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Comparison of area use and movement behavior in wild and escaped farmed Atlantic salmon (*Salmo salar* L.) before and during spawning in the river Namsen

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Abstract

The fish-farming of Atlantic salmon has been a rapidly growing industry recent years, and constitutes one of the biggest threats to the wild Atlantic salmon populations along the Norwegian coast. In the present study, I compared area use and movement behavior of wild and escaped farmed salmon before and during the spawning period in the river Namsen. Wild and escaped farmed fish were caught, tagged with radio transmitters, and released in the fjord Namsfjorden. In the Namsen watershed, the salmon were tracked by stationary receivers with data loggers positioned close to the river mouth and along the river with a manual receiver from a car. There was no difference in migration speed from the tagging sites in the fjord until entering the river in wild and farmed salmon. The proportion of tagged wild (80 %) and farmed (74 %) salmon that entered the river were not significantly different. The wild and farmed salmon stayed in the same areas of the river during both pre-spawning and spawning periods, areas holding important spawning grounds. Before and during spawning the farmed salmon stayed mainly in the upper 20 km of the river, while the wild salmon were found in the whole river stretch. Further, the predicted probability of migrating to the migration barrier at Nedre Fiskumfoss waterfall was four times higher for farmed than for wild salmon. The farmed salmon performed longer movement distances per day than wild salmon during the pre-spawning period, but not during the spawning period. These findings are important for organization of the monitoring of farmed salmon in the fall, and how to get a representative status of the proportion of escaped farmed salmon in rivers.

Sammendrag

Oppdrett av Atlantisk laks har vært en raskt voksende industri de siste årene, og utgjør en av de største truslene til populasjonene av vill Atlantisk laks langs Norskekysten. I denne oppgaven sammenlignet jeg områdebruk og vandringsadferd til vill- og rømt oppdrettslaks før og under gyting i elva Namsen. Vill- og rømt oppdrettslaks ble fanget, merket med radiosendere, og sluppet i Namsfjorden. I Namsen-vassdraget ble laksen peilet med stasjonære mottakere med dataloggere posisjonert nært elvemunningen, og langs elva ved manuell peiling fra bil. Det var ingen forskjell mellom vill- og oppdrettslaks i vandringsfart fra merkestedene i fjorden til de entret elva. Andelen av merket vill- (80 %) og oppdrettslaks (74 %) som entret elva var ikke signifikant forskjellig. Vill- og oppdrettslaks oppholdt seg i samme områder av elva før og under gyting, i områder med viktige gytegrunner. Før og under gyting befant oppdrettslaksen seg hovedsakelig i de øverste 20 km av elva, mens villaksen befant seg i alle deler av elvestrengen. Videre, den predikterte sannsynligheten for å vandre til vandringshindret på Nedre Fiskumfoss var fire ganger høyere for oppdrettslaks enn for villaks. Oppdrettslaksen vandret lengre distanser per dag enn villaksen i perioden før gyting, men ikke gjennom gyteperioden. Disse funnene er viktige for organisering av overvåkingsfiske av oppdrettslaks på høsten, og for å skaffe en representativ status av andelen rømt oppdrettslaks i elver.

Contents

1 Introduction

The fish-farming industry of Atlantic salmon (*Salmo salar* L.) has been growing rapidly in recent years. Today, Norway is the largest producer with a total production of 1 148 000 tons in 2012 (Anon. 2013a). In comparison, the total catches of wild salmon, including fisheries in the sea and in rivers, were 780 tons in the same year (Anon. 2013a). In Norwegian salmon rivers the proportion of escaped farmed salmon has been monitored since 1989 (Anon. 2013a; Diserud et al. 2010; Fiske et al. 2001). Generally, the proportion of farmed salmon is highest in the sea fisheries. In the rivers, this proportion is higher during monitoring in the fall closer to the spawning season (September-October), than during the angling season (June-August) (Fiske et al. 2006). The higher proportion of farmed salmon in the fall river catches may be because the farmed salmon ascend the rivers later than wild salmon (Anon. 2013a; Thorstad et al. 2008). In Norwegian rivers, the proportion of farmed salmon in the angling season has been on average 4-9 % (2002-2012), and during monitoring in the fall on average 11-18 % (2000-2012) (Anon. 2013a).

Escaped farmed salmon migrating into rivers may impose negative ecological and genetic consequences for the wild salmon populations (Fleming et al. 2000; McGinnity et al. 2003; Taranger et al. 2012). Further, farmed salmon differ from wild salmon in many ways, and hence, they are undesirable in the wild salmon populations for several reasons. The wild salmon populations differ in genetic composition because of local adaptations to the rivers, while the farmed salmon are based on four strains from the start of the production in the early 1970s (Skaala et al. 2005), with breading goals for optimal growth and age/size at maturity under hatchery condition (Gjøen & Berntsen 1997). In addition, it may have been a loss of genetic variation in farmed salmon because of few individuals used in the establishment of the farmed salmon strains and genetic drift (Ferguson et al. 2007; Thorstad et al. 2008). In the wild, the reproductive success of farmed salmon may be less than one third compared to wild salmon (Fleming et al. 2000), and offspring of farmed salmon, hybrids and back crosses, have less survival compared to wild offspring (McGinnity et al. 2003). The genetic introgression of farmed salmon into wild salmon populations differs between rivers, and may be density-dependent with regard to the size to the size of the wild salmon populations (Glover et al. 2012).

Wild salmon return to their natal river and the place where they grew up to spawn (Hansen et al. 1989; Harden Jones 1968). Imprinting of environmental characteristics of the river during the smolt migration phase seems pivotal for precise homing (Hansen et al. 1989). Mature farmed salmon lack this homing instinct, and do not have a ‘stop signal’ when they migrate upstream in rivers. Due to lack of river imprinting and river experience, farmed salmon individuals often migrate to the upper salmon-river stretches or to other major migration barriers. In addition, they may perform more and longer pronounced upstream and downstream movements than wild salmon during the spawning period (Heggberget et al. 1996; Thorstad et al. 1998). The migration pattern of wild salmon can prior to spawning be divided into three phases (Finstad et al. 2005; Økland et al. 2001): (1) an up-migration phase, (2) a searching phase consisting of upstream and downstream movements close to the spawning area, and (3) a holding phase prior to spawning. The migration pattern of wild salmon is well studied, while fewer have compared the wild and salmon movement pattern and area use in rivers prior to spawning and during the spawning period.

The river Namsen is one of the largest and most important salmon rivers in Norway in terms of salmon catches. It is declared as one of the National salmon rivers, which is a settlement decided by the Environmental government to strength the protection of the wild salmon (St.prp. nr. 32 (2006-2007)). Hence, the Namsen salmon should be carefully managed and protected against harmful activities.

During the fall-season monitoring of escaped farmed salmon, which in the river Namsen mainly takes place in the upper reaches of the accessible stretches for salmon, the proportion of farmed salmon has on average been 20 % (range 10-24 %) during 2004-2011 period (Anon. 2013b). There are two intensions of the monitoring of the farmed salmon in the river Namsen in the fall; (1) to monitor the proportion of farmed salmon in the population, and (2) to remove farmed salmon as much as possible from the river. Different methods can be used to remove farmed salmon from rivers depending on the size of the river and abundance of the farmed salmon. For instance may targeted angling for farmed salmon, performed to remove as many farmed salmon as possible, be an effective method in some rivers (Næsje et al. 2013a).

Based on the proportions of farmed salmon in the river catches, the river Namsen is categorized as “vulnerable” with an estimated spawning population consisting of 50-75 % wild salmon (Diserud et al. 2012). In a genetic study of salmon fry (0+) and adult salmon in Namsen in 2012, Karlsson et al. (2012) documented introgression between farmed and wild salmon by use of SNP-markers.

The aims of this thesis were to compare the area use and movement behavior of wild and escaped farmed salmon before and during spawning in the river Namsen. By using radio telemetry, I studied if escaped farmed salmon had the same area use in the river, and fjord- and river movement pattern as the wild salmon. In particular, I examined if wild and farmed salmon were located at the same river stretches before and during the spawning period - a phenomenon pertinent to introgression risk. The area use and movement behavior of wild and farmed salmon may be important in terms of future performance and design of the monitoring of farmed salmon in the fall, and how to interpret the results of it.

2 Material and methods

2.1 Study area

The river Namsen is located in Nord-Trøndelag County in Central Norway (Figure 1). It flows through municipalities Røyrvik, Namsskogan, Snåsa, Lierne, Grong, Overhalla, Høylandet and Namsos. The river mouth is located in Namsos (64°27’37’’N, 11°11’50’’ E) (Thorstad et al. 2006). The river Namsen is 210 kilometers long, and has a catchment area of 6265 km^2, and an annual flow at 290 m^3/ sec (Lien et al. 1983; Thorstad et al. 2006).

In the main river, the Atlantic salmon could originally migrate 70 kilometers up-river to the waterfall Nedre Fiskumfoss, and 60 kilometers to the waterfall Nedre Tømmeråsfoss in the tributary Sanddøla, which connects to the river Namsen at Grong, 55 km from the river mouth. In the tributary Høylandsvassdraget, which connects to the river Namsen 31 km from the river mouth, the salmon can migrate to the lake Øyvatnet. Fish ladders in the waterfalls Nedre Fiskumfoss, Nedre Tømmeråsfoss and Formofoss (Sanddøla) have increased the anadromous stretches to a total of 200 kilometers, Høylandsvassdraget included (Lien et al. 1983; Thorstad et al. 2006).

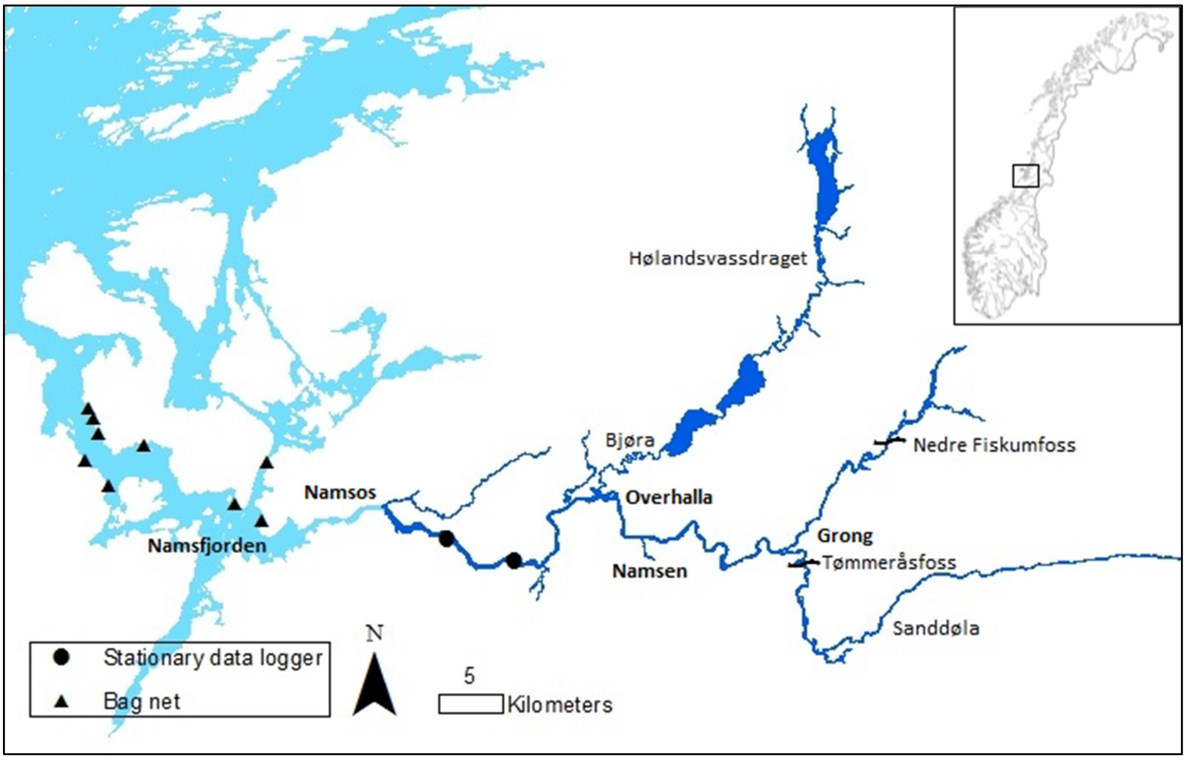

Figure 1: Namsfjorden and the Namsen river system in the middle of Norway. Location of bag nets where the fish where caught for tagging, and stationary data loggers are indicated.

