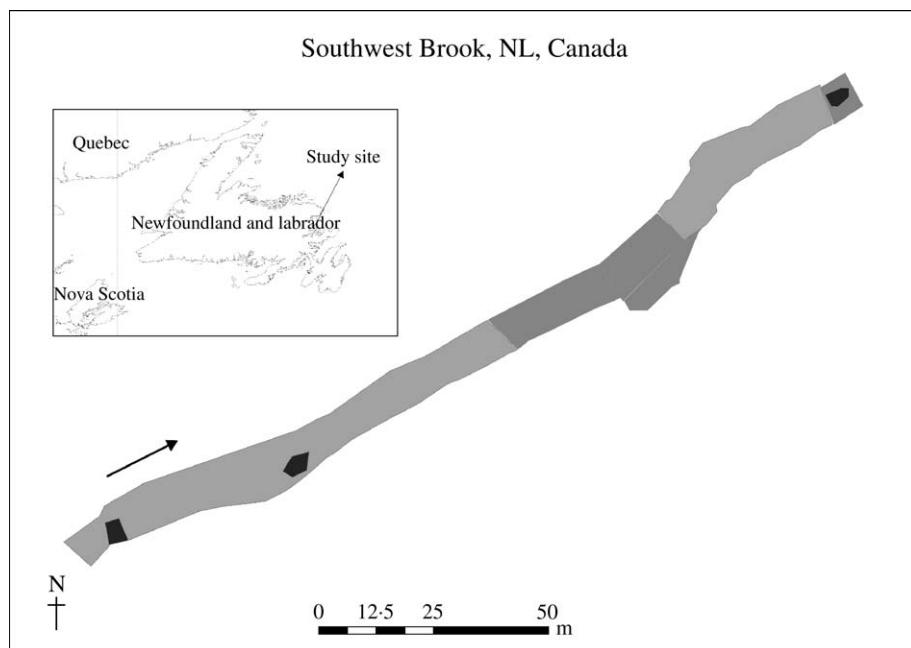
FIG. 1. Location of the study site in Southwest Brook, Terra Nova National Park, Newfoundland, Canada (48°36′ N; 53°58′ W) and the distribution of mesohabitat classes [walk (■), pool (■) and shallow (■) riffle] in ice-free conditions.

FISH TAGGING

On 24 and 25 November 2005 (water temperature, $T_W = 5.1°$ C), 81 *S. salar* parr were electrofished within the study reach using a 24 V backpack electrofisher (Smith Root Inc., Vancouver, WA, U.S.A.; model 12-B). Parr were subsequently tagged using passive integrated transponder (PIT) tags (Texas Instruments, Dallas, Texas, U.S.A.; RI-TRP-WRHP; length: 23.1 mm; diameter: 3.9 mm; mass: 0.6 g in air; tag:fish body mass ratio: minimum and maximum = 0.9 and 5.7%), and measured for fork length (L_F; ±1 mm) and body mass (M; ±0.1 g) (95% CL: L_F = 123 to 133 mm; M = 19.9 to 25.6 g). As suggested by Roussel *et al.* (2000), only parr >84 mm were tagged to ensure minimal effects of tagging. Parr were anaesthetized by immersion in an aqueous solution of clove oil (100 ppm) and placed dorsal side down on a foam pad for surgery. The incision, 6 mm long posterior to the pelvic fin, was closed with two sutures of 4–0 Ethicon braided silk. After surgery, tagged fish were held in a bucket for 20 min to recover, before they were brought to cages located in the river. Parr were kept for 24 h in the cages before release into the habitats where they had been captured. No tagging mortality was observed during the study.

TRACKING PROCEDURE

Monitoring of spatial distribution of parr was conducted during a "freeze-up" winter 2006 (20–26 January and 10–17 February) using PIT technology (Texas Instruments Inc.; TIRIS S-2000 RI-CTL-MB2A) and tracking procedures described by Roussel *et al.* (2000) and Linnansaari *et al.* (2007). Manual stream-bank tracking was conducted concurrently with two sets of hand-held antennae twice during the day (0900 and 1500 hours) and once at night (2100 hours). During nights with anchor-ice formation (23 and 24 January, and 10, 12, 14, 17 February), an additional (fourth) night tracking was

conducted (0100 hours). Maximum reading distance (700 mm) and spatial accuracy ($\pm$150 mm in *x*- and *y*-direction; Linnansaari *et al.*, 2007; pers. obs.) were tested on each tracking occasion using a test tag on the stream-bank. Tracking was done in an upstream direction to reduce the possibility of driving individuals from their positions. When an individual fish was detected, a marker was dropped and its position (*x*- and *y*-co-ordinate) was subsequently 'geo-referenced' using a theodelite (total station; Sokkia Co., Ltd, Kanagawa, Japan; SET 600; spatial accuracy = $\pm$20 mm). The morning positions were 'geo-referenced' in the afternoon, and afternoon and night positions were 'geo-referenced' on the following morning. Potential migration of individual tagged parr out of the study reach was checked by manual tracking 2 km downstream (to the estuary) and 500 m upstream (to a large pond, *c.* 5000 m^2).

