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Reduced migratory performance of farmed Atlantic salmon post-smolts from a simulated escape during autumn

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ABSTRACT: Escape of migratory finfish species from fish farms, such as Atlantic salmon *Salmo salar* L., offer a challenge when considering the environmental risks of cage culture. The migratory behaviour of groups of cultured salmon smolts and postsmolts after a simulated escape was studied in a small fjord from May to October using telemetry. Five groups of fish were released approximately every 6 wk from mid-May to late October, each of them composed of 15 to 20 fish equipped with acoustic transmitters and 1780 to 3700 individuals tagged with T-bar anchor tags. The migratory behaviour of the smolts was well developed in postsmolts for at least 6 wk after transfer to sea cages in May, but was less evident in August and was almost absent 2 mo later, when residency was prominent. In contrast to the first 2 groups that moved out of the 21 km-long fjord within a few days, fish released from August to October were being recaptured in the fjord several months after release. The actions required to mitigate the negative environmental impacts of cage-rearing therefore appear to depend on the developmental stage the fish has reached when it escapes. During the first summer months in the sea, efforts to prevent rapidly migrating smolts and postsmolts from escaping should be given priority. The chance of recapture in the small fjord used in this study increased as fish grew and dispersal rate decreased in autumn.

KEY WORDS: Atlantic salmon · Migratory behaviour · Fish farms · Escape · Recapture

INTRODUCTION

Aquaculture is the most rapidly growing animal food-producing sector with an average annual growth rate of 6.9% from 1970 to 2006. At least 40% of all fish consumed in the world is farmed (FAO 2006), with cage rearing being the most common method of production (Halwart et al. 2007). Atlantic salmon *Salmo salar* L. farming is responsible for approximately half of the total global finfish production in cages (Halwart et al. 2007). As a byproduct of this expansion, the probability of interaction between farming and the environment is increasing. Negative impacts include release of waste effluents and nutrients from the cages (Ervik et al. 1997, Islam 2005), the spread of diseases and parasites (Kusuda & Kawai 1998, Finstad et al. 2000, Krkosek et al. 2006, Skilbrei & Wennevik 2006), the attraction of wild species to fish farms (Sanchez-Jerez et al. 2008, Dempster et al. 2009) and escape of cultured individuals into the wild. The structure of natural populations is at risk from genetic interaction with escaped aquaculture conspecifics (Youngson et al. 2001).

The types of interaction with the environment depend on the developmental stage the cultured fish have reached when they escape, especially if the species held in culture is capable of performing long-distance migrations in the wild. The onset of migratory behaviour in wild fish is typically timed with the season and/or some physiological factor that triggers migration to feeding or spawning grounds (Smith 1985, Brönmark et al. 2008). If domesticated fish are disposed to migrate at the time of escape, this will determine their geographical dispersal, which in turn will influence the impact on the immediate ecosystem, the

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potential for interactions with wild stocks, and possibilities to mitigate the negative effects of escape.

Most Atlantic salmon populations have a well-defined migratory cycle: the majority of the young salmon leave the river in spring when they are 1 to 5 yr old and migrate to their feeding grounds in the open sea where they remain for at least 1 yr before returning to their home river to spawn (Youngson & Hay 1996). The smoltification process is the physiological and morphological transition that enables these fish to switch from a freshwater-adapted metabolism to a marine pelagic lifestyle, and that also marks a behavioural shift from resident to migratory behaviour (Hoar 1976, Gribson 1983, Martin et al. 2009). Cultured salmon are transferred from the hatchery to cages in the sea at the smolt stage.

Genetic introgression resulting from escaped farmed fish spawning with wild salmon is of great concern because of genetic differences between wild and domesticated strains of salmon (Lura & Sægrov 1991, McGinnity et al. 2004, Naylor et al. 2005, Skaala et al. 2005, 2006, Ferguson et al. 2007). Farmed salmon kept in fish farms until just before spawning are relatively unsuccessful in natural environments, due to competitive and reproductive inferiority resulting from domestication (Fleming et al. 1996). However, the spawning performance of fish released as smolts, which supposedly follow the natural migration pattern of wild fish, is much more comparable to that of wild salmon (Fleming et al. 1997, Hindar et al. 2006). Hansen & Jonsson (1989) found that the tag returns of released fish that were the offspring of wild parents was highest for fish released in spring. They suggested that there was a window of migration that closes during summer and hypothesized that the behaviour of the fish will change with time of release.

Assessment of the risks posed by the escape of domesticated salmon requires us to know whether, and at which stages, escapees display seaward migratory behaviour, as their return as adults may increase the risk of genetic interactions with wild populations. Such knowledge is important to enable the aquaculture industry to optimize preventive measures against escape, and to optimize recapture strategies. Migration behaviour studies at smolt and post-smolt stages during different seasons have only been performed on hatchery-reared fish with wild parents and are based on mark-recapture methods. Detailed studies of farmed salmon strains at smolt and post-smolt stages are lacking in the literature. The aims of the present study were (1) to describe the migratory behavioural patterns of cultured salmon by monitoring the movements of groups of smolts and postsmolts in a simulated escape in a small Norwegian fjord from spring to autumn and (2) to determine whether migratory behaviour changes with time of release.

