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Spawning migration and habitat use of adfluvial brown trout, *Salmo trutta*, in a strongly seasonal boreal river

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In July 2003, twenty large brown trout (*Salmo trutta*) were radio-tagged at Kiutaköngäs Falls in the Oulankajoki — a river in northern Finland — on their migration to spawning areas, to examine their movements, habitat use and overwintering in the river. The estimated average minimum daily movement of the trout before spawning was 348 m (S.D. = 139 m, n = 20), and during spawning, in late September, 208 m (S.D. = 160 m, n = 15). In winter, the fish were relatively localized (average minimum daily movement = 53 m, S.D = 23 m, n = 12). Upstream migrating trout ranged either in large, deep pool sections of the river or in rapid sections. During spawning, fish were commonly found in rapids and pool–rapid transition zones. In winter, trout resided almost entirely in deep pool sections. In spring, just after the ice break-up and rising water level due to snow melt, overwintering fish migrated downstream within two weeks, moving on average 2062 m (S.D. = 3514 m, n = 11) per day.

Introduction

Most of the available information on migration patterns of adult salmonids has focused on spawning migration of anadromous species and populations, i.e. fish that spawn in freshwater and live most of their lives in saltwater (e.g. Banks 1969, Jonsson and L'Abee-Lund 1993, Aarestrup and Jepsen 1998, Økland *et al*. 2001, Klemetsen *et al*. 2003). Spawning migration of adfluvial salmonids that live in lakes and migrate into rivers or streams to spawn has not been as extensively studied (e.g. Northcote 1992, Trepanier *et al*. 1996, Nykänen *et al*. 2004), and only few authors have focused on brown trout (*Salmo trutta*) (e.g. Alm 1950, Stuart 1957, Huusko *et al*. 1990, Arnekleiv and Kraabøl 1996, Rustadbakken *et al*. 2004). Thus the timing and pattern of the seasonal migrations of adfluvial salmonids, as well as the characteristics of the habitats used by them, are not well described. In order to better conserve and manage migratory freshwater salmonid populations — many of them presently threatened — more research is needed on their seasonal migration patterns and habitat requirements (Mills 1989, Elliott 1994, Crisp 2000, Koizumi *et al*. 2006).

In many large Fennoscandian lakes adfluvial brown trout show life history patterns often similar to those of anadromous Atlantic salmon (*Salmo salar*) and sea trout, with the exception that they live in freshwater only. After the riverine phase of 2–6 years fish migrate to the lake, where they spend 2–5 years before the first

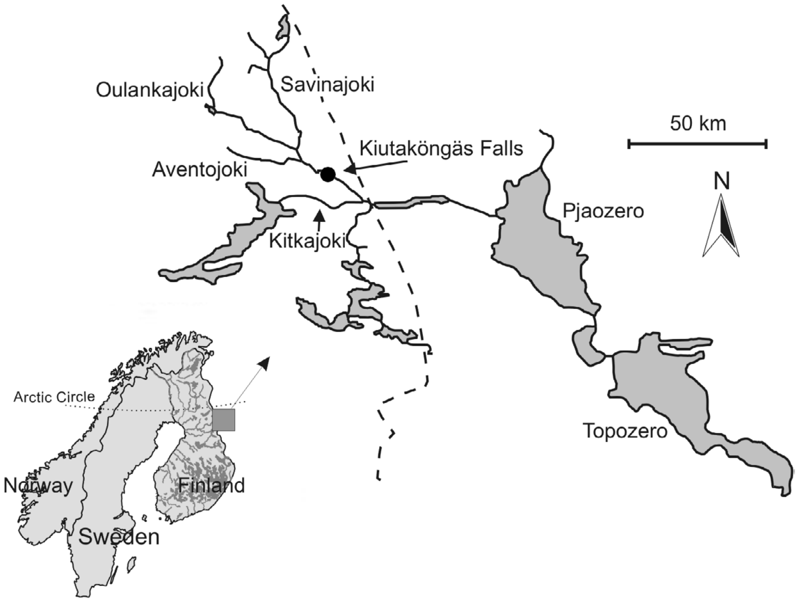

Fig. 1. Map of the Oulankajoki and some main tributaries, showing the tagging site (●; Kiutaköngäs Falls) of the brown trout. Pjaozero in Russia is the lake from where the trout were ascending. Dashed line indicates Finnish–Russian border.

ascent back to their natal river to spawn (e.g. Alm 1950, Toivonen 1972, Huusko *et al*. 1990, Nyberg *et al*. 2001, Rustadbakken *et al*. 2004). Upriver spawning migrations of the brown trout usually take place between spring and autumn, and may extend over hundreds of kilometres of the river system. The timing of the migration is dependent on the size of the river system, and in large rivers trout can start ascending as early as 6 months before settling in the spawning areas (Klemetsen *et al*. 2003). In northern areas, after spawning, fish usually overwinter in the river, descend to the lake in the following spring/early summer, reside during the summer and following winter in the lake, and then initiate their next spawning run after a one-year gap. The number of repeat-spawners in the populations is often large (Huusko *et al*. 1990).

