Homing behaviour of Atlantic salmon (S*almo salar*) during final phase of marine migration and river entry

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Homing behaviour of Atlantic salmon (*Salmo salar*) during final phase of marine migration and river entry

Abstract: Little is known about Atlantic salmon behaviour during the last phase of the marine homing migration and subsequent river entry. In this study, 56 adult Atlantic salmon in the Alta Fjord in northern Norway were equipped with acoustic transmitters. Salmon generally followed the coastline, but their horizontal distribution was also affected by wind induced spreading of river water across the fjord. Mean swimming depth was shallow (2.5–0.5 m), but with dives down to 30 m depth. Timing of river entry was not affected by river flow, diel periodicity or tidal cycles. Movements during the last part of the marine migration and river entry were unidirectional and relatively fast (mean 9.7 km day^{-1}). However, migratory speed slowed as salmon approached the estuary, with a significant lower speed in the innermost part of the estuary than in the open fjord. Migration behaviour seemed not affected by handling and tagging, as there were no behavioural differences between newly tagged fish and those captured and tagged one year before their homing migration.

Keywords: genetic assignment; migratory behaviour; returning salmon; *Salmo salar* L.; swimming depth; vertical and horizontal distribution

INTRODUCTION

Atlantic salmon (*Salmo salar* L.) is a species of great biological, cultural and economic importance. Abundance, marine survival and in some cases growth, have declined in large parts of the species distribution range for unknown reasons (Parrish et al. 1998, ICES 2011). The anadromous life cycle involves long and complex migrations through different habitats. Knowledge on migration timing and patterns and how these are affected by environmental factors is crucial to identify critical life stages and anthropogenic impacts, and to be able to implement effective mitigation measures.

Few studies have focused on the marine migration behaviour, mainly due to methodological constraints. Radio telemetry has been used to track individual Atlantic salmon in freshwater (Heggberget et al. 1993, Karppinen et al. 2004), resulting in substantial knowledge on within-river migration of adults returning for spawning (Thorstad et al. 2008). Due to the high electrolyte level, radio telemetry cannot be used in seawater. Recent improvements of acoustic telemetry methods have opened new opportunities to follow individual fish in near coastal areas (Lacroix and Voegeli 2000, Cooke et al. 2011). This has resulted in a number of studies of marine post-smolt migration towards feeding areas in the ocean (Thorstad et al. 2012), but studies of adults during their return migration are still few.

There appears to be two phases of the marine migration from the ocean to the natal river; an initial phase with navigation from feeding areas towards the coast, and a second phase with more precise orientation in coastal waters (Hansen et al. 1993). This second phase is of special concern, since near shore areas are often densely populated and heavily affected by human activities such as boat traffic, harbour and industry infrastructure, aquaculture, pollution and fishing, which may affect migration patterns (Pierce et al. 1990, Smith 1990, Alabaster et al. 1991). Near-coastal areas may also be complex habitats, forming transition zones between rivers and the ocean, being subjects to both marine (tides, waves, saline water) and riverine influences (freshwater and sediments). To collect basic information about the generally preferred migration pattern, the ideal situation is to study the migration in a natural environment with minimal anthropogenic factors possibly influencing the migratory behaviour and progression. Such information is required when evaluating the movements in declining populations from areas heavily influenced by for instance obstacles, altered water quality and global warming. Northern areas, like the Alta Fjord where this study was performed, are relatively pristine with a sparse human population and little industrial development and other constructions. Information about fish migration in these areas may therefore be important in understanding the basic migratory behavior.

A large number of studies have examined the effects of environmental factors upon the timing of river entry on adult Atlantic salmon based on data from riverine counting fences (e.g. Dahl et al. 2004, Jonsson et al. 2007). One challenge associated with detecting relationships between environmental variables and the upstream migration using such methods is the lack of information on how many fish are present downstream of the counting site (Trépanier et al. 1996). An increase in upstream counts may not necessarily mean that conditions are improved, but could reflect increased fish abundance for other reasons (Thorstad et al. 2008), or increased detection probability. On the contrary, environmental conditions may be favourable for upstream migration, but count data may show little migration activity if there are no fish available in the area. Moreover, fish counters are usually placed in fishways, traps or dams and the environmental factors important to stimulate salmon to pass such sites may be site specific and different from natural river sections with other or no migration barriers (Banks 1969, Thorstad et al. 2008). Tagging fish with acoustic transmitters enables us to follow their behaviour both before and during river entry to analyse the impacts of environmental factors on river entry in natural rivers without fishways or other obstacles.

The aim of this study was to analyse Atlantic salmon migration pattern during the last part of the spawning migration through a pristine coastal area and during river entry using acoustic telemetry methods. We tested the following hypotheses: 1) The horizontal distribution of Atlantic salmon is closer to the coastline as the fish approach the river mouth, since river water may be used as a guide for orientating to the river. 2) Swimming depths are closer to the surface as salmon approach the estuary, which may happen if olfactory clues from the river in the upper part of the water column facilitate location and recognition the river (Quinn 1990). 3) River entry is stimulated by increased water discharge in the river, and occurs mainly during the night and ebb tide, according to previous studies based on fish counts (Jonsson 1991, Potter et al. 1992, Smith and Smith 1997, Jonsson et al. 2007). 4) Marine migration speeds decline towards the river mouth, which may happen if the fish need time to ensure recognition of the home river and adapt to freshwater (Hansen and Quinn 1998). 5) Marine migration speeds increase with increasing river discharge, which may happen if increased freshwater supply to the fjord ease river recognition (Thorstad et al. 2010). 6) Migration is not affected by recent capture, handling and tagging as suggested by Thorstad et al. (2000), which may be tested by use of long lifespan telemetry tags enabling the comparison of the return migration between newly captured and tagged fish and fish tagged a year before the homing migration.

MATERIAL AND METHODS

STUDY AREA

The Alta Fjord, northern Norway (70°N 23°E), is a large open fjord, which is 15 km at its widest and 488 m at its deepest (Fig. 1). The fjord opens through three channels into the Barents Sea. The tidal range is 1.5–2.5 m. The River Alta, with a catchment area of 7 400 km^2, is the major river draining into the fjord. The estuary in this study was defined as the first 2 km of the fjord, measured from the river mouth (zone 3 and 4). The mean annual water discharge of the river is 75 $m^3 s^{-1}$, with a spring flood that is occasionally higher than 1000 $m^3 s^{-1}$. The river length accessible to Atlantic salmon is 47 km, and a hydropower plant was constructed above this stretch in 1987. River Alta is one of the northernmost Atlantic salmon rivers in the world, with annual in-river catches between 6 and 32 tonnes during 1974–2007 (Ugedal et al. 2008). Adult salmon return to the river during May–August, and the river temperature varies from 3–15° C during this period. A small town with 12 000 inhabitants is situated at the mouth of the river.