2.2 Fish tagging

Wild Atlantic salmon (24 males, 49 females, 1 unknown sex), and escaped farmed salmon (15 males, 15 females, 13 unknown sex) were caught and tagged with radio transmitters in Namsfjorden from June 10th to August 28th in 2012. The farmed salmon entered the fjord later than the wild salmon (Næsje et al. 2013b). Of the tagged fish, 71 out of 74 wild salmon were tagged in the period June 15th-July 27th, while 29 out of 43 (67 %) were caught in the period July 31st-August 29th. The tagged wild and farmed salmon had a mean length of 88 cm ± 9 (SD) (range 67-109 cm) and 78 cm ± 8 (SD) (range 64-93 cm), respectively.

The fish were caught using bag nets at Otterøya and Statland (19.4-21.8 km from the river mouth) and at Lokkaren (5.5-16.2 km from the river mouth) in Namsfjorden (Figure 1). The bag net sites were located in the two possible migration routes for salmon entering the river Namsen.

After the fish were caught, they were taken gently from the bag net in a plastic bag, and placed in a tube were they were anesthetized with 2-phenoxyethanol (EEC No 204-589-7, 1ml/1 l of water) for about one minute. Thereafter, the anesthetic solution in the tube was exchanged with seawater. During tagging the head and gills of the fish were held submerged under water. A radio transmitter (model F2120, Advanced Telemetry System (ATS), USA) was attached 0.5 cm below the dorsal fin (dimensions: 21 x 52 x 11mm, weight in air: 15 g, Figure 2). Previous research has documented that this type of transmitters does not reduce the salmon's swimming performance for individuals with body sizes comparable to fish tagged in this study (Thorstad et al. 2000). The tagging was carried out using two cannulas that were pushed through the dorsal muscle of the fish. Further, a steel wire was threaded through the cannulas, and fastened over a back plate close to the skin. The total length of the fish was measured, and 5-8 scales were sampled for wild or farmed salmon assignment. The fish was sexed based on external characters. Individuals with no or few external sex characters were characterized as "unknown sex". The tagging process lasted for about 4 minutes. When the fish was fully recovered in seawater, it was released at the catch site.

Figure 2: A wild salmon tagged with a radio transmitter. Photo: Karina Moe

The radio transmitters had frequencies in the interval 142.000-142.600 MHz, and a guaranteed battery capacity of 149-269 days, depending on pulse rate. Each radio transmitter had a unique combination of frequency and pulse rate to be able to recognize the individuals during tracking.

2.3 Tracking of tagged fish

In order to register when tagged individuals entered the river, two independent stationary radio receivers and data loggers (R4500S ATS, USA) were placed both at Steinan and Lilleøen 12.4 and 19.3 kilometers upstream from the river mouth, respectively (Figure 1). The lowermost of these stations was just upriver the tidal salt-water mixing zone in the river. The detection ranges of the receivers and nine-element antennas used, extended the river width. The radio tagged fish were automatically registered and information stored by the data-loggers. The stored data were downloaded from the data-loggers to a portable computer every 2-3 weeks.

To study area use and movement behavior of the radio tagged fish in the river, they were manually tracked from a car using a radio receiver (R4500S ATS, USA) and a car whip antennae (142MHz, Laird Technologies, Missouri, USA). Every two weeks, from July 4th to September 4th, the tagged salmon were tracked and located in the main river, as well as in the tributaries Sanddøla and Høylandsvassdraget. In addition, the tagged salmon were tracked every second day in the river Namsen from Steinan to Nedre Fiskumfoss waterfall (57 km) in the pre-spawning period from September 4th to October 4th, and in the assumed spawning period from October 5th to November 10th. The assumed spawning period of wild Atlantic salmon were based on previous studies in the river Namsen (Thorstad et al. 1998), and personal communication with local fishers.

In the pre-spawning and spawning periods, the tagged fish were manually tracked by using 75 permanent tracking stations evenly distributed in the main river between Steinan and Nedre Fiskumfoss waterfall (57 km). The car was stopped at for about 4 minutes at every station to check out all the frequencies and the fish were assigned to the tracking station it was heard the strongest at the receiver. The distance between the tracking stations was on average 760 meters. The detection length of the car receiver and antennae may have been shorter than the distance between some of the tracking stations, due to topography and vegetation at the tracking stations.

2.4 Statistical analyses and methods

Data from the survey were analyzed statistically using generalized linear mixed effect models (Pinheiro & Bates 2000; Zuur et al. 2009). The models of area use and movement distances were adapted and modeled as a function of group of fish (farmed/wild), and the individual characters body length and sex. The effect of tagging date on the movement behavior in the sea and in the river was tested within the wild and farmed groups because of small overlap between them. In order to account for within-individual dependency of the observations, ID was added as random factor in the analyses. I tested whether there were differences in migration speed of wild and farmed salmon from their tagging site in Namsfjorden to entering the river (i.e., first recording by stationary data-logger at Steinan). For the pre-spawning and spawning period, I tested whether there were differences in daily total and downstream movement distances, and daily changes in movement behavior. In addition, the probability of migrating to the migration barrier Nedre Fiskumfoss waterfall was estimated using generalized linear model with logit link function fitted to the binomial response "1" for moving all the way up to the barrier, and "0" for those that did not.

In order to estimate probabilities for staying in certain river sections in given periods (the pre-spawning and spawning periods) as function of group and covariates of interest, multinomial logit models were fitted to individual-specific mean positions data for both periods (Hosmer & Lemeshow 1989). The mean position was assigned to 1 out of 10 equally sized zones (from the lowermost receiver station to the migration barrier at Nedre Fiskumfoss waterfall). The multinomial model was fitted to predict probabilities of staying in a given zone. The models were fitted using the multinom function in the nnet package in R. Effect tests for the multinomial modes were performed using type III LogLiklihood Ratio tests running the ANOVA procedure available from the R package car.

In order to find the significant variables which had an effect on the salmons movements and changes in movement behavior, the variables with a p-value > 0.05 were backwards stepwise excluded from analyzes by calculating the models AIC-value (Akaikes information criterion) using the AICmodavg package in R (Anderson 2008). The parameter estimates of the models with a delta AIC-value less than two are presented and discussed (tables of model selection are presented in appendix 3).

The wild and farmed salmon's movement distances in the sea and in the river were calculated in ArcGIS. To calculate the movement distances in the river, a centerline in the middle of the river stretch with a known distance to the river mouth were used to calculate the distance from the river mouth at each manual and stationary tracking using the "Locate Features along routs" and "Make route event layer" tools. To calculate the migration speed from the tagging site until entering the river, the shortest distance in the sea were calculated using the "Cost Back Link" and "Cost Distance" tools.

The individuals with reliable registrations (23 farmed, 57 wild) on the data logger at Steinan (12.4 km upstream from the river mouth) were included in analyses of migration speeds in the sea. In order of short circuit at the stationary data loggers for 10 days in august, I did not have registrations of two wild and nine farmed individuals that entered the river. Only the individuals that migrated in the main river, and were not recaptured or passing the fish ladder at Nedre Fiskumfoss waterfall, were included in analyzes of the pre-spawning and spawning period. One farmed individual that migrated first in the river Namsen (upstream of where the river Sanddøla connects to the river Namsen), and thereafter to the river Sanddøla, was removed from these analyses. One farmed salmon that was recaptured October 6th, was included in the pre-spawning period analyzes, but not in the spawning period analyzes.

3 Results

3.1 Proportional use of wild and farmed Atlantic salmon of the main river and its tributaries

Of the tagged Atlantic salmon, 80 % (n = 59) wild and 74 % (n = 32) escaped farmed individuals were registered in the Namsen river system at the stationary data loggers or by manual tracking. The proportion of wild and farmed salmon that entered the river system did not differ ($\chi^2 = 0.19$, $p = 0.66$) (see appendix 1 for individual data on every tagged individuals). Four fish (2 farmed, 2 wild) were registered at the stationary data-loggers, but were never found by manual tracking in the river system.

In total, 61 (37 wild, 24 farmed) tagged salmon migrated and ended up in the main river, 11 (9 wild, 2 farmed) in the tributary Høylandsvassdraget, and 15 (11 wild, 4 farmed) in the tributary Sanddøla. The wild and the farmed salmon did not have different in distributions between the main river and the side rivers ($\chi^2 = 1.48$, $p = 0.22$). One farmed individual migrated in the river Namsen up-river from where the river Høylandsvassdraget connects to the main river before moving to the river Høylandsvassdraget. Another farmed individual migrated in the river Namsen upriver from where the river Sanddøla connects to the main river before moving to the river Sanddøla. One farmed individual passed the fish ladder at Nedre Fiskumfoss waterfall, and three wild individuals passed the fish ladder at Nedre Tømmeråsfoss waterfall in the river Sanddøla.

The movement pattern and area use of the tagged salmon that moved in the main river, the river Namsen, and were not recaptured or passed the fish ladders during the pre-spawning (19 wild, 18 farmed) and spawning period (17wild, 17 farmed) were documented (see appendix 2 for individual movement trajectories).

3.2 Sea migration

There were confirmed registrations of 23 (72 %) escaped farmed and 57 (97 %) wild Atlantic salmon at the stationary data logger at Steinan (12.4 km upstream from the river mouth). The farmed salmon had a mean movement speed of 14 km/day ± 6 (SD) (median 18, range 1-23 km/day), while the wild salmon had a mean movement speed of 17 km/day ± 8 (SD) (median 17, range 2-34 km/day) from their tagging site to Steinan.

The most supported linear model documented that sex was the only variable that had a significant effect on the tagged salmons movement speed between the tagging site and Steinan. Females ($n = 43$) moved faster than males ($n = 28$) from the tagging site until entering the river at Steinan, not depending on group ($p = 0.01$, Table 1). The second-most supported model included additive effects from group and sex, where males were estimated to migrate slower than females (Figure 3). There were no significant group effect in movement speed between the tagging site and Steinan ($p = 0.1$, Table 1), but wild salmon tended to migrate faster than the farmed salmon. The individuals with uncertain sex were excluded from these analyzes.

Table 1: Parameter estimates and effect tests for the two most supported linear models fitted to predict the migration speed from the tagging site until entering the river. Test parameters of the most supported model: one-way ANOVA: $R^2 = 0.1$, $F = 7.7$, $p = 0.01$, and the second most supported model: one-way ANOVA: $R^2 = 0.1$, $F = 4.4$, $p = 0.02$. Group levels: [Fe] = female; [Ma] = male; [Fa] = farmed salmon; [Wi] = wild salmon.

