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Movements and behaviour by juvenile Atlantic salmon in relation to ice conditions in small rivers in Canada and Norway

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Individual movements and behaviour of 144 tagged Atlantic salmon (*Salmo salar* L.) parr were monitored during two winters (2003-05) using Passive Integrated Transponder (PIT) technology. Portable antennae that allowed us to accurately locate fish in habitats ≤ 70 cm deep (measured from substrate to ice surface) were used for tracking fish during variable ice conditions (i.e. during subsurface ice formation and/or stable surface ice conditions in mid- and late winter).

Subsurface ice (54-74% of wetted area) did not initiate parr emigration from the study site. Mean ± SE movement during two subsurface ice events was 3.6 ± 1.1 m and 2.2 ± 0.9 m. Fish often chose positions under ice cover if ice was in close proximity of the initial territory of parr but did not seem to seek for it from a distance. Salmon parr residing in open water were often closely associated to the lateral growth of the edge of the surface ice. Ice build-up or break-up did not cause redistribution of fish. Net over winter movements were generally short for the winter-resident population (mean ± SE, 4.6 ± 1.5 m). Winter site fidelity was low (6.9 %, 15.4 %) in the two sites with higher gradient (1.6 %, 0.9 %; dynamic ice conditions), whereas it was high (86.7 %) for the site with lowest gradient (0.4 %; relatively stable ice conditions).

1.Introduction

In temperate and polar regions ice dominates aquatic habitats for a considerable portion of a year. Different ice formations, below and above the water surface, occur depending on the river characteristics and the local climate (e.g. Beltaos et al., 1993; Prowse, 1996). Rapidly changing ice conditions alter the aquatic microhabitats by redistributing the flow pattern such that water velocities and depths change (e.g. Prowse, 2000). In shallow streams considerable variation of the physical habitat take place even within 24-h cycle in early winter. Usually the alterations caused especially by frazil and anchor ice are described to negatively affect fish through decreased habitat availability (Maciolek and Needham, 1952; Chisholm et al., 1987; Cunjak and Caissie, 1993; Power et al., 1993; Brown and Mackay, 1995; Brown, 1999) or even direct ice-induced mortality (Tack, 1938; Benson, 1955). Increased movements of fish have been observed in response to declining water temperatures below certain species/population specific threshold (Bjornn, 1971). More, Cunjak and Power (1987) and Cunjak (1988) have shown that salmonids may have problems acclimatizing to these rapidly changing conditions during early winter and energetic deficits may arise. Further, salmonids have been shown to generally avoid stream reaches affected by subsurface ice (Jakober et al., 1998; Brown et al., 2000; Simpkins et al., 2000). These demanding conditions of early winter may create a “winter bottleneck” for survival (e.g. Letcher and Gries, 2002) but harsh conditions can follow also later during the winter (Cunjak et al., 1998)

Studies carried out during periods of significant ice build-up are challenging for data collection. Snorkeling and electrofishing have been used successfully to study winter fish movements and/or behaviour (e.g. Cunjak and Randall, 1993; Whalen et al., 1999), but their efficacy to study fish under various ice conditions is limited to relatively ice-free areas. Radio-tracking studies have proven to be a plausible method for winter studies. However, restrictions exist with this methodology as well: only relatively large fish can be used due to transmitter size and the duration of the study is dictated by the battery life of the transmitter. Further, the high cost of the transmitters usually allows for only a limited number of tagged individuals.

Recently, Roussel et al. (2004) and Linnansaari et al. (in review) have shown that active tracking of fish with Passive Integrated Transponder (PIT) -tags is possible using a portable antenna. This method has proven efficient even during the most challenging winter conditions, and permits accurate spatial positioning of the fish across different mesohabitat classes in shallow headwater streams.

In the present study we followed the movements of PIT-tagged juvenile Atlantic salmon (*Salmo salar* L.) parr under various ice conditions. Main objective was to identify any causal mechanisms between the ice formations and fish movement, behaviour and site fidelity in three shallow stream reaches which differ in their gradient and thus ice regime.

2. Study sites

We followed the behaviour and movements of Atlantic salmon parr in three small streams: 1) Catamaran Brook, a tributary to the Little South West Miramichi River, situated in northern New

Brunswick, Canada, 2) Dalåa River, a headwater tributary to the Stjørdal River, situated in Meråker, 100 km east of Trondheim, Norway and 3) Sokna River, a tributary to the Gaula River, situated in Soknedal, 70 km south of Trondheim, Norway. Within these rivers, study sites of ~ 90 - 200 meters were chosen (Table 1). These study sites were situated in the Lower Reach in Catamaran Brook (see Cunjak et al., 1990; 1993), Øyvollen Reach in Dalåa River (see Linnansaari et al., in review; Arnekleiv et al., 2002) and lowermost part of Stavilla branch (a headwater stream of Sokna River, see Gurandsrud, 2003). Each of the study sites consisted of at least one riffle-pool sequence and thus provided a range of different meso-habitat classes. Physical characteristics (length, width and bed gradient) of the study sites are shown in Table 1.