RECORDING OF SALMON BY AUTOMATIC LISTENING STATIONS AND MANUAL TRACKING

In 2007 a total of five arrays with automatic listening stations (ALS) (Vemco Inc., Canada, model VR2) were deployed in the fjord. Three arrays were deployed 31 km (array #1, 21 ALSs), 17 km (array #2, 14 ALSs) and 4 km (array #3, 11 ALSs) from the river mouth in lines across the fjord with 400 m separating each ALS (Fig. 1). The ALSs were deployed 5 m below the surface. The arrays were divided into eastern side (three ALSs from east), central part, and western side (three ALSs from west). Further, ten ALSs were deployed at 3 m depth in two arrays in the river outlet

2.8 km (array #4, 800 m between each ALS) and 2 km (array #5, 400 m between each ALS) from the river mouth. In addition, two ALSs were deployed 2 m below the surface in the river mouth (array #6) and three ALSs 5 km upstream in the river (array #7). In 2008, similar arrays were deployed 31 km (array #1), 4 km (array #3) and 2 km (array #5) from the river mouth, as well as two ALSs in the river mouth (array #6). The sea depth exceeded 30 m at all arrays in the fjord. When tagged salmon came within the range of 100–600 m from an ALS, the individual id code, depth (for 30 of the tags) and the time were recorded by the ALS (detection range depended on environmental conditions such as currents, waves, and haloclines). In array #1–5 and river mouth (array #6), the first registration of each salmon was used as the time of arrival. The last registration of each individual registered in the river mouth was used as the time of river entry. To confirm that salmon registered in the river mouth actually entered the river, manual tracking in the river was performed from a boat during July–October using a VR100 receiver (Vemco Inc., Canada).

RECORDING OF ENVIRONMENTAL VARIABLES

Water temperature, salinity, tidal cycle, light intensity, water current, and wind speed and direction were recorded in the fjord. Water temperature and discharge were recorded in the river. Salinity and temperature profiles were recorded at every second ALS across array #1–3 down to 12 m depth on 6 and 13 July 2007 at low tide, using an SD204 conductivity, temperature and depth (CTD) sonde (SAIV AS, Norway). SD6000 water current meters (Sensordata AS, Norway) were placed three meters below the surface at the south-western and north-eastern side of array #3 (Fig. 1), recording the direction and speed of the water current every 30 min. The CTD- and current meter datasets were analysed, gridded and plotted using Matlab7.0.4.365

(R14). The tidal range was measured every 10 min with a depth sensing data storage tag (Star-Oddi, Iceland, model DST-milli-L) placed at the fjord bottom 1 km from the river mouth. Light intensities and wind direction were recorded every 15 min with a light meter and an anemometer with a data logger (Onset Computer Corporation, USA, model HOBO UA-002-64) placed on a small island in the inner part of the fjord (Fig. 1).

FISH CAPTURE AND TAGGING PROCEDURE

Eighty-two Atlantic salmon were trapped in 13 different bag nets (Fig. 1) in the Alta Fjord during 3–25 July 2007. This is a gentle capture method as the salmon swim freely inside the bag net (Thorstad et al. 1998). Scale analysis (Lund and Hansen 1991, Fiske et al. 2005) confirmed that 74 of the salmon were wild fish, and only these were used in this study. Based on external sex characteristics, these were 37 females (mean fork length (L_F) = 93 cm, range 80–109 cm, S.D. = 6; mean mass = 9.6 kg, range 6.5–14.2 kg, S.D. = 1.9), 22 males (L_F = 95 cm, range 66–110 cm, S.D. = 11; mean mass = 11.0 kg, range 4.5–18.0 kg, S.D. = 3.5) and 15 of unknown sex (mean L_F = 86 cm, range 61–98 cm, S.D. = 9; mean mass = 7.9 kg, range 2.9–12.5 kg, S.D. = 2.5). There were no significant differences in fork length (Welch's t-test, d.f. = 57, P = 0.26) or mass (Welch's t-test, d.f. = 56, P = 0.07) between the sexes. According to scale analysis, mean smolt age was 4.1 years (range 3–5). Four fish had spawned once and one fish twice before this spawning season. The fish had on average spent 2.9 years (range 1–7) from smoltification until they were captured for this study. There were no differences between the sexes in age of smoltification (Welch's t-test, d.f. = 47, P = 0.76) or in time from smoltification until capture for this study (Welch's t-test, d.f. = 57, P = 0.45).

The Atlantic salmon were brought directly from the bag net into a water tank on board a small research vessel for body measurements (fork length and mass), scale sampling and tagging. They were tagged with one of four types of individually coded acoustic transmitters: Thelma AS, Norway model MP-13 (n=21 , 13 × 31 mm, mass in water/air of 7/11g); Thelma AS, Norway model LP-16-short (n=23, 16 x 36 mm, mass in water/air of 6/14 g); Vemco Inc., Canada model V13P-1L (n=21, 13 × 36 mm, mass in water/air of 6/11 g); or Vemco Inc., Canada model V16P-4H (n=9, 16x71 mm, mass in water/air of 11/25g). The 30 Vemco transmitters measured depth with a pressure sensor (accuracy 2.5 m; resolution 0.22 m) and transmitted this information together with the fish identity code. All fish were externally tagged under the dorsal fin with a modified Carlin tag with contact and reward information.

Individuals were anaesthetised by immersion in an aqueous solution of 2-phenoxy ethanol in approximately 3 min (EC No 204-589-7, SIGMA Chemical Co., USA, 0.5 ml l^{-1}). The transmitter was inserted through a 2.0–3.0 cm incision on the ventral surface anterior to the pelvic girdle. The transmitter was subsequently pushed gently forward into the body cavity. The incision was closed using two to three independent silk sutures (2.0 Ethicon, Belgium). Following recovery (5–10 minutes), the salmon were transported 300 m away from the bag net (to avoid recapture in the same bag net) and released. Mean distance from the release site to the river mouth was 24 km (range 19–34 km, S.D. = 4) (Fig. 1).

To assess possible effects of being newly tagged on fish behaviour, the results were compared to a ‘control’ group of eight Atlantic salmon that were acoustically tagged in the same river as kelts in May 2007 (see Halttunen et al. 2009 for details), and recorded during return migration as multiple spawners more than one year later, in 2008.