MATERIALS AND METHODS

Fish and tagging. The fish studied were of the domesticated Aqua Gen strain that is widely used in fish farming in Norway and were produced at the hatchery at Matre Research Station (Institute of Marine Research), Matre, Masfjord. One-year-old smolts were transferred to a 5.5 × 5.5 m wide and 7 m deep sea cage at the fish farm located close to the station in the inner part of the fjord which was the release site (Fig. 1). Each release group was produced by tagging 1780 to 3700 fish with T-bar anchor tags (Hallprint) and 15 to 20 individuals with 9 mm telemetry transmitters with depth sensors (MP-9-Short, Thelma; length 24 mm, weight in water 2.2 g, min to max delay: 40 to 120 s) (Table 1). The first tagging was done in the hatchery on 9 May 2008, when the fish were still in freshwater, 2 d prior to transfer to seawater, the others were done at 5 to 7 wk intervals from 20 June to 21 October 2008 at the sea cage facility. Each group was tagged 6 to 9 d before release and held in a separate net pen until release (Table 1). The mean size of the fish equipped with acoustic transmitters increased from <0.2 to >1.5 kg during the release period; however, the size ranges of the fish of successive releases overlapped considerably (Table 1). The acoustic pingers were surgically inserted in the abdomen of the fish as described in Skilbrei et al. (2009). According to fish size, tag size was clearly within the recommendations for the use of such tags to study swimming performance (Anglea et al. 2004, LaCroix et al. 2004). The experiment and the tagging procedures were approved by the Norwegian committee for the use of animals in scientific experiments (FDU).

Hydrography. The regulated Matre River and a hydroelectric power plant supply the inner bay of Masfjord with fresh water (Fig. 1), establishing a brackish surface layer which is typical of Norwegian fjords. Salinity and temperature profiles were recorded on 8 to 22 and 16 to 22 d per month at the fish farms at Solheim and Matre from May 2008 to October 2008, respectively. At Matre, the mean salinity (±SD) at 1 m depth was 14.1 ± 4.3 during this period, but fluctuated frequently between days, usually between 9 and 21. At 5 m depth, salinity was much more stable, with a mean of 27.9 ± 2.7 and ranged from 26.9 to 28.4 between months. At Solheim, salinities were slightly higher and less variable. At 1 m depth, salinity usually varied between 12 and 25 with a mean of 16.7 ± 3.7. At 5 m depth, mean salinity was 29.0 ± 1.4 and ranged from 28.1 to 29.9 between months.

Mean monthly temperature at Matre at 1 m depth increased steadily from May to August from 8.1°C to 14.0°C, and then declined to 10.0°C in October. At Solheim the corresponding temperatures were 2.1 to

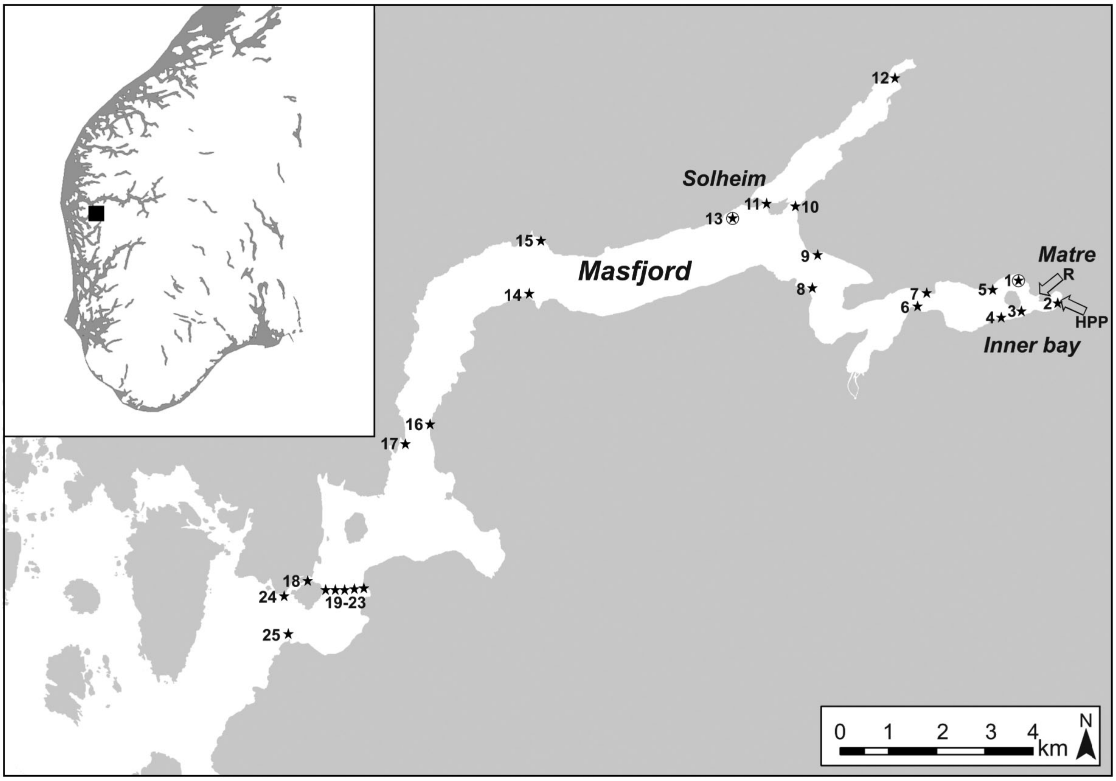

Fig. 1. Location of the acoustic receivers in Masfjord (1–25), of Matre River (R) and the hydropower plant (HPP). The receivers located at the fish farm at Matre (release site) and the other fish farm in the fjord at Solheim (nos. 1 and 13, respectively) are circled

2.9°C higher until August and more similar thereafter. Temperatures were higher at both locations at 5 m depth. At Matre, temperature increased from 9.7 to 16.7°C from May to August and fell to 13.1°C in October. Temperatures at Solheim were 0.2 to 0.5°C higher than at Matre.