PHYSICAL HABITAT CHARACTERIZATION

Water level and discharge were automatically monitored every hour at a gauging station (pressure sensor; Campbell Scientific, Logan, UT, U.S.A.) located 100 m upstream of the study reach. Due to backwater effects caused by ice formation, discharge was manually measured (SonTek, San Diego, CA, U.S.A.; flow tracker handheld velocity meter) twice during the survey in January and February to ensure correct discharge values. The measurements were taken across one transect located in an area with minimal heterogeneity in flow conditions, which was determined visually. Data on formation and distribution of ice were collected using: (1) the total station (*x*- and *y*-co-ordinates), (2) a fixed video camera with time lapse recording every 30 min (only during light hours) and (3) visual observations during every tracking period.

Mesohabitat classification was conducted using a modified version of the method by Borsányi *et al.* (2004). The classification system was modified due to the small size of the stream, by reducing the boundary limit of water depth of the different mesohabitat classes from 0·7 to 0·4 m. Three classes were used: (1) shallow riffle, (2) walk and (3) pool. Thus, boundaries of water depth and flow velocity of each mesohabitat class are given as follows: shallow riffle: $\leq$0·4 m and $\geq$0·5 m s^{-1}; walk: $\leq$0·4 m and $\leq$0·5 m s^{-1}; pool: $\geq$0·4 m and $\leq$0·5 m s^{-1}. Classification of size of substrata and 'embeddedness' were conducted using the Wentworth Scale (Wentworth, 1922) and the method proposed by Schälchli (2002), respectively. In the method of Schälchli (2002), five embeddedness classes (0–20, 20–40, 40–60, 60–80 and 80–100%) were used to visually determine the degree of outer substrata embeddedness within the reach. Lower numbers relate to low embeddedness and thus providing better cover for fish; while higher numbers reflect high embeddedness and thus less cover availability.

DATA ANALYSIS

Three approaches were used to investigate the effect of anchor-ice dams on habitat use of parr. (1) A characterization of the physical changes (water depth, flow velocity and mesohabitat composition) caused by anchor-ice dams, (2) the effect of these physical changes on parr habitat use with respect to spatial distribution and movements within and between mesohabitat, and (3) site fidelity on the basis of calculated home ranges.

Concerning the first approach, three distinct anchor-ice dams formed on six events on 23 and 24 January and 10, 12, 14 and 17 February within the study reach. The three ice dams formed under equal discharge conditions (0·4 m^3 s^{-1}). To reflect the spatial changes caused by these ice dams, three different measurements of the physical habitat were conducted before and after formation of ice dams: (1) surface water elevation reflecting changes in the longitudinal direction, (2) water depth and flow velocity measured along three transects located upstream an ice dam reflecting changes in a cross-wise direction and (3) mesohabitat classification reflecting in-stream habitat changes. As the hydraulic effects of the ice dams were similar considering the hydraulic heterogeneity, only two different compositions of mesohabitat were used in the further

analyses, *i.e.* mesohabitat composition before and after the formation of anchor-ice dams.

In the second approach, the effect of anchor-ice dams on parr habitat use was analysed with respect to: (1) mesohabitat use, (2) movement and (3) distance to the stream-bank. A group of five parr positioned in the uppermost part (50 m) of the study reach (east direction <9715 m; Fig. 2) unaffected by anchor-ice dams was used as a control group. (1) Parr distribution within different mesohabitat classes was separated into two periods: periods without anchor-ice dams and periods with presence of ice dams. To analyse whether changes in parr distribution between mesohabitat classes were due to active movements rather than due to shifting mesohabitat boundaries, the spatial direction, the length and the timing of movements of individual parr were investigated. For example, if a parr was observed to shift between habitats, it was investigated whether it actively moved or if the mesohabitat boundaries shifted. If parr actively switched between mesohabitats, the timing and direction of the parr movement were compared with timing of the formation of anchor-ice dams. (2) Movements by individual parr were calculated as Euclidean distance between two consecutive positions (*x*- and *y*-direction) based on the tracking intervals. (3) The use of stream bank habitat was analysed to investigate whether parr prefer this habitat, both in relation to anchor-ice dam presence or absence and to diurnal scale. Linear distance between the positions of individual parr and the nearest stream-bank (distance to stream-bank, DS) was calculated using ArcInfo 9.2 (ArcGIS, ESRI Inc., Redlands, CA, U.S.A.). Then, each DS was related to the wetted width on the specific location, hereafter assigned relative DS or RDS (Mäki-Petäys *et al.*, 2004). For positions near the stream-bank, RDS approaches 0% whereas at mid-river positions, RDS approaches 50%.