Parameter estimates			**Effect test**				
Model: Sea speed ~ Sex							
	Estimate	SE		Df	SS	F	P
Intercept [Fe]	18.6	1.1	Sex	1	424	7.6	0.01
Sex [Ma]	-5.0	1.8					
Model: Sea speed ~ Group + Sex							
	Estimate	SE		Df	SS	F	P
Intercept [Fa, Fe]	16.5	2.3	Group	1	158.5	2.9	0.10
Group [Wi]	2.4	2.3	Sex	1	324	5.9	0.02
Sex [Ma]	-4.5	1.9					

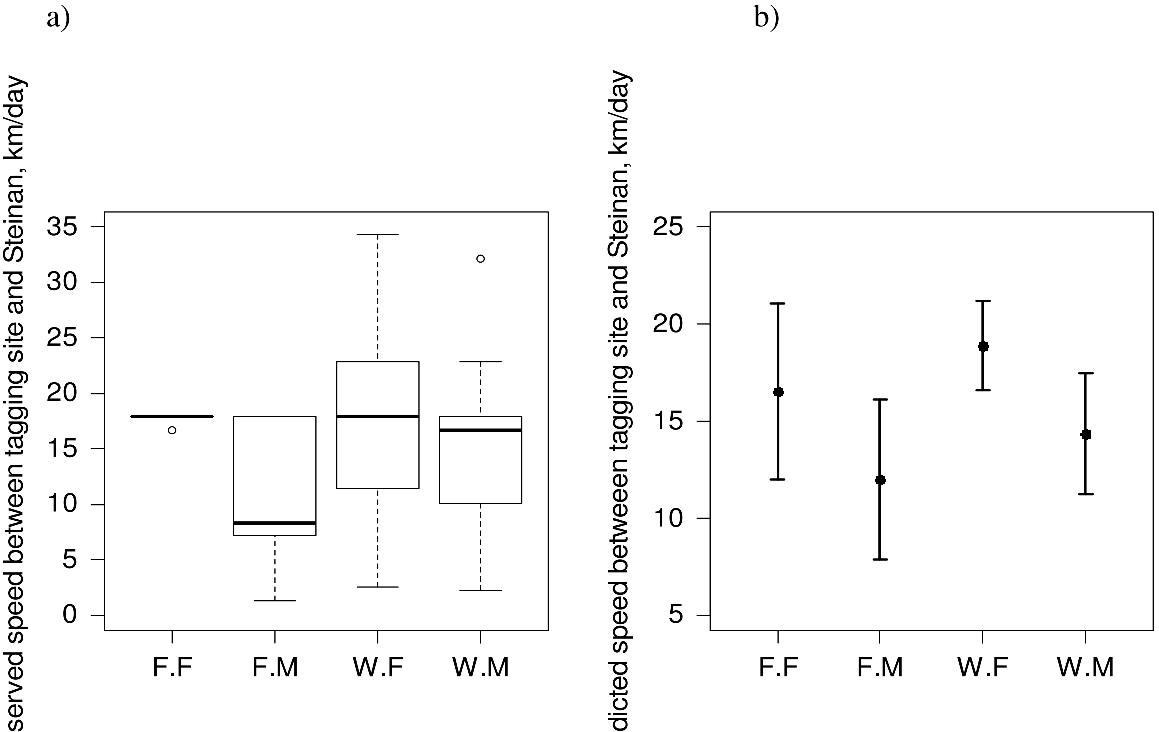

Figure 3: Boxplots of observed (a) and the predicted (b) sea migration speed as function of group and sex. The boxes include 50 % of the observations, outer horizontal lines span 90 % of the observations, and the bold horizontal line represent the median value. Predictions have been retrieved from the second-most supported linear model provided in table 1. N = 5 farmed females (F.F), 38 wild females (W.F), 9 farmed males (F.M), 18 wild males (W.M.). The bars in b) represent the 95 % confidence intervals of the prediction.

Wild salmon tagged early in the tagging period performed a higher sea migration speed between the tagging site and Steinan compared to wild salmon tagged later (p = 0.02, Table 2), while the date of tagging did not explain any variation in sea migration speed in farmed salmon (p = 0.93).

Table 2: Parameter estimates and effect tests for the two most supported linear models fitted to predict the movement speed from the tagging site until entering the river. The movement speed is explained by the variable date of tagging within the wild and farmed groups. Test parameters on the wild salmon model: One-way ANOVA: $R^2 = 0.01$, F = 5.9, p = 0.02, n = 57, and the farmed salmon model: one-way ANOVA: $R^2 = 0.0$, F = 0.01, p = 0.93, n = 23.

Parameter estimates			**Effect test**				
Model: Sea speed ~ Date of tagging (Wild)							
	Estimate	SE		Df	SS	F	P
Intercept	53.9	15.1	Date of tagging	1	351.6	5.9	0.02
Date of tagging	-0.2	0.1					
Model: Sea speed ~ Date of tagging (Farmed)							
	Estimate	SE		Df	SS	F	P
Intercept	16.1	21.7	Date of tagging	1	0.29	0.0	0.93
Date of tagging	0.0	0.1					

3.3 Area use

Pre-spawning period

The distribution of wild and escaped farmed Atlantic salmon differed throughout the pre-spawning period (September 4th to October 4th, Figure 4-5). On September 4th, early in the pre-spawning period, six (33 %) of the tagged farmed salmon in the main river were located in the pool just below the migration barrier at Nedre Fiskumfoss waterfall, while on the 6th of September there were two (11 %). Throughout the pre-spawning period the farmed salmon were distributed in the in the upper 30 kilometers of the river stretch, while three stayed in the lower part during the whole period. Two other farmed salmon stayed in the lower reaches for shorter periods. The wild salmon were evenly spread over the river stretch (Figure 4).

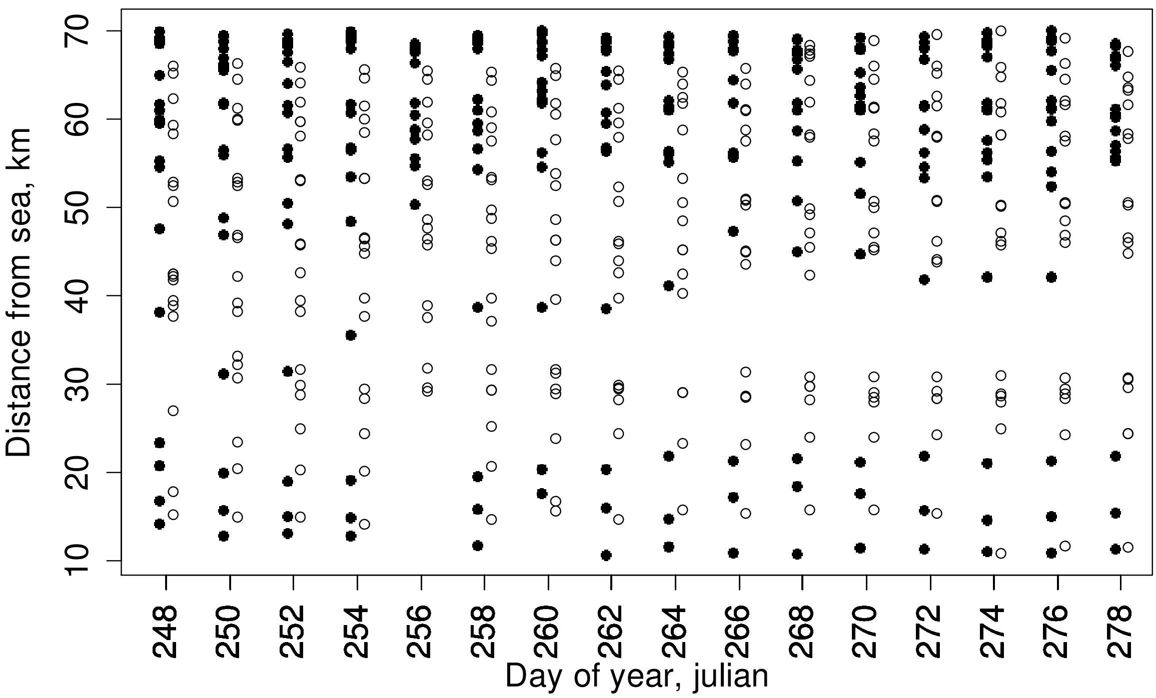

Figure 4: The location (distance from the river mouth) of farmed (filled circles) and wild salmon (open circles) on day 248-278 (September 4th-October 4th). At day 256 (September 12th), the lower 28 kilometers were not manually tracked. In order to ease reading of the figure minor temporal separation of wild and farmed salmon observations have been made.

The most supported multinomial model fitted to explore effects on river-stretch use during the pre-spawning period constituted a fully factorial structure between group, sex and day of year – however without including the three-way interaction between these predictors (see appendix 4 for parameter estimates, and LR effect test). In particular, there was a significant group*sex effect on river stretch distributions during the pre-spawning period (LR $x^2 = 84.01$, df = 8, $p < 0.0001$). The farmed salmon males had a higher probability of using the river stretches between 50 km from the river mouth and the migration barrier at Nedre Fiskumfoss (69.4 km from the river mouth), than both sexes of wild salmon (Figure 5). The farmed salmon females were estimated to have a higher probability for using the lower reaches (< 17.4 km), or the upper reaches (> 62.9), than of being elsewhere in the river stretch. The wild salmon were estimated to use all reaches of the river stretch during the period (Figure 5).

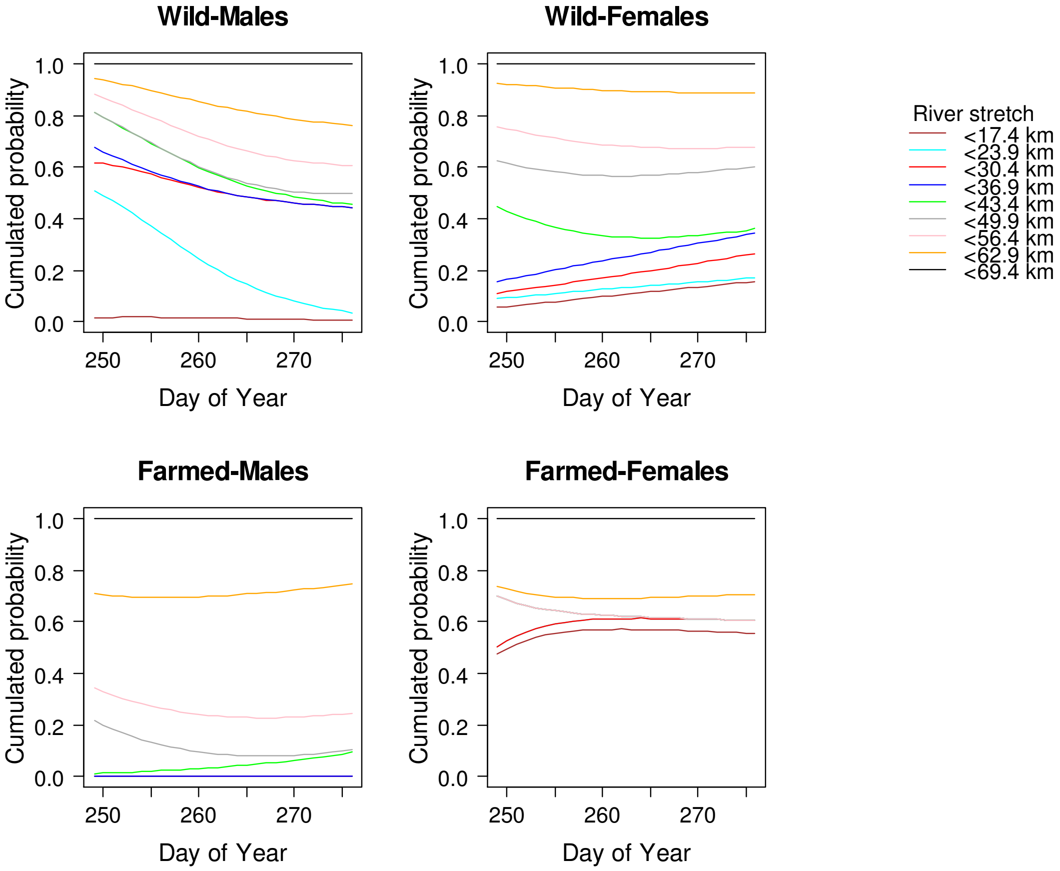

Figure 5: The predicted probability of use of river stretches (zones) in the pre-spawning period as function of group, sex and day of year. Predictions have been retrieved from the most supported multinomial model provided in the table in appendix 4.

Spawning period

All the escaped farmed Atlantic salmon except three individuals stayed in the upper 20 kilometers of the river (Figure 6). There were no tagged farmed salmon in the middle 30 kilometers of the river stretch. The wild salmon were evenly spread over the river stretch.