The influence of environmental conditions on the upstream migration of anadromous salmonids has been studied and discussed over several decades (e.g. Banks 1969, Trepanier *et al*. 1996). River flow, temperature and light conditions, together with their interrelationships, are frequently cited as influencing the river ascent both in anadromous (Jonsson 1991) and also in adfluvial salmonid populations (Trepanier *et al*. 1996, Rustadbakken *et al*. 2004). In this study, our objectives were to study the migration and the concurrent changes in the habitat use of boreal adfluvial brown trout in the Oulankajoki, a river in northern Finland. This is among the first studies focused on adfluvial brown trout, and by extending almost over a year (July–May) it also described the period rarely reported in scientific literature, i.e. post-spawning and descent phases of the spawning run. The study included minimum daily movements and habitat use of 20 radio-tagged fish determined separately for upstream migration period, spawning season, overwintering, and migration back to the lake. Discharge and temperatures were correlated with movements.

Material and methods

Study area

The study was conducted in the Oulankajoki (66°2´N, 29°19´E), a river in northern Finland (Fig. 1). The flow regime of the river (annual mean 25.5 $m^3 s^{-1}$) is natural and typical for boreal streams (Petersen *et al*. 1995). Minimum flows (down to 3 $m^3 s^{-1}$) occur in late winter and peak flows soon after snowmelt (in May–June, up to 249 $m^3 s^{-1}$). Most of the river is ice-covered from mid-November to early May, and water temperature is highest (up to 21–23 °C) in July. The main branch of the river is mostly 40–80 m wide, with the riparian community dominated by conifer trees. The streambed is dominated by cobbles and boulders in the riffles and rapids, and by finer particles in the pool sections that are up to 500-m wide. At mean discharge, depth is 0.5–1.0 m in most fast-flowing sections and over 10 m in pools. The Oulankajoki is located in a wilderness area with a natural channel form. Fish species present in the river are: brown trout, European grayling (*Thymallus thymallus*), northern pike (*Esox lucius*), alpine bullhead (*Cottus poecilopus*), perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernuus*), roach (*Rutilus rutilus*), minnow (*Phoxinus phoxinus*), whitefish (*Coregonus lavaretus*), burbot (*Lota lota*), and nine-spined stickleback (*Pungitius pungitius*).

Fish tagging

The brown trout for the study were caught at the Kiutaköngäs Falls on the Oulankajoki. These natural falls form a partial obstacle for brown trout migration and are located approximately 60 km upstream from Pjaozero, which is the aquatic system where the fish spent their lake years (Fig. 1). On their ascent, fish gather below the falls to wait for optimal flow and/or temperature conditions to enable them to continue their upstream migration. Since 1965, local fisheries managers have annually caught with a small seine and tagged (with Carlin tags) tens of trout in order to transport them above the falls to ensure that at least these fish manage to pass the falls regardless of environmental conditions. Tag returns have determined that migrating brown trout have been recaptured at maximum distance of 71 km upstream from the falls (A. Huusko and M. Saraniemi unpubl. data).

Experimental fish (n = 20, mean and range of total length, mass, and age: 62.5 (53–71) cm, 2443 (1500–3670) g, and 7.6 (5–14) years, respectively) were taken from the catch of the fisheries managers between 9 and 15 July 2003 at the Kiutaköngäs Falls. At the time of capture and tagging, water temperature at the falls ranged between 16.9 and 18.2 °C. One fish was male and the other 19 were females. Sex was determined from external morphological characters (shape of head, hook on lower jaw). The female dominance among the migrant fish has been persistent during the 40 years when the fish have been transported above the Kiutaköngäs Falls (A. Huusko and M. Saraniemi unpubl. data), the same was previously observed also in some other adfluvial brown trout populations (e.g. Alm 1950, Huusko *et al*. 1990), and in other salmonids as well (Jonsson and Jonsson 1993, Koizumi *et al*. 2006).