In the third approach, site fidelity by parr was examined using home-range sizes. In addition, overlaps in home ranges between individual parr were investigated to illustrate potential intraspecific competition between tagged individuals. Home-range size was calculated using the 100% minimum convex polygon (MCP) method (ArcInfo 9.2, ArcGIS, ESRI Inc.). As the estimates of the MCP method are sensitive to sample size (White & Garrot, 1990), only parr that were observed >20 times were included in the analysis (*n* = 32). Dry land components were excized from the home ranges. To describe home range size relative to the stream size, individual home-range sizes were divided by the available wetted area within the study reach limited by the most lower and upper fish position observed, and hereafter termed relative home-range size.
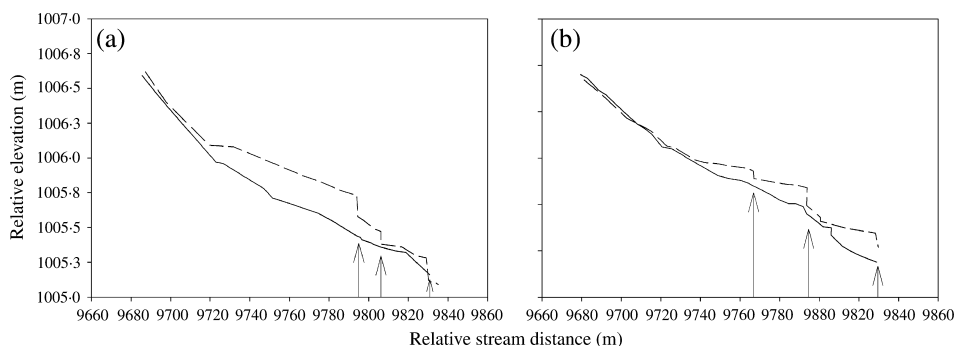

FIG. 2. The influence of anchor-ice dams on the water level in longitudinal direction during the study periods (a) January and (b) February 2006. ——, the water level in the absence of anchor-ice dams [(a) 25 January 2006 and (b) 13 February 2006]; ----, the water level in the presence of anchor-ice dams [(a) 24 January 2006 and (b) 14 February 2006]. Location of the ice dams is indicated by vertical arrows.

STATISTICAL ANALYSIS

During the two surveys in January and February, 44 parr (54% of tagged individuals) were relocated by manual tracking, in which 32 (40%) were found in both periods. The 12 parr that were not found in both periods were removed from the analysis to see if their presence had any significant effect on the results. As the inclusion of these individuals did not alter the conclusions, these individuals were included in the further analyses.

In all cases, highly skewed distributions were observed (by using Shapiro–Wilk's test for normality). Hence, non-parametric tests (Mann–Whitney U-test and Kruskal–Wallis test) were used, including statistics on median, range, skewness and kurtosis, to examine trends and clustering. Statistical analyses were performed using SPSS 15.0 for Windows (SPSS Inc., Chicago, IL, U.S.A.), and considered significant at the level of $P = 0.05$.

RESULTS

INFLUENCE OF ANCHOR-ICE DAMS ON WATER LEVEL, FLOW VELOCITY AND MESOHABITAT COMPOSITION

Along stream banks, surface ice was present in both periods (average cross-sectional extent $= 0$–1 m, *i.e.* 0–10%). Anchor-ice formation occurred in riffle and walk mesohabitats, on top of submerged substrata. The anchor ice could be characterized as 'cotton-like' because a finger could easily penetrate through the ice. Furthermore, anchor-ice dams formed during the night, and predominantly close to mid-stream locations in proximity to large, emergent boulders. Anchor-ice dams disappeared around mid-day (1100 and 1500 hours; 4–8 h after sunrise) and were not observed to last throughout daytime. In January, three anchor-ice dams, reaching a maximum height of 0.75 m, formed within the study reach (23 and 24 January) resulting in backwater effects [Fig. 2(a)]. After the formation of anchor-ice dams, a maximum water elevation difference of 0.70 m was recorded on 24 January. Backwater effect and decreased water velocities upstream of the dams changed the mesohabitat composition from riffle to walk (Table I). In February 2006, three smaller anchor-ice dams up to 0.40 m in height were formed (10, 12, 14 and 17 February) causing similar effects as observed in January [Fig 2(b)]. Water depth increased to a maximum of 0.40 m on 14 February (Table I). Based on the three transects located in the mid-part of the study reach, water depth increased by 37% and average flow velocity decreased by 40% after the establishment of an anchor-ice dam: 12 February (Table II).