All of the study sites were affected by variable ice formations between October/November and April and all/most of the surface area was ice covered by January. The water temperature regime during the study period is shown in Figure 1.

Juvenile Atlantic salmon was the dominant fish species in all of the study sites, being of wild stocks in Catamaran Brook and Stavilla study sites, but originates from young-of-the-year stockings in the Øyvollen site (Arnekleiv et al. 2002). Additionally, small populations of brown trout (*Salmo trutta* L.) and brook trout (*Salvelinus fontinalis*, Mitchill) co-existed in the Norwegian and Canadian study sites, respectively.

The data used in this paper were collected from October 2003 to May 2004 in the Stavilla study site, and from November 2004 to May 2005 in the Catamaran Brook and Øyvollen study sites.

3. Methods

We used Passive Integrated Transponder (PIT) -tags in juvenile Atlantic salmon for subsequent active tracking of individual fish. Initial capture of the fish was by standard backpack electrofishing procedures (see e.g. Bohlin et al., 1989).

The transponders were 23-mm in length, 3.9-mm in diameter, weighted 0.6 grams in air and were manufactured by Texas Instruments. The tagging procedure was as described by Linnansaari et al. (in review) and followed the general rule of using only fish > 84mm FL as suggested by Roussel et al. (2000). The fish were kept in substrate filled liveboxes for a minimum of 12-h following the tagging to ensure that all the fish were released in good condition and to determine tag retention. The tagging dates, overall number of tagged individuals and morphometric parameters for the tagged population in each study site are listed in Table 1.

The “recapture” of the fish was done by recovering the individual code from the PIT-tag using a portable antenna that was connected to a backpack reader device (Texas Instruments Radio Frequency Identification System, Series 2000) and a palmtop computer for the code identification. The portable antenna system had a maximum reading distance of up to 70 cm when a transponder was oriented parallel to the plane of the antenna inductor coil loop. Ice and water did not have notable effect on the reading distance. Further details of the portable antenna system are described in Linnansaari et al. (in review) and Roussel et al. (2000).

Active tracking was carried out multiple times during daylight and hours of darkness. Occasionally repeated (3-13) trackings were conducted over a 24-h cycle. In open water conditions, the tracking was carried out in an upstream direction, moving from bank to bank. When surface ice was prevalent, tracking was carried out both in up- and downstream directions. Upon encountering a tagged fish, the "blind-spot method" (Linnansaari et al., in review) was used to determine the exact fish position; this was marked with a colored sinker. Ice conditions at these locations (i.e. ice "use" by fish) were recorded each time. The tracking occasions and the number of fish found during each occasion are listed Table 2.

After the tracking survey, the fish locations were georeferenced using a total station (Leica TC307 or TC400) or by measuring the distance from the fish location to at least two adjacent downstream bench marks with known coordinates (distributed every ~ 5 metres on the river banks). The spatial distribution and thus amount of different ice formations (i.e. ice "availability") was also measured using the same methodology and are presented in Table 3.

Movement, as used in this paper, is measured as the linear distance between the position of a fish on two consecutive tracking occasions (i.e. net movement). Movement could not be calculated for the Øyvollen Reach during 2 and 9 Dec due to erratic coordinate data.

4. Results

Site fidelity

Considerable number of fish disappeared from all of the study sites before the first ice formations (Table 2). By November, 36.2 %, 56.0 % and 72.2 % of the originally tagged salmon parr were found in the Stavilla, Øyvollen and Catamaran Brook study sites, respectively. The body condition factor was not different between the fish residing in the study site and the fish that were absent (t-test, $p = 0.181$, $p = 0.565$ and $p = 0.173$ for Stavilla, Øyvollen, and Catamaran Brook, respectively). In Catamaran Brook, the proportion of absent mature parr was higher than that of immature parr (odds ratio 4 to 1) but the difference was statistically non-significant (Fisher exact test, $p = 0.179$).

Overwinter site fidelities were low in Catamaran Brook and Stavilla study sites. In May 2005, only six fish were located in the Catamaran Brook study site, and two of these were dead. Thus, the fidelity was 15.4 % of the fish that were residing in the study site during the first tracking. In Stavilla study site, four fish were found in the end of March (19.0 % fidelity), whereas 86.7 % of the fish that were residing in the Øyvollen study site during the first tracking were still found in end of April. There was a high negative correlation between the overwinter site fidelity and the gradient of the study reach ($r = -0.787$), but the correlation was statistically non-significant (t-test, $p = 0.423$) due to low sample size.

Overwinter site fidelity did not depend on the body condition factor. There was no difference in the condition factor between the resident and emigrant salmon parr groups in any of the study sites (Mann -Whitney U-test, $p =0.076$, $p = 0.395$ and $p = 0.486$ for Stavilla, Øyvollen and Catamaran Brook, respectively).