DATA ANALYSES

Differences in the horizontal distribution along the different ALS arrays and differences in the horizontal distribution between periods with and without wind were tested with Chi-square tests. To take into account the time lag of wind forces on the water currents, mean average wind speed and direction from the last two hours before the passage of salmon in the ALS array were used. Due to the low number of salmon registered at each ALS array (range 26–33), the wind speeds were divided into only two categories: "no wind" was defined as wind speeds less than 3.0 m s^{-1} and "wind" as wind speeds from 3.1–13.4 m s^{-1} (highest measured value). Brackish water was defined as salinity < 30.

Since the individual swimming depths had unequal variance, difference in swimming depth between the different ALS arrays was tested with Welch's *t*-test (two-way *t*-test assuming unequal variance).

The relationship between time of river entry and river flow the same day and cumulative changes in river flow from one, two and three days before river entry, were tested with linear regression analyses. To test if salmon entered the river during day or night, night was defined as 2000–0800 hours, which during the study period corresponded to light intensities less than 20 000 lx. Chi-square-tests were used to test for differences between river entry at day or night, during different stages of the tidal cycle (divided into three hour phases: high, ebbing, low or flooding tide) and between the different combinations of day and night and different stages of the tidal cycle. In order to explore if timing of river entry (day-of-the-year, day or night, river flow, tidal cycle) depended on fork length or body mass, a redundancy analysis (RDA, Legendre and Legendre 1998) was used as ordination method. The proportion of the constrained inertia (the sum of the variance from all included parameters) from the total inertia was calculated, which in RDA gives the proportion of variance. The package “Vegan” (Oksanen 2008) was used in the software program R 2.8 (http://www.r-project.org). Day and night and the tidal cycle groups were coded as dummy variables.

Time spent in the different parts of the fjord system and migratory speeds were calculated for those salmon registered at two subsequent ALS arrays. Since not all salmon were registered by all arrays, the sample sizes for these analyses were smaller than the total number of salmon registered. Migratory speed was estimated as individual body lengths (L_F) per second and km per day by using the shortest distance between the actual ALS recording the detection and the river mouth, thus giving minimum estimates (Thorstad et al. 2004). Individual mean and median values were used to calculate the populations mean and median in order to keep the data points independent. Differences in swimming speeds between the four zones were tested as unbalanced unreplicated repeated measurements by fitting a linear mixed model using the restricted maximum likelihood (REML) method. The resulting zone term in the fitted model was when tested with a likelihood ratio test against the null model. The package “lme4” (Bates and Maechler 2010) was used in the software program R 2.12 (http://www.r-project.org).

Relationships between migratory speed and river flow the same day as river entry and cumulative changes in river flow from one, two and three days before river entry were tested with linear regression analyses. Possible significant *p*-values were corrected for multiple comparisons using the Bonferroni procedure.

RESULTS

Fifty-nine of the 74 confirmed wild salmon (80%) were registered in the river mouth (array #6) and 56 (76%) entered the river. Of those 15 fish that did not enter the river mouth, five were recaptured by anglers in the fjord, seven left the fjord (registered in array #1) and the remaining three were only registered some few times at array #2. Genetic assignment tests supported the homing of the 56 salmon to their natal river (J.G. Davidsen, unpublished data). Data from these 56 salmon are used in the following analyses.

ENVIRONMENTAL DATA

The river flow in River Alta decreased during the period 5–26 July from 130 $m^3 s^{-1}$ to 75 $m^3 s^{-1}$. Thereafter it increased again (Fig. 2).

In summer, the surface layer in the Alta Fjord consists of brackish water due to the large freshwater supply from the river. The Alta fjord is a wide fjord where the Coriolis effect on the circulation is considerable (Svendsen 1995), allowing cross-fjord gradients in current velocities, salinity and temperature. Theoretically, the brackish water would therefore follow the eastern side of the Alta fjord towards the sea. This was clearly seen in the conductivity, temperature and depth (CTD) sections from July 13 (Fig. 3), when the lowest salinities were measured on the eastern side of the fjord on array #1–3 (only array #2 and #3 are shown in the figure). One week earlier, the vertical salinity gradients were stronger in the upper 4 m, while the horizontal gradients were weaker. This difference can be explained by the larger river runoff in early July than mid-July combined with stronger winds (up to 8 $m s^{-1}$) with northerly components, spreading the surface water across the fjord. Thus, in array #1 and #2 the brackish water (salinity less than 30) was found only along the eastern side on the 13 July, while covering the entire fjord section one week earlier. At array #3 the brackish water covered the upper 3–4 m all along the array both days.

The currents at both current meter locations were highly variable, and did not co-vary (Fig. 4). Surface temperature varied during the study period between 11 and 17 ºC.

HORIZONTAL DISTRIBUTION

Most of the salmon ($n = 70$, 95%) were captured, tagged and released on the eastern side of the fjord. Only four salmon (5%) were captured on the western side (Fig. 1). When passing the array #2, where 55 of the 56 salmon were registered, the horizontal distribution corresponded to the distribution at release (Chi-square test, $P = 0.22$, $n = 55$). Forty salmon (73%) were registered on the eastern side, 11 (20%) in the central part and four (7%) on the western side.

When passing the array #3 (Fig. 1), more salmon migrated in the central and south-western part of the fjord (Chi-square test, $P < 0.001$, $n = 55$). Twelve salmon (22%) were registered on the north-eastern side, 23 (42%) in the central part and 20 (36%) on the south-western side. In the array #4 and #5, salmon were equally distributed between the eastern (45% / 46%, respectively) and western side (41% / 50%, respectively), but only few individuals migrated in the central part (14% / 4%, respectively). The horizontal distribution along the third AL array #3 in 2007 differed between periods with and without wind. During periods with no wind, most salmon passed the array on the north-eastern side, while when the wind was blowing from the north (321–50°) most salmon were found in the central part of the array (Chi-square test, d.f. = 2, $P < 0.01$). Such difference was not observed when salmon passed array #2, #4 or #5.

There was no correlation between the passage time at array #3 and the current direction (in/out of the fjord) at either the north-eastern (Chi-square test, d.f. = 1, P = 0.86) or south-western current meter (Chi-square test, d.f. =1, P = 0.16) (Fig. 4). The current speeds (< 20 cm s^{-1}, Fig. 4) were consistently well below the estimated migratory speed of the salmon between the river mouth (array #6) and array #1 (average 63 cm s^{-1}).

