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Migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during and after spawning in a Norwegian river

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Abstract

The migratory behaviour of adult wild and escaped farmed Atlantic salmon, *Salmo salar* L., before, during after spawning in the River Namsen, Norway, was analysed using radio telemetry. The fish were caught, radio tagged and released into the fjord between 7 and 25 km from the river mouth. A significantly higher proportion of wild (74%) than farmed (43%) salmon was subsequently recorded in the river. Wild salmon (33%) were more frequently captured in the sea and in rivers than farmed salmon (14%). The migration speed from release to passing a data logger 11 km upstream from the river mouth was not significantly different between wild (20.6 km day^{-1}) and farmed (19.8 km day^{-1}) salmon. Wild salmon tagged when water flow in the river was increasing had a significantly higher migration speed than wild salmon tagged when water flow was decreasing. This was not true for farmed salmon. Farmed salmon were distributed significantly higher up the river than wild salmon during spawning, although both types of fish were found together in spawning areas. Thus, there was no geographical isolation to prevent spawning between wild and escaped farmed salmon. Farmed salmon had significantly more and longer up- and downstream movements than wild salmon during the spawning period. Unlike farmed salmon, the number of riverine movements by wild salmon increased significantly when variation in water flow increased. A smaller proportion of wild (9%) than farmed (77%) salmon survived through the winter after spawning.

Introduction

The fish farming industry in Norway has increased rapidly during the last 2 decades (Tilseth, Hansen & Møller 1991) and large numbers of farmed Atlantic salmon, *Salmo salar* L., have been released accidentally. The mean proportion of farmed salmon recorded in Norwegian rivers during spawning has varied between 20% and 38% (Lund, Hansen & Økland 1994).

Escaped farmed salmon lack river imprinting and seem to return to the area of release at maturation (e.g. Sutterlin, Saunders, Henderson & Harmon 1982; Heggberget, Hvidsten, Gunnerød & Møkkelgjerd 1991). Later in the season, the fish seem to enter rivers in the release area at random (Hansen, Døving & Jonsson 1987). Escaped farmed salmon are spawning in these rivers (Lura & Sægrov 1991, 1993; Lura & Økland 1994), but the spawning success seems reduced when compared with wild salmon (Lura & Sægrov 1993; Økland, Heggberget & Jonsson 1995; Fleming, Jonsson, Gross & Lamberg 1996).

A detailed analysis of the migratory patterns of wild and farmed salmon was carried out by using radio telemetry in the River Alta, northern Norway (Heggberget, Økland & Ugedal 1993, 1996; Økland *et al.* 1995). Wild salmon were captured in the fjord during the return migration and farmed salmon were released from a fish farm to simulate a natural escape. A higher proportion of wild salmon than farmed salmon was recorded after release (Heggberget *et al.* 1993). The farmed salmon spent a longer time in the sea before entering the River Alta (Heggberget *et al.* 1993). The farmed salmon also spread further up the river and showed a greater up- and downstream movement pattern than the wild salmon (Heggberget *et al.* 1996).

In the present study, corresponding investigations were carried out in the River Namsen on escaped farmed salmon that had spent a period of time in the wild after release. Both wild and farmed salmon were captured for tagging in the fjord during the return migration of wild salmon. The farmed salmon in the present study were of unknown origin and the time from escape to tagging was also unknown. The present study aims to analyse possible behavioural differences during the return migration of wild and escaped farmed salmon. The results from the River Namsen are compared to those from the River Alta to analyse possible differences between farmed salmon that have spent some time in nature after escaping from the farm and newly released salmon.

Materials and methods

The River Namsen is situated in Middle Norway at 64° N (Fig. 1). Mean annual water flow at the outlet is 290 $m^3 s^{-1}$. Salmon can migrate 60 km upstream in the mainstem of the River Namsen and a total of 200 km of the watercourse is accessible for fish migrating upstream (Paulsen, Rikstad & Einvik 1991). The peak migration of adult salmon occurs from mid-June through July. Peak spawning takes place during the last half of October. Spawning areas are widely distributed along the accessible stretches above Sellæg (Fig. 1). Atlantic salmon is the dominant fish species in the river and there are small numbers of andromous brown trout, *Salmo trutta* L. Proportions of between 0.3% and 12.7% of farmed salmon have been recorded in the River Namsen during the fishing season in summer, and between 10.0% and 72.2% during spawning time (Paulsen *et al.* 1991; Lund *et al.* 1994). Several fish farms are situated in the fjord about 50 km from the river outlet (Lund *et al.* 1994).