Immediately after capture, the fish were surgically implanted with radio transmitters (cylindrical ATS (Advanced Telemetry Systems) Model F1840: 52 mm long, 17 mm wide, mass 20 g in air, expected battery life 383 days, individual transmitter frequencies starting from 42.40 MHz with 20 kHz intervals) following the procedure described in Nykänen *et al*. (2001). Four to five simple sutures (Deknalon 3-0 non-absorbable line attached to a cutting needle) were used to close the incision. After surgery, the fish were allowed to recover in a net pen in the river until they had regained their posture and alertness. All the fish were released near the capture site within one hour after their capture. Five fish were released below and 15 fish above the falls, the latter group included the single male fish.

Fish movements and habitat characteristics

Fish were manually tracked from the shore or boat using an ATS Model R2100 receiver with an ATS loop antenna. The fish were located once each week between 8 a.m. and 4 p.m. from 9 July 2003 to 27 May 2004 until fish left Finnish side of the river system. Using triangulation, we were able to determine fish positions with an accuracy of ±25 m; coordinates of the positions were recorded on the spot with a Trimble GeoExplorer 3 GPS device with differential correction and an accuracy of 2 m. All fish positions were plotted on a computerised map of the river channel. For movement analyses, mean daily movement of the fish were determined as the net distance (measured along river channel and rounded to the nearest 50 m) between fish locations on two consecutive tracking occasions divided by the total number of days between trackings. This is a minimum estimate of daily movements, as the fish likely moved more between successive trackings.

Habitats used by fish were described qualitatively by classifying them according to stream velocity, turbulence and gradient criteria into pools (mean velocity < 10 cm s^{-1}, no turbulence, low gradient), runs (mean velocity > 10 cm s^{-1}, no turbulence, moderate gradient) and rapids (mean velocity > 10 cm s^{-1}, turbulent, moderate to high gradient). Additionally, sites just above the runs and rapids with relatively low velocity, turbulence and gradient were classified as transition zones. All habitat assessments were carried out by eye.

Records of discharge and local air and water temperatures were obtained from the Oulanka Research Station (University of Oulu) adjacent to the river about 1.5 km upstream from the tagging site. Air temperatures used in the analysis were mean daily values, while discharge and water temperatures were measured once during the daytime and they may deviate little from daily averages. Water temperatures were only available until the start of ice formation on 12 November.

Data analysis

Seasonal changes in the fish movement patterns and habitat use were examined after data for each fish were divided into four periods: (1) upstream migration, (2) spawning season, (3) overwintering and (4) migration back to the lake. Firstly, upstream migration was the period from tagging to the initiation of spawning. Secondly, spawning season was determined individually for each fish based on the movement pattern of the fish (moving from pool dominated areas to potential spawning areas) together with local information on water temperatures at which the eggs of hatchery-reared brown trout are ripe for spawning (the Oulankajoki and nearby Kitkajoki stocks). Thirdly, the period after the spawning season was designated as overwintering, which extended to period of ice melt and onset of the spring flood. Finally, the spring flood initiated the descending period, which ended up with fish migrating out of the tracking range to the Russian side of the river system. In respect of autumn migrating fish, the descend period started immediately after the spawning.

Seasonal differences in the mean minimum daily movement of the fish were examined with univariate repeated measures ANOVA. A Spearman rank order correlation analysis was used to examine the relationship between the mean minimum daily distance covered by fish and daily environmental variables (discharge, water temperature, and air temperature) over the entire study period. Where appropriate, data were normalized by natural log-transformation to enable the use of parametric tests. Null hypotheses were rejected at $p < 0.05$.

Results

Movements

Upstream migration

After tagging most trout rested for a few days near the release location. Three fish released above the falls fell back below the falls soon after release, and one of them remained there until it spawned and migrated downstream. All others, including those released below the falls, migrated upstream within a few weeks (Fig. 2).