Location and validation of acoustic receivers. All 25 receivers (VR2 and VR2W, Vemco) were attached to floats moored to the bottom and kept at a depth of ca. 2 m.

The inner bay was covered by 5 receivers (nos. 1 to 5, Fig. 1). All the individuals that reached the fjord mouth had previously been recorded by one or both of each pair of receivers located on both sides of the fjord during their outward movement (receiver pairs 4/5, 6/7, 8/9, 14/15 and 16/17; see Fig. 1), except for 2 individuals (5% of the total) that missed nos. 14 and 15. In addition, 86% of all the migrating fish (44 from 51 ind.) were recorded by receiver no 13 (see Fig. 1 for locations).

At the fjord mouth, 21 km away from the release site, a single receiver covered a narrow strait (no. 18, see Fig. 1), and a monitoring array of 5 receivers stretched 800 m across the fjord at intervals of approximately 200 m (nos. 19 to 23). During passage of the array, signals from 93% of the fish were detected by several

Table 1. *Salmo salar*. Number of fish tagged with T-bar anchor tags and acoustic transmitters (AT), dates for tagging and releases in 2008, mean weight and length (± SD) of release groups and size range (min. to max.) of AT fish

	T-bar (n)	AT (n)	T-bar date	AT date	Release date	AT Weight (kg)	AT Range (kg)	AT Length (cm)	AT Range (cm)	T-bar Weight (kg)	T-bar Length (cm)
May	3700	20	7–8 May	9 May	16 May	0.16 (±0.03)	0.09–0.19	24.7 (±1.7)	20.2–27.5	0.15 (±0.04)	23.7 (±2.2)
June	2000	18	18 Jun	20 Jun	26 Jun	0.24 (±0.07)	0.13–0.33	27.6 (±2.5)	22.5–31.0	0.19 (±0.05)	25.8 (±2.1)
Aug	2000	17	6 Aug	7 Aug	14 Aug	0.51 (±0.19)	0.25–0.92	35.0 (±3.9)	28.3–41.2	0.45 (±0.14)	33.2 (±3.2)
Sep	2000	16	10 Sep	9 Sep	17 Sep	0.95 (±0.27)	0.56–1.49	41.5 (±3.5)	36.4–47.8	0.87 (±0.26)	39.6 (±3.8)
Oct	1780	15	20 Oct	21 Oct	27 Oct	1.56 (±0.42)	0.90–2.30	47.0 (±4.0)	40.0–54.0	1.30 (±0.34)	44.6 (±4.0)

receivers simultaneously, and single pings from 48% of the fish reached both ends of the array. After the passage of the array, 91% of the fish (and no previously undetected individuals) were recorded at one or both of the outermost receivers that served as extra checkpoints (nos. 24 and 25). It is assumed that the receiver coverage was sufficient to describe the movements of the fish within the fjord with a high degree of accuracy.

Recapture of tagged fish. The letters HI (Norwegian acronym for the Institute of Marine Research; IMR), the IMR internet address (www.imr.no) and postal code were printed on the T-bar tags in addition to an individual alphanumeric code. The reward was 100 NOK per T-bar anchor tag returned, and 500 NOK for an acoustic tag. Information about the pinger and the rewards were available on the IMR internet home page.

Acoustic tags and T-bar anchor tags were returned by fishers after capture by rod or gill-net in the inner and middle part of the fjord. More than 90% of the fish taken by rod were angled from the 2 fish farms or in the effluent water from a hydropower plant that attracts escaped farmed salmon and is a popular site for anglers (requires a fishing licence) (Fig. 1). The angling effort at the fish farm at Solheim was probably much higher in August to November than in winter because fish were angled by personnel that were engaged in different research projects going on at the fish farm during this period. All the gill-netted salmon were reported from the inner part of the fjord (between receivers 3 to 12, Fig. 1), 85% of them by a single fisher who was the only professional fisher in the fjord. The fisher used mainly 60 to 63 mm mesh-sized gill-nets and fished regularly during autumn, except for the first 3 wk of December. He was also engaged by the project to take part in field activities and to recapture fish on a weekly basis from late December onwards.

Missing tags. Eleven tagged fish disappeared during the 3 post-release weeks, 8 of them while they were active in the inner basin in the proximity of several receivers, while another 3 were recorded in the middle part of the fjord before their disappearance. In addition to predation and unreported catches, tag malfunction may have contributed to the loss of recordings. The tags were expected to last for at least half a year. However, the batteries of several of the tags returned by fishers were completely discharged when tested 4 to 6 wk after release, while others appeared to work properly. The tag manufacturer checked some of these tags and discovered that battery life had been reduced possibly due to a previously unidentified problem with a seal. Water may have penetrated into some tags and increased the consumption of current due to fissures that may have developed in the glue/casting material attaching the depth sensor unit.

