

## Upstream migration of Atlantic salmon in three regulated rivers

E. B. Thorstad<sup>1\*</sup>, P. Fiske<sup>1</sup>, K. Aarestrup<sup>2</sup>, N. A. Hvidsten<sup>1</sup>, K. Hårsaker<sup>3</sup>, T. G. Heggberget<sup>1</sup> and F. Økland<sup>1</sup>

<sup>1</sup>Norwegian Institute for Nature Research (NINA), Tungasletta 2, NO-7485 Trondheim, Norway. Tel. +47 73 80 14 00, Fax +47 73 80 14 01. \*Corresponding Author, email: eva.thorstad@nina.no

<sup>2</sup>Danish Institute for Fisheries Research, Dept. of Inland Fisheries, Silkeborg, Denmark.

<sup>3</sup>NTNU, Museum of Natural History and Archaeology, Department of Natural History, Trondheim, Norway.

**Key words:** *Salmo salar*, hydropower development, power station, residual flow, artificial freshets, radio telemetry.

### Abstract

Atlantic salmon (*Salmo salar* L.) were studied during their upstream migration in three Norwegian regulated rivers; the Rivers Mandalselva, Nidelva and Orkla (mean annual water discharge 88, 123 and 71 m<sup>3</sup>s<sup>-1</sup>, respectively). A total of 169 salmon (body length 51-108 cm) were radio tagged during 1996-2002. The studies were focussed on migration past power station outlets, residual flow stretches (6, 2.6 and 22 km long, respectively), over dams and weirs and on the effects of artificial freshets. The salmon were delayed at power station outlets. The behaviour at the outlets seemed dependent on water discharge and design of the outlet. The salmon were further delayed by low water discharge (3-5 m<sup>3</sup>s<sup>-1</sup>) and a number of weirs and dams on the residual flow stretch in the Rivers Nidelva and Mandalselva. Some salmon even reversed direction and migrated downstream again after entering the residual flow stretches, probably due to confusion by the much lower water discharge than in the river below the power station outlet. In contrast, the higher residual flow in the River Orkla (10-20 m<sup>3</sup>s<sup>-1</sup>) did not seem to delay the upstream migration, although the dam at the power station intake did. The studies showed that even dams and weirs that seemed not physically difficult for salmon to pass acted like migration barriers. Positive effects on the upstream migration by artificial freshets were found in the River Mandalselva one of the years, but not in the River Orkla (artificial freshets were not studied in the River Nidelva). However, the migration speeds in the River Mandalselva were so low, and the movements generally so erratic, that the importance of the freshets in stimulating the salmon to pass the residual flow stretch was insignificant.

### Introduction

The installation of hydroelectric power stations on rivers may hinder or harm migrating salmonids. Downstream migrating smolts are reported to suffer mortality when passing through dams or turbines (Raymond, 1988; Hvidsten and Johnsen, 1997). Upstream migration to the spawning grounds may be affected by altered water discharges, dams, weirs, fish passages and other migration barriers (Webb, 1990; Laine *et al.*, 2002; Karpinen *et al.*, 2002). Outflows from hydropower stations may also attract fish and delay the upstream migration (Andrew and Geen, 1960;

Brayshaw, 1967; Arnekleiv and Kraabøl, 1996).

Water discharge is the factor most frequently reported to control the upstream migration of salmonids (Banks, 1969; Jonsson, 1991). Water discharge appears to be an important factor stimulating adult Atlantic salmon (*Salmo salar* L.) to enter rivers from the sea (e.g. Huntsman, 1948; Saunders, 1960; Potter, 1988; Smith *et al.*, 1994). Upstream migration in rivers also appears to be stimulated by elevated flow (e.g. Huntsman, 1948; Hayes, 1953; Dunkley and Shearer, 1982; Baglinière *et al.*, 1990). However, the relationship between physical factors and migration is complex, and many other factors may also affect the migration (Banks, 1969;

Jonsson, 1991). In regulated rivers with possibilities of controlling the water discharge, artificial freshets may be used to stimulate the upstream migration of Atlantic salmon (Huntsman, 1948; Hayes, 1953; Banks, 1969). However, little is known about the effects of different water discharges and duration of such freshets on migration.

The aim of this paper is to present and synthesise results from studies of upstream migration of radio tagged Atlantic salmon in three Norwegian regulated rivers; with focus on power station outlets, residual flow stretches, dams and weirs and on the effects of artificial freshets. The purpose is to determine factors important for the passage of salmon past hydropower installations and affected river stretches.

## Materials and methods

### *Study area*

Atlantic salmon were studied during their upstream migration past power stations in the Rivers Mandalselva, Nidelva and Orkla (Fig. 1). The power stations are similar in that they have water intake just above a dam in the main river and the outlet in the main river some km downstream (Fig. 2). The river stretch between the intake and the outlet (residual flow stretch) has a reduced water discharge. The rivers differ in mean annual water discharge, minimum discharge in residual flow stretch, discharge of artificial freshets, number of weirs/dams in the residual flow stretch and origin of the salmon (Table 1).

The fish populations in the Rivers Mandalselva and Nidelva are negatively affected by acid precipitation. The native Atlantic salmon populations are extinct, and the Atlantic salmon entering these rivers during the 90s were non-native, mainly originating from neighbouring rivers and salmon farm escapes. (The River Mandalselva is currently limed and a salmon population being re-established.) The River Orkla has a native salmon population. The rivers and power stations are described in further detail in Hvidsten (1993), Thorstad and Heggberget (1998) and Thorstad *et al.* (2003).