Wild and farmed salmon were caught in bag nets in the Namsen Fjord between 7 and 25 km from the outlet of the River Namsen (Fig. 1). During the tagging procedure, the fish were not anaesthetized, but kept in a water-filled tube with their head in darkness. Radio transmitters (Model 16M from Advanced Telemetry Systems, ATS) were attached externally to the fish below the dorsal fin. The transmitters were flat, with outline dimensions of 49 × 25 × 10 mm, and a weight of 25 g in air and 11 g in water. Transmitters of this size should not cause any long-term effects on fish larger than 60 cm (Mellas & Haynes 1985; Heggberget, Hansen & Næsje 1988). The fish were released immediately after tagging at the site of capture, except for 12 individuals that spent a night in a net pen.

During the period from 19 June to 17 September

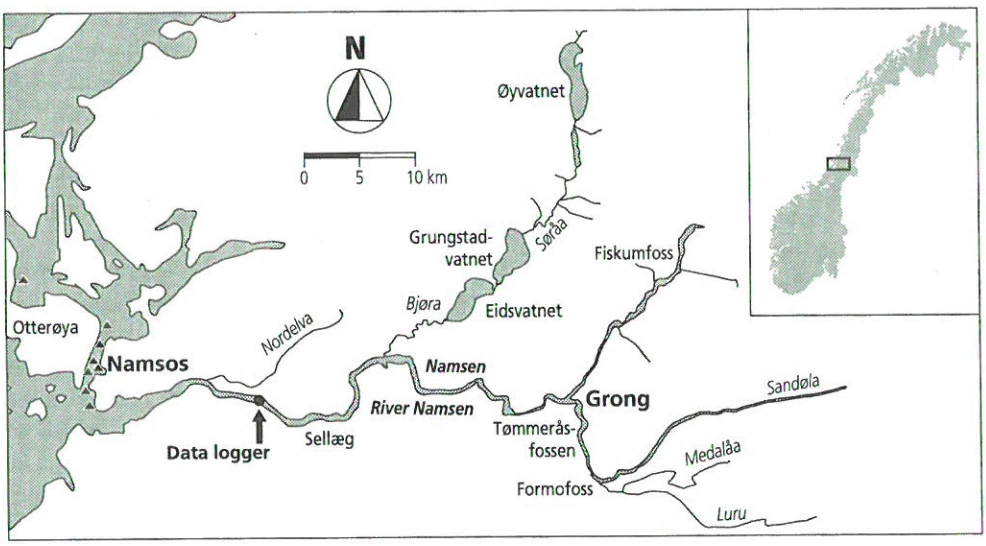

Figure 1 The location of the River Namsen and the Namsen Fjord, Middle Norway: (▲) bag net sites where wild and escaped farmed salmon were caught, tagged with radio transmitters and released; and (●) the location of a data logger recording signals from passing radio-tagged fish.

1993, 84 wild salmon (mean total length = 88.6 cm; range = 63–116 cm; SD = 11.3) and 28 farmed salmon (mean total length = 73.0 cm; range = 60–92 cm; SD = 10.3) were tagged. Most of the wild salmon (90%) were tagged in June and July, and most of the farmed salmon (82%) were tagged in August and September. The present authors were not able to capture farmed salmon earlier than this time because these fish entered the inner fjord areas later than the wild salmon. Wild and farmed salmon were identified according to their external characteristics and from scale analysis (Lund, Hansen & Järvi 1989).

Water flow and water temperatures were measured at Fiskumfoss (Fig. 1) every day at 0700 h. During the period of tagging, water flow varied between 65 and 510 $m^3 s^{-1}$, and water temperatures between 5.9 and 14.8 °C.