RESULTS

Movements of fish equipped with acoustic transmitters

The 2 groups released in mid-May and late June moved rapidly out of the fjord, and all survived (Table 2, Figs. 2 & 3). Approximately 90% of the smolts released on 16 May moved out of the inner bay within the first 6 h and out of the fjord during the first day (Figs. 2 & 3). The postsmolts released on 26 June took an extra day before 90% of them had passed the outer receivers. The smolts released in May moved significantly more rapidly from the inner bay to the fjord mouth than the postsmolts released in June; 1.36 ± 0.34 (± SD) versus 0.78 ± 0.48 body lengths s^{-1} (Student's *t*-test, $p < 0.001$), because more postsmolts reversed direction and moved inwards before they continued their outward migration in June. When the outward and recorded inward movements were summed, the overall rate of movement was not significantly different, 1.47 ± 0.35 versus 1.23 ± 0.52 body lengths s^{-1} (*t*-test, $p = 0.20$) for the smolts and postsmolts respectively, corresponding to 0.38 and 0.37 m s^{-1}. Both the May and June groups moved close to the surface during outward migration, at a mean depth of 1.7 ± 0.3 and 1.2 ± 0.3 m, respectively, with a low degree of individual variability. Mean swimming depths of the individual fish of the first and second releases ranged from 1.06 to 2.43 m and from 0.77 to 1.82 m depth, respectively. No recordings were done below 4.8 m depth.

The postsmolts attained a mean weight of 0.5 kg in early August (Table 1). After release, most of them moved rapidly out of the inner basin (72%, n = 13, Fig. 2), but further migration out of the fjord was slow.

Table 2. *Salmo salar*. Locations of fish equipped with acoustic transmitters following each of the 5 releases. Percentage (numbers in parentheses) represent fish that have either moved out of the fjord, were reported as captured, disappeared from the experiment, or were still present in the fjord on days 7 and 21 post-release

Release group	Out of fjord	Captured	In fjord	Missing tags
One wk post-release				
16 May	100 (20)	0	0	0
26 Jun	94 (17)	0	6 (1)	0
14 Aug	41 (7)	6 (1)	47 (8)	6 (1)
17 Sep	6 (1)	38 (6)	50 (8)	6 (1)
27 Oct	0	13 (2)	67 (10)	20 (3)
Three wk post-release				
26 Jun	100 (18)	0	0	0
14 Aug	53 (9)	12 (2)	18 (3)	18 (3)
17 Sep	13 (2)	38 (6)	25 (4)	25 (4)
27 Oct	13 (2)	20 (3)	40 (6)	27 (4)

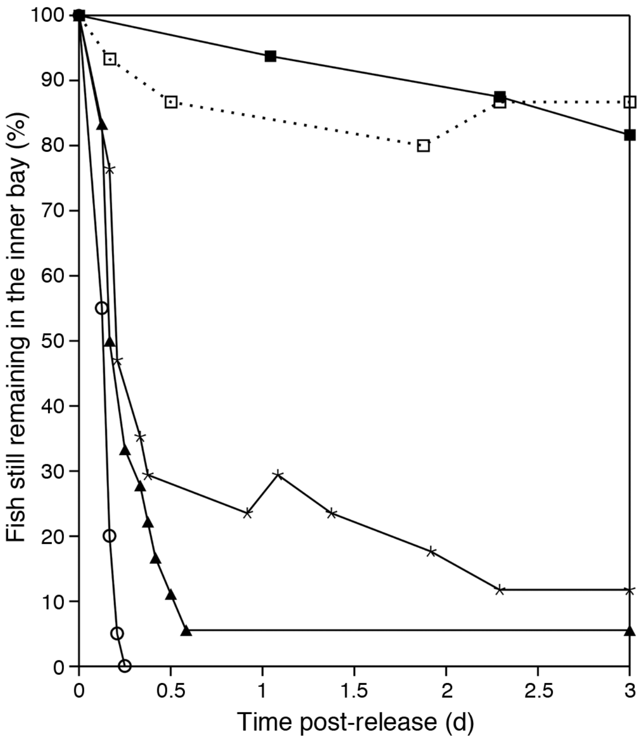

Fig. 2. *Salmo salar*. Presence of fish (%) in the inner bay (receivers, 1–5, see Fig. 1) during the first 72 h following the 5 releases in May (○), late June (▲), August (*), September (■) and October (□)