Water temperature was warmest (up to 22.8 °C) at the beginning of August (Fig. 3) and fish remained relatively stationary at this time, residing in deep pools. Within two weeks, movements were again more variable with two different patterns apparent: (1) some individuals stayed localized in small areas until spawning, whereas (2) others migrated progressively resting in pools as needed (Fig. 2). On occasion, the progressive migrators headed temporarily downstream, but the main direction was upstream. The mean individual minimum daily movement varied between 52 and 568 m and an overall mean was 348 m day^{-1} (S.D. = 139 m, $n = 20$, Table 1). The mean distance from the release site to relocation sites varied among fish, between 1.5 and 16.1 km, with the furthest observation made 29.6 km upstream from the release location. During their upstream migration, trout were located primarily in the main channel, but as the spawning approached, they also moved into the

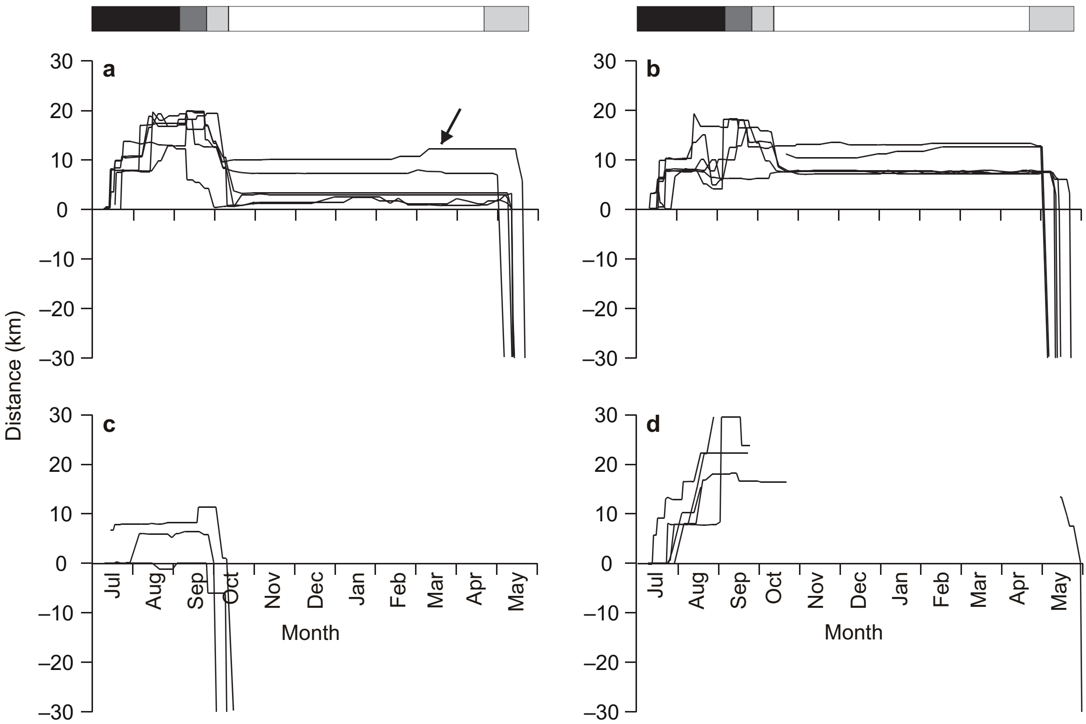

Fig. 2. Weekly locations of radio-tagged brown trout relative to the release site (0 km) in the Oulankajoki. **a** and **b**: 12 individuals with descend migration in the spring, divided into two line graphs for clarity; **c**: three fish with descend migration in the autumn; **d**: four fish that were lost and one that was not located during spawning and winter. Positive figures are distances upstream as measured along the centre line of the river, negative figures are distances downstream. Rectangle above gives the phases of the spawning migration and post spawning period (black = ascent phase, dark grey = spawning period, light grey = descent phase (both in autumn and spring), white = overwintering). The migration pattern of the single male fish tagged is indicated in **a** with an arrow.