The radio tags transmitted signals within the 142.010–142.500 MHz range. To recognize individual fish, each radio tag had a unique combination of frequency and pulse rate. Radio signals are not transmitted in salt water because of the high electrolytic content. A data logger (DCC II Model 05041 from ATS) 11 km upstream from the mouth of the River Namsen (Fig. 1) recorded signals from passing radio-tagged salmon. Atmospheric and local signal disturbance made it difficult to recognize transmitter signals, but 57% of the upstream migrating salmon recorded by manual tracking were recorded by the data logger (30 wild and 12 farmed salmon).

Radio-tagged salmon that entered the River Namsen were tracked from a car once a week during the period from 1 September to 28 November 1993, every second week from 10 April to 31 July 1994 and three times between the two periods (Receiver Model R2100 from ATS). During spawning, 33 wild and nine farmed salmon were tracked in the river. Fishermen returned transmitters from captured fish both in the sea and in rivers. Proportions of fish observed after release are based on these efforts. Differences in the proportions of wild and farmed salmon were analysed by Yates-corrected chi-squared calculations (Zar 1984).

The results concerning migratory pattern were based on individuals that the present authors were able to record every week during the period from 1 October to 15 November 1993. Because of previous findings (Power & McCleave 1980; Jonsson, Jonsson & Hansen 1990, 1991; Økland *et al.* 1995), a more up- and downstream migratory pattern was expected in farmed than wild salmon. The results concerning migratory pattern in relation to water flow were based on individuals that the present authors were able to record every week during the period from 18 September to 27 November 1993, and on 8 and 19 December 1993. Per cent survival through the winter was based on trackings made the following spring and summer. Survivors gradually migrated downstream until the radio signals eventually disappeared when the fish reached the estuary between April and June. Individual fish were assumed dead when the transmitters continued to broadcast signals from the same pool (last tracking 31 July 1994).

Results

Proportions of fish recorded after release

A higher proportion of wild than farmed salmon was recorded after release ($\chi^2 = 14.8$, $P < 0.001$) and subsequently in the River Namsen ($\chi^2 = 7.6$ $P = 0.006$) (Table 1). There were no differences in the proportion of river entry between the sexes for either wild or farmed salmon (wild salmon: $\chi^2 = 0.16$, $P = 0.69$; farmed salmon: $\chi^2 = 0.000$, $P = 1.0$). There were no differences in body length between the salmon that entered and did not enter the Namsen river system either for wild or farmed salmon (Mann–Whitney *U*-test, wild salmon: $U = 533.5$, $P = 0.13$; farmed salmon: $U = 81.0$, $P = 0.51$). A significantly higher proportion of wild (35%) than farmed (14%) salmon was captured in the sea and rivers after release ($\chi^2 = 4.1$, $P = 0.042$) (Table 1).

Migration speed in the estuary and the lowest part of the River Namsen

There were no differences in migration speed between wild and farmed salmon from release to passing the data logger 11 km upstream in the River Namsen (Mann–Whitney *U*-test: $U = 178.0$, $P = 0.96$) (Table 2). There were no differences in migration speed between the sexes for either wild or farmed salmon (Mann–Whitney *U*-test, wild salmon: $U = 86.0$, $P = 0.28$; farmed salmon: $U = 12.0$, $P = 0.50$). The fish were tagged and released at eight different bag net sites, thus individual fish had different migration distances from the release site to the river mouth, but had the same migration

Table 1 Atlantic salmon radio tagged in the Namsen Fjord. Recordings after release are based on data logging in the River Namsen, regular trackings in the Namsen river system and captures reported from commercial and sports fisheries