DISTRIBUTION AND MOVEMENT BY PARR BETWEEN AND WITHIN MESOHABITAT CLASSES

In ice-free conditions, parr inhabited both shallow riffle and walk but were seldom found in the pool habitat (shallow riffle $= 77\%$; walk $= 18\%$; pool $= 5\%$). Although parr distribution within-habitat classes changed when anchor-ice dams were present (shallow riffle $= 7\%$; walk $= 74\%$; pool $= 19\%$), individuals were not observed to actively shift between habitats. Comparisons of parr positions observed shortly before and after the formation of anchor-ice dams demonstrated that most parr maintained their holding or

TABLE I. Physical conditions and mesohabitat composition before and after formation of anchor-ice dams. Observations are based on data upstream (0–100 m) of the uppermost anchor-ice dam [see Fig. 2(b)]. Mesohabitat compositions (1) and (2) are based on before and after formation of anchor-ice dams, respectively, for both the January and the February period

Time period	Maximum difference in water elevation	Change in mesohabitat class	Flow (cm^3 s^{-1})
21–26 January	+0·7 m (24 February)	Shallow riffle → walk	0·4
10–17 February	+0·4 m (14 February)	Shallow riffle → walk	0·4
January and February		Walk → pool	0·4
Mesohabitat composition (1)	Shallow riffle: 83%	Walk: 13%	Pool: 4%
Mesohabitat composition (2)	Shallow riffle: 25%	Walk: 53%	Pool: 22%

sheltering position, or made only small movements (median movement = 0·5 m, range = 27·6 m; Fig. 3).

Five parr were detected to migrate out of the study reach and down to a low-gradient reach (walk and pool mesohabitat). Within the study reach, few movements occurred between the shallow riffle, walk and pool mesohabitat ($n = 44$; 5% of total; Table III). Of these movements, conducted by 11 individuals, 23% were made from shallow riffle or walk into pool (movement range: 10·1 m), 20% were from pool into shallow riffle (movement range: 0·1–4·7 m) and 48% were made from shallow riffle to walk or *vice versa* (movement range: 73·0 m). Two individuals displaying four movements actively switched to another habitat patch in the absence of anchor-ice dams. Both individuals moved from an upstream riffle to a downstream riffle (86·7 m), and back. The first parr returned close (<2 m) to its original position within 24 h (24–25 January), whereas the second parr was not observed until 26 days later after its downstream habitat shift. In the uppermost area, that was not affected by

TABLE II. Physical conditions measured during an event with anchor-ice dam of 0·40 m height (12 February 2006) and without an anchor-ice dam (13 February 2006). Data are based on measurements from three transects located upstream (1, 3 and 5 m) of the middle anchor-ice dam [see Fig. 2(b)]. Values are means

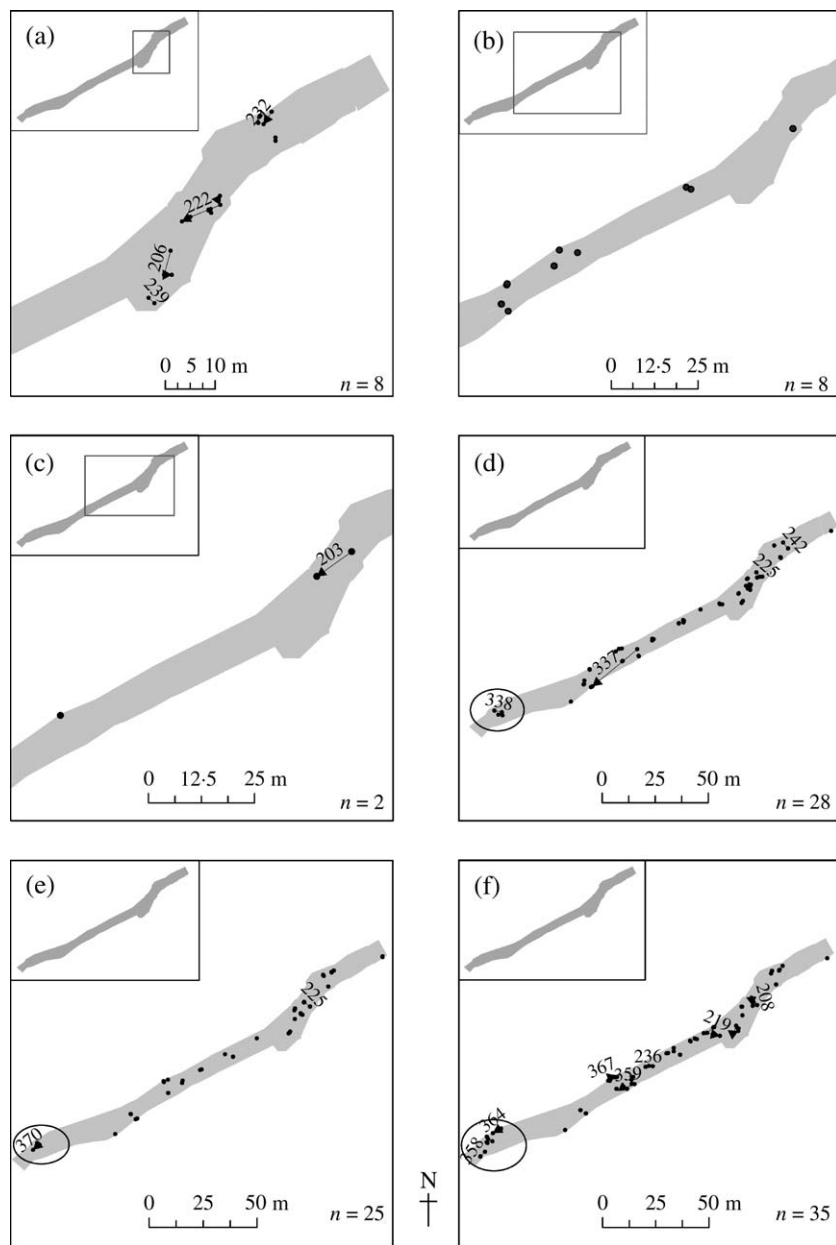| Transect measurement	Flow velocity (m s^{-1})	Water depth (m)	Flow (cm^3 s^{-1})
Pre anchor-ice dam	0·53	0·26	0·4
Post anchor-ice dam	0·32	0·36	0·4
Net change (%)	−40	+37	0