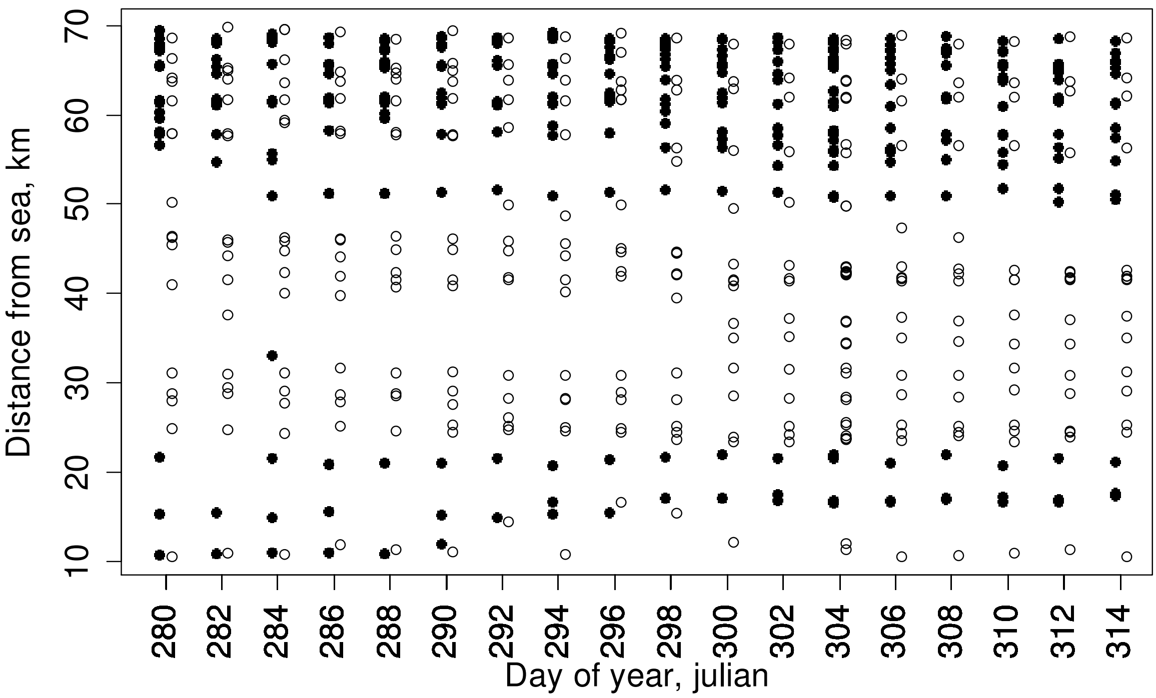

Figure 6: The location (distance from the river mouth) of farmed (filled circles) and wild salmon (open circles) on day 280-314 (October 6th-November 10th). In order to ease reading of the figure minor temporal separation of wild and farmed salmon observations have been made.

The most supported multinomial model fitted to explore effects on river-stretch use during the spawning period had exactly the same model structure as for the most supported pre-spawning multinomial model (see appendix 4 for parameter estimates, and LR effect test). As for the pre-spawning model, there was a significant group*sex effect on river stretch distributions during the spawning period (LR $x^2 = 56.77$, df = 8, $p < 0.0001$). The farmed salmon males had a higher probability of using the river stretch from 50 km from the river mouth and the migration barrier than both sexes of wild salmon (Figure 7). The farmed salmon females had a higher probability of using the river stretches below 56.4 km from the river mouth or the upper reaches (> 62.9) than middle part of the river. The wild salmon were estimated to use all reaches of the river stretch during the period (Figure 7). For the salmon females, the estimated probability of using the lower and middle river stretches increased with the day of year, indicating that they moved downstream after some time into the assumed spawning period of wild salmon.

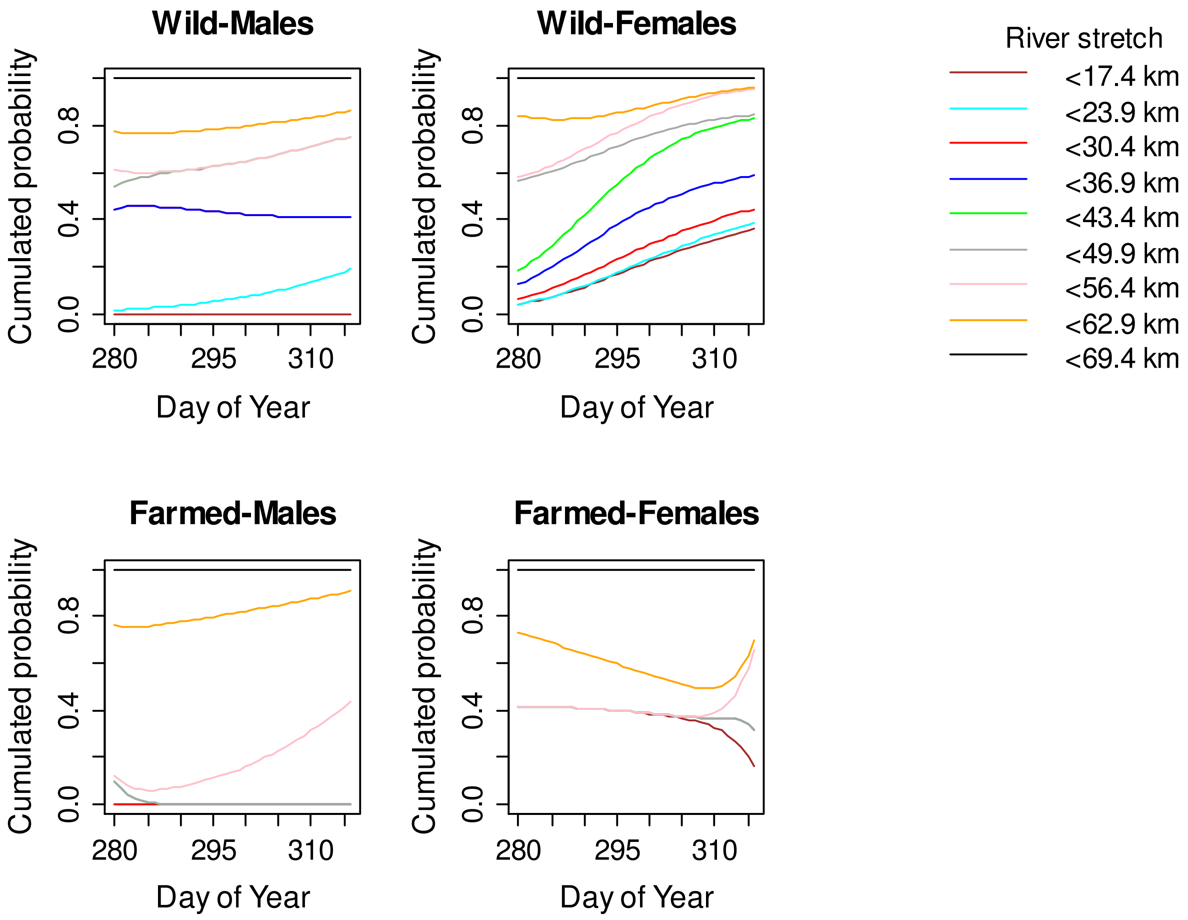

Figure 7: The predicted probability of use of river stretches (zones) during the spawning period as function of group, sex and day of year. Predictions have been retrieved from the most supported multinomial model provided in appendix 4.

3.4 River movement behavior

Pre-spawning period

The wild Atlantic salmon (n = 19) moved a mean total distance of 540 m/day ± 487 (SD) (median 436, range 118-1946 m/day), while the escaped farmed salmon (n = 18) moved a mean total distance of 867 m/day ± 515 (SD) (median 719, range 293-2295 m/day).

The two most supported linear models of the daily total movement distances, indicated that the group and the interaction parameter between group and body length was the significant variables, indicating that the farmed salmon performed longer total movement distances than the wild salmon (p = 0.04, Table 3). In addition, the interaction parameter between group and body length had a significant effect (p = 0.02), indicating that the body length had a different effect on the movement distances in farmed and wild salmon (Figure 8).

Table 3: Parameter estimates and effect tests for the two most supported linear models fitted to predict the daily total migration distances. The most supported model indicated that body length had a different effect on the total movement distances (one-way ANOVA: $R^2 = 0.25$, F = 3.6, p = 0.02). Group levels: [Fa] = farmed salmon; [Wi] = wild salmon.

Parameter estimates			**Effect test**				
Model: distance/day ~ Group * Length							
	Estimate	SE		Df	SS	F	P
Intercept [Fa]	-1136	1111	Group	1	988190	4.43	0.04
Group [Wi]	3814	1654	Length	1	292	0.00	0.97
Length	25	14	Group * Length	1	1416145	6.35	0.02
Group [Wi] * Length	-49	19					
Model: distance/day ~ Group							
	Estimate	SE		Df	SS	F	P
Intercept [Fa]	867	118	Group	1	988190	3.94	0.05
Group [Wi]	-327	165					

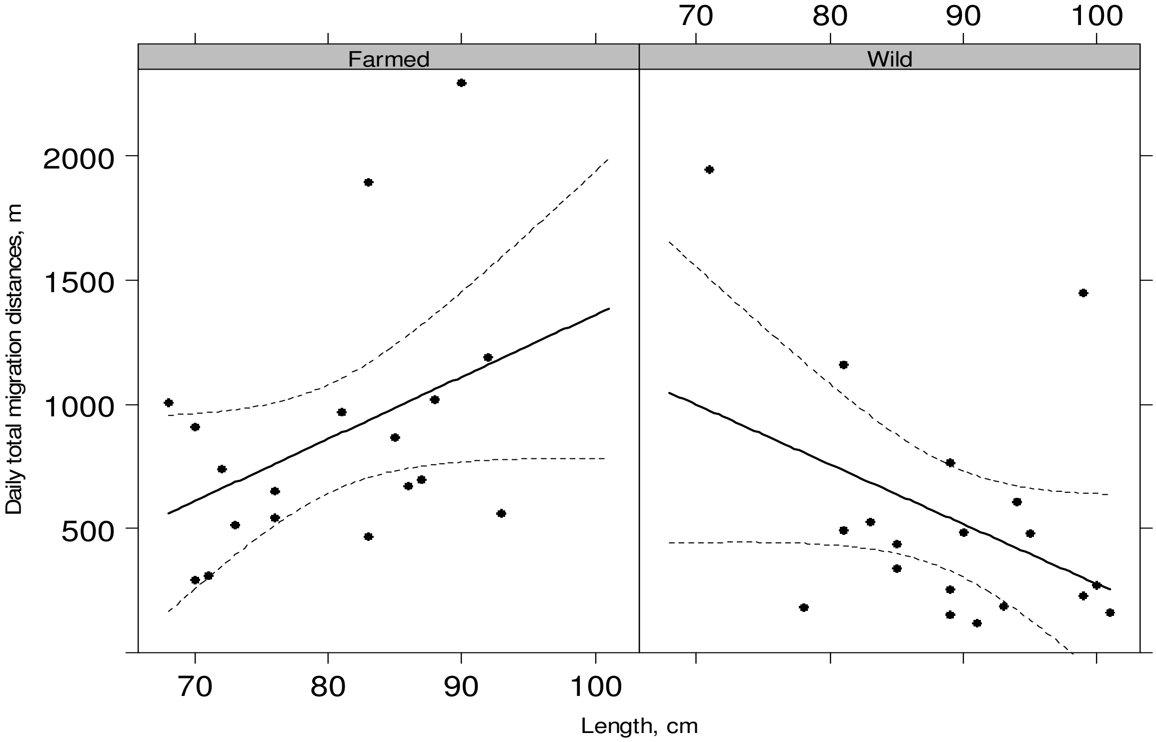

Figure 8: The observed daily total migration distances plotted as a function of body length (dots), and the predicted daily total migration distance as a function of length and group (solid line), with upper and lower 95 % confidence intervals (dotted lines). The predictions have been retrieved from the most supported linear model provided in table 3. N = 19 wild, 18 farmed.

The wild salmon moved a mean downstream distance of 289 m/day ± 238 (SD) (median 280, range 0-799 m/day), while the farmed salmon moved a mean downstream distance of 427 m/day ± 312 (SD) (median 367, range 0-117 m/day).

The most supported linear model of the daily downstream distances indicated that body length and the interaction variable between group and body length were significant parameters (Table 4). That indicated that the body length had an effect on the migration distances (p = 0.05), but in a different way in wild and farmed salmon (p = 0.01, Table 4). The daily downstream movement distances increased with body length in farmed salmon, while it tended to decrease with body length of the wild salmon (Figure 9). There were no significant difference in daily downstream movement distances of the wild and the farmed salmon (p = 0.1).

Table 4: Parameter estimates and effect tests for the most supported linear models fitted to predict the daily downriver migration distances. The most supported model indicated that body length had a different effect on the total movement distances (one-way ANOVA: $R^2 = 0.27$, $F = 3.8$, $p = 0.02$). Group levels: [Fa] = farmed salmon; [Wi] = wild salmon.