SWIMMING DEPTH

The mean swimming depth when crossing array #2–5 varied from 0.5–2.4 meter (Table 1). When approaching the estuary, salmon swam closer to the surface. There was no difference in swimming depth between males and females. Seven of the ‘control’ fish (the fish that returned to the river again in 2008) had depth sensing tags. Mean migration depth was 5 m (range 0–8, S.D. = 2) at array #1, 4 m (range 0–6, S.D. = 2) at array #3 and 5 m (range 0–9, S.D. = 3) at array #5, which was slightly deeper than the newly tagged fish.

TIMING OF RIVER ENTRY

Females entered the river on average six days before the males (Welch’s t-test, d.f. = 42, P = 0.02). Timing of river entry did not depend on river flow on the day of entry (r^2 = 0.16, P = 0.06), or on cumulative changes from one (r^2 = 0.007, P = 0.70), two (r^2 = 0.003, P = 0.81) or three days before entry (r^2 = 0.003, P = 0.80). No difference in the timing of river entry was found in relation to the tides (Table 2). There was also no difference in the timing of river entry (day-of-the-year, day or night, river flow, tidal cycle) in relation to fork length or body mass, since only 14%

of the variation (Table 3) of the constrained axes in the redundancy analysis was explained by the timing of river entry between different sizes of salmon.

There was a clear difference in the light intensities between day (50 000–209 424 lx) and night (183–20 000 lx) during the study period (5–24 July), but no significant difference was observed in the timing of river entry between day and night or in the combination of tidal water and day or night (Table 2). Thirty salmon entered the river during day-time and 26 during night time (Chi-square test, d.f. = 1, *p*-value = 0.62).

MIGRATORY SPEEDS

Mean migratory speed from release to river entry was 9.7 km day^{-1} (0.1 L_F s^{-1}), but with large individual variation (n = 54, range 0.7–33.1 km day^{-1}, S.D. = 8.0). The mean speed was lower (Welch's t-test, d.f. = 50, P = 0.003) from release to the array #2 (9.3 km day^{-1}/0.1 L_F s^{-1}, n = 52, range 0.5–71.0 km day^{-1}, S.D. = 12.2) than from array #2 to the river mouth (16.5 km day^{-1}/0.2 L_F s^{-1}, n = 51, range 0.6–61.0 km day^{-1}, S.D. = 13.7). Median migratory speed (Fig. 5) was fastest in zone 1 (0.6 L_F s^{-1}) and decreased as the fish migrated towards the river mouth (0.1 L_F s^{-1}) (0.5 L_F s^{-1}, 0.4 L_F s^{-1}and 0.1 L_F s^{-1}for zones 2-4 respectively, Linear mixed-effects model, n = 159, P < 0.001).

Migratory speed from ALS array one to the river mouth did not depend on the river flow on the day of river entry (r^2 = 0.007, P = 0.55) or on cumulative changes in water flow from one (r^2 = 0.019, P = 0.31), two (r^2 = 0.028, P = 0.22) or three days before entry (r^2 = 0.013, P = 0.41). There was also no relationship between migratory speed in zone four (the last 2 km before river entry) and river flow on the day of river entry (r^2 = 0.033, P = 0.29) or changes in river flow from the day before entry (r^2 = 0.037, P = 0.27).

For the eight returning Atlantic salmon in 2008 (‘control’ group tagged the year before), the median migratory speed decreased as they approached the inner part of the fjord, similar to the newly tagged fish (Fig. 5). Median migratory speed from array #1 to the river mouth was 27.2 km day^{-1} (range 1.9–53.8 km day^{-1}, S.D. = 19.9), which was higher than when salmon were tagged and initially studied in 2007. However, while the ‘control’ group was registered at array #1, the registrations in 2007 started at array #2. Therefore, a larger part of the fjord was included in 2008.

DISCUSSION

These results from the relatively pristine Alta Fjord confirmed the hypothesis that horizontal adult migration path was closer to the coastline as the fish approached the river mouth, but the distribution was influenced by brackish water distribution: northerly winds spread the brackish water across the fjord and the Atlantic salmon seemed to follow this. Further, the results supported the hypothesis that the migration occurred closer to the surface as the salmon approached the river mouth, however the findings could not confirm that river entry was facilitated by increased water discharge and ebb tide and occurred mainly during the night. The results confirmed the hypothesis that the marine migration speed of returning Atlantic salmon declined towards the river mouth, however the hypothesis that marine migration speeds increased with increasing river discharge was not supported. A similar behaviour between newly tagged fish and those tagged the year before their homing migration, supported the hypothesis that the migration pattern was not largely affected by short-term capture, handling and tagging effects.

HORIZONTAL DISTRIBUTION

Atlantic salmon generally followed the coastline during their homing migration, which may suggest that the coastline was used as a guide for orientating to the river. The complex interface between open ocean and up-river migration pose special challenges, and salmon may use elements of many orientation systems (Quinn et al. 1989, Pascual and Quinn 1991, Olson and Quinn 1993). It is widely accepted that salmon at least partly, rely on olfactory information to orientate to their home river (Brannon 1981, Stabell 1982, Quinn 1990). The fact that most of the returning adults were observed on the eastern side in the outer and central part of the fjord, where the lowest salinities were measured, may suggest that the fish used this side of the fjord because it provided the best conditions to locate and recognise the river. At array #3, in the inner part of the fjord, the brackish layer covered the entire array and here the returning adults utilized both sides of the fjord.

Despite finding no correlation between the current direction measured at 3 m depth and migratory pattern at array #3, there was a significant relationship between wind direction and horizontal distribution of salmon when passing this array. This may indicate that the salmon distribution was influenced by wind induced spreading of river water across the array. The same pattern was observed during the outward post-smolts migration studied in the same fjord in the same year (Davidsen et al. 2009).

Despite the wind induced spreading of river water across the fjord mean migratory speed was always higher than measured current velocities, so it seems that salmon had an active swimming behaviour when passing the array #3. In other studies, Atlantic salmon have been found to be influenced by the tidal current by generally moving with the tide (e.g. Aprahamian et al. 1998), but also to swim with lower ground speed during ebb tide and higher during flood tides (Smith et al. 1981).