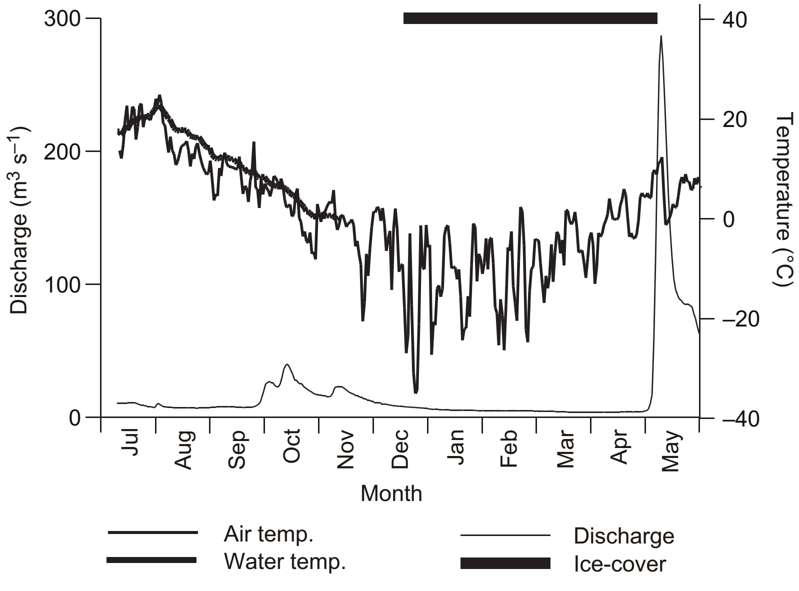

Fig. 3. Daily discharge, water temperature, mean daily air temperature, and the period of ice cover in the Oulankajoki during the study. The water temperature data were available only to the 12 November.

two main tributaries, the Aventojoki and the Savinajoki (Fig. 1). The furthest observation (29.6 km upstream from the Kiutaköngäs Falls) was made in the main channel.

Spawning season

Three fish were lost before spawning and two of them were caught by fishermen since their radio-tags were subsequently returned. One additional fish was lost after spawning. Most obviously these two lost fish with unknown fate were also caught by fishermen but were not reported. Two other fish were not located during spawning. One was later found at its overwinter location. The other one was relocated only during its downstream migration after ice break-up. Migrations and locations of the remaining 15 fish were observed without any specific problems.

Most fish started to find their way to suitable spawning areas by mid-September, at the water temperature of 12 °C. Altogether, the spawning migration from the Kiutaköngäs Falls onwards took the fish on average 9 weeks.

The estimated spawning season lasted from mid-September to the first days in October and spawning sites were distributed throughout the area of 0–19.5 km from the Kiutaköngäs Falls (Fig. 2). Most fish remained localized for at least two weeks. The mean individual minimum daily movement on the spawning site varied between 13 and 526 m and an overall mean was 208 m day^{-1} (S.D. = 160 m, n = 15, Table 1). By the completion of the spawning period the water temperature had decreased to 9 °C (Fig. 3).

Table 1. Basic statistics of the average minimum daily movements (metres per day) of radio-tagged brown trout in the Oulankajoki in the ascent phase, during spawning, over-winter, and in the descent phases. The values are calculated from the mean values for each fish.

	Ascent	Spawning	Winter	Descent
Mean	348	208	53	2062
S.D.	139	160	23	3514
Range	52–568	13–526	17–84	112–11371
Median	361	186	59	717
n	20	15	12	11

Winter

After the spawning season, radio-tagged brown trout showed considerable variation in migratory behaviour. The most common pattern was a directed downstream movement to overwintering habitats. Only one fish moved 1.4 km upstream. Most fish (12 of 15 fish) spent the winter along the main branch of the Oulankajoki while three fish migrated downstream to lakes in Russia immediately after spawning (Fig. 2). Migration to winter habitats occured mainly in the first half of October at the mean water temperature of 6 °C (Fig. 3).

All fish staying in the river found overwintering areas upstream of Kiutaköngäs Falls, with the mean distance from the falls varying between 1.3 and 13.2 km. During winter brown trout were clearly stationary (Fig. 2), with mean minimum daily distances moved by trout varying between 17 and 84 m, and an overall mean of 53 m day^{-1} (S.D. = 23 m, n = 12, Table 1). However, more extensive movements were observed at the end of December and at the beginning of January and February with few fish moving more than 1 km between weekly observations. The most severe frost (minimum air temperature –35.8 °C) during that winter took place at the same time (Fig. 3). It is also noteworthy that fish moved back and forth rather than remaining at the secondary site selected. The winter season lasted on average 32 weeks and ended with the downstream migration. None of the fish staying in the river died during winter.

Descent to the lake

Spring migration from the river started at the time of ice break-up. The river was ice-free on 7 May. Altogether the migration lasted about a month beginning at the end of April with the highest intensity taking place in the first half of May (Fig. 2).