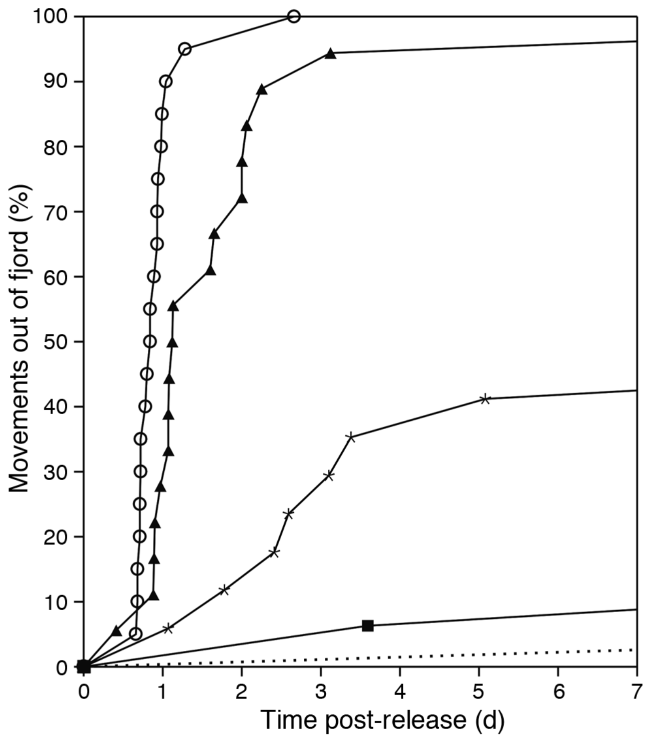

Fig. 3. *Salmo salar*. Percentage of fish detected migrating out of Masfjord in the course of the first week following the 5 releases in May (○), late June (▲), August (*), September (■) and October (······)

Only 41% moved out during the first week, and few followed in the course of the next 2 wk (Fig. 3, Table 2). The mean size of the fish that moved out during the first week were not significantly different from the size of those that remained in the fjord (0.47 ± 20 versus 0.57 ± 0.19 kg, respectively. Student's *t*-test, $p = 0.31$). Many fish (41%, $n = 7$) seem to have been attracted to the fish farm at Solheim 7 km away from the release site (no 13, Fig. 1). During the 3 wk after release, the receiver at the fish farm made numerous recordings of 6 individuals during an average of 11 d, and another individual was angled there after 5 d. A high percentage of the T-bar tagged fish were also captured at this site (see details in next section). No other concentrations of fish in the vicinity of single receivers in this or outer part of the fjord were observed. The mean swimming depth of the fish released in August that moved out of the fjord during the first week was not significantly different from those that did not (1.75 ± 0.35 versus 1.62 ± 0.35, $p = 0.85$). Mean individual swimming depth ranged from 1.32 to 2.30 m depth. Most recorded movements below 4 m depth were single observations or rapid dives. The exceptions were 5 individuals that moved between 4 and 9 m for a limited period of time (<2 h) before they moved closer to surface, and 2 individuals that were recorded at 13 to 15 m depth shortly before they disappeared.

The large postsmolts, which had grown to mean weights of 0.9 kg in September and 1.3 kg in late October, did not move rapidly out of the fjord (Tables 1 & 2, Figs. 2 & 3). Only 1 fish moved out of the fjord during the first week, and only 13% of both groups did so before the third week (Table 2). Of the fish still present in the fjord after 3 wk, one of the 4 from release 4, and 5 of 6 fish (33% of the total number released) from release 5 moved exclusively between the receivers in the inner basin. The mean swimming depth of the fish released in September was 2.7 ± 1.2 m (individual range 0.9 to 4.9 m), which was significantly closer to the surface compared with the swimming depth of the fish released in October at 4.2 ± 1.53 m (range 1.1 to 6.2 m) (*t*-test, $p < 0.01$). Maximum depth varied widely (from 4 to 51 and 5 to 51 m depth for releases 4 and 5, respectively), between the individuals in both groups, the maximum depth observed is probably close to the deepest part of the inner bay area.

Recapture of fish with external tags

The percentages of the fish recaptured and the timing of the catches varied between the release groups (Fig. 4). Reported recaptures of T-bar tagged fish in the fjord following the May, June, August, September and

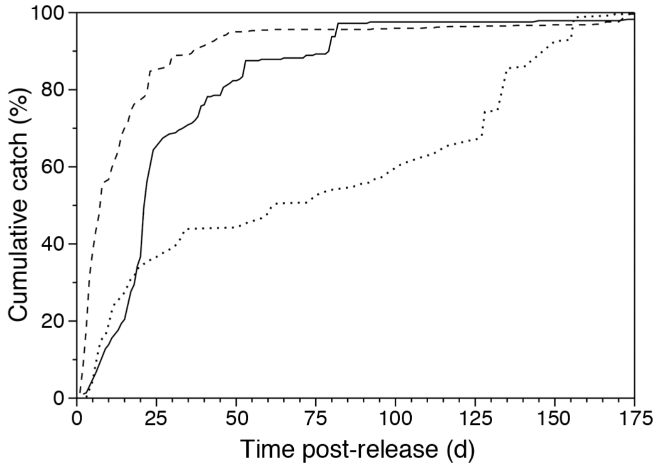

Fig. 4. *Salmo salar*. Cumulative catches in Masfjord following the August (——), September (– – –) and October releases (·····)

October releases were 0.0, 0.2, 14.5, 35.1 and 29.2% (corresponding to n = 0, 7, 290, 702 and 520 fish), respectively. The recapture rate of the fish released in August was lower ($p < 0.05$, 2×2 *G*-test, Sokal & Rohlf 1981), and significantly delayed by approximately 2 wk compared with the fish released in September ($p < 0.05$, Kolmogorov-Smirnoff 2-sample test, Sokal & Rohlf 1981, my Fig. 4). Behavioural differences between the 2 groups, angling at the fish farm at Solheim and a less efficient gill-net fishery on the smaller individuals released in August may have contributed to these differences. The fish released in August moved more rapidly out of the inner part of the fjord compared with those in the following releases, and were less likely to be recaptured there (Fig. 2). Unlike subsequent releases, many fish concentrated around the fish farm at Solheim and were recaptured there (50% of the catch, n = 145). Furthermore, the fish released in August that were gill-netted during the following 2 mo were 30% larger than the angled fish (0.70 ± 0.83 versus 0.54 ± 0.95 kg, Student's *t*-test, $p < 0.001$). The proportion of the catch that were caught by rod (as opposed to gill-netting) fell significantly during the autumn, from 85.3% (n = 247) following the August release, to 36.2% (n = 254) for the September release and 10.2% (n = 53) for the fish released in October, when almost 90% (n = 497) of the catch was gill-netted ($p < 0.01$, 2×2 *G*-tests).