				Captured		
		Recorded in the sea and rivers	Recorded in the Namsen river system	Total	Sea	Rivers
	No. tagged	*n* (%)	*n* (%)	*n* (%)	*n* (%)	*n* (%)
Wild fish:						
males	38	35 (92%)	28 (74%)	11 (29%)	5 (13%)	6 (16%)
females	46	40 (87%)	34 (74%)	18 (39%)	6 (13%)	12 (26%)
Farmed fish:						
males	9	5 (56%)	4 (44%)	3 (33%)	2 (22%)	1 (11%)
females	19	10 (53%)	8 (42%)	1 (5%)	—	1 (5%)
Total:						
wild fish	84	75 (89%)	62 (74%)	29 (35%)	11 (13%)	18 (21%)
farmed fish	28	15 (54%)	12 (43%)	4 (14%)	2 (7%)	2 (7%)

Table 2 The migration speed of radio-tagged Atlantic salmon from release in the Namsen Fjord (between 7 and 25 km from the mouth of the River Namsen) to passing a data logger 11 km upstream in the River Namsen

	Migration speed (km day^{-1})		
	Mean	*n*	SD
Wild fish:			
males	17.3	14	12.4
females	23.5	16	17.3
Farmed fish:			
males	18.9	4	11.0
females	20.2	8	9.1
Total:			
wild fish	20.6	30	15.3
farmed fish	19.8	12	9.3

distance from the river mouth to passing the data logger. The migration speed of wild and farmed salmon was not dependent on migration distance from the release site to passing the data logger (linear regression analysis, wild salmon: $r^2 < 0.001$, $P = 0.94$; farmed salmon: $r^2 = 0.14$, $P = 0.23$), which means that the fish migrated at the same speed from site of release to the river mouth as from the river mouth to passing the data logger.

Migration speed and fish size

Migration speed from release to passing the data logger was not dependent on total body length in either wild or farmed salmon (linear regression analysis, wild salmon: $r^2 = 0.088$, $P = 0.11$; farmed salmon: $r^2 = 0.21$, $P = 0.14$).

Migration speed and time of tagging

Migration speed from release to passing the data logger was not dependent on the time of the season the fish were tagged in either wild or farmed salmon (linear regression analysis, wild salmon: $r^2 = 0.015$, $P = 0.70$; farmed salmon: $r^2 < 0.001$, $P = 0.97$).

Migration speed and water flow

Migration speed from tagging to passing the data logger was not dependent on water flow ($m^3\ s^{-1}$) on the date of tagging in either wild or farmed salmon (linear regression analysis, wild salmon: $r^2 = 0.10$, $P = 0.088$; farmed salmon: $r^2 = 0.094$, $P = 0.33$).