Behaviour during subsurface ice events

We tracked salmon parr on two separate occasions during considerable subsurface ice accumulation in Catamaran Brook study site.

Prior to tracking on November 9th, negligible surface ice was present in the study reach and no subsurface ice events took place prior to this date. The first tracking on Nov 9th (5 pm, Table 4) took place before subsurface ice formation and most of the fish were residing in open water (Table 4). After the initialization of frazil ice build-up, almost all the fish (92%) were observed to be active. Fish showed high site fidelity during the event (Table 4). Indeed, no fish left the study site during the subsurface ice event, although 54.4 % of the area was affected by anchor ice during the nigh. Moreover, fish resided within considerably small areas during the event (Figure 2); the maximum net movement observed between the trackings was 7.1 m. By the morning (3rd tracking, 8.30 am) salmon parr were found, on average, within 1.7 ± 0.3 metres from their original location. In the morning, majority of the fish chose a daytime shelter under an ice formation rather than in open water (Table 4). Indeed, more fish would have been expected to reside in open water based on the amount of the open water surface in the reach (log-likelihood ratio test, $p<0.001$) and thus there was an indication of preference towards ice cover.

Subsurface ice formation and accumulation continued between the trackings on 10th and 16th November. Only one (mature) salmon parr disappeared during this period indicating 96.2 % site fidelity. The average net movement distance between the last position on 10th Nov and first position on 16th Nov was 3.6 ± 1.1 metres. Net movement distance between the two dates did not correlate with body condition factor of the fish (Pearson $r = -0.191$, $p = 0.382$).

The second tracking was carried under extensive anchor ice build-up (up to 74.4 % of river bed covered in anchor ice) on 16th to 17th Nov (six repeated trackings over 24-h). At the beginning of the second tracking survey (9 am, Table 4), all fish were sheltering in locations covered by scattered surface/border ice formations during the daylight. At dusk, large proportion of the fish entered the open water for the early part of the night (Table 4). Many fish that were staying under surface ice followed the lateral growth of the ice edge during the night. The proportion of the fish in open water decreased during the course of the night and by the morning all the fish were found again under ice cover (Table 4). This behaviour reflected the availability of ice cover (Yates corrected χ^2–test, $p > 0.05$) rather than preference to shelter under ice.

Mean net movements between the trackings during the 24-h period were short and generally similar in extent (Table 5). Mean net distance between the initial and the final location of salmon parr was 2.2 ± 0.9 metres (Table 5) and indicated that anchor ice formations did not force fish to move far from their original location (Figure 2). Maximum extent of movements was 19.2 metres (Figure 2, fish 408). All the salmon parr resided within the study site during the subsurface ice event.

No salmon parr mortalities were evident between 9th and 17th November even if some salmon parr (N=8) resided under anchor ice that was in direct contact with the substrate and was up to 30 cm thick.

Behaviour in relation to surface (partial and full) ice and overwinter movements

All the study sites froze over almost completely during the course of study. In Stavilla and Catamaran Brook study sites surface ice build-up precluded any further active tracking in most or all parts of the study site (by February, 44% of the study site could be tracked in Stavilla; no tracking was possible in Catamaran Brook between December and April).

In the Stavilla study site, the active tracking was inefficient under the (thick) border ice. Thus, most fish were observed in open water (Table 3). Fish residing in open water were in close proximity of the ice edge (on average 0.9 m on 23rd Oct and 1.4 m on 18th Nov). Especially when fish were in active state (i.e. during hours of darkness) majority (71.4 %) of salmon parr were in closer association with ice edge than middle point of the open area. Association was not as pronounced during daylight (57.1 % of fish closer to ice than mid-channel). In February, only two fish were found and they both resided under full surface ice during all of the 13 repeated tracking occasions over a 24-h cycle.

At the Øyvollen site, efficient tracking was possible even after surface ice build-up. The reach became initially ice covered in the end of November (Table 3, tracking # 2), but the ice was lost during the first weeks of December (see Figure 1, peak in water temperature). During the next tracking in February, the study reach was again under full ice cover that lasted until the spring ice break-up in early April. Regardless of the ice build-up and break-up patterns, the vast majority of net movements of the resident parr were relatively short between the consecutive trackings (Figure 3) indicating that the changes in ice conditions did not initiate long-scale movement in the population staying in the study reach. The extent of net movements between the trackings was similar (two-way ANOVA without replication, controlled for the time difference between the trackings, $F_{3,34}$, $p > 0.50$). The few longer scale movements (i.e. > 20 metres, Figure 3) resulted because of a notable movement pattern of few individuals (three fish moving upstream direction into areas with considerably smaller substrate sizes under full surface ice and then moving back to their original tagging station by April).

Generally short between-tracking movements resulted in considerably short overwinter net movement; mean ± SE net overwinter movement was 4.6 ± 1.5 m (N=24), as measured between the initial (4th Nov) and the final (20th Apr) daytime location.