The fish released in October dispersed much more slowly out of the fjord compared with the following releases. The period of recapture lasted several months longer compared to the previous releases ($p < 0.05$, Kolmogorov-Smirnoff 2-sample tests, Fig. 4). The difference in the timing of the recaptures between the September and the October release could not be explained by an increased catchability in gill-nets due to the larger size of the fish. The fish released in September that were gill-netted during the first 2 mo were significantly smaller than the angled fish (0.83 ± 0.21 versus 0.95 ± 0.19 kg, $p < 0.001$). The 2 categories were not significantly different after the October release (1.48 ± 0.35 of gill-netted versus 1.36 ± 0.37 kg of angled fish, p = 0.07).

DISCUSSION

This study demonstrates that migratory behaviour was well developed in domesticated Atlantic salmon smolts and postsmolts during summer, but was gradually lost in cage-reared salmon over the course of the autumn.

The speed of migration of the smolts and postsmolts released in May and late June, respectively, was higher than or comparable to the fastest moving groups in several other telemetry studies of migrating cultured and wild smolts (Thorstad et al. 2004, 2007, Økland et al. 2006, LaCroix 2008). Rapid migration towards the ocean does not seem to be limited to a few weeks during smoltification. One possible reason for the unexpectedly high survival during migration out of the fjord may be that the simultaneous releases of several thousand fish could have stimulated school formation. Cultured smolts released from cages are capable of forming rapidly migrating schools (Skilbrei et al. 1994a,b). Schooling fish benefit from lower predation intensity and improved migratory behaviour (Partridge 1982, Pither 1986, Bakshtanskiy et al. 1988, Roccanova 1993).

The fish released in mid-August performed intermediately between the groups released on earlier and later dates. Besides, they appeared to be attracted to, and were angled at, the fish farm in the middle of the fjord. It appears that migration motivation had declined and that feeding behaviour was more pronounced at this time of the year. Migratory patterns may be viewed as seasonally fluctuating trade-offs between predator avoidance and foraging gains (Brönmark et al. 2008).

The low level of migratory behaviour following the October release, the aggregation of the fish in the inner bay for several weeks, and their lengthy recapture period in the vicinity of the release site, combine to demonstrate that a significant proportion of the fish were actively residing in the fjord. When compared with the rapid displacement of the released smolt in the present study and other experiments (Finstad et al. 2005, Økland et al. 2006, Sivertsgård et al. 2007, LaCroix 2008), these results may be interpreted to indicate that the fish dispersed randomly throughout the fjord system rather than having performed active migration. Fish that remain close to, and move between, fish farms offer a challenge to fish health management. Escaped salmon and wild fish such as saithe *Pollachius virens*, that congregate around fish farms (Uglem et al. 2009), may act as vectors of disease and parasites that spread towards both fish farms and local wild salmonid populations, and may also increase the spread of drugs, used for treatment of diseases and parasites, in the vicinity of the fish farms (Ervik et al. 1994, Skilbrei et al. 2010).

Recapture of rapidly migrating smolts and postsmolts is very difficult in practice, particularly when they have escaped from fish farms located in larger fjords or on the coast, where they can potentially move in several directions. Gill-netting and surface trawling have been used to collect samples of released and wild smolts and postsmolts (Sturlaugsson 1994, Holm et al. 2000), but most fish farmers lack the resources or technology required at such short notice to organize an effective fishery that can target and catch small fish that are moving rapidly away from the escape site.

It may be possible to capture a considerable proportion of fish that escape in late autumn, as recapture is easier when the motivation to migrate decreases and the cage-reared fish have grown large enough for angling and capture by means of traditional fishing gear. The size selectivity of the gill-nets contributed to the results in this study, especially following the release in August when many fish may have been too small for the gill-nets used. However the very low rod catches compared with gill-net catches of the fish released in October indicate that some aspect of post-release behaviour changed during autumn and affected their catchability by different gear types, for example, this group moved deeper in the water than the previous release groups.

The behaviour of adult escapees and the success of their recapture also depend on the locality of the fish farm. The differences in post-release behaviour between fish that have a high or a low migratory motivation at the time of release will probably be more pronounced in small fjords than in larger fjords, or from exposed localities at the coast where the fish may disperse more rapidly. Following several releases at different times of the year of adults in a simulated escape in the Hardanger-Fjord, one of the largest fjords in Norway, recaptures were comparable and even higher than in the present study, but the fish were more dispersed, both vertically and horizontally (Skilbrei et al. 2009, 2010). The fish moved within the fjord basin for many weeks and did not show any clear signs of migratory behaviour. Following releases of adult farmed salmon, Hansen (2006) reported that most recaptures were made in areas close to the fish farms within the first 60 d after release, but the distance of the successive recaptures from the fish farms increased with time as fish appeared to move with the currents. The time required to recapture the fish released in September in the present study is comparable to the time periods in larger fjords reported in the above studies, but a considerable proportion of the fish released in October stayed much longer in the fjord, possibly showing that dispersal may be slower in small and narrow rather than in large fjord systems.