### *Capture and tagging of fish*

A total of 169 Atlantic salmon were captured and radio tagged during 1996-2002 (Table 1). In the River Mandalselva, the salmon were captured in a fish passage and released in the lower part of the residual flow stretch, just above the tunnel outlet. In the River Nidelva, the fish were captured in bag nets and released 2 km downstream from the power station outlet, or collected in the fish passage at the dam and transported downstream to the same release site. No differences were found between salmon collected at the dam and salmon captured in bag nets in migratory speeds or behaviour (Thorstad *et al.*, 2003). In the River Orkla, the fish were captured by hook and line and released in the pool downstream the power station outlet. Ideally, the fish should be captured in the sea outside the river mouth for studies of upstream migration, since capture in the river may disturb the migration pattern. However, resources for capture in the sea were not available for these studies, and fish were caught in bag nets in the river or collected from fish ways, which are also gentle catch methods. In the River Orkla, where there is no fish ways (and no bag nets available), the fish had to be captured by hook and line. In all three rivers, the fish were either tagged and released immediately after captured or kept for up to 12 days (most of the fish less than six days) in a net pen or wooden boxes until tagging and release. This was done to standardise release dates for groups of fish. Negative effects of keeping fish like this is not known.

Radio transmitters (Model 2040 or 2120, Advanced Telemetry Systems, ATS) were externally attached to the fish below the dorsal fin, as described in Økland *et al.* (2001). The transmitters had weight in air of 10-11 g and weight in water of 6-8 g. Swimming performance of similarly sized salmon was not affected by such transmitters in laboratory trials (Thorstad *et al.*, 2000). To recognise individual fish, each radio tag had a unique combination of frequency and pulse rate.

### *Recording of the fish after release*

During upstream migration, the fish were positioned by manual tracking (within  $\pm 250$  m or less, receiver model R2100, ATS) every third day in the

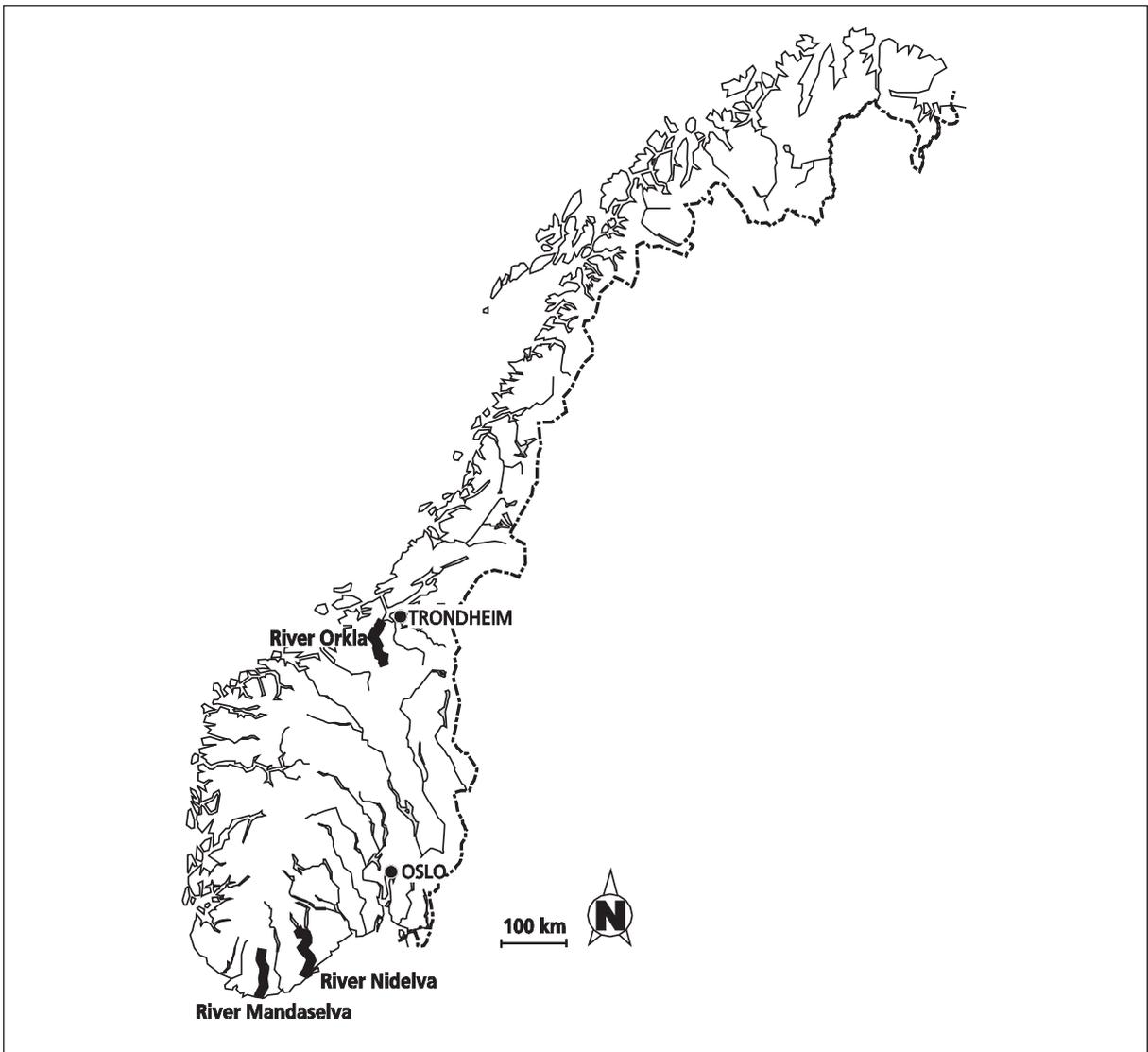


Fig. 1 – Map of Norway showing the Rivers Orkla, Nidelva and Mandalselva.