Downstream migrations in the autumn (n = 3) and spring (n = 13) were notably fast with daily distances covered reaching up to 22.5 km (Fig. 2). Two fish were more unhurried in their movements and rested 1–2 weeks in pools before continuing downstream migration. The

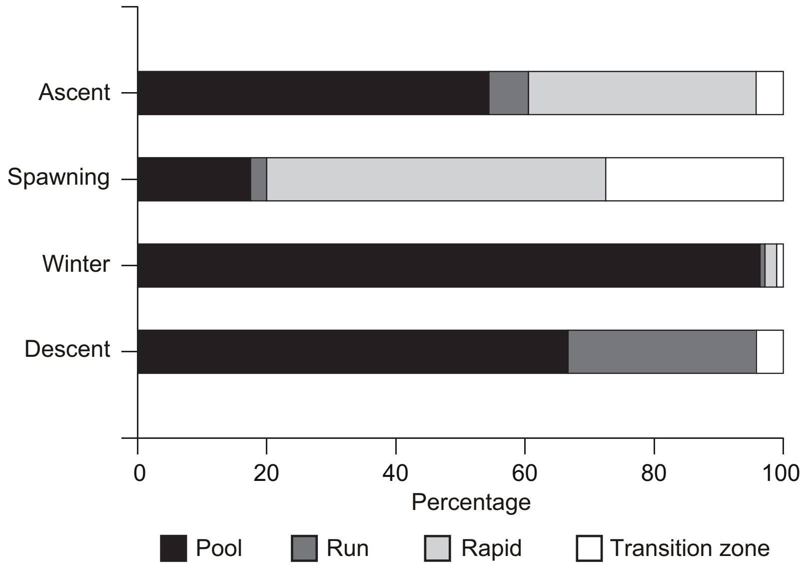

Fig. 4. Habitat use (percentages from the total number of fixes in each period) by radio-tagged brown trout during the phases of the spawning migration and post-spawning period. *See* text for the description of the habitat class characteristics.

mean individual minimum daily movement of the downstream migration varied between 112 and 11 371 m, with an overall mean of 2062 m day^{-1} (S.D. = 3514 m, n = 11, Table 1).

Overall movements

Trout moved less in winter than during either the upstream (repeated measures ANOVA: $F_{3,18}$ = 10.86, $p < 0.001$, n = 7, followed by Tukey's test with pairwise comparisons, $p = 0.011$) or downstream migrations (pairwise comparisons: $p < 0.001$). The trout were relatively localized during spawning and there was no significant difference in movement between spawning and winter seasons (pairwise comparisons: $p = 0.363$), whereas the difference was significant between spawning and downstream migration (pairwise comparisons: $p = 0.022$). Fish made their longest mean minimum daily movements during the upstream and downstream migrations, and no difference in movement activity was detected between these two periods (pairwise comparisons: $p = 0.540$). As compared with females, the single male fish tagged did not show any differences in migration pattern (Fig. 2).

Mean minimum daily distance covered by the fish correlated positively with daily discharge (Spearman rank order correlation: $r_S = 0.266$, n = 318, $p < 0.001$) and air temperature ($r_S = 0.658$, n = 318, $p < 0.001$) over the entire study period. There was also a positive correlation between mean minimum daily movements and water temperature ($r_S = 0.526$, n = 127, $p < 0.001$), but the data on water temperature was available only until 12 November.

Habitat use

During upstream migration radio-tagged brown trout selected primarily deep pool sections of the river (Fig. 4). Half of the observations were made at sites with low velocity. The areas where trout remained localized for two or more weeks, especially during hot weather in late July and early August (Fig. 3), were 4–28 m deep. During migration to spawning areas fish were often detected in rapids as well.

During spawning, brown trout favoured sites of moderate stream velocity. Fish were commonly detected in pool–rapid transition zones, but also in relatively low velocity areas in rapids. Eight individuals spawned in the Savinajoki (up to 19.6 km from Kiutaköngäs upwards) and one in the Aventojoki, while the remaining fish spawned in the main channel of the Oulankajoki within a distance of 16 km from the tagging site.

In winter, radio-tagged brown trout strongly selected pool habitats (96% of observations). Overwintering sites in the river were situated in more restricted area than in the previous two seasons (i.e. the pre-spawning migration and during spawning). All trout tracked during winter resided in the main channel within the 13-km river section from the Kiutaköngäs Falls to the junction of the main side channels (Fig. 1). In comparison with winter behaviour, downstream migrating fish were again more variable in their habitat selection, and in addition to the pools, they were often also found in runs.