CONCLUSIONS

The present study illustrates that the challenges involved in mitigating the environmental impacts of a migratory species escaping from fish farms depend on the developmental stage of the fish at the time of escape. The post-escape behaviour changed radically over the course of 4 mo, from rapid and synchronous ocean migration to a high level of residency in the fjord. Due to the challenges involved in recapturing rapidly moving small fish at smolt and postsmolt stages, efforts to prevent escapes should be given particularly high priority by fish farms throughout the first summer that the fish spend in the sea in order to reduce negative effects of interactions with wild populations. At a later stage, when the escaped smolts return as adults to spawn, it would require a massive effort to catch, identify and remove non-native fish from salmon rivers and furthermore may be difficult to perform if the fish are geographically dispersed. The reduced migratory behaviour as fish grew larger during autumn showed that the probability of recapture may increase over time, but also indicated that the risk of interactions between escaped fish and the environment around the fish farm increased.

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LITERATURE CITED

Anglea SM, Geist DR, Brown RS, Deters KA, McDonald RD (2004) Effects of acoustic transmitters on swimming performance and predator avoidance of juvenile chinook salmon. N Am J Fish Manag 24:162–170

Bakshtanskiy EL, Nesterov VS, Neklyudov MN (1988) Development of schooling behaviour in juvenile Atlantic salmon, *Salmo salar*, during seaward migration. J Ichthyol 28:91–101

Brönmark C, Skov C, Brodersen J, Nilsson PA, Hansson LA (2008) Seasonal migration determined by a trade-off between predator avoidance and growth. PLoS ONE 3(4), e1957

Dempster T, Uglem I, Sanchez-Jerez P, Fernandez-Jover D, Bayle-Sempere J, Nilsen R, Bjørn PA (2009) Coastal salmon farms attract large and persistent aggregations of wild fish: an ecosystem effect. Mar Ecol Prog Ser 385: 1–14

Ervik A, Thorsen B, Eriksen V, Lunestad BT, Samuelsen OB (1994) Impact of administering antibacterial agents on wild fish and blue mussel *Mytilis edulis* in the vicinity of fish farms. Dis Aquat Org 18:45–51

Ervik A, Hansen PK, Aure J, Stigebrandt A, Johannessen P, Jahnsen T (1997) Regulating the local environmental impact of intensive marine fish farming. I. The concept of the MOM system (Modelling-Ongrowing fish farms-Monitoring). Aquaculture 158:85–94

FAO (2006) State of world aquaculture 2006. FAO Fisheries Technical Paper 500, FAO, Rome

Ferguson A, Fleming I, Hindar K, Skaala Ø, McGinnity P, Cross TF, Prodöhl P (2007) Farm escapes. In: Verspoor E, Stradmeyer L Nielsen JL (eds) The Atlantic salmon: genetics, conservation and management. Blackwell Science, Oxford, p 357–398

Finstad B, Bjørn PA, Grimnes A, Hvidsten NA (2000) Laboratory and field investigations of salmon lice [*Lepeophtheirus salmonis* (*Krøyer*)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts. Aquacult Res 31:795–803

Finstad B, Økland F, Thorstad EB, Bjørn PA, McKinley RS (2005) Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. J Fish Biol 66:86–96

Fleming IA, Jonsson B, Gross MR, Lamberg A (1996) An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). J Appl Ecol 33:893–905

Fleming IA, Lamberg A, Jonsson B (1997) Effects of early experience on the reproductive performance of Atlantic salmon. Behav Ecol 8:470–480

Gibson RJ (1983) Water velocity as a factor in the change from aggressive to schooling behaviour and subsequent migration of Atlantic salmon smolts (*Salmo salar*). Nat Can 110: 143–148

Halwart M, Soto D, Arthur JR (2007) Cage aquaculture – regional reviews and global overview. FAO Fish Tech Paper 498, FAO, Rome

Hansen LP (2006) Migration and survival of farmed Atlantic salmon (*Salmo salar* L.) released from two Norwegian fish farms. ICES J Mar Sci 63:1211–1217

Hansen LP, Jonsson B (1989) Salmon ranching experiments in the River Imsa: effect of timing of Atlantic salmon (*Salmo salar*) smolt migration on survival to adults. Aquaculture 82:367–373

Hindar K, Fleming IA, McGinnity P, Diserud O (2006) Genetic and ecological effects of salmon farming on wild salmon: modeling from experimental results. ICES J Mar Sci 63: 1234–1247

Hoar WS (1976) Smolt transformation; evolution, behaviour and physiology. J Fish Res Board Can 33:1234–1252

Holm M, Holst JC, Hansen LP (2000) Spatial and temporal distribution of postsmolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. ICES J Mar Sci 57:955–964

Islam MS (2005) Nitrogen and phosphorus budget in coastal and marine cage aquaculture and impacts of effluent loading on ecosystem: review and analysis towards model development. Mar Pollut Bull 50:48–61

Krkosek M, Lewis MA, Morton A, Frazer LN, Volpe JP (2006) Epizootics of wild fish induced by farm fish. Proc Natl Acad Sci USA 103:15506–15510