Parameter estimates			**Effect test**				
Model: distance/day ~ Group * Length							
	Estimate	SE		Df	SS	F	P
Intercept [Fa]	-1497	577	Group	1	176427	2.93	0.10
Group [Wi]	2086	859	Length	1	247260	4.11	0.05
Length	24	7	Group * Length	1	441839	7.34	0.01
Group [Wi] * Length	-27	10					

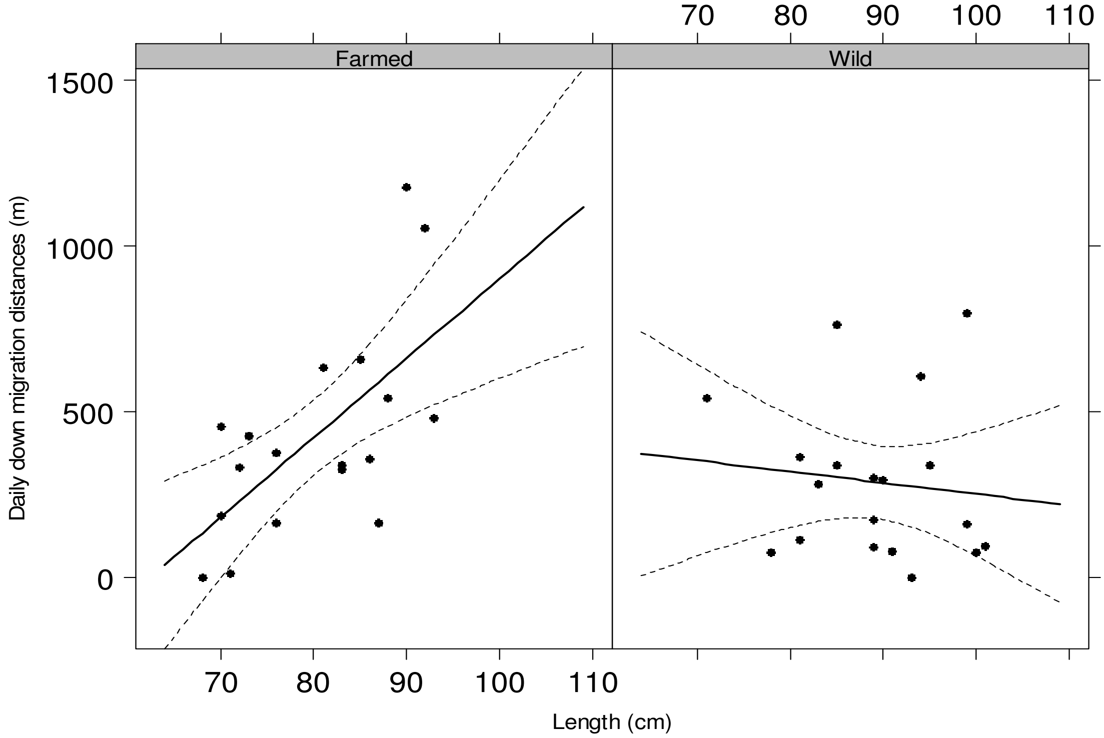

Figure 9: The observed daily downstream migration distances plotted as a function of body length (dots), and the predicted daily total migration distance as a function of length and group (solid line), with upper and lower 95 % confidence intervals (dotted lines). The predictions have been retrieved from the most supported linear model provided in table 4. N = 19 wild, 18 farmed.

Of the salmon that stayed in the main stream and were not recaptured, nine farmed salmon (42 %,), and two wild salmon (5 %) moved to the barrier at Nedre Fiskumfoss waterfall. The generalized linear model analyzes confirmed that the group (wild/farmed) were the only significant variable exploring the probability of migrating to the migration barrier (p = 0.01, Table 5). The farmed salmon had a predicted probability of 0.5 (95 % conf. interv. 0.28-0.72), and the wild salmon 0.1 (95 % conf. interv. 0.02-0.34) of moving to the barrier at Nedre Fiskumfoss waterfall.

Table 5: Parameter estimates and effect tests of the three most supported generalized linear models fitted to predict probabilities of migrating to the barrier at Nedre Fiskumfoss waterfall. Parameters are on logit-scale. Group levels: [Fa] = farmed salmon; [Wi] = wild salmon.

Parameter estimates			**Effect test**				
Model: to the barrier ~ Group							
	Estimate	SE		Df	Chi square	Df	P
Intercept [Fa]	-8E-16	0.47	Group	1	7.29	35	0.01
Group [Wi]	-2.14	0.88					
Model: to the barrier ~ Group + length							
	Estimate	SE		Df	Chi square	Df	P
Intercept [Fa]	-4.94	4.28	Group	1	7.29	35	0.01
Group [Wi]	-2.78	1.09	Length	1	1.43	34	0.23
Length	0.06	0.05					
Model: to the barrier~ Group * length							
	Estimate	SE		Df	Chi square	Df	P
Intercept [Fa]	-8.33	5.36	Group	1	7.29	35	0.01
Group [Wi]	9.42	9.71	Length	1	1.43	34	0.23
Length	0.10	0.07	Group * Length	1	1.50	33	0.22
Group [Wi] * Length	-0.14	0.11					

A change in movement direction was defined as moving either upstream or downstream from one manual tracking position to the next. The wild salmon changed movement direction on average 0.26 times/day ± 0.12 (SD) (median 0.23, range 0.07-0.53 times/day), while farmed salmon changed movement direction on average 0.38 times/day ± 0.12 (SD) (median 0.37, range 0.13-0.67 times/day).

The most supported linear models showed that group (wild/farmed) and the sex were the variables that had a significant effect on daily changes in movement direction. The farmed salmon had more changes in movement behavior than the wild salmon (p = 0.02, Table 6), and the females changed movement direction more often than males in both groups (Figure 10). The interaction parameter between group and sex indicated that sex had the same effect in both wild and farmed salmon (p = 0.12, Table 6). The salmon with unknown sex were not included in these analyzes.

Table 6: The parameter estimates of the most supported linear models fitted to predict the number of daily changes in movement direction. The most supported model indicated that males had a fewer changes in movement direction than females in both wild and farmed salmon (one-way ANOVA: R^2 = 0.33, F = 6.4, p = 0.003). Group levels: [Fa] = farmed salmon; [Wi] = wild salmon; [Fe] = female, [Ma] = male.

Parameter estimates			**Effect test**				
Model: change movement direc. ~ Group + Sex							
	Estimate	SE		Df	SS	F	P
Intercept [Fa, Fe]	0.43	0.04	Group	1	0.072	5.71	0.02
Group [Wi]	-0.12	0.04	Sex	1	0.104	8.29	0.01
Sex [Ma]	-0.12	0.04					
Model: change movement direc. ~ Group * Sex							
	Estimate	SE		Df	SS	F	P
Intercept [Fa, Fe]	0.47	0.05	Group	1	0.072	6.03	0.02
Group [Wi]	-0.19	0.06	Sex	1	0.104	8.75	0.01
Sex [Ma]	-0.20	0.06	Group * Sex	1	0.030	2.55	0.12
Group [Wi] * Sex [Ma]	0.13	0.08					

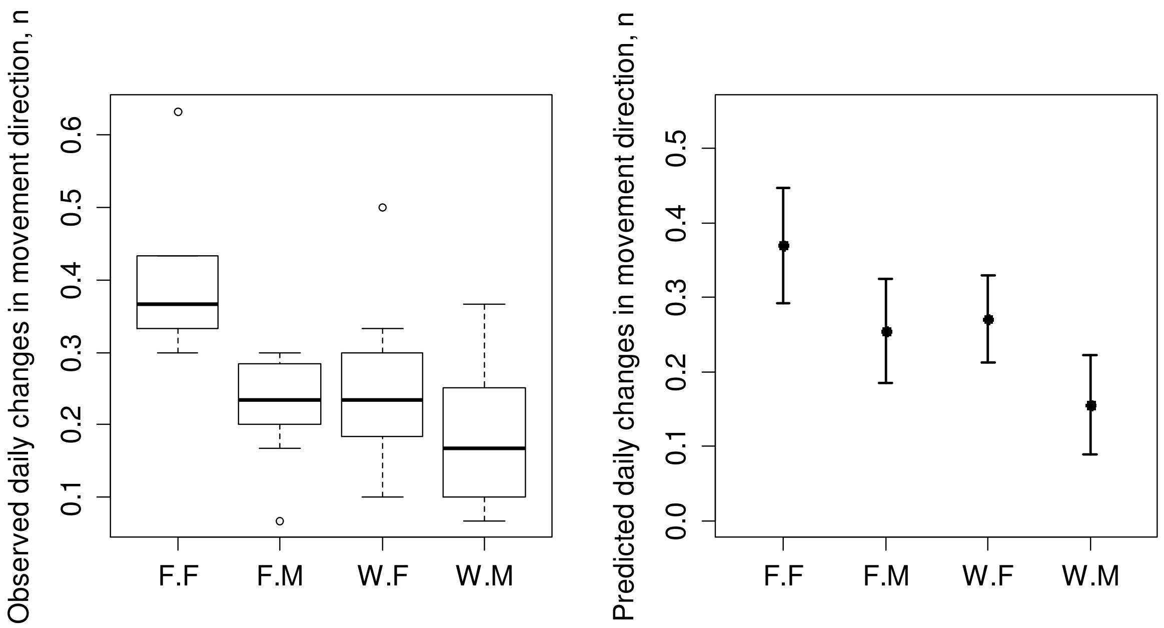

Figure 10: The observed (a) and predicted (b) number of changes in movement direction as function of group and sex, with 95 % confidence intervals (bars). The boxes include 50 % of the observations, outer horizontal lines span 90 % of the observations, and the bold horizontal line represent the median value. Predictions have been retrieved from the most supported linear model provided in table 6. N=11 wild females (W.F), 8 wild males (W.M), 5 farmed females (F.F), and 7 farmed males (F.M).

Spawning period

The escaped farmed Atlantic salmon moved a mean total distance of 356 m/day ± 503 (SD) (median 204, range 44-2173 m/day), while the wild salmon moved a mean total distance of 390 m/day ± 311 (SD) (median 326, range 0-1150 m/day). Daily total movement distances in the salmon were not depending on group (wild/farmed), sex or body length (one-way ANOVA: all p-values ≥ 0.1).

The farmed salmon moved a mean downstream distance of 207 m/day ± 286 (SD) (median 138, range 0-1215 m/day), while wild salmon moved a mean downstream distance of 295 m/day ± 248 (SD) (median 253, range 0-854 m/day). Daily total downstream movement distances in salmon were not depending on group (wild/farmed), sex or body length (one-way ANOVA: all p-values ≥ 0.15).

The farmed salmon changed movement direction mean 0.2 times/day ± 0.1 (SD) (median 0.2, range 0-0.43 times/day), while wild salmon changed movement direction mean 0.2 times/day ± 0.1 (SD) (median 0.2, range 0-0.54 times/day). Daily changes in movement direction in salmon were not depending on group (wild/farmed), sex or body length (one-way ANOVA: all p-values ≥ 0.4).

4 Discussion

4.1 Proportional use of wild and farmed Atlantic salmon of the main river and its tributaries

In the present study, there was no significant difference between wild and escaped farmed Atlantic salmon in the proportion of tagged fish entering the river, being 80 % and 74 % respectively. In the studies of radio tagged wild and farmed salmon in the river Namsen in 1993 (Thorstad et al. 1998) and the river Alta in 1991 (Heggberget et al. 1993), there was a higher proportion of wild than farmed salmon registered and tracked in the river systems. Smolts of wild salmon have been suggested to imprint information of their natal river when migrating to sea, which they use to find their way back to the river for spawning (Hansen et al. 1989; Harden Jones 1968). Since the farmed salmon do not undergo this imprinting process from a home river, I expected that a larger proportion of the tagged wild than the farmed salmon would enter the river. In 1993, only one out of 28 tagged farmed salmon migrated to Bjøra in Høylandsvassdraget (Thorstad et al. 1996). In another study, five out of 40 farmed salmon tagged and released from a fish farm in Altafjorden, entered neighboring rivers to the main river Alta (Heggberget et al. 1993). The fish that did not enter the river may have migrated to rivers that were not tracked. However, my findings suggest that the farmed salmon were just as motivated as the wild salmon to enter the Namsen river system when they had arrived Namsfjorden. This means that fjord catches may also give a reliable indication of the proportion of farmed salmon in the river.

