

Incidence and timing of wild and escaped farmed Atlantic salmon (*Salmo salar*) in Norwegian rivers inferred from video surveillance monitoring

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Abstract – Run timing of escaped farmed Atlantic salmon *Salmo salar* vs. wild fish was compared by the use of video camera surveillance in 15 rivers over several years, covering 1600 km of the Norwegian coastline (from 58°N to 69°N). Annual runs of wild salmon varied among rivers from <200 fish to more than 10 000. During the surveillance period that for most rivers extended from late May to early October, larger-sized salmon (fish ≥ 65 cm) generally entered the rivers earlier than small fish. The percentage of salmon identified as escaped farmed fish ranged from 0.1% to 17% across rivers with an average of 4.3%. Estimates of escapees are, however, assumed to represent minimum values because an unknown number of farmed fish passing the video cameras may have been misclassified as wild fish. By the use of a linear mixed model and generalised additive mixed models, it was found that the relationship between run timing and fish length differed significantly between farmed and wild salmon. While small-sized farmed and wild fish (<65 cm) entered the river at about the same time, wild large salmon returned on average 1–2 weeks earlier than similarly sized escapees. The proportion of large-sized farmed escapees also increased until late August and decreased thereafter. In contrast, there was a relatively constant and lower proportion of small-sized escapees throughout the season. Within the surveillance period, there was no evidence of any exceptionally late runs of fish classified as escaped farmed salmon.

Key words: Atlantic salmon; run timing; video surveillance; farmed escapees; fish size

Introduction

Concerns associated with potential impacts of escaped farmed Atlantic salmon (*Salmo salar*) on wild populations have persisted for many years both in Europe (e.g. Gausen & Moen 1991; Heggberget et al. 1993) and in North America (e.g. Carr et al. 1997; Morris et al. 2008). This is often a result of observations showing declines in wild stocks in areas proximate to aquaculture operations (e.g. Ford & Myers 2008) and the potential for interactions as a result of outbreeding and subsequent loss of fitness

(McGinnity et al. 2003), competition for food and space (Jonsson & Jonsson 2011), disruption of breeding behaviour (Fleming et al. 2000; Jensen et al. 2010) and transmission of disease and parasites (Finstad et al. 2011; Harris et al. 2011). Even small percentages of escaped farmed salmon have the potential to affect natural populations negatively (Hutchings 1991), and recent studies provide strong evidence of genetic impacts, suggesting that escaped farmed salmon can lead to persistent reduced wild population fitness with an increased contribution of maladapted cultured fish in the population (Glover et al. 2012,

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2013; Baskett et al. 2013). This is particularly relevant in areas where production of farmed salmon is high, such as Norway.

During the past 30+ years, the annual production of farmed Atlantic salmon in Norway has increased from <5000 tons in 1980 to more than 1 200 000 tons by 2014 (ICES 2015). Based on the information from Norwegian fish farms, the number of annual reported escaped fish has varied between 38 000 (2012) and 921 000 (2006) with a total reported escapement of over 3 million salmon during the 10-year period 2005–2014 (<http://www.fiskeridir.no/Akvakultur/Statistikk-akvakultur/Roemningsstatistikk>). It has been suggested that not all escapees are reported (Jonsson & Jonsson 2012), a situation that is not unique to Norway (Sepúlveda et al. 2013), and Skilbrei et al. (2014) estimated that during the period 2005–2010, more than 1.5 million farmed salmon have escaped annually from Norwegian fish farms. By comparison, during the last 10 years, <125 000 wild Atlantic salmon have been reported captured annually along the Norwegian coast or in Norwegian rivers (Anon 2015), and thus, the number of escaped farmed Atlantic salmon along the Norwegian coast likely exceeds the number of wild conspecifics.

The behaviour of escaped farmed fish is often uncertain with the majority of escapees suffering mortality (Skilbrei 2010) due to starvation or predation. While escaped smolts may migrate towards the open sea, mature adults may enter nearby rivers for spawning (Fleming et al. 1996; Jonsson & Jonsson 2011). In a simulated-escapement event in a Norwegian fjord system, farmed adult Atlantic salmon moved rapidly away from the release site (Solem et al. 2013; Skilbrei et al. 2014), in accordance with a similar experiment using farmed postsmolts (Skilbrei 2010). Homing to the area of release in adult fish and of escaped postsmolts that returned as adults after one or more years at sea has been described (Skilbrei et al. 2014). Several studies have also noted that the highest occurrence of farmed salmon is often found in rivers located in areas with the highest salmon farming activity (Youngson et al. 1997; Fiske et al. 2006), suggesting there may be some level of homing behaviour to rivers proximate to areas where fish escaped (see Jonsson & Jonsson 2011 and references therein).