The number of salmon parr using ice as cover reflected its availability (i.e. proportion of ice cover of the wetted area, Table 3) in the Øyvollen reach. Only exception seemed to be during the tracking period on 14th December (Table 3, tracking # 5), when more fish resided in open water than was expected based on the bulk ice abundance in the whole study reach (Yates corrected log-likelihood test, $p < 0.05$). However, the ice was not evenly distributed in the reach; most of the ice was in the upstream part of the study reach. In contrast, large proportion of the fish (43 %) had their initial territories in the downstream part of the reach where the ice consisted only 9.3 % of the wetted area. When the uneven ice distribution within the reach was taken into account, it was observed that fish were found under ice cover according to the ice availability (Yates corrected log-likelihood test, $p > 0.10$). Thus, fish did not seek ice cover when it was located at a distance from their original (i.e. prior ice) territories.

5. Discussion

Our data showed that higher number of salmon parr disappeared from study sites with higher gradient. This was, however, not related to more dynamic subsurface ice regime in the higher gradient reaches during the early phase of the study. In general, no ice form caused avoidance but instead fish tended to stay under any ice formation if it was in close proximity of its original territory. Further, surface ice allowed a “predator-free” dispersal opportunities to low-cover areas later during the winter.

Loss of the tagged individuals was observed in all of the study sites already in the early phase (i.e. prior ice) of the study. This was expected as leptokurtic movement distributions are common for many animal populations (e.g. Fraser et al., 2001) including overwintering fish (e.g. Jakober et al., 1998; Muhlfeld et al., 2001). Some emigration was probably caused due to tagging and capturing the fish (Nordwall, 1999). The tagged population also included mature parr that were observed to emigrate in higher extent in Catamaran Brook in comparison with immature individuals. Similar results were obtained for Øyvollen reach in a former study (Linnansaari et al., in review) and have been seen also elsewhere (Whalen et al., 1999).

The movement to winter habitats was not a probable cause of the emigration as it is described to take place when the water temperature decline under 10 ^{o}C (e.g. Rimmer et al., 1983). Tagging of the fish took place in our study sites in water temperatures of ~ 5 ^{o}C. Jakober et al. (1998) observed that additional movements occurred in a salmonid population even after the major shift to overwintering habitats; these additional movements were observed when water temperature declined to 0 ^{o}C. Similar movements might have further reduced the number of the tagged fish in our study sites before first trackings.

In contrast to the relatively high emigration before ice initiation, our data from Catamaran Brook showed no evidence that frazil and anchor ice formation/accumulation would initiate long scale movements. Majority of former studies indicate that in addition to movements to overwintering sites, a second period of long scale movements indeed takes place during the subsurface ice events (Brown et al., 1993; Brown and Mackay, 1995; Jakober et al., 1998; Brown, 1999; Brown et al. 2000; Simpkins et al., 2000; but see Roussel et al., 2004). It appears, however, that our results are not in contradiction to these studies; they rather reflect different behavioural strategy that is utilized by small sized rheophilic fish. Indeed, Heggenes et al. (1993) described that small sized salmonids (like in our study) hide in the interstices of the substrate material during the day in winter whereas larger individuals (i.e. fish that are commonly used in radio-tracking studies) do not easily find such shelter and aggregate in pools or hide in aquatic vegetation and log-jams. These habitats used by larger sized fish become easily filled (pools, log-jams) or destroyed (aquatic vegetation clusters) by frazil ice due to its adhesive properties and thus fish are forced to move (Brown and Mackay, 1995; Griffith and Smith 1995; Simpkins et al., 2000). In comparison, anchor ice rarely penetrates into the substrate due to warmer microtemperatures the hyporheic layer in winter (Caissie and Giberson, 2003) and thus small sized fish hiding within the substrate are not in physical contact with the subsurface ice. Roussel et al. (2004) have also observed similar response to anchor ice as described in this study. They suggested, that fish could experience warmer microtemperatures even in the actual watercolumn when residing under anchor ice accumulations. On occasion we observed similar behaviour during the hours of darkness, but we never saw fish staying in the watercolumn under such ice structures during the daytime.

Further, we did not observe subsurface ice induced salmon parr mortalities during the period when active tracking of the fish was possible (one white sucker (*Catostomus commersoni* (La.)), appr. 11 cm in length, died during the second tracking survey due to entrapment in anchor ice). However, we only observed the fish under conditions where the anchor ice partially lifted up during the daytime. As this took place, "corridors" for movement were formed within the anchor ice mass. Because we could not perform any further tracking later in November/December in Catamaran Brook, it is not known if detrimental conditions can arise when anchor ice remained on the substrate for extended periods (days/weeks). Fish can presumably survive such period without being able to feed due to lower metabolism during winter. However, the oxygen in the hyporheic water is mainly supplied from the interchange of water between water column and substrate (Sheridan, 1962). Thus, it is possible that thick anchor ice accumulations may reduce the oxygen availability within the substrate and thus cause fish mortality.