River Mandalselva and in the River Nidelva in 1999, every fourth day in the River Nidelva in 1997 and every second day in the River Orkla. After the upstream migration period, the fish were tracked less often, but after standardised tracking schemes, until December or January. During artificial freshets in the Rivers Mandalselva and Orkla, the fish were located just prior to every freshet, twice a day during the freshets (morning and evening) and the morning after the freshets.

In the River Mandalselva in 1996, a data logger (DCC II, ATS) was installed at two of the weirs locally considered as migration barriers to continuously and automatically record tagged fish in these areas. In the River Nidelva, a data logger was installed at the tunnel outlet both years. A multiplex (ATS) connected to the DCC II provided the ability to automatically select and monitor four antennae separately. Antenna 1 covered the area downstream the tunnel outlet, antenna 2 the area outside the out-

Table 1 – Information on studies of radio tagged salmon past Laudal power station in the River Mandalselva, Rygene power station in the River Nidelva and Svorkmo power station in the River Orkla. Information on water discharges is given for the study periods, except mean annual water discharge.

	River Mandalselva	River Nidelva	River Orkla
Mean annual water discharge ( $\text{m}^3\text{s}^{-1}$ )	88	123	71
Minimum water discharge in residual flow stretch ( $\text{m}^3\text{s}^{-1}$ )	3	3-5	10-20
Water discharge through power station ( $\text{m}^3\text{s}^{-1}$ )	0-110	36-176	0-60
Length of residual flow stretch (km)	6	2,6	22
Number of weirs/dams on residual flow stretch	12	4	1
Screen to prevent fish from entering the power station tunnel	yes	no	yes
Study period	1996 and 1997	1997 and 1999	2002
Number of salmon tagged	76	59	34
Origin of salmon	non-native	non-native	native
Body size of tagged salmon (cm)	51-96	52-108	58-108
Catch method	fish trap	bag net and fish way	angling
Period when tagged salmon were released	9 Aug-18 Sept	21 Aug-2 Oct	15 Jun-27 Jul
Studies carried out at power station outlet	no	yes	yes
Studies carried out in residual flow stretch	yes	yes	yes
Studies on artificial freshets	yes	no	yes
Water discharge of artificial freshets ( $\text{m}^3\text{s}^{-1}$ )	8-13	-	23-30
Water discharge in residual flow stretch prior to artificial freshets ( $\text{m}^3\text{s}^{-1}$ )	3	-	10-21
Duration of artificial freshets (h)	8-48	-	6-15

let, antenna 3 (underwater antenna) a small area just outside the outlet, and antenna 4 the area upstream the outlet. It was thus possible to record when fish stayed outside the outlet, or when they entered the tunnel and the residual flow stretch (see Thorstad *et al.* 2003). In the River Orkla, a data logger was installed at the power station outlet and at the dam at the power station intake.

#### Study design

In the River Mandalselva, migration in the residual flow stretch ( $3 \text{ m}^3\text{s}^{-1}$ ) and further upstream, and the effects of artificial freshets in the residual flow stretch, were studied for two years (Table 1). The design of the dam limited the maximum rate at which water could be released to  $13 \text{ m}^3\text{s}^{-1}$ . Six different freshets were released in 1996 (Thorstad and Heggberget, 1998), and two similar freshets in 1997 (each freshet consisted of increased water discharge to  $13 \text{ m}^3\text{s}^{-1}$  in two following days from 8:30 to 20:30 hours).

In the River Nidelva, migration past the power station outlet and in the residual flow stretch was studied for two years; one year with residual discharge of  $3 \text{ m}^3\text{s}^{-1}$ , and the following year of  $5 \text{ m}^3\text{s}^{-1}$ , to see if increased discharge stimulated the migration (Table 1).

In the River Orkla, migration past the power station outlet, in the residual flow stretch and further upstream was studied for one year (Table 1). The effects of artificial freshets in stimulating salmon to pass the power station outlet and residual flow stretch were studied during four freshets (lasting from 6 to 15 hours, with water discharge of  $23\text{-}30 \text{ m}^3\text{s}^{-1}$ , Table 1). Two of the freshets were released in connection with rain and a natural increase in water discharge. The residual discharge in the River Orkla was minimum  $20 \text{ m}^3\text{s}^{-1}$  until 1 September and  $10 \text{ m}^3\text{s}^{-1}$  thereafter (Fig. 3). Salmon that migrated downstream after catch and release and stayed in the downstream parts of the rivers, were not included in the analyses.