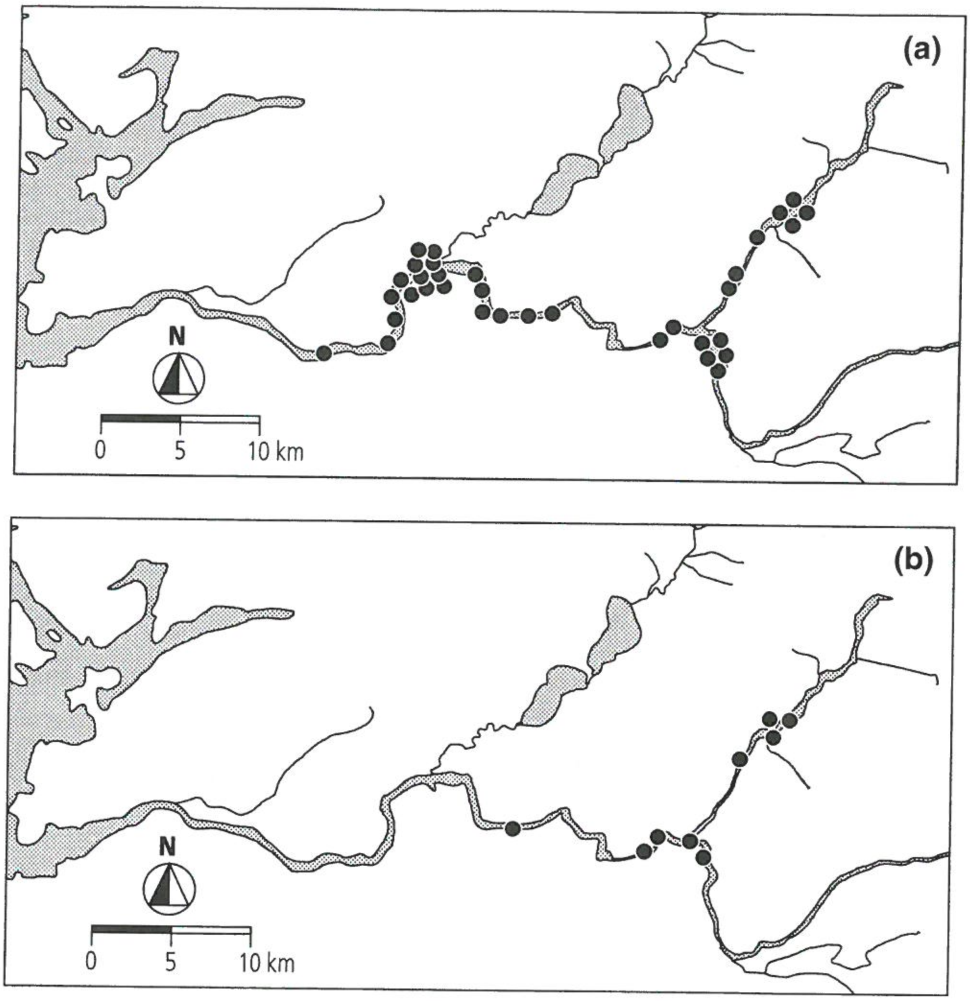

Figure 2 The distribution of (a) wild (n = 33) and (b) farmed (n = 9) radio tagged Atlantic salmon in the River Namsen on 30–31 October 1993 (during spawning time).

However, wild salmon tagged when water flow was increasing (n = 9) had a higher migration speed than wild salmon tagged when water flow was decreasing (n = 21) (Mann–Whitney U-test: U = 37.0, P = 0.0093). There were no differences in migration speed between farmed salmon tagged when water flow was increasing (n = 4) and those tagged when water flow was decreasing (n = 8) (Mann–Whitney U-test, U = 14.0, P = 0.73).

Distribution in the river during spawning

Farmed salmon were distributed higher up the river than wild salmon on 30–31 October 1993 (Kolmogorov–Smirnov two-sample test, Z = 1.45, P = 0.030) (Fig. 2; Table 3). Wild and farmed

Table 3 Distribution of radio-tagged Atlantic salmon in the River Namsen on 30–31 October 1993 (during spawning time)

	Distance from the river mouth to the position held in the river (km)		
	Mean	***n***	**SD**
Wild fish:			
males	37.1	16	16.8
females	42.7	17	15.1
Farmed fish:			
males	54.9	3	7.8
females	54.2	6	10.0

salmon had different distributions in the river, but were not geographically separated (Fig. 2). The radio-tagged farmed salmon stayed in important wild salmon spawning areas. The position of individual radio-tagged salmon on 30–31 October 1993 was not dependent on the date of tagging (linear regression analysis: $r^2 = 0.33$, $P = 0.25$).

Migration pattern during the period from 1 October to 15 November 1993

Farmed salmon were located more frequently at a new position in the river than wild salmon the next time the fish were tracked (Mann–Whitney *U*-test, $U = 51.0$, one-tailed $P = 0.031$) (Table 4). Farmed salmon had longer movements in the river than wild salmon (Mann–Whitney *U*-test, $U = 33.5$, $P = 0.0077$) (Table 4). In wild salmon, 28 out of 57 (49%) recorded movements during the period were downstream, while in farmed salmon, 23 out of 37 (62%) were downstream. The proportions were not significantly different (Yates-corrected chi-square calculations, $\chi^2 = 1.06$, $P = 0.30$).

The number of movements up- and downstream by wild salmon increased with variation in water flow (the absolute difference between the highest and lowest water flow during the period between two trackings; linear regression analysis, $r^2 = 0.41$, $P = 0.025$). The same was not true for farmed salmon (linear regression analysis, $r^2 = 0.18$, $P = 0.16$).