The two wild and the two farmed individuals that were registered at the stationary data loggers, but never manually tracked in the river system, probably turned and migrated back to sea, or stayed in the lower reaches of the river that were not manually tracked.

The wild and the farmed salmon did not differ in their dispersal between the main river (37 wild, 24 farmed) and the tributaries Høylandsvassdraget and Sanddøla (20 wild, 6 farmed).

Hence, the farmed and wild salmon may spawn together also in the tributaries, as well as in the main river.

The differences in results of farmed salmon of the present study and what Thorstad et al. (1998) found in the river Namsen in 1993, may be a result of annual variations of proportions of farmed salmon which entered the river. The farmed salmon used in the 1993 and 2012 may have had different origin (i.e., different age when escaping and/or location of escape site). In addition, artificial selection of farmed salmon to optimal growth and age/ size at maturity (Gjøen & Berntsen 1997), may have resulted in different properties in farmed salmon in 1993 and 2012.

4.2 Sea migration

The migration speeds of the tagged wild and escaped farmed Atlantic salmon between the tagging sites in Namsfjorden and Steinan, 12.4 km upstream from the river mouth, was on average 17 and 14 km per day, respectively. These results support the suggestion that farmed salmon were just as motivated as the wild salmon to enter the river when present the fjord. Similar results were found in a study of tagged salmon in Namsfjorden in 1993 (Thorstad et al. 1998). In contrast, Heggberget et al. (1996) found that farmed salmon had a slower migration speed compared to wild salmon from the tagging site in the fjord to the river mouth of the river Alta. In the study in Altafjorden (Heggberget et al. 1996), the farmed salmon were tagged and released from fish farms to simulate an escape event, while in the river Namsen study in 1993 (Thorstad et al. 1998) and the present, the farmed salmon were captured using bag nets in the fjord.

Females migrated significantly faster than males both within wild and farmed salmon. This is in contrast to comparable studies of wild and farmed salmon in the river Namsen (Thorstad et al. 1998) and in the river Alta (Heggberget et al. 1996), where they did not document differences between the sexes in migration speed from the tagging sites in the fjords until entering the river. The wild salmon studies in the river Lærdalselva (Finstad et al. 2005) and the river Tana (Økland et al. 2001) did neither find differences between the sexes in migration speed from tagging until entering the rivers.

Wild salmon tagged later in the season migrated more slowly to the river mouth than those tagged earlier, – a pattern not observed in farmed salmon. The date of tagging explained only a small part of the variation ($R^2 = 0.1$), but it was highly significant. As far as I know, no privious studies have demonstrated differences in migration speed in the sea depending on the date of tagging in wild salmon.

4.2 Area use

Pre-spawning period

During the pre-spawning period (September 4th-October 4th), the wild and the escaped farmed Atlantic salmon were differently distributed among areas in the main river stretch of Namsen. The farmed salmon mainly stayed in the upper 30 km of the salmon stretch of the river, while wild salmon were distributed over all parts of the river stretch. A higher proportion of the farmed salmon (42 %) than wild salmon (5 %) moved to the migration barrier at Nedre Fiskumfoss waterfall, resulting in a four times higher predicted probability of moving to the barrier for farmed than for wild salmon. This finding supports the suggestion that farmed salmon, as opposed to the wild salmon, lack river- and spawning-site imprinting and thus do not have a ‘stop signal’ when migrating upstream rivers (Butler et al. 2005; Heggberget et al. 1996; Thorstad et al. 1998). Consequently, farmed individuals end up and aggregates at the migration barrier far up in the river. Non-maturity or poor physiological condition in some of the farmed salmon may be a reason that not all of them migrate to the upper parts. Alternatively, some of the farmed salmon escaped at an early life stage, for instance at the smolt stage, and may have migrated to the river Namsen in an earlier year. In the river Namsen 1993, five out of 28 tagged farmed salmon reached the river by early September (Thorstad et al. 1996). These individuals were distributed throughout the main river stretch (Thorstad et al. 1996), while in the previously mentioned Alta study, the farmed salmon distributed themselves in the upper reaches of the river after entering the river (Økland et al. 1995). The fact that farmed salmon mainly used the upper reaches of the main river, may affect the proportion of farmed salmon in the monitoring of farmed salmon in the fall during the pre-spawning period, – the proportion will be dependent on angling location and point of time. For instance, the proportion of farmed salmon may be higher in the upper reaches of the river than the lower and middle reaches of the main river. In addition, the proportion of farmed salmon may be higher in the middle and lower reaches of the main river during their up-migration phase than later in period.

The number of radio tagged farmed salmon that stayed in the pool under the migration barrier at Nedre Fiskumfoss waterfall varied throughout the study period. Consequently, the proportion of farmed salmon during the monitoring of farmed salmon in the fall in the pool under Nedre Fiskumfoss waterfall may be dependent on the day of angling.

Spawning period

Escaped farmed and wild Atlantic salmon were differently distributed in main the river during the spawning period (October 5th-November 10th). All tagged farmed salmon, except three in the lower reaches, stayed in the upper 20 km of the salmon stretch of the river, and there was no tagged farmed salmon in the middle 30 kilometers of the river. During the same period, the wild salmon were found over the whole river stretch. This is in accordance with the dispersal of wild salmon in compared to farmed salmon in the river Namsen in 1993 and in the river Alta (Heggberget et al. 1996; Thorstad et al. 1998). Both in the river Namsen in 1993 and in the river Alta, the farmed salmon were distributed higher up in the river than the wild salmon during the spawning period (Heggberget et al. 1996).

The spawning success for farmed males was 24 % of that of wild males, and for farmed females 32 % of that of wild females in a controlled study in the river Imsa (Fleming et al. 2000). The upper parts of the river Namsen main river are important spawning grounds for the wild salmon (Næsje et al. 2013b). Both wild- and farmed salmon stayed in these reaches during the spawning period. Hence, it is likely that spawning between wild and farmed salmon takes place in these areas. Recently, Karlsson et al. (2012) documented introgression of farmed salmon into the wild salmon in the river Namsen, both in adults and in fry (0+). From my findings of spatial variation in the degree of overlapping area use between wild and farmed salmon during spawning time, one can expect a varying degree of introgression among different parts of the river.

Some of the wild females moved downstream after some time into the anticipated spawning period. Heggberget et al. (1996) found the same tendency in the wild females in the river Alta in 1991. When the salmon females are done spawning, after a median of 5-6 days after the time, they do not defend their spawning site but leave their spawning area and, most often moves downstream, while the males stay at the spawning ground as long as they have strength and energy to spawn (Fleming 1996).

4.3 River movement behavior

Pre-spawning period

The escaped farmed Atlantic salmon had a longer total movement distance per day than wild salmon in the pre-spawning period, while there was no significant difference in downstream movements between the two groups. This may be because a proportion of farmed salmon had not finished their upstream migration in the river when the study period started (September 4th), while all the wild salmon had entered the river earlier and may have finished their searching and had started their holding phase close to the spawning area (Finstad et al. 2005; Økland et al. 2001).

The most supported models of daily total and downstream movement distances showed that the movement distances increased with body length in farmed salmon, while body length had no or little effect on the wild salmon. Two farmed individuals had a large effect on the linear model parameter estimates, but the results were significant even when they were excluded from the dataset analyses. As far as I know, no previous studies have found that movement distances of farmed salmon are depending on their body length.

The females changed movement direction more often than males in both wild and farmed salmon. The reason may be that females actively searched for a suitable nesting site by 'test-digging' of nests at different localities prior to spawning (Fleming 1996). Karppinen et al. (2004) found that wild females tended to have a more erratic migration pattern than wild males in the river Tana, while Økland et al. (2001) did not find a significant difference in movement pattern in the same river. Neither did Finstad et al. (2005) find sex differences in erratic movement behavior in wild salmon in the river Lærdalselva.

Spawning period

During the assumed wild-salmon spawning period, there were no differences in daily total and downstream movement distances between wild and escaped farmed Atlantic salmon. Further, there was no difference in changes in movement direction between wild and farmed salmon. However, in other similar studies, more extensive up- and downstream movements in farmed than wild salmon during the spawning period have been documented (Thorstad et al. 1998; Økland et al. 1995). In the present study, wild and farmed salmon had similar movement patterns during the spawning period, with substantial among-individual variations within both groups. A possible reason for not documenting differences in movement behavior between wild and farmed salmon may be that it was a low accuracy on the manual tracking, and thus it was too low for detecting smaller movements of the fish. For instance, movements between spawning grounds located 200 meter apart in the same area of the river would not have been documented. Further, the individuals may have moved and returned during the approximate two days between the manual tracking days. Hence, the estimated movement distances and the changes in movement behavior are most likely underestimated. Another factor that may have affected the results on area use and movement behavior is that not all the tagged salmon were located at every manual-tracking day. However, most of the wild and farmed salmon had a high number of detections in the pre-spawning (14-16 out of 16) and spawning (17-19 out of 19) periods. Hence, I believe the results in the present study are reliable for analyses of comparing of area use and movement behavior between wild and farmed salmon.

4.4 Methods used and suggestions of improvements

The present study has documented and compared the movement speed from the tagging site in the fjord until entering the river and area use and movement behavior before and during the assumed spawning period of wild and escaped farmed Atlantic salmon. A higher spatial accuracy of the tracking of the fish would have resulted in higher resolution of the results. This may be improved in future studies by smaller distances between the manual tracking stations along the river, and manual tracking more often than every second day.

Because of small overlap of tagging periods of the wild and farmed salmon that entered the river, the effect of tagging date on movement behavior and area use could be compared only within the farmed and the wild groups and not between the groups. This may be difficult to accomplish because farmed salmon often seem to enter the fjord later than the wild salmon (Thorstad et al. 2008), which also was the case in the tagging period of the present study.

Of the tagged fish, 13 farmed and one wild individual did not have clear sex characters, and were consequently characterized as “unknown sex”. These individuals were taken out from analyses when sex had a significant effect on river movements or area use, which resulted in a smaller number of individuals in the analyses where sex was a significant variable. If I had information on the sexes of these salmon, I might have been able to document differences between the sexes also in farmed salmon.

5 Conclusion and management implications

The tagged wild and escaped farmed Atlantic salmon stayed in the same areas of the river Namsen during both pre-spawning and spawning periods, in areas holding important spawning grounds. However, the wild and farmed salmon had different spatial distributions in the river during the spawning period, where farmed salmon stayed mainly in the upper 20 km of the river, while wild salmon were found in the whole river stretch. The present study indicates that wild and farmed salmon were in the same spawning areas at the same time in the upper reaches of the river, and hence, may have spawned together. None of the tagged farmed individuals were found in the middle reaches, and hence, the probability of breeding between wild and farmed salmon in this area was low.

The wild and farmed had different movement behavior during the pre-spawning period, but not in the assumed spawning period for wild salmon. This indicates that the farmed salmon had the same behavior as the wild during the spawning period.

The results of the present study suggest that the catch proportion of escaped farmed salmon in wild populations in the fall will differ between parts of the river, depending on the location and time of angling. In general, the results of the present study may be of importance when examining the proportion of farmed salmon in rivers in the fall. A changing distribution of farmed salmon between parts of the river indicates that the monitoring of proportion of farmed fish should be performed in all the parts of the river to give a representative sample of the situation of farmed salmon in the whole river system. In addition, targeted angling to remove as much farmed salmon as possible from the wild populations in the river Namsen, should be performed in the upper 20 km where the density of farmed salmon was highest both prior to and during spawning. Fishing for removal of escaped farmed salmon in the upper part of the river might also be recommended for other rivers with similar distribution of escaped farmed salmon as the river Namsen.

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Appendix 1

Individual data on every Atlantic salmon tagged with radio transmitters in Namsfjorden in 2012. ID*: Id-number of the fish*, Group: *whether the individual was a wild (W) or farmed (F) fish*, Sex: *whether the individual was a male (M), female (F) or a fish with unknown sex (U)*, Date: *date of tagging*, Length: *body length (cm),* Entered river: *whether the individual entered a river or not*, Recap.: *whether the individual was recaptured or not*, Detections pre-spawning: *number of detections by manual tracking in the period*, Detections spawning: *number of detections by manual tracking in the period*, River: *which part of the watershed the fish ended up in*.