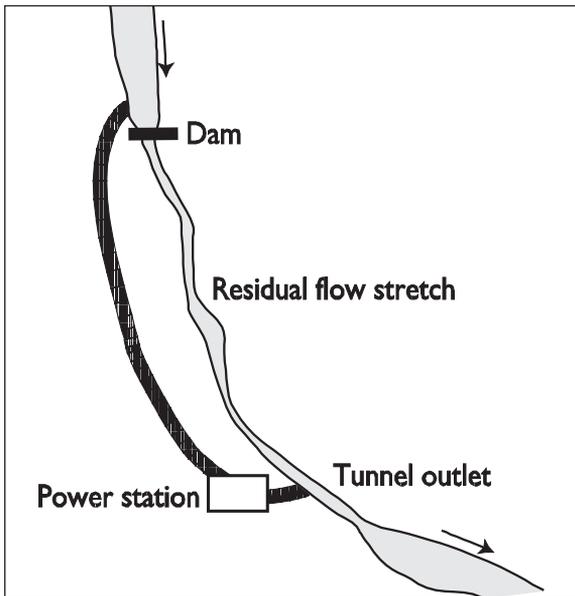


Fig. 2 – Schematic outline of the Laudal power station in the River Mandalselva, Rygene power station in the River Nidelva and Svorkmo power station in the River Orkla, which all have intake and outlet in the main river.

#### *Previously published results*

Two previous publications are produced from these studies. One publication analysed the effects of artificial freshets in the River Mandalselva in 1996, concluding there were no significant effects of the six freshets released (Thorstad and Heggberget, 1998). The other publication analysed the results from the River Nidelva in 1997, concluding that salmon were delayed by the power station outlet and in the residual flow stretch at a water discharge of  $3 \text{ m}^3\text{s}^{-1}$  in the residual flow stretch (Thorstad *et al.*, 2003). Previously published results are not repeated in this paper, but are referred to as a basis of comparison to the new results presented in this paper.

#### *Data analyses*

The data did not meet the assumptions of parametric tests, and non-parametric tests were therefore used. Mann-Whitney U tests were used to test whether two independent samples came from the same population. The Kruskal-Wallis test was used

in the case of more than two independent samples, whereas the Wilcoxon signed ranks test was used when comparing two related samples. A Yates-corrected Chi-square calculation was used to compare observed and expected frequencies in two categories to test whether the categories contained the same proportion of values.

## Results

#### *Delays at power station outlets*

In the **River Nidelva** in 1999, when water discharge in the residual flow stretch was  $5 \text{ m}^3\text{s}^{-1}$ , 74% ( $n=31$ ) of the tagged salmon migrated upstream to the tunnel outlet after release, where they stopped for on average 4.1 days (range 0-39). This was a shorter stop than in 1997, when the residual discharge was  $3 \text{ m}^3\text{s}^{-1}$  (average 22.4 days, Mann-Whitney U test,  $U=91.0$ ,  $P<0.001$ ). However, the fish seemed to be attracted by the tunnel outlet also in 1999, and returned to the outlet one or more times after up- or downstream movements. In total, the fish was recorded at the outlet on average during 27% (range 0-92%) of the tracking surveys. Results from the data logger and manual tracking showed that in 1999, the fish rather stayed outside the power station tunnel, instead of entering the tunnel and mainly staying inside the tunnel as they did in 1997. In 1999, only seven salmon had a longer stay than 1 h inside the tunnel (up to 77 h). However, the proportion of salmon entering the residual flow stretch was not different between the two years (10 of 17 in 1997 *versus* 25 of 31 in 1999, Yates-corrected Chi-square calculation,  $\chi^2=2.65$ ,  $P=0.20$ ).

In the **River Orkla**, salmon also stopped at the power station outlet, before migrating further upstream (on average 42 days, range 0-101,  $n=25$ ). The salmon were not recorded immediately at the tunnel outlet, but stayed in the pool 150-200 m downstream from where the water from the tunnel and the residual flow stretch run together.

#### *Migration on residual flow stretches*

In the **River Mandalselva**, 17% ( $n=9$ ) of the radio tagged salmon passed the residual flow stretch and