In addition to subsurface ice, also ice forms above the water surface provide overhead cover for fish. Our data suggests that salmon parr chose positions under surface ice formations when ice forms in close proximity to the initial (prior-ice) fish territory. However, if the ice cover was formed at a distance (e.g. upstream part of the reach when fish at downstream part), fish did not seek for these areas if the microhabitat at the fish territory offered other suitable cover. Thus, juvenile Atlantic salmon were not attracted by the ice formations *per se*. Fish has been observed to take advantage of ice cover also in other studies (Maciolek and Needham, 1952; Logan, 1963; Meyers et al., 1992; Cunjak et al., 1998).

It was further observed that salmon parr entered the area that was not covered by ice during the hours of darkness. However, fish were staying in close proximity of surface or border ice cover at all times. Also Muhlfeld et al. (2003) observed that bull trout (*Salvelinus confluentus* Suckley) appeared to areas without overhead cover during the nights in winter. We further observed that the fish staying under the border ice during the night were spatially located in a close proximity to the edge of ice and they consistently followed the edge as it moved towards the middle of the channel due to its lateral growth during night. In addition to cover, fish will experience reduced water velocities when staying under the due to overhead friction layer for water flow (e.g. Beltaos et al., 1993). Fish might also be able to take advantage of higher net amount of invertebrate drift in open water without being obliged to stay in the faster moving water (i.e. fish can enter the open water area to catch prey item and move back under ice).

Once the river reach was frozen over, the general movements were very short and fish could be encountered from the same mesohabitats almost without exception. Jakober et al. (1998) have observed similar results in a headwater stream with stable ice conditions. Our results, however, may reflect our inability to follow the movements beyond the study site. Thus, our results are only applicable for the "winter-resident" population. All the "large" scale movements (i.e. tens of metres) observed between December and February were directed upstream, either towards areas with small substrate sizes and limited (substrate-) cover, or continued within this section. It seems that this movement pattern did not take place before the formation of full surface ice cover. Further, all these fish moved back to areas with coarse substrate when the surface ice degraded. Similar ‘homing’ behaviour in late winter or spring has been observed also by Cunjak and Randall (1993).

The observed movement pattern may indicate that large substrate size and association with other in-stream cover structures may not be as important for fish that are residing under full ice cover. Also Gregory and Griffith (1996) observed in stream enclosures that juvenile rainbow trout (*Oncorhynchus mykiss* Walbaum) concealed themselves less frequently under surface ice. As the wintertime sheltering behaviour is believed to be a consequence of the need to hide from the endothermic predators like mink (*Mustela vison* Screber) or otter (*Lutra lutra* L.) (e.g. Valdimarsson and Metcalfe, 1998), the need to find shelter should be decreased under full surface ice when the predators have limited access into water. Thus, once the ice cover was established, it offered safe dispersal opportunities for salmon parr into new areas that did not provide cover before the ice build-up. Further, if movements can be done under low risk conditions, it might be beneficial to move into areas with lower densities of conspecifics and thus reduce competition for food and space.

Build-up and break-up of ice may facilitate both large- and small-scale movements during winter (Jakober et al., 1998; Whalen et al., 1999; Brown et al. 2001) and can cause significant fish losses (Doyle et al., 1993). Our data showed very localized movements of the salmon parr in the Øyvollen reach even after two ice build-up and two break-up periods. This implies that the severity of these events was not overwhelming in this low gradient study reach and that the microhabitat at the fish residence provided sufficient shelter to overcome any adverse effects that these events may have caused. This might not have been the case in the two other study reaches where especially the ice break-up might have been harsh due to higher gradient and may explain the observed lower overwinter site fidelity. Indeed, the higher emigration took place in the sites with steeper gradient. Also Chisholm et al. (1987) observed that a higher extent of adult brook trout emigration took place in stream reaches with higher gradient in Wyoming. Even if the gradient does not induce movements *per se,* it is a surrogate for ice and microhabitat conditions within the reach. Thus, the correlation between the site fidelity and gradient may indicate that a complexity of factors dictates the population dynamics of streams during winter. These relationships will require further research.

In summary, we observed that the relationship between the fish life and supercooled flows and the resulting subsurface ice is much more complex than previously though; the mere fact that frazil and anchor ice exists in a stream reach does not necessarily make the area unsuitable for juvenile Atlantic salmon. Though, large generalizations about unsuitability of stream reaches during subsurface ice events should be avoided as the conditions may remain suitable at least for smaller sized individuals of the population whereas larger fish may experience these conditions avoidable. Further, surface ice formations may provide fish with beneficial habitat features. Build-up and break-up of ice, when taking place in a low gradient reach with abundance of in-stream cover, did not initiate redistribution of small salmon parr.