ID	Group	Sex	Date	Length	Entered river	Recap.	Detect. pre-spawning	Detect. spawning	River	Comment
40	W	M	7.5.12	78	Yes	(Yes)	14	19	Namsen	C&R in the sea
79	F	F	7.25.12	88	Yes	No			Namsen	Over Fiskumfoss
87	F	F	7.31.12	76	Yes	No	15	16	Namsen	
91	F	F	8.6.12	83	Yes	No	16	17	Namsen	
94	F	F	8.8.12	85	Yes	No	14	14	Namsen	
104	F	F	8.18.12	70	Yes	No	16	19	Namsen	
105	F	F	8.18.12	76	Yes	No	15	18	Namsen	
63.5	F	M	7.17.12	86	Yes	No	16	19	Namsen	
78	F	M	7.25.12	92	Yes	No	15	19	Namsen	
102	F	M	8.16.12	73	Yes	No	15	19	Namsen	
111	F	M	8.24.12	71	Yes	No	14	17	Namsen	
112	F	M	8.25.12	70	Yes	No	16	19	Namsen	
116	F	M	8.29.12	68	Yes	No	16	19	Namsen	
49	F	U	7.11.12	83	Yes	No	16	19	Namsen	
85	F	U	7.31.12	87	Yes	No	16	19	Namsen	
89	F	U	8.6.12	90	Yes	No	16	18	Namsen	
97	F	U	8.13.12	81	Yes	No	15	19	Namsen	
100	F	U	8.15.12	72	Yes	No	15	18	Namsen	
103	F	U	8.17.12	88	Yes	No	16	19	Namsen	
8	W	F	6.15.12	101	Yes	No	15	16	Namsen	
17	W	F	6.21.12	89	Yes	No	16	18	Namsen	
22	W	F	6.21.12	89	Yes	No	16	19	Namsen	
27	W	F	6.22.12	93	Yes	No	16	16	Namsen	
34	W	F	6.29.12	85	Yes	No	14	19	Namsen	
38	W	F	7.5.12	90	Yes	No	16	19	Namsen	
55	W	F	7.12.12	83	Yes	No	16	19	Namsen	
57	W	F	7.13.12	99	Yes	No	15	18	Namsen	
62	W	F	7.13.12	94	Yes	No	16	0	Namsen	
63	W	F	7.13.12	95	Yes	No	16	18	Namsen	
66	W	F	7.18.12	71	Yes	No	16	19	Namsen	
6	W	M	6.15.12	99	Yes	No	16	19	Namsen	
29	W	M	6.28.12	81	Yes	No	6	0	Namsen	
36	W	M	6.29.12	85	Yes	No	16	19	Namsen	
41	W	M	7.5.12	89	Yes	No	16	19	Namsen	
46	W	M	7.6.12	91	Yes	No	16	19	Namsen	

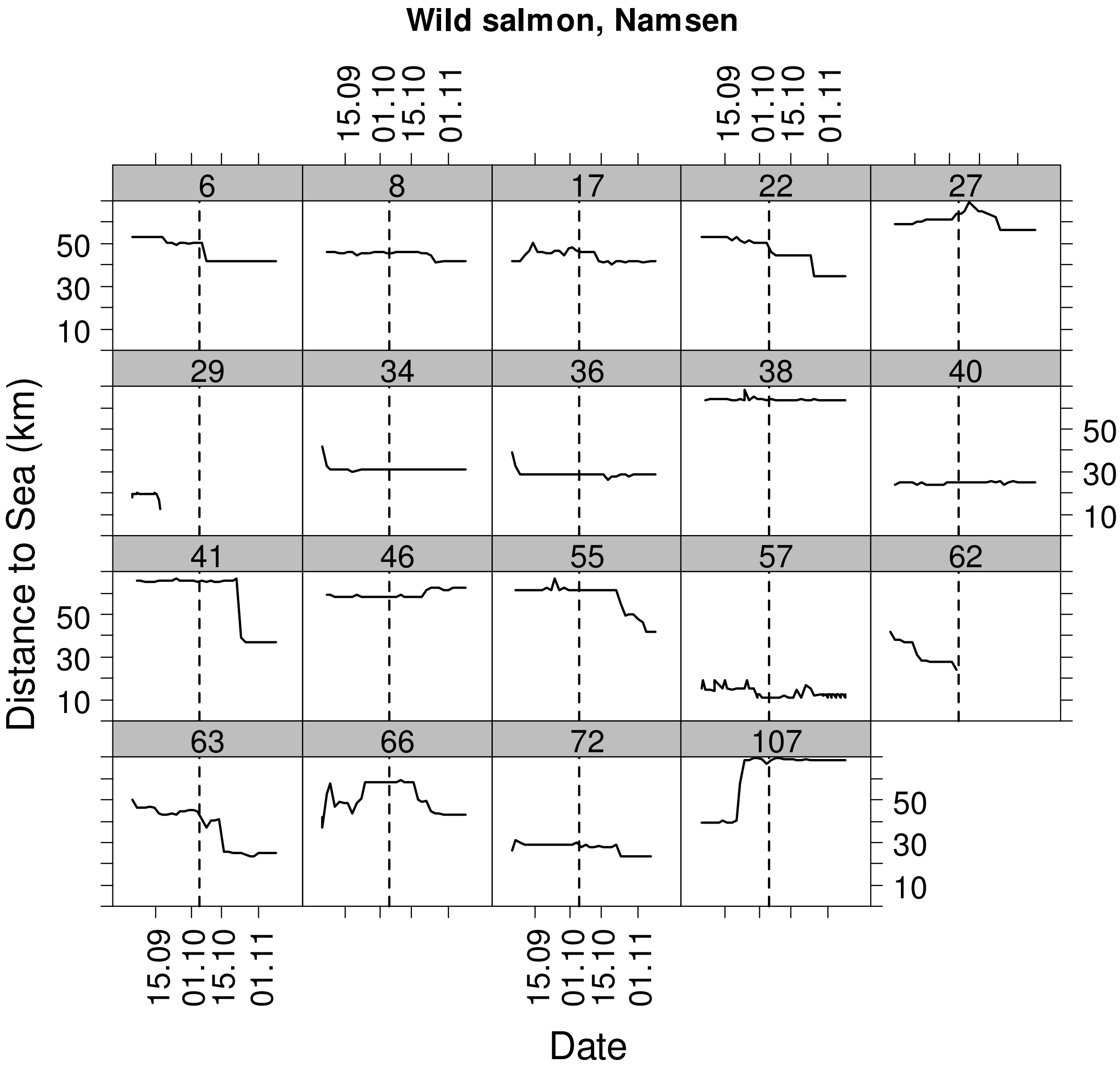
ID	Group	Sex	Date	Length	Entered river	Recap.	Detect. pre-spawning	Detect. spawning	River	Comment
72	W	M	7.18.12	100	Yes	No	16	18	Namsen	
107	W	M	8.21.12	81	Yes	No	16	19	Namsen	
88	F	M	8.2.12	68	Yes	Yes			Namsen	
92	F	M	8.6.12	80	Yes	Yes			Namsen	
98	F	M	8.13.12	93	Yes	Yes	16		Namsen	Recapture fall fisheries
76	F	U	7.20.12	80	Yes	Yes			Namsen	
96	F	U	8.12.12	65	Yes	Yes			Namsen	
101	F	U	8.16.12	69	Yes	Yes			Namsen	
1	W	F	6.15.12	83	Yes	Yes			Namsen	
5	W	F	6.15.12	98	Yes	Yes			Namsen	
7	W	F	6.15.12	92	Yes	Yes			Namsen	
10	W	F	6.15.12	76	Yes	Yes			Namsen	
12	W	F	6.15.12	101	Yes	Yes			Namsen	
13	W	F	6.15.12	95	Yes	Yes			Namsen	
16	W	F	6.21.12	108	Yes	Yes			Namsen	
21	W	F	6.21.12	88	Yes	Yes			Namsen	
23	W	F	6.22.12	93	Yes	Yes			Namsen	
24	W	F	6.22.12	94	Yes	Yes			Namsen	
31	W	F	6.28.12	82	Yes	Yes			Namsen	
52	W	F	7.11.12	83	Yes	Yes			Namsen	
54	W	F	7.12.12	94	Yes	Yes			Namsen	
20	W	M	6.21.12	100	Yes	Yes			Namsen	
37	W	M	7.5.12	80	Yes	Yes			Namsen	
42	W	M	7.6.12	77	Yes	Yes			Namsen	
43	W	M	7.6.12	78	Yes	Yes			Namsen	
109	W	U	8.24.12	67	Yes	Yes			Namsen	
113	F	M	8.26.12	75	Yes	No			Sanddøla	
90	F	M	8.6.12	71	Yes	No			Sanddøla	
106	F	M	8.21.12	80	Yes	No			Sanddøla	
110	F	M	8.23.12	86	Yes	No			Sanddøla	
19	W	F	6.21.12	93	Yes	No			Sanddøla	
30	W	F	6.28.12	93	Yes	No			Sanddøla	
68	W	F	7.18.12	76	Yes	No			Sanddøla	
73	W	F	7.18.12	91	Yes	No			Sanddøla	
75	W	F	7.20.12	86	Yes	No			Sanddøla	
25	W	F	6.22.12	86	Yes	No			Sanddøla	
74	W	M	7.19.12	103	Yes	No			Sanddøla	
59	W	M	7.13.12	81	Yes	No			Sanddøla	
60	W	M	7.13.12	80	Yes	No			Sanddøla	
26	W	F	6.22.12	81	Yes	Yes			Sanddøla	
39	W	F	7.5.12	77	Yes	Yes			Sanddøla	Recapture Namsen
115	F	M	8.29.12	81	Yes	No			Høylandsvassdraget	
108	F	M	8.23.12	81	Yes	No			Høylandsvassdraget	
28	W	F	6.28.12	87	Yes	No			Høylandsvassdraget	
64	W	F	7.18.12	85	Yes	No			Høylandsvassdraget	

ID	Group	Sex	Date	Length	Entered river	Recap.	Detect. pre-spawning	Detect. spawning	River	Comment
69	W	F	7.18.12	77	Yes	No			Høylandsvassdraget	
83	W	F	7.27.12	85	Yes	No			Høylandsvassdraget	
18	W	M	6.21.12	81	Yes	No			Høylandsvassdraget	
35	W	M	6.29.12	93	Yes	No			Høylandsvassdraget	
48	W	M	7.11.12	83	Yes	No			Høylandsvassdraget	
81	W	M	7.27.12	93	Yes	No			Høylandsvassdraget	
2	W	M	6.15.12	83	Yes	Yes			Høylandsvassdraget	Recapture Namsen
51	W	F	7.11.12	96	No	Yes			Nidelva	
4	W	F	6.15.12	85	No	Yes			Orkla	
53	F	F	7.12.12	79	No	Yes			Sea	
9	W	F	6.15.12	80	No	Yes			Sea	
15	W	F	6.21.12	88	No	Yes			Sea	
44	W	F	7.6.12	99	No	Yes			Sea	
70	W	F	7.18.12	80	No	Yes			Sea	
71	W	F	7.18.12	109	No	Yes			Sea	
56	W	M	7.12.12	82	No	Yes			Sea	
67	W	M	7.18.12	83	No	Yes			Sea	
50	W	M	7.11.12	82	No	Yes			Åsgårdselva	
11	F	F	6.15.12	68	Yes	No				Logged, not manually tracked
14	F	F	6.20.12	80	No	No				
33	F	F	6.29.12	77	No	No				
77	F	F	7.20.12	78	No	No				
80	F	F	7.25.12	72	No	No				
95	F	F	8.12.12	64	No	No				
99	F	F	8.14.12	82	No	No				
114	F	F	8.28.12	85	No	No				
47	F	U	7.10.12	90	Yes	No				Logged, not manually tracked
65	F	U	7.18.12	66	No	No				
84	F	U	7.27.12	69	No	No				
86	F	U	7.31.12	75	No	No				
3	W	F	6.15.12	98	Yes	No				Logged, not manually tracked
32	W	F	6.28.12	95	No	No				
58	W	F	7.13.12	81	No	No				
61	W	F	7.13.12	81	Yes	No				Logged, not manually tracked
82	W	F	7.27.12	95	No	No				
93	W	F	8.7.12	102	No	No				
45	W	M	7.6.12	101	No	No				