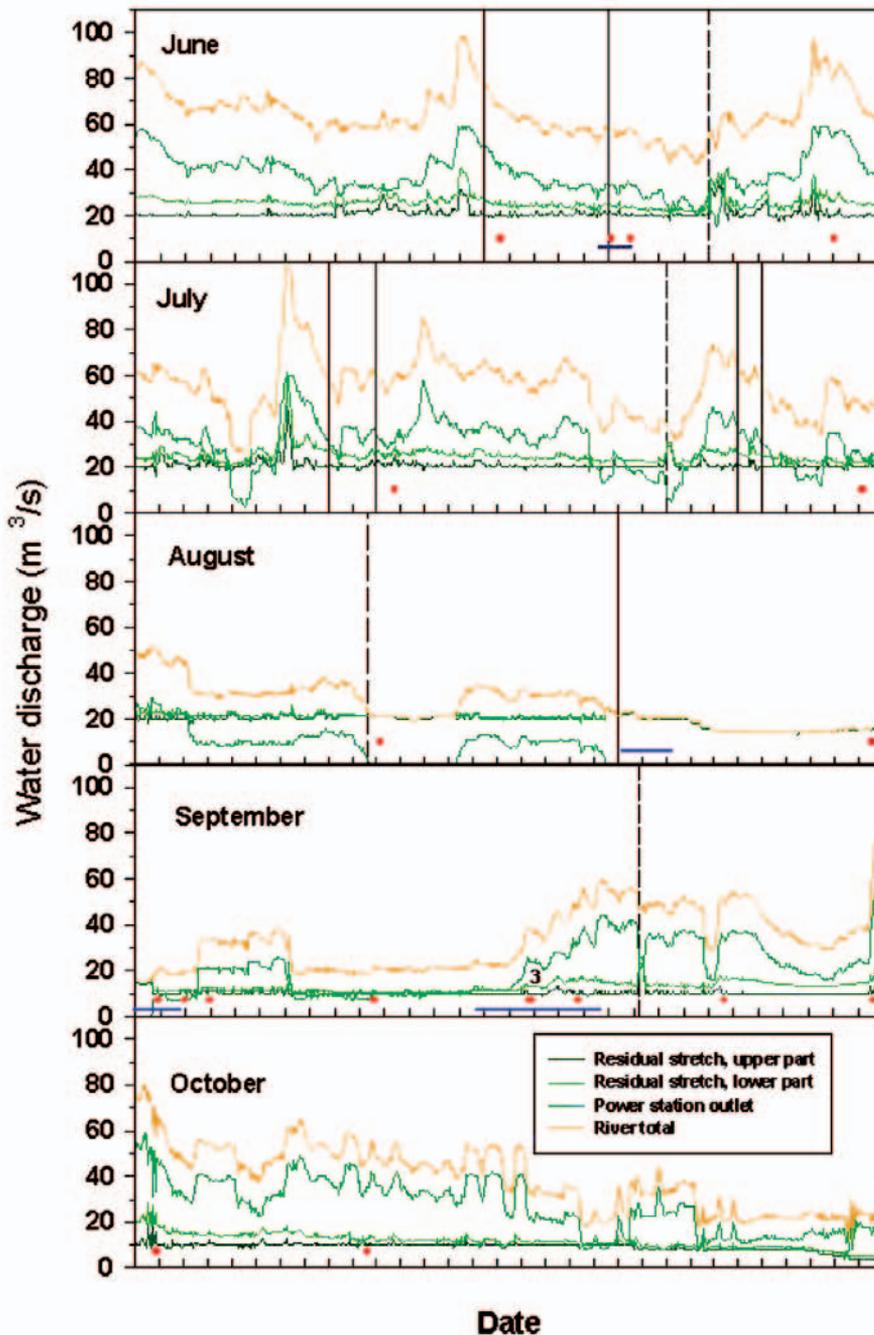


Fig. 3 – Timing of upstream migration of individual salmon (red dots [note that three salmon passed the same day in mid September] or blue lines when the exact timing was uncertain) from the tunnel outlet in the River Orkla in relation to artificial freshets (dotted vertical lines) and water discharge. Solid vertical lines indicate dates when salmon were radio tagged. Data on hourly water discharge during 1 June to 31 October was provided by the Power Stations in Orkla (KVO), and is shown from the first to the last date every month.

migrated further upstream the river. This was a larger proportion than in previous years with a lower residual discharge ( $0.25 \text{ m}^3\text{s}^{-1}$  in 1993 and  $1.5 \text{ m}^3\text{s}^{-1}$  in 1994-1995), when 1.5% (1993) and 3.7% (1994-1995) of the salmon passed the residual flow stretch according to results from fish traps catching all salmon entering and leaving the stretch those years (Yates-corrected Chi-square calculation,  $\chi^2=5.20$ ,  $P=0.023$ ). The radio tagged salmon spent on average 42 days (range 14-69) in passing the residual flow stretch, corresponding to a migration speed of  $0.15 \text{ km}(\text{day}^{-1})$ . After passing the residual flow stretch, average migration speed for the same individuals increased to  $3.6 \text{ km}(\text{day}^{-1})$ .

In the **River Nidelva**, none of the salmon managed to pass the dam at the power station intake. Both in the **River Mandalselva** and **River Nidelva**, salmon distributed themselves over the entire residual flow stretch, and generally showed an erratic movement pattern with up- and downstream movements. Based on where the salmon stopped, or turned and migrated downstream in the two rivers, none of the weirs could be identified as more serious migration barriers than the others, except the dam at the power station intake and one of the other weirs in the **River Mandalselva**. The two weirs locally considered as migration barriers in the River Mandalselva did not appear to delay salmon more than the others. Some of the salmon turned and migrated downstream again just after entering the residual flow stretch. This was especially notable in the **River Nidelva** in 1999, where 24% ( $n=6$ ) of the salmon moved downstream again after being recorded just upstream the outlet, and they did not enter the residual flow stretch again later in the season.

In the **River Orkla**, salmon seemed not to be delayed in passing the residual flow stretch. The salmon spent on average 9.7 days in passing the stretch, which corresponded to an average migration speed of  $3.1 \text{ km}(\text{day}^{-1})$ . This was not different from the migration speed further upstream the river, which was on average  $3.7 \text{ km}(\text{day}^{-1})$  for the same individuals (Wilcoxon signed ranks test,  $Z=-0.31$ ,  $P=0.75$ ). However, the salmon seemed to be delayed at the dam at the power station intake, where they spent on average 11 days (range 2-24) before passing.

#### *Effects of artificial freshets*

In contrast to no effects in 1996, positive effects of the artificial freshets on the upstream migration were found in the **River Mandalselva** in 1997. Number of weirs passed per hour was higher during both of the freshets (including a 10-13 hour period after the freshet) than during the remaining upstream migration period (Wilcoxon signed ranks tests,  $Z=-2,28$ ,  $P=0.023$ ;  $Z=-2,11$ ,  $P=0.035$ ), and distance moved was higher during one of the freshets (Wilcoxon signed ranks test,  $Z=-2,58$ ,  $P=0.010$ ). However, the migration speeds in question were so low ( $0.2-0.5 \text{ km}(\text{day}^{-1})$  during freshets and  $0.08 \text{ km}(\text{day}^{-1})$  during the remaining upstream migration period), and the movements generally so erratic, that the importance of the freshets in stimulating the salmon to pass the residual flow stretch was insignificant. Freshets were not obligatory for the passage of any of the weirs, as all the weirs at some occasion were passed during residual water discharge.