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Table 1. Tagging dates and numbers of PIT-tagged juvenile Atlantic salmon in each study section with morphometric measures (mean ± SD) describing the tagged population. Lower part of the table describes basic characteristics of each study reach.

	Catamaran	Øyvollen	Stavilla
N	36	50	58
Total length (mm) ± SD	106 ± 17	125 ± 11	109 ± 14
Weight (g) ± SD	10.4 ± 5.4	14.1 ± 4.5	10 ± 5[a]
Tag/Fish weight (%) ± SD	7.0 ± 2.7	4.6 ± 1.2	7.0 ± 2.6
Maturity (%)	22.2	44.0	6.9
Tagging date	21 Oct 2004	27 Sept 2004	24-25 Sept 2003
Reach length (m)	91	225	102
Reach width (m)	9	15	9
Reach bed slope (%)	0.9	0.4	1.6

[a] Weights recorded without decimals

Table 2. The timing of active tracking surveys during the study and the number of fish found (N, number of mortalities in brackets) at each time. Column Time indicates whether the tracking was carried in daylight (day), during hours of darkness (dark) or multiple times within the 24-hour cycle (whereat number of trackings is indicated in brackets).

Study site	#	Date	Time	n
Stavilla	1	23-Oct-03	dark	8
Stavilla	2	06-Nov-03	day	5
Stavilla	3	18-Nov-03	day	7
Stavilla	4	06-Feb-04[a]	24-h (13)	4 (2)
Catamaran	1	09-Nov-04	24-h (3)	26
Catamaran	2	16-Nov-04	24-h (6)	25
Catamaran	3	16-May-05	day	6 (2)
Øyvollen	1	04-Nov-04	day,dark	28
Øyvollen	2	22-Nov-04	day,dark	25
Øyvollen	3	02-Dec-04	dark	18
Øyvollen	4	09-Dec-04	day	23
Øyvollen	5	14-Dec-04	day	28
Øyvollen	6	18-Feb-05	24-h (10)	23
Øyvollen	7	20-Apr-05	day	27

[a] Only 44 % of the study area was tracked due to ice and snow accumulation

Table 3. Ice conditions and proportion of salmon parr found under each category during the active tracking surveys. Columns Open, SI/BI and SSI indicate the coverage of each ice category of the wetted perimeter of the reach and next three columns describe the percentage of fish found using each category. SI: surface ice, BI: border ice, SSI: subsurface ice, N/A: data not available, #: number of tracking occasion (see Table 2 for dates).

Study site	#	Ice "availability"			Ice "use"		
		Open (%)	SI/BI (%)	SSI (%)	Fish open (%)	Fish SI/BI (%)	Fish SSI (%)
Stavilla	1	54.1	42.7	3.2	87.5[a]	12.5	0
Stavilla	2	100.0	0	0	100	-	-
Stavilla	3	61.5	38.5	0	100[a]	N/A	-
Stavilla	4	19.7	80.3	0	0	100	-
Catamaran	1	22.2[b]	23.4[b]	54.4[b]	**[d]	**[d]	**[d]
Catamaran	2	15.9[c]	9.7[c]	74.4[c]	**[d]	**[d]	**[d]
Catamaran	3	100	0	0	100	-	-
Øyvollen	1	100.0	0	0	100	-	-
Øyvollen	2	1.0[e]	99[e]	N/A	0	100	N/A
Øyvollen	3	N/A	N/A	N/A	5.6	94.4	N/A
Øyvollen	4	N/A	N/A	N/A	0	100	N/A
Øyvollen	5	63	37	N/A	85.7	14.3	N/A
Øyvollen	6	1	99	N/A	8.7	91.3	N/A
Øyvollen	7	100.0	0	0	100	-	-

[a] Tracking of the fish was inefficient in the areas affected by above-surface ice formations due to low reading range by the time of tracking and might cause a disproportionately high number of fish in open water.

[b] Ice coverage during night. By the morning, subsurface ice reached the water surface and turned into surface ice or anchor ice lifted up and floated away. The ice distribution during the next day was 41.6 % open, 42.4 % SI/BI and 16 % SSI.

[c] As in b. The ice distribution during the next day was 15.9 % open, 84.1 % SI/BI.

[d] Results are shown in Table 4 due to multiple observations over a 24-h cycle.

[e] Visually estimated

Table 4. The observed fish in relation to ice formations during the 24-h trackings in Catamaran Brook study site in November 2005. SI: surface ice, BI: border ice, SSI: subsurface ice.

	Date and time 9 - 10 Nov 2005			Date and time 16 - 17 Nov 2005					
	17:00	22.30	8.30	9:00	19:30	22.30	2:00	5:00	7.30
Fish under SI/BI	4	4	13	23	11	12	16	21	22
Fish under SSI	-	3	11	0	2	2	3	2	1
Fish in open water	21	18	2	0	11	11	6	2	0
Total	25	25	26	23	24	25	25	25	23

Table 5. Mean net movement ± SE and mean net movement ± SE per hour between the tracking periods in Catamaran Brook study site on 16 – 17 Nov 2005. Last column indicates the mean distance between daytime locations between these two days.