SWIMMING DEPTH

As salmon approached the estuary, they swam closer to the surface. Since the brackish water from the river outlet is in the upper part of the water column, one explanation for this behaviour may be that they use the brackish water layer to locate and recognise the river (Quinn 1990). The attraction may be due to both the lower salinity level and the river odour. Earlier gillnet studies have shown that returning Atlantic salmon usually remain near the surface (1–5 m depth), but occasionally make downwards movements in the water column (Stasko et al. 1973). Westerberg (1982) and Døving et al. (1985) reported that Atlantic salmon with acoustic tags moved up and down in the water column in association with fine-scale hydrographic stratification, and they both concluded that salmon searched for vertical gradients of odours from the home river rather than horizontal gradients. Another reason to migrate closer to the sea surface when approaching the river is to acclimate to the fresh water. Quinn (1990) suggested that by migrating in and out of the brackish water layer at the top of the water column in the estuary, salmonids can adjust to the salinity of their environment as they make the transition from salt water to freshwater.

TIMING OF RIVER ENTRY

Females entered the river in average six days earlier than males, which is consistent with findings in other studies (Dahl et al. 2004, Niemelä et al. 2006). Dahl et al. (2004) suggested that the earlier river entry of female Atlantic salmon may be due to females being older than males when performing their spawning migration.

Several previous studies indicate that older (larger) fish usually arrive earlier than younger (smaller) individuals (Power 1981, Jonsson et al. 1990a). However, in the present study there were no differences in size or age between the two sexes.

Changes in river flow did not influence the timing of river entry. Increased water discharge appears to be an important proximate factor stimulating adult Atlantic salmon to enter small rivers from the sea (Jonsson et al. 2007). However, this stimuli may act in combination with other environmental factors such as water temperature, light, tides and water chemistry (Jonsson 1991, Potter et al. 1992, Smith and Smith 1997). The fact that no correlation between river flow, tidal cycle and river entry was found in this study may be due to the generally large discharge of the River Alta (75–130 $m^3 s^{-1}$ during the study). In a large river like this, it may not be critical for salmon to enter the river at high river flow in order to safely migrate upstream or have the ebb tide to facilitate the recognition of the outflowing fresh water from the home river. This is supported by the fact that day-of-the-year, day or night time, river flow and tidal cycle at the time of river entry in total explained only 14% of the variation between different sizes of the salmon. This suggests that parameters other than those included in the analysis may be important for timing of river entry, or that timing of river entry in the River Alta simply depends on the time salmon reach the estuary and river mouth. If the latter is the case, timing of river entry may depend on factors influencing the migration in the outer fjord or open sea.

It has been suggested that the correlation between increased discharge and the time of river entry in large rivers is not due to the stimulus for Atlantic salmon to enter the river *per se*, but rather that increased freshwater supply to near coastal areas may aid salmon to recognise and find their natal river, increasing the number of fish entering fresh water compared to low flow periods (Thorstad et al. 2010). In the present study, there was no correlation between time of river entry and changes in river flow, one, two and three days before entry. However, since salmon were tagged and monitored in the last part of the spawning run, there may already have been enough freshwater in the fjord system to guide the salmon. The observation that river entry not is correlated with river flow in large rivers is also supported by other studies (Dahl et al. 2004, Karppinen et al. 2004).

Adult salmon entered the river during all phases of the tidal cycle. It has been suggested that Atlantic salmon entering the river during strong ebb currents may have been attracted by the outward flow of fresh water (Potter et al. 1992). However, there is little consensus among studies about the relationship between tidal phase and river entry (Potter 1988, Potter et al. 1992, Smith and Smith 1997, Karppinen et al. 2004). Given the wide variation in the physical, chemical and hydrographic characteristics of estuaries, this variation in the migratory responses of Atlantic salmon to the tidal cycle is perhaps not surprising (Smith and Smith 1997). In general, different sizes, forms and shapes of rivers may result in different relationships between Atlantic salmon behaviour and environmental factors.

The absence of a clear diel pattern in the timing of river mouth passage differed from that observed in a post-smolt study in the River Alta, when more post-smolts passed the river mouth at night during migration towards the sea (Davidsen et al. 2009). Nocturnal migration is thought to be an adaptive behaviour to reduce predation by visual predators like seals (Solomon 1982) and has been observed in several studies of returning Atlantic salmon (e.g. Potter 1988, Smith and Smith 1997). Even though the northern River Alta is situated on a latitude with midnight sun, light intensities were still lower than 20 000 lx at night, in contrast to the 50 000–200 000 lx measured during day time. The fact that no difference in the diel migration pattern was observed for adult salmon may be because they do not experience the same predation level as the smaller post-smolts.

MIGRATORY SPEEDS

The migratory speed slowed as salmon approached the estuary, and salmon had a lower migratory speed in the innermost part of the estuary (zone four) than in the open fjord (zone one–three). This change in travel rates may be an indication of a physiological need to adapt to the fresh water in the river, time to orientate towards the river mouth and to recognise the home river (Hansen and Quinn 1998), or to wait for optimal conditions for upstream migration (Jonsson et al. 1990b). The finding of decreasing travel rates when approaching the estuary confirm results from mark and recapture studies (Hansen et al. 1993, Hansen and Quinn 1998).

CONTROL FISH TAGGED THE PRECEDING YEAR

The migration behaviour of the eight returning Atlantic salmon in 2008 (‘control’ group tagged the year before) did not differ from the newly tagged fish. Similar to the newly tagged fish, median migratory speed decreased as they approached the inner part of the fjord, and the fish migrated close (4–5 m) to the surface. The migration behaviour seemed therefore not affected by capture, handling and tagging. This is in accordance with a laboratory study indicating that swimming performance of Atlantic salmon was not affected by transmitters used in the present study (Thorstad et al. 2000). To our knowledge, this study is first one using multiyear tags to capture the migration behaviour of Atlantic salmon, while Welch et al. (2011) have used this method on juvenile Pacific salmon.

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TABLES

Table 1: Mean swimming depth registered at the time Atlantic salmon (*Salmo salar*) passed the array #2–5 in the Alta Fjord. Mean values are based on individual means. Welch's *t*-test was used to test for significant difference between male and female swimming depth.