The upstream migration from the power station outlet in the **River Orkla** were not highly stimulated by freshets, as only one salmon (4%) migrated upstream during a freshet (Fig. 3). Of the salmon migrating upstream later in the season, 17 (68%) stayed outside the outlet during at least one of the freshets without passing (two of the salmon stayed during four freshets, two salmon stayed during three freshets and four salmon stayed during two freshets). The upstream migration happened during a wide range of water discharges, both in the residual flow stretch (between 11 and  $28 \text{ m}^3\text{s}^{-1}$ ) and from the tunnel outlet ( $0-55 \text{ m}^3\text{s}^{-1}$ ), during increasing, decreasing and stable water discharges (Fig. 3). Water discharge from the power station varied from 0 to 2.8 times higher than from the residual flow stretch when salmon passed the tunnel outlet and migrated further upstream (this relationship varied between 0 and 3.6 during the season, and was on average 1.3 times). Migration in the residual flow stretch also did not seem to be stimulated by the freshets, but the sample size was low, except during the last freshet, when there was no difference in distance moved between the days before, during and after the freshet (Kruskal-Wallis test,  $n=14$ ,  $\chi^2=1.5$ ,  $P=0.46$ ).

## Discussion

### *Delays at power station outlets*

Results in the present study showed that both native and non-native salmon were delayed at power station outlets during their upstream migration, even though the localities in the River Nidelva and River Orkla did not seem to imply any physical migration barriers (passage of power station outlet was not studied in the River Mandalselva). Salmon may naturally stop in some pools during their upstream migration, but the stops at the tunnel outlets both in the River Nidelva and Orkla were much longer than what was observed in comparable pools in the River Tana (average 5-9 days in the most popular pools, Økland *et al.*, 2001). The shorter delay observed in the River Nidelva than in the River Orkla may be because the salmon were tagged later in the season, closer to spawning. The results in the present study are in accordance with other studies describing delays at power station outlets (Andrew and Geen, 1960; Brayshaw, 1967; Webb, 1990; Chanseau and Larinier, 1999).

Behaviour at the outlets seemed to be affected by both water discharge and the design of the outlet. Effects of water discharge were demonstrated in the River Nidelva, where the salmon mainly stayed inside the power station tunnel the first year of the study (Thorstad *et al.*, 2003), whereas they mainly stayed in the river outside the outlet the second year, when the residual discharge was higher. No other factors were known to differ between the two years. However, the increase in water discharge was not sufficient to increase the proportion of salmon entering the residual flow stretch. The design of the outlet seemed to affect where the fish stayed at the outlets. In the River Nidelva, where the tunnel empties straight into the river, the most “natural” migration route is into the tunnel, and salmon must keep slightly to the right to enter the residual flow stretch. In the River Orkla, the tunnel empties into a side stream, which run together with the residual flow stretch 100 m downstream from the tunnel outlet. Upstream migrating salmon must either turn left to enter the side stream from the tunnel outlet, or slightly to the right to enter the residual flow stretch. These differences between the rivers

may be the reason why the fish stayed inside or just outside the tunnel outlet in the River Nidelva, whereas they stayed in the pool downstream from where the water from the side stream and the residual flow stretch run together in the River Orkla.

One may think that factors such as water discharge in the residual flow stretch, water discharge from the power station, or the relationship between these two, would affect the upstream migration past tunnel outlets. However, the artificial freshets did not seem to affect the upstream migration from the outlet in the River Orkla, and the passage by individuals happened during a wide range of water discharges in the residual flow stretch and through the power station in both rivers (for results from the River Nidelva, see Thorstad *et al.*, 2003). In the River Orkla, the water discharge was usually 1-2 times higher from the tunnel outlet compared with the residual flow stretch when upstream migration from the outlet occurred. The power station was closed for a period in August, without stimulating the migration, which may be due to unusually warm weather conditions and low water discharges during the period. Closing the power station in a period with rain and higher water discharge would maybe stimulate the upstream migration.

It can be concluded from these studies that relatively short and small artificial freshets in large regulated rivers may be a waste of water and money in stimulating Atlantic salmon to pass power station outlets. However, Arnekleiv and Kraabøl (1996) found positive effects by artificial freshets on trout (*Salmo trutta*) migration past a tunnel outlet, and effects by water discharge also on Atlantic salmon cannot completely be ruled out. Complex relationships may exist, and for example changes in water discharge or quality on a micro scale may be important. Furthermore, water discharge may not be important until the salmon is motivated for migration.

### *Migration on residual flow stretches*

A water discharge of  $20 \text{ m}^3\text{s}^{-1}$  in the residual flow stretch in the River Orkla did not seem to reduce the migration speed. The migration speed was both comparable to migration speeds on river stretches upstream the residual flow stretch and in other rivers

(e.g. Johnsen *et al.*, 1998; Hayes *et al.*, 1953; Smirnov, 1971), although other studies have reported higher migration speeds, such as Hawkins and Smith, 1986; Aarestrup *et al.*, 2000). In contrast, the much lower residual flow in the Rivers Mandalselva and Nidelva seemed to delay the migration, probably together with a number of weirs constituting migration barriers (see below). The importance of increased water discharge on residual flow stretches was also demonstrated by the fact that an increase in residual discharge in the River Mandalselva from 0.25 to 3 m<sup>3</sup>s<sup>-1</sup> increased the proportion of salmon passing the residual flow stretch.