FIG. 3. Spatial distribution (●) and movement direction (→) of *Salmo salar* parr being affected by the formation of anchor-ice dams. (a)–(f) Six separate events with formation of ice dams are presented, including the number of parr (*n*) at each event being observed. Three digit numbers illustrate individual parr that made one single movement during the ice event, *i.e.* moved during the night when the ice dams formed. Individuals enclosed by circles are parr that were situated in the upstream part of the study reach not affected by anchor-ice dams.

TABLE III. Movement of *Salmo salar* parr related to number of movements (n), range and median, between mesohabitat classes (shallow riffle, walk and pool)

Movements between habitat classes	n	Range (m)	Median (m)
Walk/riffle → pool	10	0·0–10·1	1·8
Pool → walk/riffle	9	0·1–10·5	0·9
Walk ↔ riffle	21	0·0–73·0	4·0
Riffle → riffle	4	86·3–109·2	*

*Median value is not included as only four movements were observed.

anchor-ice dams, no parr made a habitat shift, but demonstrated small movements (median movement: 0·9 m, range: 5·7 m) similar to parr in the anchor-ice dam affected areas.

Movement by parr within mesohabitat classes was considered small, and differed significantly between the habitat classes (Kruskal–Wallis test, $P < 0·01$; Fig. 4). Smallest movements were observed in pools (median values: shallow riffle = 0·2 m, walk = 0·8 m and pool = 0·0 m). The distribution of movements in all habitat classes was positively skewed and kurtotic (kurtosis: shallow riffle = 103·5, walk = 3·8 and pool = 9·0; Shapiro–Wilk's test for normality: $P < 0·001$), indicating clustering around short movements, although individual variation was observed (movement range: shallow riffle = 0·0–65·2 m, walk = 0·0–10·1 m and pool = 0·0–0·9 m).

RELATIVE DISTANCE TO STREAM-BANK

Parr demonstrated low preference to stream-bank habitats using most of the wetted width (median, 5 and 95 percentile: $RDS_{January}$ = 23·7, 5·7 and 46·2%;
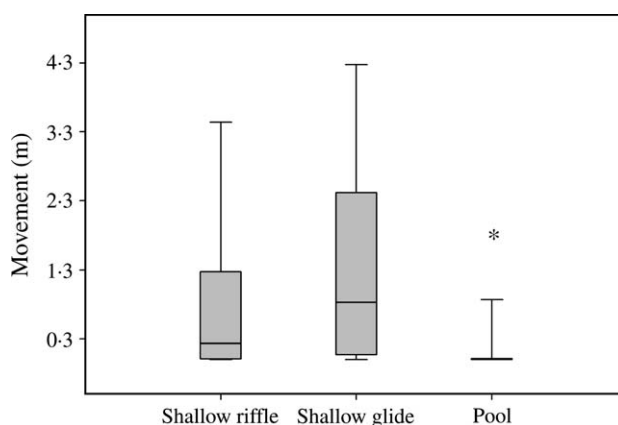

FIG. 4. Movement by *Salmo salar* parr within mesohabitat classes shallow riffle ($n = 39$ parr; $n = 739$ movements), walk ($n = 7$ parr; $n = 145$ movements) and pool ($n = 3$ parr; $n = 9$ movements), during freeze-up periods in January and February 2006. Boxes are 25 and 75 percentiles, whiskers 5 and 90 percentiles and solid line the median value. *, significant difference at $P < 0·05$.