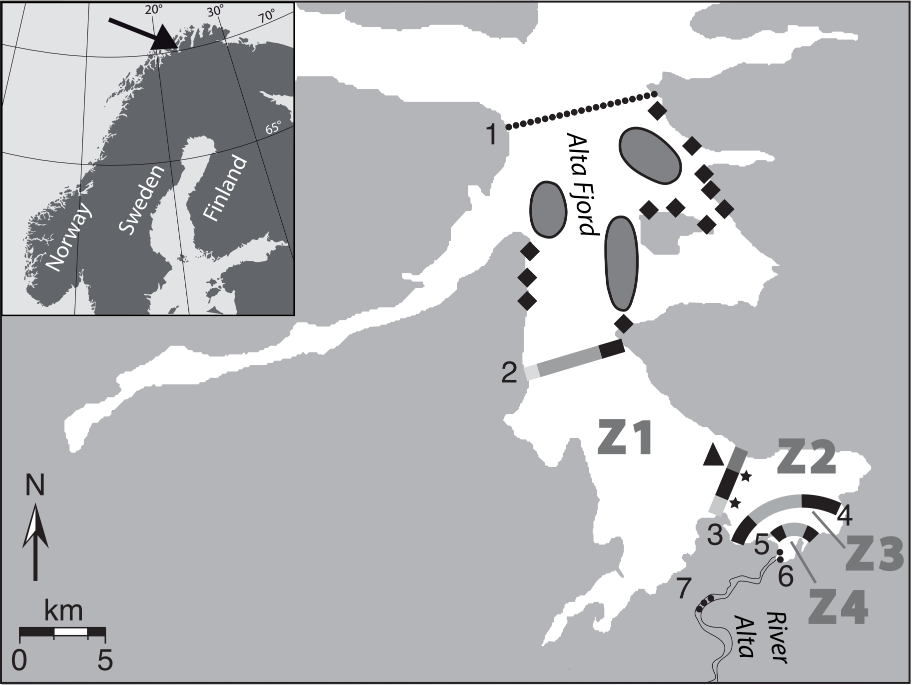
ALS Array	*n*	Mean (m)	S.D. individual mean (range) (m)	Deepest individual recording (m)	Mean depth females (m)	Mean depth males (m)	*p*-value (between sexes)
2	23	2.4	3.7 (0.0–16.1)	29.7	2.6	1.8	0.57
3	24	1.1	1.5 (0.0–6.4)	18.9	0.9	1.4	0.36
4	18	1.5	1.9 (0.0–6.7)	10.9	1.4	1.7	0.75
5	21	0.5	0.7 (0.0–1.8)	14.6	0.4	0.9	0.18

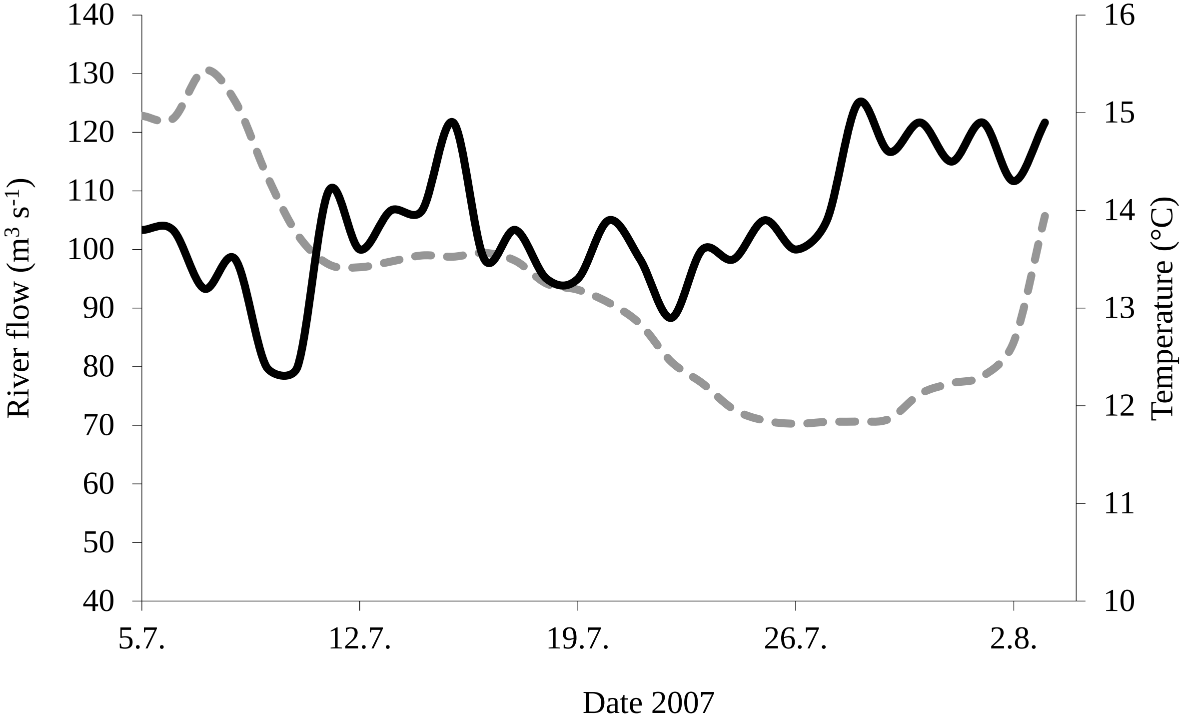
Table 2: Comparisons of the number and proportions of homing Atlantic salmon (*Salmo salar*) entering the river during 1) different stages of the tidal cycle, and 2) for different combinations of day and night and different stages of the tidal cycle. Chi-square-tests were used to test for differences between different stages of the tidal cycle and between the different combinations of day and night and different stages of the tidal cycle.

	Number (n =56)	%	P-value
High tide	15	27	
Ebbing tide	13	23	
Low tide	9	16	
Flooding tide	19	34	0.29
High tide day time	7	13	
High tide night time	8	14	
Ebbing tide day time	7	13	
Ebbing tide night time	6	11	
Low tide day time	5	9	
Low tide night time	4	7	
Flooding tide day time	11	20	
Flooding tide night time	8	14	0.71