Large-grown salmon and sea trout may enter small rivers (3-5 m<sup>3</sup>s<sup>-1</sup>) seemingly without any problems. The delays seen in the residual stretches in the River Mandalselva and Nidelva is, therefore, probably related to salmon entering a big river and then suddenly finding themselves on a river stretch with a much lower water discharge. This may also have been the reason why some salmon turned and migrated downstream again after entering the residual flow stretch. Such behaviour was also observed for sea trout entering fish passages, and it was speculated that the fish tried to find an alternative route or wait for better conditions (Aarestrup *et al.*, 2003). As for passage of power station outlets, relatively small and short artificial freshets did not seem to stimulate migration in residual flow stretches to a large extent, although small effects were found one of the years in the River Mandalselva. A large number of studies have reported that increases in water discharge have stimulated the upstream migration of salmon (see e.g. references in the introduction). Strikingly few studies have reported that they found no relationship between upstream migration and water discharge (but see Hawkins and Smith, 1986; McKinnell *et al.*, 1994). One may speculate that studies finding no effects are under-reported and, thus, the effect of water discharge on the upstream migration exaggerated, especially in large rivers with a generally high water discharge.

#### *Migration barriers*

Dams and weirs delayed upstream migration in all the three rivers, although none of them seemed to be

physically difficult migration barriers. In the Rivers Mandalselva and Nidelva, there were no weirs where all salmon stopped or where they only passed at increased discharge, and it seemed like the motivation to migrate was reduced due to a combination of low water discharge and a high number of obstacles. Salmon in the Rivers Mandalselva and Nidelva probably had no previous experience of the rivers, which may have decreased their motivation to migrate upstream compared with native salmon. However, escaped farmed salmon in two other Norwegian rivers appeared motivated to migrate upstream and distributed themselves further upstream than the wild salmon during spawning (Økland *et al.*, 1995; Heggberget *et al.*, 1996; Thorstad *et al.*, 1998). The lack of motivation to migrate upstream in the Rivers Mandalselva and Nidelva may, therefore, not be explained by origin or lack of river imprinting. This was confirmed by the results from the River Orkla, where native salmon also seemed to be delayed by the dam, although it seems not to be a physically difficult obstacle to pass. It can be concluded from the results in this study that seemingly easy obstacles to pass may considerably delay salmon in their upstream migration. Ovidio and Philippart (2002) concluded from a five-year study in the same way that some small obstacles are not as insignificant as initially thought and can significantly disrupt and/or obstruct fish upstream movements.

Delays in the upstream migration may obviously create conflicts in the organisation of a sport fishery when salmon arrive in the upper parts of the watershed later after hydropower development. However, the biological importance of such delays is not known, as long as the salmon arrive on the spawning grounds in time for the spawning season. Atlantic salmon often enter the rivers several months before spawning (Nordqvist, 1924; Hawkins and Smith, 1986), and may hold position at the spawning grounds for one to two months before spawning (Økland *et al.*, 2001). As pointed out by Fleming (1996), there is no satisfactory adaptive explanation for the early river entry time of adult Atlantic salmon. If the early river entry is associated with some kind of advantages, delays during the upstream migration will involve corresponding disadvantages.

## Acknowledgements

The studies were financed by the Office of County Governor in Vest-Agder, Flerbruksplan Mandalsvassdraget, Aust-Agder Power Company and The Norwegian Water Resources and Energy Directorate (NVE). We would like to thank all those who participated in catch and tracking of the fish and others who contributed to various parts of the projects. We would also like to thank the power companies for their assistance and co-operation.