Escaped salmon that do return to freshwater are often reported to enter rivers later in the season by comparison with wild fish (Gudjonsson 1991; Gausen & Moen 1991; Carr et al. 1997; Crozier 1998), although not necessarily consistent among all studies (Økland et al. 1995). It has also been reported that farmed fish are more likely to spawn in the lower sections of rivers and sometimes later in the year (Webb et al. 1991). As the incidence of escaped

farmed salmon in Norwegian rivers is often determined from samples obtained by rod fishing in late autumn at relatively few sites (Anon 2015), and wild and farmed fish may have a different behaviour as to how fish react to angling gear, estimates of farmed fish may be biased by differential catchability (see Fiske et al. 2006).

An alternative means to quantify escapees is to observe the total ascending run of salmon during the spawning migration period rather than depend on a limited samples taken at few selected locations in a river. Accordingly, the objective of the current study is to examine the incidence and run timing of escaped farmed salmon vs. wild fish in a series of Norwegian rivers using video camera surveillance. It was hypothesised that escaped farmed salmon enter the rivers later in season compared with wild salmon and that the general pattern for size- and age-dependent ascendance of wild salmon is less pronounced in escaped farmed salmon. Implications of differential migration times could ultimately influence management strategies designed to ensure conservation of the wild population.

Materials and methods

Study sites and monitoring

Video camera surveillance systems were operated in 15 rivers ranging from river Mandalselva in the south (58°02'N) to river Laukhella in the north (69°23'N) (Table 1; Fig. 1). Rivers varied in length from 3.6 to 51 km, with respective drainage areas ranging from 43 to 4011 km² (Table 1). The period of monitoring (2003–2013) varied from 1 to 12 years, depending on the river (Table 1). All video surveillance was performed by Scandinavian Nature Surveillance AS (Ltd), where migration data have been routinely collected over a 15-year period in various Norwegian rivers (see reports at: www.ferskvannsbiologen.net). The video tapes and hard disks have been archived by Scandinavian Surveillance Ltd and are accessible to those who might want to use them. Several rivers are included in the National Salmon Watercourse (see Table 1) scheme and identified as requiring additional conservation measures (Vøllestad et al. 2014).

Video cameras were generally installed from late April to late May and removed in most rivers before freezing, that is between late September and mid-November (Table 1). Camera systems (Lamberg Bio-Marin, Trondheim, Norway) were similar to those that have been previously used to monitor salmon abundance in Norwegian or Finnish rivers (e.g. Davidsen et al. 2005; Orell et al. 2007; Borgstrøm et al. 2010) or used in other fisheries surveillance

Table 1. Location, drainage area, river length and distance from sea to location of video cameras for the rivers included in this study.

River name	MapNo	Drainage area km ²	River length (km)	Distance from video/trap to sea (km)	River sections vs. fishways (FW)	No of cameras	Years covered	No of years	Week of the year	Total no of fish		No of large fish	
										Wild	Farmed	Wild	Farmed
Arendalselva	1	4011	20.5	0.500	FW	1	2004-2006	3	25-45	748	18	404	17
Mandselva†	2	1817	51	34.000		4	2011-2012	2	21-40	3280	2	2244	2
Suldalselva†	3	1463	20.6	0.200		8	2012	1	21-44	1845	15	1498	14
Aurlandselva	4	801	15.6	0.500		8	2005	1	22-40	108	7	46	5
Gaula†	5	632	13.6	0.001	FW	1	2005-2013	9	22-42	10 682	156	6551	131
Nausta†	6	278	9.8	2.500	FW	1	2003-2013	11	22-41	9585	53	5822	43
Hustadelva	7	43	17.7	0.600		4	2009-2011	3	21-41	609	2	128	1
Stordalselva†	8	374	25.4	1.200	FW	1	2011-2012	2	21-40	1641	13	653	11
Moelva	9	433	34.5	1.200		4	2008-2013	6	17-41	2168	442	784	391
Urvollelva	10	63	3.6	0.050		4	2006-2010	5	21-38	305	19	92	14
Futelva	11	46	5.5	0.250	FW	1	2006-2009, 2011	5	25-41	931	3	130	
Sagvatnan	12	243	13	0.050	FW	1	2013	1	26-40	133	20	35	18
Skjoma	13	185	12.8	0.500		8	2001-2012	12	20-41	1573	94	1086	74
Roksdalselva†	14	51	14.5	0.120		4	2004-2012	9	19-47	18 814	57	4316	34
Laukhella	15	207	20	0.650		4	2008-2012	5	20-39	3265	337	1021	294

National Salmon Watercourses are marked with an (†). MapNo corresponds to the number used to show respective river cameras used at each river is provided, and in Laukhella, barriers were used to divert salmon into a narrow migration window where video cameras were placed. Large salmon are defined as fish ≥ 65 cm.