The number of movements was not dependent on variation in water flow when movements upstream (linear regression analysis, wild salmon: $r^2 = 0.24$, $P = 0.1077$; farmed salmon, $r^2 = 0.063$, $P = 0.43$) or downstream (linear regression analysis, wild salmon: $r^2 = 0.088$, $P = 0.35$; farmed salmon, $r^2 = 0.21$, $P = 0.14$) were examined independently.

The results concerning migration pattern during the period from 1 October to 15 November are based on wild salmon that were larger than the farmed salmon (Mann–Whitney *U*-test, $U = 36.5$, $P = 0.012$) (Table 4).

Survival after spawning

A smaller proportion of wild (9%, three males) than farmed (78%, two males and five females) salmon survived through the winter and moved downstream during the next spring (Fisher's exact probability test, $P < 0.001$).

Discussion

A higher proportion of wild (74%) than farmed (43%) salmon was observed in the River Namsen after release in the inner Namsen Fjord. The results are similar to those of Heggberget *et al.* (1993) from the Alta Fjord, indicating that a higher proportion of escaped farmed than wild salmon never reach the spawning areas in these rivers. The reasons may be that: (1) the farmed salmon experience a higher mortality rate at this stage of spawning migration; (2) the farmed fish do not leave salt water because these animals are either immature or are very late

Table 4 The migration pattern of radio-tagged Atlantic salmon in the River Namsen during the period from 1 October to 15 November 1993. The fish were tracked once a week during this period

		Total length of fish (cm)		Number of times located to a new position since last tracking		Length of the movements (km)	
	Number	Mean	SD	Mean	SD	Mean	SD
Wild fish:							
males	9	93.6	10.1	2.6	1.9	0.45	0.37
females	11	88.7	10.0	3.1	1.5	1.00	0.69
Farmed fish:							
males	3	72.3	17.2	3.7	0.6	2.20	1.50
females	6	78.2	9.6	4.3	1.5	2.20	2.30

maturing; or (3) the farmed fish enter other small rivers in the area. Farmed salmon in the Alta study showed a more random distribution to neighbouring streams than wild salmon, but not enough to explain the differences in proportions of wild and farmed salmon entering the River Alta (Heggberget *et al.* 1993). In the present study, no farmed salmon were captured in rivers other than the River Namsen, which supports the results from the Alta study and suggests that large rivers attract higher numbers of escaped farmed salmon than small rivers.

A higher proportion of wild (33%) than farmed (14%) salmon was captured in the sea and rivers after release, which is probably explained by the fact that the farmed salmon arrived in the inner fjord areas during the last part of the fishing season or after the fishing season had ended. Thus, prevailing fishing regulations seem to exploit wild more than farmed salmon.

Farmed salmon enter the rivers later in the season than wild salmon (Eriksson & Eriksson 1991; Gausen & Moen 1991; Gudjonsson 1991; Lund, Økland & Hansen 1991; Økland, Lund & Hansen 1993; McKinell, Lundqvist & Johansson 1994). In the present study, the farmed salmon were caught later in the season than the wild salmon in the inner Namsen Fjord. However, the fish migrated as fast as the wild salmon in the estuary and the lower part of the river. In contrast, radio-tagged farmed salmon that entered the River Alta had a significantly slower migration speed than wild salmon from release to entering the river (Heggberget *et al.* 1993). This may be a result of the method of releasing farmed salmon directly from a fish farm. The newly released salmon in the Alta study probably needed some time to adjust to the free life in the sea. The nearest fish farms in the Namsen Fjord are situated about 50 km from the site of capture, which means that the farmed salmon in the present study had stayed in the fjord before tagging. Farmed salmon in the River Alta migrated upstream as fast as the wild salmon after they had passed the river mouth (Heggberget *et al.* 1996).

A number of factors affect the time of river entry in salmon (Mills 1989). Water flow appears to be an important factor stimulating adult Atlantic salmon to enter rivers from the sea (e.g. Hayes 1953; Banks 1969; Smith, Smith & Armstrong 1994). Water flow in the River Namsen on the day of release did not significantly affect the migration speed from release in the fjord to passing the data logger 11 km upstream the River Namsen in either wild or farmed salmon in the present study. However, wild salmon released when water flow was increasing had a significantly higher migration speed than wild salmon released when water flow was decreasing. This was not true for farmed salmon.