## References

- Aarestrup, K., Jepsen, N., Rasmussen, G., Økland, F., Thorstad, E.B. & Holdensgaard, G. 2000. Prespawning migratory behaviour and spawning success of sea-ranched Atlantic salmon, *Salmo salar* L., in the River Gudena, Denmark. *Fish. Mgmt. Ecol.*, 7: 387-400.
- Aarestrup, K., Lucas, M.C. & Hansen, J.A. 2003. Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecol. Freshw. Fish*, 12: 160-168.
- Andrew, F.J. & Geen, G.H. 1960. Sockeye and pink salmon production in relation to proposed dams in the Fraser River system. *Bull. Int. Pac. Salm. Fish. Comm.*, 11: 10-30.
- Arnekleiv, J.V. & Kraabøl, M. 1996. Migratory behaviour of adult fast-growing brown trout (*Salmo trutta*, L.) in relation to water flow in a regulated Norwegian river. *Reg. Riv. Res. Mgmt.*, 12: 39-49.
- Baglinière, J.L., Maise, G. & Nihouarn, A. 1990. Migratory and reproductive behaviour of female adult Atlantic salmon, *Salmo salar* L., in a spawning stream. *J. Fish Biol.*, 36: 511-520.
- Banks, J.W. 1969. A review of the literature on the upstream migration of adult salmonids. *J. Fish Biol.*, 1: 85-136.
- Brayshaw, J.D. 1967. The effects of river discharge on inland fisheries. In P.G. Isaac, ed. *River Management*, pp. 102-118. London, MacLaren.
- Chanseau, M. & Larinier, M. 1999. The behaviour of returning adult Atlantic salmon (*Salmo salar* L.) in the vicinity of Baigts hydroelectric power plant on the Pau River as determined by radiotelemetry. *Bull. Fr. Pêche Piscic.*, 353/354: 239-262. (In French with English summary)
- Dunkley, D.A. & Shearer, W.M. 1982. An assessment of the performance of a resistivity fish counter. *J. Fish Biol.*, 20: 717-737.
- Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev. Fish Biol. Fish.*, 6: 379-416.
- Hayes, F.R. 1953. Artificial freshets and other factors controlling the ascent and population of Atlantic salmon in the LaHave River, Nova Scotia. *Bull. Biol. Board Can.*, 99: 1-47.
- Hawkins, A.D. & Smith, G.W. 1986. Radio-tracking observations on Atlantic salmon ascending the Aberdeenshire Dee. *Scott. Fish. Res. Rep.*, 36: 1-24.
- Heggberget, T.G., Økland, F. & Ugedal, O. 1996. Prespawning migratory behaviour of wild and farmed Atlantic salmon (*Salmo salar*) in a North Norwegian river. *Aquacult. Res.*, 27: 313-322.
- Huntsman, A.G. 1948. Freshets and fish. *Trans. Am. Fish. Soc.*, 75: 257-266.
- Hvidsten, N.A. 1993. High winter discharge after regulation increases production of Atlantic salmon (*Salmo salar*) smolts in the River Orkla, Norway. *Can. Spec. Publ. Fish. Aquat. Sci.*, 118: 175-177.
- Hvidsten, N.A. & Johnsen, B.O. 1997. Screening of descending Atlantic salmon (*Salmo salar* L.) smolts from a hydropower intake in the River Orkla, Norway. *Nordic J. Freshw. Res.*, 73: 44-49.
- Johnsen, B.O., Jensen, A.J., Økland, F., Lamberg, A. & Thorstad, E.B. 1998. The use of radiotelemetry for identifying migratory behaviour in wild and farmed Atlantic salmon ascending the Suldalslågen river in Southern Norway. In M. Jungwirth, S. Schmutz & S. Weiss, eds. *Fish migration and fish bypasses*, 55-68 pp. Oxford, Fishing News Books, Blackwell Science, 438 pp.
- Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. *Nordic J. Freshw. Res.*, 66: 20-35.
- Karppinen, P., Mäkinen, T.S., Erkinaro, J., Kostin, V.V., Sadkovskij, R.V., Lupandin, A.I. & Kaukoranta, M. 2002. Migratory and route seeking behaviour of ascending Atlantic salmon in the regulated River Tuloma. *Hydrobiologia*, 483: 23-30.
- Laine, A., Jokivirta, T. & Katopodis, C. 2002. Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L., passage in a regulated northern river - fishway efficiency, fish entrance and environmental factors. *Fish. Mgmt. Ecol.*, 9: 65-77.
- McKinnell, S., Lundqvist, H. & Johansson, H. 1994. Biological characteristics of the upstream migra-

- tion of naturally and hatchery-reared Baltic salmon, *Salmo salar* L. *Aquacult. Fish. Manage.*, 25 (Suppl. 2): 45-63.
- Nordqvist, O. 1924. Times of entering of the Atlantic salmon (*Salmo salar* L.) in the rivers. *Rapp. P.-V. Reun. CIESM Mediterr.*, 33: 1-58.
- Ovidio, M. & Philippart, J.-C. 2002. The impact of small physical obstacles on upstream movements of six species of fish. *Hydrobiologia*, 483: 55-69.
- Økland, F., Heggberget, T.G. & Jonsson, B. 1995. Migratory behaviour of wild and farmed Atlantic salmon (*Salmo salar*) during spawning. *J. Fish Biol.*, 46: 1-7.
- Økland, F., Erkinaro, J., Moen, K., Niemelä, E., Fiske, P., McKinley, R.S. & Thorstad, E.B. 2001. Return migration of Atlantic salmon in the River Tana: phases of migratory behaviour. *J. Fish Biol.*, 59: 862-874.
- Potter, E.C.E. 1988. Movements of Atlantic salmon, *Salmo salar* L., in an estuary in South-west England. *J. Fish Biol.*, 33 (Suppl. A): 153-159.
- Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River basin. *N. Am. J. Fish. Mgmt.*, 8: 1-24.
- Saunders, J.W. 1960. The effect of impoundment on the population and movement of Atlantic salmon in the Ellerslie Brook, Prince Edward Island. *J. Fish. Res. Bd. Can.*, 17: 453-473.
- Smironov, Y.A. 1971. Salmon of Lake Onega. *Fish. Res. Bd. Can. Transl. Ser.*, 2137: 1-212.
- Smith, G.W., Smith, I.P. & Armstrong, S.M. 1994. The relationship between river flow and entry to the Aberdeenshire Dee by returning adult Atlantic salmon. *J. Fish Biol.*, 45: 953-960.
- Thorstad, E.B. & Heggberget, T.G. 1998. Migration of adult Atlantic salmon (*Salmo salar*); the effects of artificial freshets. *Hydrobiologia*, 371/372: 339-346.
- Thorstad, E.B., Heggberget, T.G. & Økland, F. 1998. Migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during and after spawning in a Norwegian river. *Aquacult. Res.*, 29: 419-428.
- Thorstad, E.B., Økland, F. & Finstad, B. 2000. Effects of telemetry transmitters on swimming performance of adult Atlantic salmon. *J. Fish Biol.*, 57: 531-535.
- Thorstad, E.B., Økland, F., Kroglund, F. & Jepsen, N. 2003. Upstream migration of Atlantic salmon at a power station on the River Nidelva, Southern Norway. *Fish. Mgmt. Ecol.*, 10: 139-146.
- Webb, J. 1990. The behaviour of adult Atlantic salmon ascending the Rivers Tay and Tummel to Pitlochry dam. *Scott. Fish. Res. Rep.*, 48: 1-27.