RDS$_{February}$ = 24·8, 1·2 and 45·0%), both during daytime (median, 5 and 95 percentile: RDS$_{Day}$ = 25·0, 1·2 and 45·3%) and night-time (median, 5 and 95 percentile: RDS$_{Night}$ = 24·0, 1·2 and 45·4%). Further, RDS of parr was not significantly different between periods with anchor-ice dams compared to those without anchor-ice dams (Mann–Whitney *U*-test, $P > 0.05$; Fig. 5). No individual actively searched stream-bank habitats at daytime or night-time, either during periods with or without anchor-ice dams. In periods without anchor-ice dams, RDS of fish inhabiting shallow riffle, walk and pool was significantly different (Kruskal–Wallis test, $P < 0.01$; Fig. 4). Lowest median RDS was found in pool habitat (7·7%), while parr in shallow riffle and walk had a median RDS of 23·5 and 28·3%, respectively. In periods with anchor-ice dams, parr in pools were positioned closer to mid-stream than in periods without anchor-ice dams (median RDS = 28·9%). Parr in shallow riffle and walk maintained similar positions relative to those maintained before the anchor-ice dam formation (median RDS: riffle = 22·6%; walk = 29·6%).

Parr located in the uppermost part of the stream not affected by anchor-ice dams, demonstrated similar patterns in their distribution as parr in areas affected by anchor-ice dams. Unaffected parr seemed to demonstrate low stream-bank preference using the whole wetted width (median, 5 and 95 percentile RDS: 19·9, 4·8 and 48·0%). No difference was found in the RDS between the periods with and without presence of anchor-ice dams (Mann–Whitney *U*-test, $P > 0.05$).

HOME-RANGE SIZE

The home-range size of parr ($n = 32$) were considered small (range = 0·1–154·7 m^2; 0·0–6·8% in relative home-range size) (Fig. 6), and observed to overlap with other tagged parr. A positive skewness and kurtosis (skewness = 2·0; kurtosis = 2·8; Shapiro–Wilk's, $P < 0.001$) indicated a higher number of small
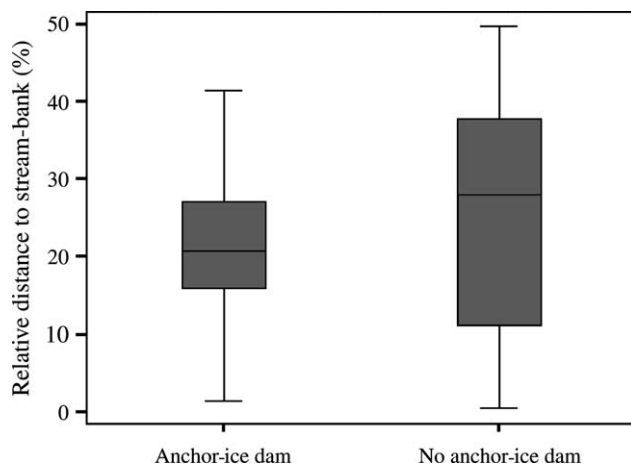

FIG. 5. The distribution of *Salmo salar* parr relative to the stream-bank with and without presence of anchor-ice dams during the study period, January and February 2006. Boxes are 25 and 75 percentiles, whiskers the 5 and 90 percentiles and solid line the median value.
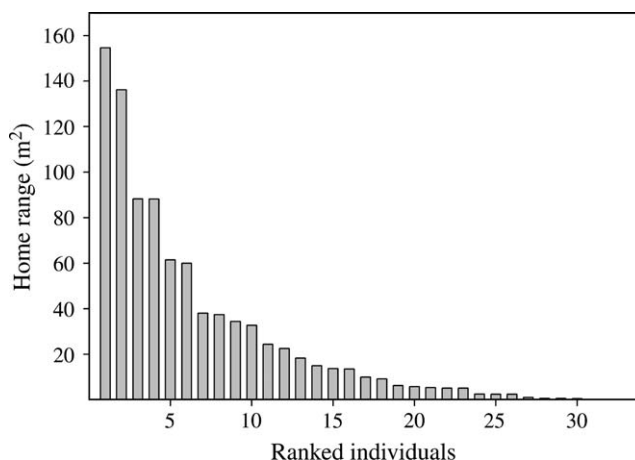
FIG. 6. Ranked 100% minimum curve polygon (MCP) home ranges and relative (%) use of home range represented by 32 *Salmo salar* parr.

home-range sizes (median home range $= 11\cdot7$ m^2; median relative home range $= 0\cdot5\%$) with only a few parr having larger home-range sizes. Five (16%) individuals had home ranges of $<1\cdot0$ m^2 ($1\cdot0\%$ in relative home range), and six (19%) individuals had home ranges >60 m^2 ($2\cdot6\%$ in relative home range). The two largest home ranges ($136\cdot2$ m^2, 6% in relative home range, and $154\cdot7$ m^2, $6\cdot8\%$ in relative home range) belonged to two of 11 individuals that shifted between mesohabitat.