Farmed salmon in the present study were distributed higher up the river than wild salmon during spawning time. The same results occurred in the River Alta (Økland *et al.* 1995; Heggberget *et al.* 1996). Wild salmon seem to relocate nursery areas in the river after the marine migration (Heggberget, Lund, Ryman & Ståhl 1986; Heggberget *et al.* 1988; Heggberget 1989). However, farmed salmon lack river imprinting and may distribute themselves higher up the river than wild salmon in the absence of a 'stop signal' in a particular area. In contrast, Power & McCleave (1980) and Webb, Hay, Cunningham & Youngson (1991) concluded that farmed salmon most likely stay in the lower parts of the rivers. However, these authors studied farmed salmon that had earlier experienced fresh water from the lower sections of the rivers, either during hatchery rearing, or transport and release. This return to lower river sections indicates homing to areas previously experienced, rather than a preference for lower parts of the river. An alternative hypothesis is that the river fills up with fish from the top of the accessible stretches for salmon, and that fish arriving later are progressively inhibited from moving as far upstream by the presence of earlier entrants (Hawkins & Smith 1986). This hypothesis is not supported by the present study; the date of tagging did not significantly affect the location of the fish during spawning period.

Radio-tagged wild and farmed salmon in the River Namsen were found together in spawning areas, which is comparable to the results reported from the River Alta (Økland *et al.* 1995; Heggberget *et al.* 1996). Thus, no geographical separation seems to exist that will prevent spawning between wild and farmed salmon.

Upstream migration in rivers appears to be stimulated by elevated flow (e.g. Hayes 1953; Dunkley & Shearer 1982; Baglinière, Maisse & Nihouarn 1990). In the present study, the number of movements of wild but not of farmed salmon within the river increased when variation in water flow increased. Farmed salmon showed a more up- and downstream migration pattern than wild salmon in the river during spawning time. Farmed salmon lack river imprinting, which may result in a more erratic migration pattern than wild salmon. Farmed salmon may have less success in spawning interactions (Fleming *et al.* 1996), and therefore, migrate from spawning ground to spawning ground, or these fish could be competitively inferior (Fleming *et al.* 1996) and may be chased. Several characteristics of farmed salmon may, singly or together, affect the competitive ability and spawning success of these animals relative to wild salmon. Farmed salmon have a higher fat content than wild salmon (Thorstad, Finstad, McKinley, Økland & Booth 1997). Farmed salmon also show morphological differences from wild salmon, such as decreased rayed-fin sizes and body streamlining (Fleming, Jonsson & Gross 1994). Farmed salmon may also have different experiences in intraspecific interactions and aggressiveness than wild salmon. In the River Imsa, a higher frequency of injuries was found in farmed than wild salmon (Jonsson *et al.* 1990), which suggests that farmed fish are more often involved in conflicts.

The radio-tagged farmed salmon in the present study were smaller than the radio-tagged wild salmon, which may explain differences in the riverine migration pattern. Body size alone does not prevent spawning in the absence of mate competition (Hutchings & Myers 1985; Myers & Hutchings 1987), but differences in body size may lead to a different competition strength and spawning success (Gross 1985; Hutchings & Myers 1985; Fleming & Gross 1992), and hence, differences in migration behaviour. Schroder (1982) found that relatively small and/or weak chum salmon, *Oncorhynchus keta* (Walbaum), males probably had to search longer and travel greater distances to find females when levels of male competition were high. The size distribution of farmed salmon in relation to that of wild salmon in a population may be of significant importance concerning the spawning success of farmed salmon in a river.

The farmed salmon in the present study had a higher survival (77%) than wild salmon (9%) through the winter following spawning. The migration pattern of the farmed salmon (more frequent movements) seemed more energetically costly than the migration pattern of the wild salmon. The explanation for the higher survival of farmed salmon than wild salmon may be related to larger energy stores as a result of previous feeding in a fish farm (Thorstad *et al.* 1997).

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