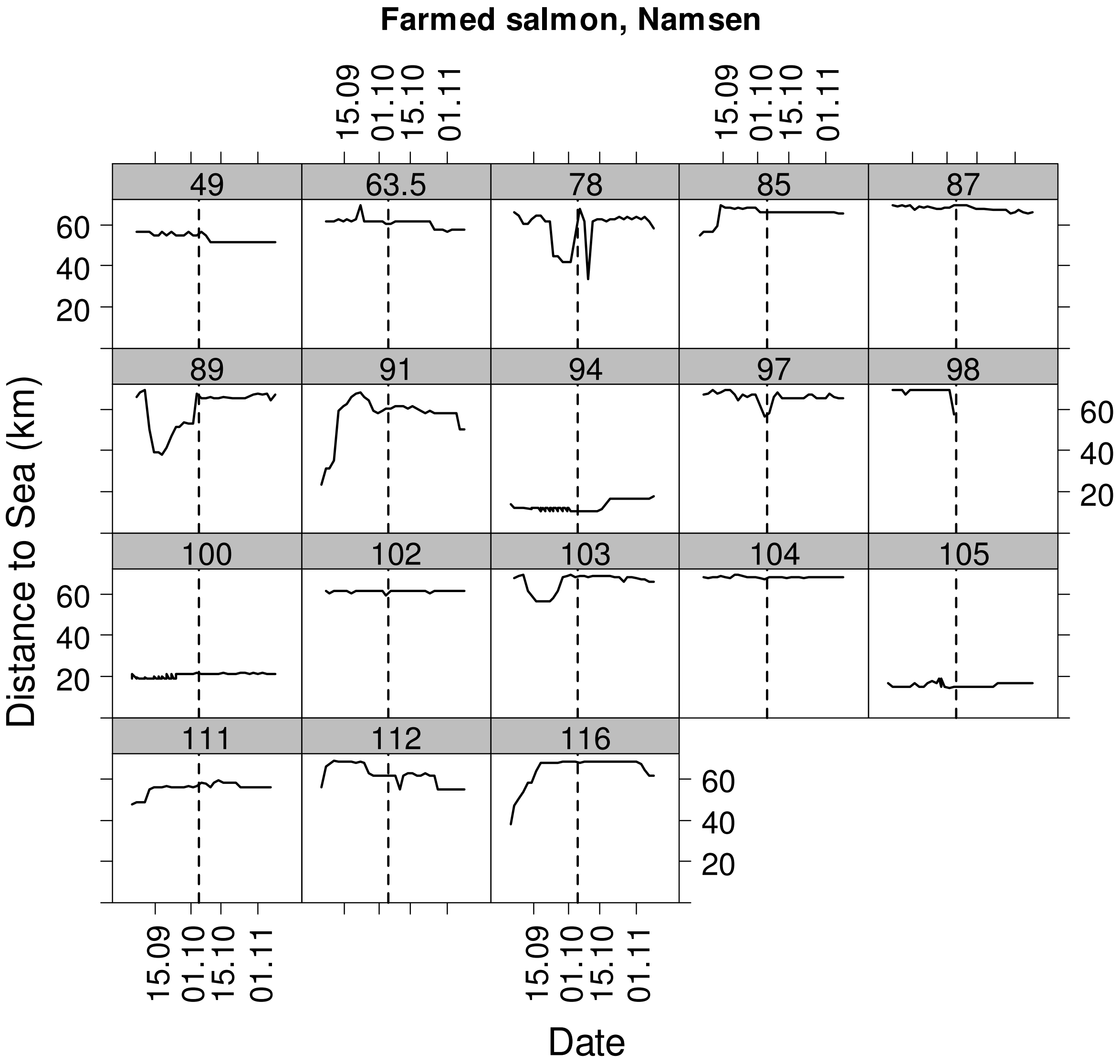
Appendix 2

Movement trajectories of the wild (a) and the farmed (b) salmon that migrated and ended up in the main river and were not recaptured. The pre-spawning (September 4th to October 4th) and the spawning (October 5th to November 19th) periods are marked with a dotted line. The numbers in the rectangle boxes are the individuals ID. Fish number 98 (farmed) was recaptured in the spawning period. Fish number 29 and 62 (wild) probably migrated back to the sea in the pre-spawning period.

a)



b)


Farmed salmon, Namsen
49
63.5
78
85
87
89
91
94
97
98
100
102
103
104
105
111
112
116
15.09
01.10
15.10
01.11
60
40
20
Distance to Sea (km)
Date

Appendix 3:

Ranked model selection tables based on AIC-values of the linear models on migration speed in the sea, the movement distances in the river, and changes in movement behavior. In addition the ranked model selection table of the GLM-models of the probability of migrating to the barrier at Nedre Fiskumfoss. K: *numbers of parameters estimated*, AICc: *the corrected (according to number of observations) Akaike's Information Criterion*, Delta AICc: *the difference in AICc value of the particular model and the most supported model*. The most supported models (with a delta AICc-value less than two) are highlighted.

Model selection of migration speed (km/day) from the tagging site to the first registration at the stationary data logger at Steinan.

Model structure	**K**	**AICc**	**Delta AICc**
Sex	4	551.2	0.0
Group + Sex	5	552.4	1.1
Sex + Length	5	553.5	2.3
Group	3	554.2	3.0
Group * Sex	6	554.4	3.2
Group + Length + Sex	6	554.6	3.4
Group + Length	4	556.4	5.2
Length	3	556.8	5.6
Group * Length + Sex	7	556.9	5.7
Sex * Length	7	557.8	6.5
Group * Length	5	558.6	7.4
Group + Length * Sex	8	558.9	7.6

Model selection of daily total migration distances (m/day) in the pre-spawning period.

Model structure	**K**	**AICc**	**Delta AICc**
Group * Length	5	568.4	0.0
Group	3	569.7	1.3
Group * Length + Sex	7	571.2	2.8
Sex	4	571.9	3.6
Group + sex	5	572.1	3.8
Group + Length	4	572.2	3.8
Length	3	572.8	4.4
Sex + Length	5	573.6	5.3
Group * Sex	6	574.7	6.4
Group + Length + Sex	6	574.9	6.6
Sex * Length	7	575.8	7.5
Group + Length * Sex	8	578.1	9.8

Model selection of the daily down migration distances (m/day) in the pre-spawning period.

Model structure	**K**	**AICc**	**Delta AICc**
Group * Length	5	519.9	0.0
Group * Length + Sex	7	523.4	3.5
Group + length	4	524.6	4.8
Group	3	525.7	5.8
Sex	4	526.7	6.8
Length	3	527.4	7.5
Group + Length + Sex	6	528.2	8.3
Group + Sex	5	528.2	8.3
Sex + Length	5	528.6	8.7
Group * Sex	6	529.0	9.1
Sex * Length	7	533.1	13.2
Group + Length * Sex	8	533.6	13.7

Model selection of the probability of migrating to the barrier Nedre Fiskumfoss waterfall.

Model structure	**K**	**AICc**	**Delta AICc**
Group	2	42.1	0
group + Length	3	43.0	0.9
Group * Length	4	44.1	2.0
Group + Sex	4	45.9	3.8
Sex	3	47.2	5.1
Group + Length + Sex	5	47.6	5.5
Group * Sex	5	48.6	6.5
Group * Length + Sex	6	49.3	7.2
Length	2	49.3	7.2
Sex + Length	4	49.7	7.6
Sex * Length	6	49.8	7.7
Group + Length * Sex	7	49.9	7.8

Model selection of the daily changes in movement behavior in the pre-spawning period.

Model structure	**K**	**AICc**	**Delta AICc**
Group + Sex	5	-47.2	0.0
Group * Sex	6	-46.9	0.2
Group + Length + Sex	6	-45.1	2.1
Sex + length	5	-43.9	3.3
Sex	3	-43.2	4.0
Group	4	-42.3	4.9
Group + length * Sex	7	-42.2	5.0
Group * Length + Sex	8	-42.1	5.0
Sex * Length	4	-40.9	6.3
Group + Length	7	-39.8	7.4
Length	5	-38.3	8.9
Group * Length	3	-37.9	9.2

Appendix 4:

Logit parameter estimates for the most supported multinomial model fitted to predict probabilities of river-section use during the pre-spawning (a) and spawning (b) periods. DoY = Day of year; Group levels: [Fa, Fe] = female farmed salmon; [Wi] = wild salmon; [Ma] = male.

a) Pre-spawning period

Response	Parameter estimates (±SE)						
River stretch	Intercept[Fa, Fe]	Group[Wi]	DoY	Sex[Ma]	Group[Wi]*DoY	Group[Wi]*Sex[Ma]	DoY*Sex[Ma]
<23.9 km	-6.6341±0.009	22.8935±0.0132	0.0153±0.0017	-0.2638±0.006	-0.0827±0.0026	3.3345±0.006	0.0033±0.0034
<30.4 km	-2.6306±0.0577	-2.5777±0.0577	-0.075±0.0007	-6.2856±0.0382	0.092±0.0007	-8.2701±0.0382	0.0701±0.0031
<36.9 km	61.9376±0.0196	-57.7007±0.0209	-0.2523±0.0025	61.3251±0.0001	0.2345±0.0028	1.0177±0.0001	-0.2446±0.0041
<43.4 km	-35.6328±0.0419	74.1853±0.0276	0.1011±0.0026	-3.0053±0.0189	-0.2493±0.0026	-19.9571±0.0094	0.0942±0.0032
<49.9 km	27.8616±0.164	-20.0159±0.1481	-0.2284±0.0034	-16.7511±0.0173	0.2016±0.0034	-46.5806±0.0013	0.2354±0.0039
<56.4 km	-11.6488±0.1773	27.1547±0.1043	0.0087±0.002	-6.9384±0.1108	-0.0675±0.0021	-21.2996±0.0404	0.1156±0.0032
<62.9 km	-9.663±1.4153	18.2526±0.8575	0.0289±0.0055	-9.7433±0.8382	-0.0589±0.0037	-15.6368±0.3046	0.1029±0.0046
<69.4 km	-0.2645±0.9801	6.2904±0.4589	-0.0013±0.0038	-15.0884±0.6469	-0.0217±0.0022	-12.8682±0.3028	0.116±0.0038

Effect test:

	LR Chisq	Df	P
Group	16.7	8	0.0334
Julian	12.9	8	0.116
Sex	2.5	8	0.963
Group * Julian	19.3	8	0.013
Group * Sex	84	8	> 0.0001
Julian * Sex	12	8	0.16

b) Spawning period

Response	Parameter estimates (±SE)						
River stretch	Intercept[Fa, Fe]	Group[Wi]	DoY	Sex[Ma]	Group[Wi]*DoY	Group[Wi]*Sex[Ma]	DoY*Sex[Ma]
<23.9 km	-107.001±0.002	97.262±0.001	0.338±0.002	-32.565±0.001	-0.316±0.003	16.757±0.016	0.139±0.064
<30.4 km	4.336±0.010	5.275±0.010	-0.189±0.182	15.676±0.008	0.152±0.182	-23.055±0.008	0.111±0.064
<36.9 km	26.534±0.005	-15.265±0.005	-0.148±0.022	42.425±0.001	0.109±0.022	-20.523±0.001	-0.076±0.043
<43.4 km	3.01±0.006	3.245±0.007	-0.115±0.037	-11.399±0.001	0.094±0.037	-8.861±0.001	0.148±0.064
<49.9 km	21.832±0.005	23.124±0.005	-0.139±0.042	-1.192±0.001	-0.014±0.042	-12.599±0.001	0.062±0.083
<56.4 km	-173.555±0.036	174.164±0.059	0.551±0.002	92.571±0.060	-0.557±0.002	-2.148±0.828	-0.244±0.064
<62.9 km	8.003±0.024	42.384±0.009	-0.03±0.001	-62.685±0.033	-0.144±0.001	11.634±0.518	0.254±0.064
<69.4 km	-8.312±0.004	37.952±0.022	0.028±0.001	-42.488±0.021	-0.129±0.001	13.297±0.497	0.179±0.064

Effect test

	LR Chisq	Df	P
Group	33.5	8	> 0.0001
Julian	34.4	8	> 0.0001
Sex	18.5	8	0.018
Group * Julian	33.5	8	> 0.0001
Group * Sex	56.8	8	> 0.0001
Julian * Sex	24.8	8	0.002

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