DISCUSSION

A dynamic winter environment evoked small effects on distribution and meso-habitat use of *Salmo salar* parr. Periodic formation of local anchor-ice dams resulted in rapid (<12 h) temporal shifts in the hydraulic heterogeneity and mesohabitat class composition, shifting between riffle and walk dominated habitats. Despite the dynamic conditions, parr demonstrated high site fidelity, occupying small home ranges and undertaking only few active movements between different mesohabitats. Moreover, large individual variability in in-stream distribution was evident. Parr exploited most of the wetted width with no specific association towards stream-bank or pool habitat. Also, neither dynamic ice formation nor the diel cycle seemed to influence this pattern. These findings are consistent with previous winter studies confirming limited movements of juvenile stream salmonids during winter (Huusko *et al.*, 2007), but bring into question the importance of hydraulic variables such as water depth, flow velocity and anchor ice as single habitat features in habitat selection models by juveniles stream salmonids during winter.

Identification of critical habitats is crucial for habitat management, conservation of freshwater fish populations and for the development of effective and realistic habitat models. Previous studies on juvenile stream salmonids have led to the development of a range of habitat preference systems and models for various spatial and temporal scales. Knowledge on habitat use in ice-affected

streams, however, is scarce (Huusko *et al.*, 2007). The majority of the previous habitat studies suggest that juvenile stream salmonids select deeper and slow flowing habitats such as pools and back eddies during winter (Cunjak & Power, 1986; Cunjak, 1988; Heggenes, 1996; Bremset, 2000; Annear *et al.*, 2002; Harper & Farag, 2004) to avoid predators (Valdimarsson & Metcalfe, 1998) and energy-demanding flow velocities (Rimmer *et al.*, 1983). Although the majority of the literature identifies the pool habitat as an important winter habitat for juvenile stream salmonids, a few studies have reported fast flowing habitat, such as riffles, as suitable during winter, especially for juvenile *S. salar* (Smirnov *et al.*, 1976; Rimmer *et al.*, 1983; Cunjak, 1988; Roussel *et al.*, 2004). Findings of the present study concur with the latter, suggesting that fast-flowing habitat is indeed suitable winter habitat. According to Fausch & White (1981), access to suitable cover can be a primary factor in habitat use by juvenile stream salmonids. In particular, the importance of substrata size and low embedded substrata to juvenile stream salmonids has been emphasized for optimal winter conditions (Rimmer *et al.*, 1984; Heggenes, 1996; Mäki-Petäys *et al.*, 1997). This has not yet been linked, however, to anchor-ice formation or to dynamic conditions as found in streams with steep riverbed gradient. In Southwest Brook, the influence of low embedded substrata on high site fidelity was evident in terms of small home range sizes and few long movements. According to Heggenes *et al.* (1993), microhabitat selection by juvenile stream salmonids is driven by two mechanisms during winter: (1) access to areas providing substrata with large interstitial spaces suitable for shelter during the day, and (2) the need for low flow velocity areas to minimize energy expenditure during the activity at night. Thus, coarse and less embedded substrata, as found in Southwest Brook, may offset the need of parr to relocate into pool habitat. The riffle habitat provides cover for both day sheltering and against energy demanding water velocities or ice formation in the active phase of parr at night.

In constricted areas, however, interspecific and intraspecific competition may control the number of individuals, and hence explain the absence of parr found in pool habitat in this study. For example, *S. salar* and *S. fontinalis* have differences in their body morphology leading to a natural habitat partitioning (Gibson, 1973). *Salmo salar* is better suited to riffle habitat due to their enlarged pectoral fins allowing them to maintain position on the substrata with minimal energy expenditure. *Salmo salar* is also more aggressive, possibly out-competing other species for preferred habitat. *Salvelinus fontinalis* may out-compete *S. salar* in pool habitat because they emerge earlier as fry (Gibson, 1981), thus, having a size advantage. But, as interspecific competition has been stated to be less important during winter in unstable conditions (Larkin, 1956; Mäki-Petäys *et al.*, 2004), competition may be less important and thus have less effect on the results from the present study. This suggestion is also supported by the observation of overlapping home ranges, indicating low competition between parr during winter when cover is present, although the abundance of non-tagged parr or *S. fontinalis* could not be estimated. Furthermore, notwithstanding the possibility that the small number of available pools in this study reach could bias the results, two larger pools (70 m^2, water depth <2 m) were accessible in both upstream and downstream

direction within 100 m. Also, the pool habitat within the study reach increased in size due to backwater effects when anchor-ice dams formed. Still, parr were not observed to actively move into pool habitat, suggesting that pool habitat may be of less importance during winter than earlier thought, even when dynamic ice conditions dominate and formation of anchor ice occurs.