Discussion

Adfluvial brown trout migrations to spawning areas in the Oulankajoki were similar to movement patterns observed in anadromous salmonids studies. Anadromous salmonids have been reported to move in phases during migration from the river entry to spawning areas: (1) steady progress with periods of active swimming alternating with stationary episodes, (2) followed by a relatively long residence period, and (3) finally short upstream migration just before spawning (e.g. Bagliniere *et al.* 1990, Thorstad *et al.* 1998, Erkinaro *et al.* 1999, Økland *et al.* 2001). In this study, once brown trout got above the Kiutaköngäs Falls, they continued their upstream movement quickly towards potential spawning areas. Some fish remained localized for most of the pre-spawning time, while others (53%) were more active and sometimes even moved in a downstream direction. Similar behaviour has previously been reported for anadromous Atlantic salmon in the River Tana, northern Norway (Økland *et al.* 2001). The variable movement pattern observed among fish was considered to involve selection of a spawning site, finding potential mates, or locating a position where to spend the time until spawning and this behaviour was classified as a search phase (Økland *et al.* 2001). In addition to these factors, the reason for bi-directional movements in the Oulankajoki may have been related to a search for deep pools in order to find refuge from high water temperatures (up to 22.8 °C) at the beginning of August 2003. Salmonids are commonly cool-water species, and the brown trout are known to prefer water temperatures from 3 to 20 °C (Crisp 2000). At lower or higher temperatures migration can cease (Crisp 2000). In the depths of the pools fish may have been able to find preferable holding sites. In addition to the pools, brown trout has been seen to use also small groundwater fed streams as cool water refuges (Clapp *et al.* 1990, Garret and Bennett 1995).

This study did not reveal any factors affecting the onset of the spawning migration from the lake. The fish were captured and tagged on their spawning migration below the Kiutaköngäs Falls, approximately 60 km upstream from the lake. Therefore the data reflects the later phase of the pre-spawning migration, and fish could also have spent some time below the falls before being captured. However, it is very likely that the spawning run started soon after the ice melting in late May–early June, and therefore the brown trout ascended into the Oulankajoki well before the spawning (Khalturin 1971). Overall, during their stay in the river the radio-tagged trout seemed to move more during high discharges and elevated air and water temperatures. This is logical because during winter period fish were very localized and discharge did not vary much, while most of the longest mean minimum daily movements took place during upstream and downstream migrations associated with higher discharges and temperatures. Fish tracking was performed only once per week which does not permit a very detailed analysis of factors affecting movements within a migration phase. For example, river flow can change rapidly within hours or days, and fish observations collected at a coarser level of temporal resolution are unsuitable for analysing whether rising or falling flow levels have the impact on movement activity (Trepanier *et al.* 1996). In general, considerable data supports the view of river flow affecting salmonid upstream migration but no joint consensus exists on the effect and its mechanisms (Banks 1969, Trepanier *et al.* 1996, Thorstad *et al.* 1998, Erkinaro *et al.* 1999, Økland *et al.* 2001).

Exact spawning sites were not located in this study, but generally fish during the spawning phase favoured typical salmonid spawning habitats (Frost and Brown 1967, Elliott 1994). Brown trout were observed mostly in rapids and pool–rapid transition zones which were characterized by moderate stream velocity and gravel substrate. The movement to spawning areas and spawning period for brown trout in the Oulankajoki occurred at warmer water temperatures than expected. According to the literature, brown trout spawn generally at the water temperature of 2–6 °C (e.g. Elliott 1994), while in this study spawning occurred between 9 and 12 °C. Water temperatures in the Oulankajoki decreased to 6 °C only by mid-October and by that time most of the radio-tagged trout had already moved to their winter habitats. It is possible that due to cold nights the water temperatures were lower at night than during the day when they were measured, and reported temperatures may be somewhat higher than average daily values. In general, day length and water temperature are considered key factors in regulating the start of spawning, but there is large variability in the absolute values between populations and rivers (Crisp 2000, Armstrong *et al.* 2003). Brown trout spawn earlier in the north than in the south since the water temperature during the winter is lower and it takes more time for eggs to develop (Klemetsen *et al.* 2003). Day length seems to have major impact on the timing as the fish spawn approximately at the same time every year. However, the most important factor is physiological readiness to spawn, as when the right time is getting closer other factors seem to lose their significance (Crisp 2000).