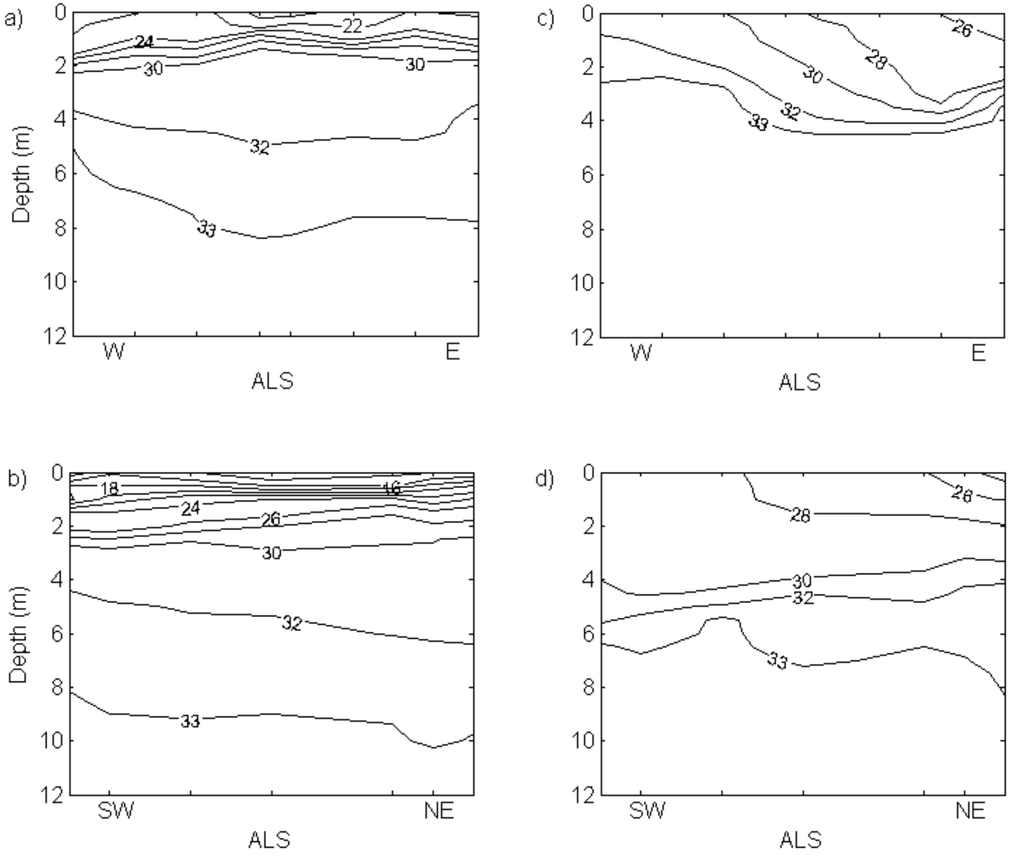
Table 3: Results from a redundancy analysis (RDA) exploring whether timing of river entry (day-of-the-year, day or night, river flow, tidal cycle) of Atlantic salmon (*Salmo salar*) depended on fork length or body mass. The proportion of constrained and unconstrained inertia (the sum of the variance from all included parameters) from total inertia was calculated, which in RDA gives the proportion of variance.

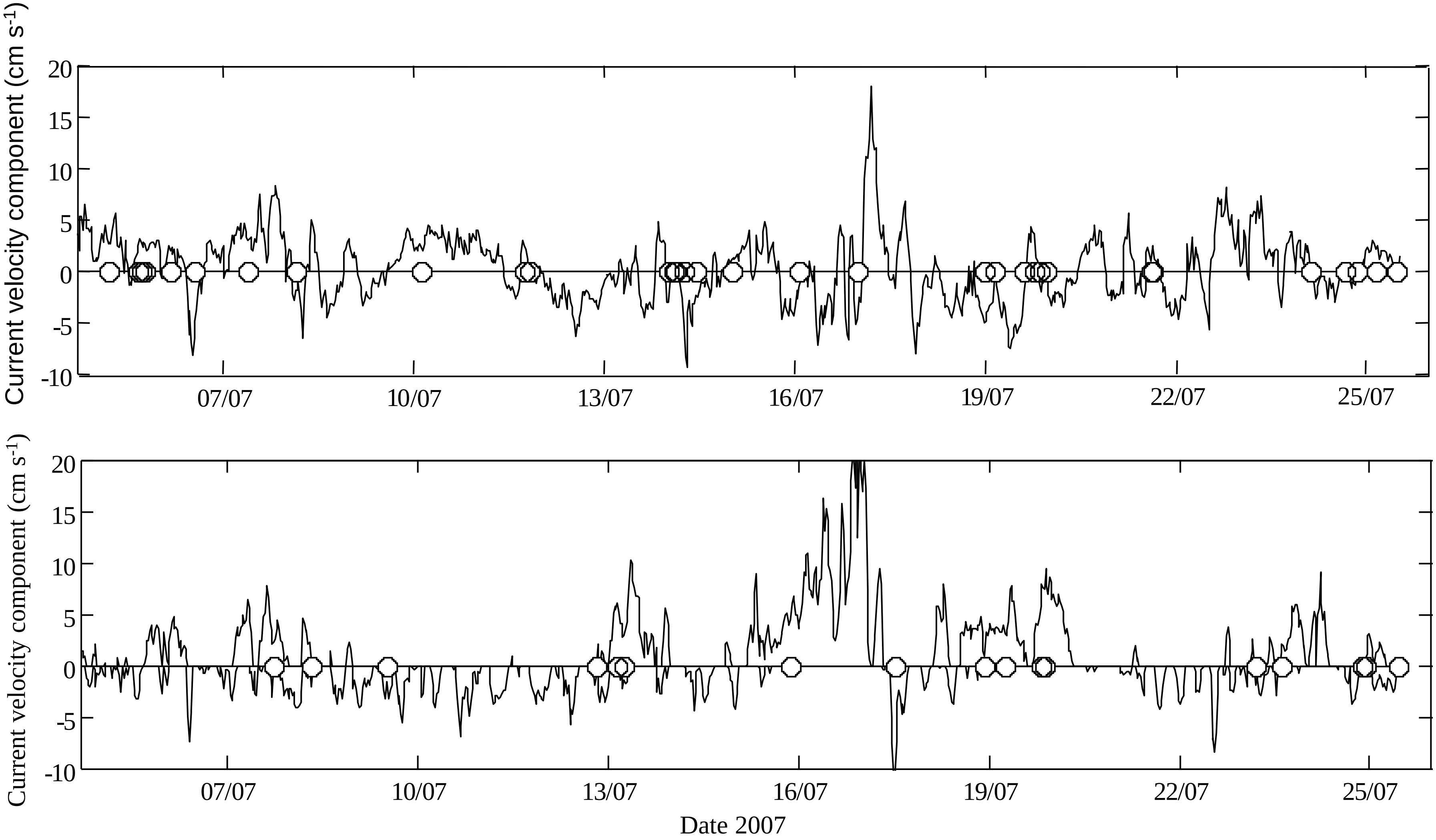
	Inertia	Proportion
Total	2.0000	1.0000
Constrained	0.2846	0.1423
Unconstrained	1.7154	0.8577


20°
30°
70°
65°
Norway
Sweden
Finland
1
Alta Fjord
2
Z1
Z2
3
4
Z3
5
6
Z4
7
River
Alta
N
km
0
5