Kusuda R, Kawai K (1998) Bacterial diseases of cultured marine fish in Japan. Fish Pathol 33:221–227

LaCroix GL (2008) Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. Can J Fish Aquat Sci 65:2063–2079

LaCroix GL, Knox D, McCurdy P (2004) Effects of implanted dummy acoustic transmitters on juvenile Atlantic salmon. Trans Am Fish Soc 133:211–220

Lura H, Sægrov H (1991) Documentation of successful spawning of escaped farmed female Atlantic salmon, *Salmo salar*, in Norwegian rivers. Aquaculture 98:151–159

Martin F, Hedger RD, Dodson JJ, Fernandes L, Hatin D, Caron F, Whoriskey FG (2009) Behavioural transition during the estuarine migration of wild Atlantic salmon (*Salmo salar* L.) smolt. Ecol Freshw Fish 18:406–417

McGinnity P, Prodöhl P, Maoiléidigh NÓ, Hynes R and others (2004) Differential lifetime success and performance of native and non-native Atlantic salmon examined under communal natural conditions. J Fish Biol 65:173–187

Naylor R, Hindar K, Fleming IA, Goldburg R and others (2005) Fugitive salmon: assessing the risks of escaped fish from net-pen aquaculture. BioScience 55:427–437

Økland F, Thorstad EB, Finstad B, Sivertsgård R, Plantalech N, Jepsen N, McCinley RS (2006) Swimming speeds and orientation of wild Atlantic salmon post-smolts during the first stage of the marine migration. Fish Manag Ecol 13: 271–274

Partridge BL (1982) The structure and function of fish schools. Sci Am 246:114-123

Pither TJ (1986) Functions of shoaling behaviour in teleosts. In: Pitcher TJ (ed) The behaviour of teleost fishes. Blackwell Science, Oxford, p 294–337

Roccanova LP (1993) Evolution of bright coloration in schooling fish. Anim Behav 45:1034

Sanchez-Jerez P, Fernandez-Jover D, Bayle-Sempere J, Valle C, Dempster T, Tuya F, Juanes F (2008) Interactions between bluefish *Pomatomus saltatrix* (L.) and coastal seacage farms in the Mediterranean Sea. Aquaculture 282: 61–67

Sivertsgård R, Thorstad EB, Økland F, Finstad B and others (2007) Effects of salmon lice infection and salmon lice protection on fjord migrating Atlantic salmon and brown trout post-smolts. Hydrobiologia 582:35–42

Skaala O, Taggart JB, Gunnes K (2005) Genetic differences between five major domesticated strains of Atlantic salmon and wild salmon. J Fish Biol 67:118–128

Skaala Ø, Wennevik V, Glover KA (2006) Evidence of temporal genetic change in wild Atlantic salmon, *Salmo salar* L., populations affected by farm escapees. ICES J Mar Sci 63: 1224–1233

Skilbrei OT, Wennevik V (2006) Survival and growth of searanched Atlantic salmon, *Salmo salar* L., treated against sea lice prior to release. ICES J Mar Sci 63:1317–1325

Skilbrei OT, Holm M, Jørstad KE, Handeland SO (1994a) Migration motivation of cultured Atlantic salmon, *Salmo salar* L., smolts in relation to size, time of release and acclimatization period. Aquacult Fish Manag 25:65–78

Skilbrei OT, Jørstad KE, Holm M, Farestveit E, Grimnes A, Aardal L (1994b) A new release method for coastal ranching of Atlantic salmon (*Salmo salar*) and behavioural patterns of released smolts. Nord J Freshw Res 69:84–94

Skilbrei OT, Holst JC, Asplin L, Holm, M (2009) Vertical movements of 'escaped' farmed Atlantic salmon (*Salmo salar*) — a simulation study in a western Norwegian fjord. ICES J Mar Sci 66:278–288

Skilbrei OT, Holst JC, Asplin L, Mortensen S (2010) Horizontal movements of simulated escaped farmed Atlantic salmon (*Salmo salar* L.) in a western Norwegian fjord. ICES J Mar Sci 67:1206–1215

Smith RJF (1985) The control of fish migration. Springer-Verlag, Berlin

Sokal RB, Rohlf JF (1981) Biometry. WH Freeman, San Francisco, CA

Sturlaugsson J (1994) Food of ranched Atlantic salmon (*Salmo salar* L.) post-smolts in coastal waters, west Iceland. Nord J Freshw Res 69:43–57

Thorstad EB, Økland F, Finstad B, Sivertsgård R, Bjørn PA, McKinley RS (2004) Migration speed and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system. Environ Biol Fishes 71:305–311

Thorstad EB, Økland F, Finstad B, Sivertsgård R, Plantalech N, Bjørn PA, McKinley RS (2007) Fjord migration and survival of wild and hatchery-reared Atlantic salmon and wild brown trout post-smolts. Hydrobiologia 582:99–107

Uglem I, Dempster T, Bjørn PA, Sanchez-Jerez P, Økland F (2009) High connectivity of salmon farms revealed by aggregation, residence and repeated movements of wild fish among farms. Mar Ecol Prog Ser 384:251–260

Youngson A, Hay D (1996) The lives of salmon. Swan Hill Press, Shrewsbury

Youngson AF, Dosdat A, Saroglia M, Jordan WC (2001) Genetic interactions between marine finfish species in European Aquaculture. J Appl Ichthyology 17:153–162

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