Stream-bank habitats are suggested as important winter refuges for juvenile stream salmonids (Cunjak, 1996; Mäki-Petäys *et al.*, 2004). Like pool habitat, stream-bank habitats are assumed to provide cover (surface ice, overhanging or undercut cover) against homoeothermic predators (*e.g.* mink, otter or birds) and refuges against energy-demanding flow velocities during low water temperatures. Stream-banks may also be important night habitats for juvenile stream salmonids, when actively feeding as the optimization of energy is important for winter survival (Heggenes, 1996). In Southwest Brook, parr demonstrated a wide variety in distribution, covering most of the wetted width with no association with stream-bank habitats, and with no relationship with ice formation or diel patterns. These findings are consistent with Heggenes & Saltveit (1990), who observed little use of and small seasonal differences in stream-bank affiliation of juvenile *S. salar* and *S. trutta*. In contrast, Cunjak (1988) hypothesized that parr move towards the stream-bank at night to feed. Correspondingly, Heggenes *et al.* (1993) found juvenile *S. trutta* seeking cover along stream-banks at night suggesting that the observed behaviour enabled avoidance of entrapment in anchor ice. Likewise, Riehle & Griffith (1993) found the majority of juvenile rainbow trout *Oncorhynchus mykiss* (Walbaum) near banks during the day in winter, and similarly, Griffith & Smith (1993) found juvenile cutthroat trout *Oncorhynchus clarkii* (Richardson) and *S. trutta* along stream-banks in daytime during winter. In a larger sub-arctic river, *S. salar* parr were also positioned closer to the stream-banks during winter in comparison to summer, although diel differences and ice formation were not considered (Mäki-Petäys *et al.*, 2004). In a recent winter study considering anchor-ice formation, *S. salar* parr inhabiting pool habitat positioned themselves closer to the stream-bank compared to parr in riffle habitat (Roussel *et al.*, 2004). A similar finding was also obtained in the present study, although this observation may be biased as the stream-bank shifted inland when the water depth increased. Nevertheless, findings from the present study suggest that the importance of stream-bank habitat can be questionable and may be overridden by the importance of substrata cover.

Movement by juvenile stream salmonids during winter has been reported as limited (Saunders & Gee, 1964; Fraser *et al.*, 1993; Jakober *et al.*, 1998; Hiscock *et al.*, 2002; Scruton *et al.*, 2005; Stickler *et al.*, 2008), but rarely related to specific mesohabitats (Roussel *et al.*, 2004). In Southwest Brook, within-habitat movement by parr was limited in all three habitat types, shallow riffle, walk and pool, confirming the suggested low winter activity. As density-independent factors have been suggested to be more important than density-dependent factors during winter (Chapman, 1966), however, it is implicit that the degree and severity of density-independent factors affect habitat selection of juvenile salmonids. The observed limited movement could therefore be because the observed anchor ice was not extensive in terms of its density

and that it formed only on top of the substratum. Hence, potential cover underneath the anchor ice could offset the need to relocate. For example, in the study by Stickler *et al.* (2007), anchor ice filling interstitial substrata was hypothesized to cause out-migration of parr from the riffle habitat. In other similar winter studies, longer movement during winter by juvenile stream salmonids has been reported. Such movements have mostly been related to specific winter events, such as sudden changes in water level (Gillooly *et al.*, 2001), but also related to specific ice events (Brown *et al.*, 2000; Simpkins *et al.*, 2000). In Southwest Brook, a few large movements were detected. Five individuals made large downstream movement (>200 m) to a low riverbed gradient reach, and eight individuals made large within-reach movements. The reason for these displacements remains unknown, as they could not be related to hydraulic changes or to ice formation. Nonetheless, the observed large movements might be explained by 'explorative migration', presence of diurnal predators, or by parr being disturbed when tracking, although latter is less probable as parr were observed to keep position at night despite the tracking.

Investigation of potential critical habitats and behavioural responses by juvenile stream salmonids on a seasonal scale is an important task to enhance future fisheries habitat management and to develop efficient habitat modelling tools. In particular, knowledge on winter behaviour of juvenile stream salmonids are lacking for northern temperate regions, where various forms of ice are present. Thus, it will be important to understand the role of physical habitat features including water depth, flow velocity, substrata and different forms of ice, not only as single variables but also in combination. Observations from the present study reflect the facts of the hydraulic complexity and dynamics that can be found in steep stream environments during winter and their effect on parr distribution, habitat use and movement. The observed behavioural responses by parr to formation of anchor ice and anchor-ice dams question the importance of hydraulic heterogeneity and dynamic ice formation as single habitat features. As this study is limited in space and time, and considering that there is a general lack of knowledge on winter dynamics and behavioural responses of juveniles, further studies and with larger spatio-temporal scales are recommended. Finally, future winter research may need to place more focus on cover availability in terms of low embedded substrata than hydraulics and ice.

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