140
130
120
110
100
90
80
70
60
50
40
River flow (m3 s-1)
16
15
14
13
12
11
10
Temperature (°C)
5.7.
12.7.
19.7.
26.7.
2.8.
Date 2007


a)
0
2
4
6
8
10
12
Depth (m)
22
24
30
30
32
33
W
E
ALS
c)
0
2
4
6
8
10
12
26
28
30
32
33
W
E
ALS
b)
0
2
4
6
8
10
12
Depth (m)
18
16
24
26
30
32
33
SW
NE
ALS
d)
0
2
4
6
8
10
12
26
28
30
32
33
SW
NE
ALS


Current velocity component (cm s-1)
20
15
10
5
0
-5
-10
07/07
10/07
13/07
16/07
19/07
22/07
25/07
Current velocity component (cm s-1)
20
15
10
5
0
-5
-10
07/07
10/07
13/07
16/07
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22/07
25/07
Date 2007

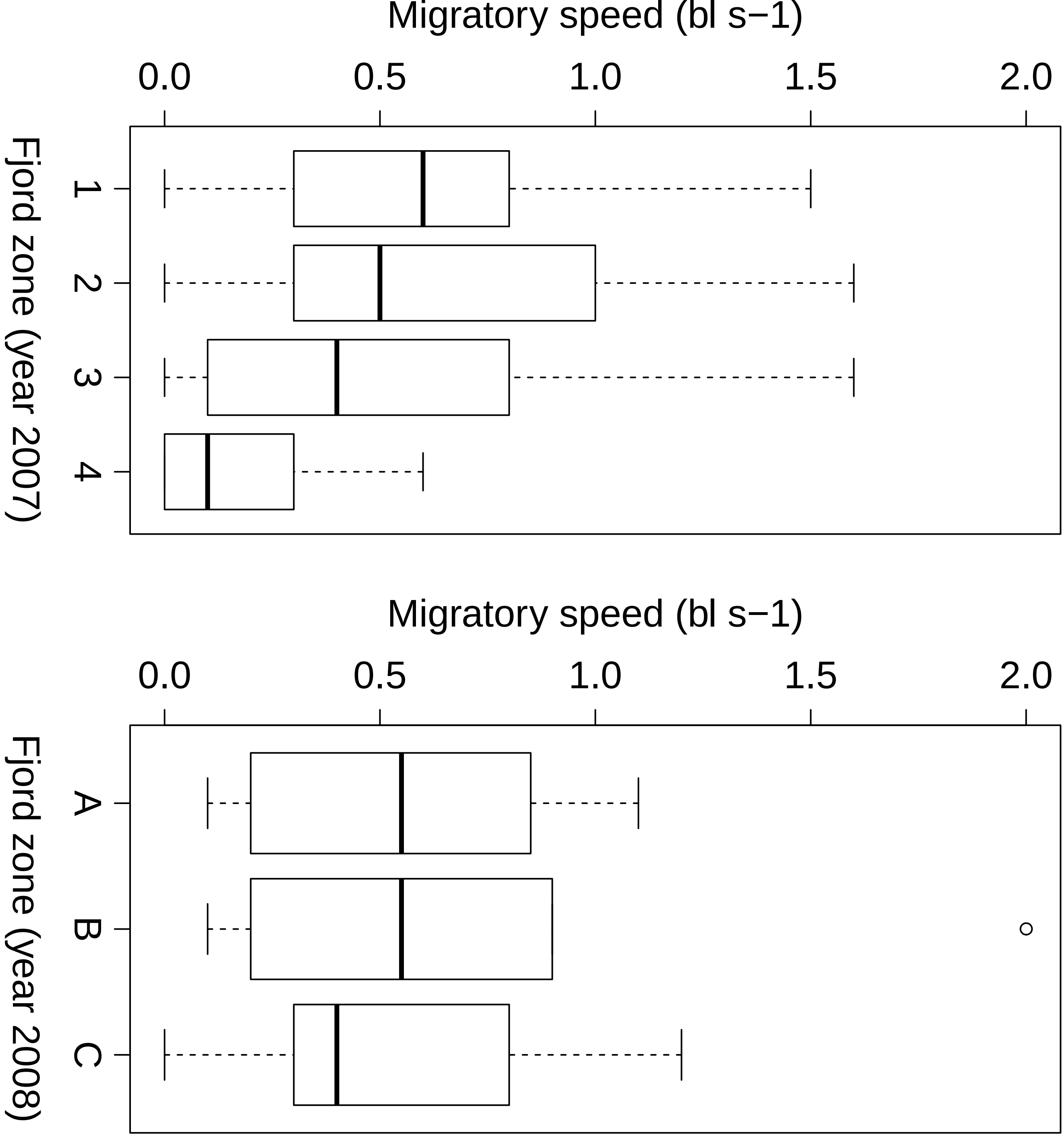
Migratory speed (bl s−1)
0.0
0.5
1.0
1.5
2.0
Fjord zone (year 2007)
1
2
3
4
Migratory speed (bl s−1)
0.0
0.5
1.0
1.5
2.0
Fjord zone (year 2008)
A
B
C

FIGURE CAPTIONS

Figure 1. Map of the lower part of River Alta and the Alta Fjord showing the position of the bag nets (◆) and the release sites (⬬). ALS array #1 is indicated with (•••••), while ALS arrays #2–5 are indicated by grey and black lines. Most fish passed these ALSs in the darker parts of the lines. The two ALSs in the river mouth (array #6) and the three ALSs (array #7) in the river are given by (•). The map also shows the position of the two current meters in ALS array #3 (✶), the four zones (Z1–4) and the weather station (▲). In the following year (2008) were only array #1, #3, #5 and #6 present.

Figure 2. Daily river flow (- - - - -) and water temperature (—) in the River Alta.

Figure 3. Salinity distribution recorded at 0–12 m depth across ALS array #2 (a & c) and ALS array #3 (b & d) in the Alta Fjord on 6 July (a & b) and 13 July (c & d) 2007.

Figure 4. Current velocity components at 3 m depth at the north-eastern (upper panel) and south-western (lower panel) side of the Alta Fjord at the ALS array #3. Positive values are towards the fjord head, and negative values are towards the fjord mouth. ○ indicates time of individual Atlantic salmon (*Salmo salar*) passage.

Figure 5. Migratory speeds of homing Atlantic salmon (*Salmo salar*) in the Alta Fjord in 2007 and 2008. In 2007, the fjord was divided into four zones (see map, Fig. 1). In 2008, zone A was the area from ALS#1–3, zone B from ALS#3–5 and zone C from ALS#5–6. The box-and-whisker plots give the median values (black lines), the interquartile ranges (box, 50% of the data falling into this) and the 5th and 95th percentiles (whiskers).