Interestingly, most of the tagged brown trout (13 of 16 individuals) overwintered in the Oulankajoki, and returned to the lake in spring. There were thus two different behavioural patterns, the autumn and the spring descent-migrations after spawning. Unfortunately, many telemetric studies of salmonid spawning migrations cover only the ascent phase and spawning without any focus on the behaviour after the spawning (e.g. Trepanier *et al.* 1996, Jensen *et al.* 1998, Erkinaro *et al.* 1999, Økland *et al.* 2001). Rustadbakken *et al.* (2004) reported that all land-locked brown trout in a small southeastern Norwegian river descended to the lake soon after the spawning. It may well be that in northern rivers, overwintering of the spawners in rivers is more common than in southern rivers. Habitat hydraulic conditions of the river, particularly the availability of suitable overwintering habitats, the migration distance for spawners, size of the spawners, and many other factors likely play a role in the process. Spawning demands a huge energy input, and therefore it might be better to rest and recover in the river for the winter and return to the lakes with the spring flood (Jonsson 1991, Jonsson and Jonsson 1993). Activity, feeding and growth would be low during the winter — in the lakes as well — so after spawning the fish do not lose much energetically by staying in rivers, which are often poorer feeding areas. Available overwintering habitats in rivers may be restricted, which may cause fish to migrate to lakes after spawning in the autumn. This propensity to migrate immediately after spawning may be more common in relatively small rivers (Rustadbakken *et al.* 2004), where e.g. ice conditions can be very severe over winter (Brown and Mackay 1995, Brown 1999, Huusko *et al.* 2007).

The brown trout in the Oulankajoki dispersed after spawning from rapid/run habitats mainly downstream to the deeper and more slowly flowing river sections, and during winter the fish were very localized. Habitat selection of the adult trout clearly differed between summer and winter so that during the cold season the fish used deeper water and lower current velocities than in the summer. This seasonal change in behaviour and habitat use is typical for adult salmonids in boreal regions as water temperatures decrease (Clapp *et al.* 1990, Brown and Mackay 1995, Klemetsen *et al.* 2003, Carlsson *et al.* 2004, Huusko *et al.* 2007). Habitats with slow water flow, such as pools, are often used as overwintering sites by adult salmonids. In regions with subzero air temperatures, fish usually settle down in these sites before the development of ice cover (Clapp *et al.* 1990, Brown and Mackay 1995, Brown 1999, Nykänen *et al.* 2004), as was the case in our study river.

In midwinter, some overwintering trout in the Oulankajoki made movements that differed from the general pattern of staying localized in a pool. Although ice conditions were not quantified in the study, it is possible that ice-related changes in the pool areas of the Oulankajoki caused the habitat shifts observed in midwinter. The very low air temperatures (up to –35.8 °C) probably changed ice and habitat conditions in the river. Studies on other salmonids have shown that fish generally move long distances in the winter only if the changing ice conditions force them to leave their preferred pool habitats (Brown 1999, Brown *et al*. 2000, Nykänen *et al*. 2004). For example, as a result of ice accumulation, water velocity and depth conditions change and can become unfavourable for the fish (Brown and Mackay 1995, Cunjak 1996, Brown *et al*. 2000, Kylmänen *et al*. 2001). These kinds of changes are perhaps most evident in strongly seasonal northern regions, such as our study area, where the rivers are fully or partially ice-covered for almost half of the year, making conditions in the river variable due to surface and underwater ice accumulation (Alfredsen and Tesaker 2002). Due to ice, there are a limited number of suitable winter habitats in the river (Komadina-Douthright *et al*. 1997, Huusko *et al*. 2007), which was also a probable reason for more restricted occurrence of the brown trout in the Oulankajoki area in the winter than during other seasons.

In general, radio-tagged brown trout stayed in relatively large stream channels on their spawning migration as they ranged only in the main channel and two main tributaries of the Oulankajoki. The summer and autumn of 2003 were exceptionally dry in the study river: mean discharge in July 2003 was 10 m^3 s^{-1} whereas in 1991–2000 it averaged 22 m^3 s^{-1}. Low discharge probably limited the migration area and in summers with higher flows fish may migrate and spawn in smaller tributaries as well. Seasonal changes in water temperature, river hydrology and habitat characteristics continually modify the spatio-temporal environment of both purely resident and migratory riverine fish (Rabeni and Sowa 1996). Fish respond to environmental changes by selecting and shifting habitats according to their individual needs so that at all times their fitness remains as high as possible (Kramer *et al*. 1997). The furthest observation during our study was about 30 km upstream from the Kiutaköngäs Falls, however, it is likely that at least one other fish spawned and overwintered somewhere further upstream. This individual was not located between 23 September 2003 and 12 May 2004 and its last observation, before being 'lost', was 24 km up from the tagging location. Despite extensive tracking throughout the watershed, it was not located until the spring migration suggesting it must have spawned and overwintered somewhere in the upper reach of the Oulankajoki. Therefore, in spite of efficient methods and considerable tracking effort, there is always room for more efficient technologies to observe fish and refinement of the research efforts (Scruton *et al*. 2002).

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