	Track 1 - 2	Track 2 - 3	Track 3 - 4	Track 4 - 5	Track 5 - 6	Track 1 - 6
N	22	24	25	25	23	22
Net movement (m) ± SE	2.2 ± 0.6	2.1 ± 0.5	1.5 ± 0.4	1.6 ± 0.3	3.1 ± 0.6	2.2 ± 0.9
Net movement (m) / h ± SE	0.5 ± 0.1*	1.0 ± 0.2	0.6 ± 0.2*	0.8 ± 0.2	1.9 ± 0.4[a]	

[a] Net movement between 5th and 6th tracking was considered longer than those marked with an asteristic; otherwise movements were similar in extent (repeated measures ANOVA with log(x+1) transformed data, $F_{4,80}$, p<0.001, followed by Tukey-test)

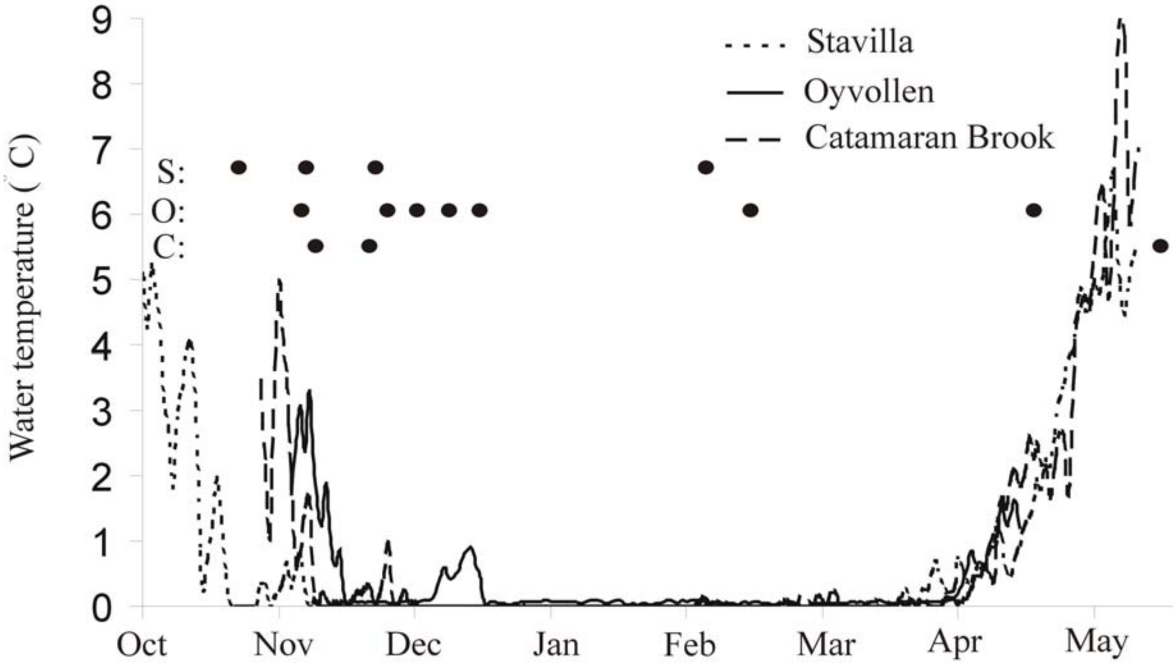

Figure 1. Water temperature fluctuation in 2003-04 in Stavilla River and 2004-05 in Øyvollen reach and Lower reach of Catamaran Brook. Active PIT-tracking periods are indicated by black dots, S=Stavilla River, O= Øyvollen reach and C=Catamaran Brook.

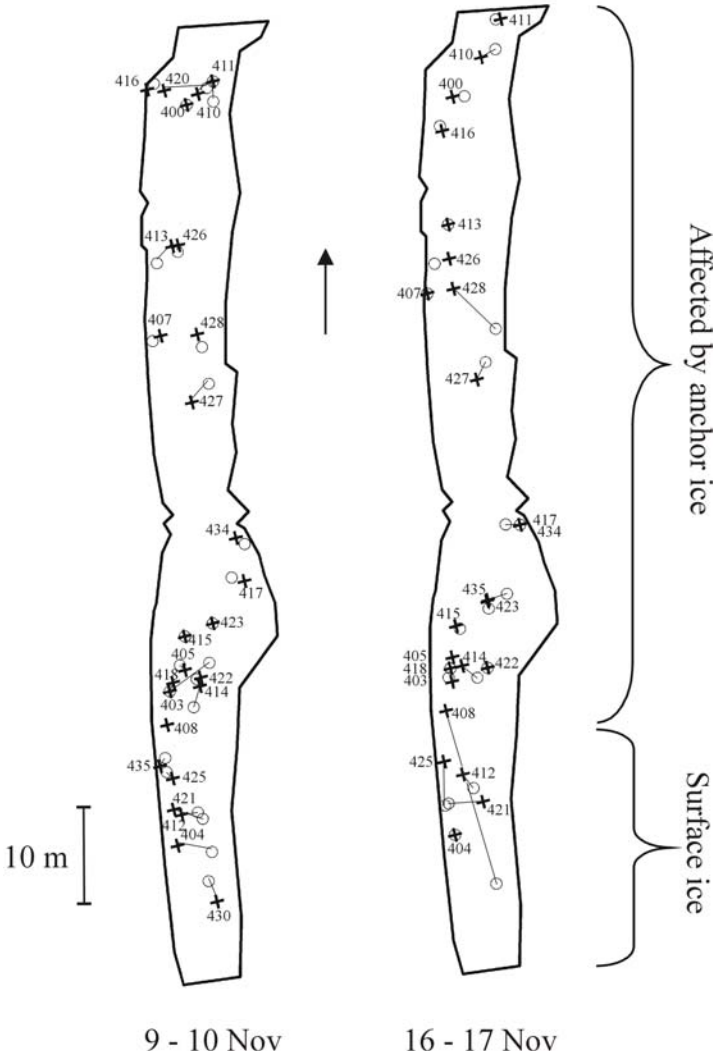

Figure 2. Movements of PIT-tagged Atlantic salmon parr during two subsurface ice events in Catamaran Brook study site in November 2005. Open circle and black cross represent the initial and the final position of each individual, respectively. Arrow indicates the main flow direction. Fish identification numbers are situated close to their final position. Ice formations are not drawn in the figure for more convenient outlook, but the dominating ice category is indicated by parentheses.

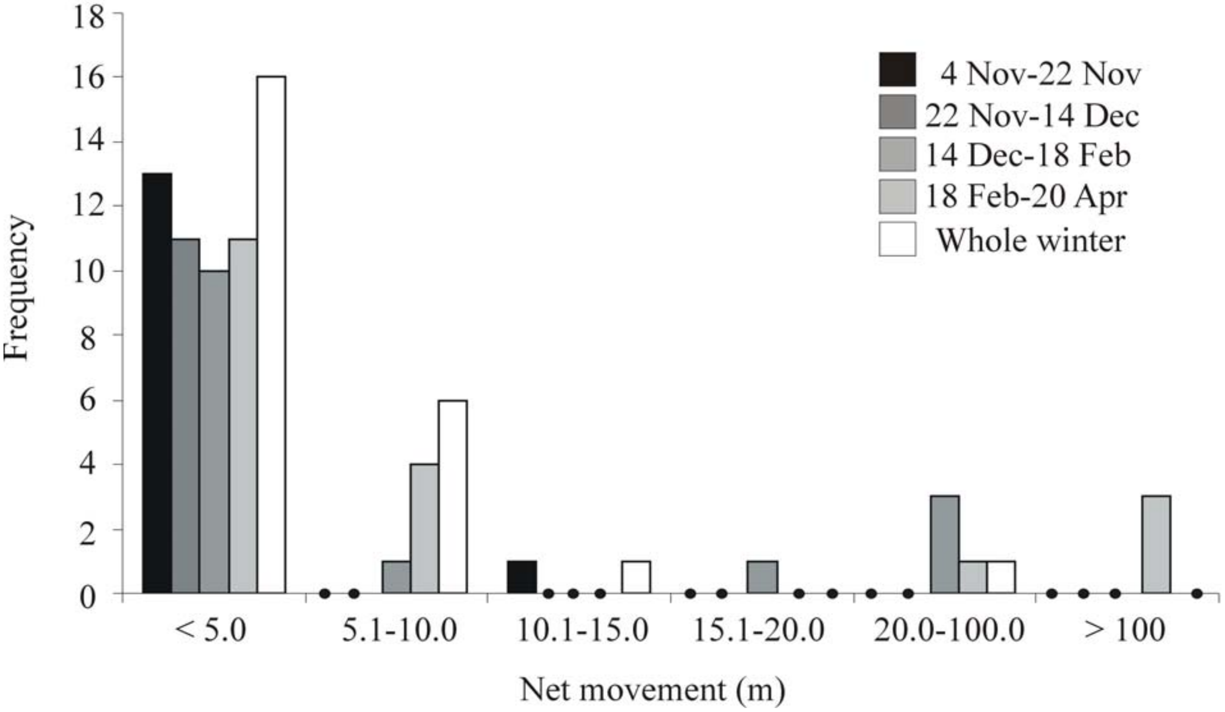

Figure 3.The frequency distribution of the net movements of salmon parr between consecutive tracking occasions in the Øyvollen reach. Distance is measured as the linear distance between daytime locations. Black dots on the x-axis represent a bar with value of 0. Note the different range in the categories on x-axis.