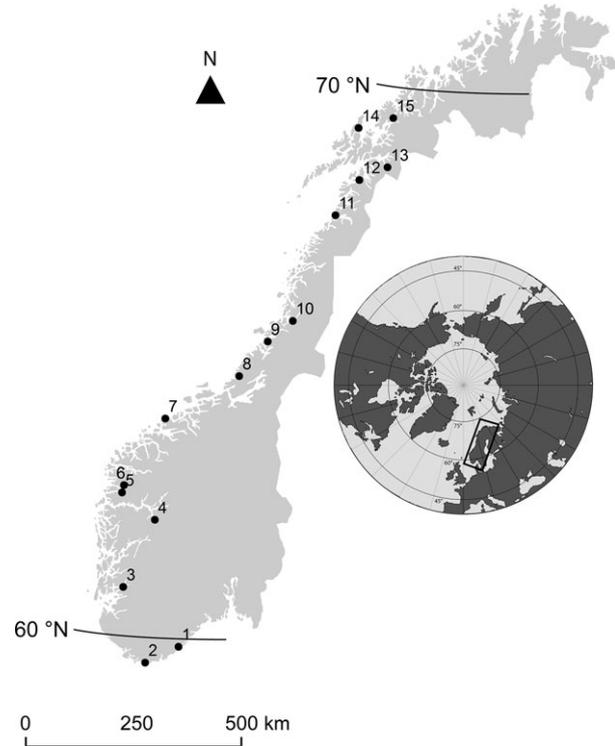


Fig. 1. Map showing the location of rivers where video camera surveillance (1 – 15) was used to determine the incidence and timing of wild and escaped farmed salmon. Details pertaining to the rivers are summarised in Table 1.

programs (Dempster et al. 2009; Uglem et al. 2009). In some locations, an array of cameras was used across a transect of the river, while in other rivers, individual cameras were placed in fishways (see Table 1). Turbidity may vary both among rivers and throughout the season. Rivers draining from lakes are less influenced by changes in flow (due to ‘lake storage’ of water) than riverine systems without lakes and thus are less likely to be impacted by variable turbidity during the season. Therefore, in riverine systems without lakes, the number of cameras used is usually increased by comparison with ‘lake’ systems to try and ensure migrating fish are not missed. Further details pertaining to the video recording system are provided by Davidsen et al. (2005).

Two main types of video systems were used in enumerating upstream migrating salmon, that is a single or dual camera used in fishways and multi-camera array used in open river cross sections. In both systems, cameras deliver SD video (standard PAL resolution 720 × 576 pixels) and with resolution being approximately 550 TV lines. Camera field of view was approximately 70 degrees measured horizontally under water. Under water LED light (Intellilight, Amber) supplied artificial light to the cameras during dark hours. In single camera systems, the camera was placed about 70 cm from the passing

fish. In multicamera systems, the distance between cameras varied from 1.2 to 2.5 m, directed perpendicular to the water flow. In some systems, fences were used to reduce the width of the monitored cross section resulting in a distance between cameras and fish passing by of approximately 1.2 m. The video signals in both types of systems were recorded on hard disks in 'time lapse' mode with a frame rate varying from two to four frames per second. In addition, a sensor trigger was used in fish ladders producing video clips of each passing fish with a frame rate of 50 frames per second. The 'time lapse' video was analysed on high-resolution monitors (1000 TV lines) with playback speeds varying from 10 to 30 times real time. The same type of camera was used in all rivers, while the numbers of cameras varied with river width. In fish ladders, only one or two cameras were used. The video cameras were located from 10 to 650 m from the sea in 11 of the 15 rivers, from 1.2 to 2.5 km in three of the rivers and 34 km from the sea in one river (Table 1).

Of the total number of 56 925 salmon classified from 15 rivers, 55 900 fishes were measured for length and partitioned into two life-history size groups, as described in detail by Borgström et al. (2010). *Small* salmon were defined as fish <65 cm in length ($N = 30\,041$), while *large* salmon were defined as fish ≥ 65 cm ($N = 25\,859$). As noted by Borgström et al. (2010), small salmon are predominately 1SW fish while large salmon are mostly MSW and repeat spawners.

Fish length was measured to the nearest centimetre by the use of a reference scale in the picture. Salmon migrating into fish ladders must swim through a narrow stainless steel channel, 22 cm wide, with little room for the fish to move sideways. Based on the position of the fish in the channel and the distance from the camera to the fish, the estimated length of, say, a 70-cm-long salmon would be determined correctly if the fish was positioned adjacent to the side closest to the camera, but could result in an estimated length of 65 cm if the fish was positioned

proximate to the side that was more distant to the camera. A larger fish of 100 cm could only move 2–3 cm sideways in the channel, resulting in an underestimated length of about 98 cm as the fish has little opportunity to move laterally. Where video cameras were operated in an array across an open section of river, fish length was estimated in a two-step procedure. First, when setting up the cameras, a measuring stick was moved sequentially along the 'heterogeneous' river bed and recorded by the camera images. These images were used as a reference during the analysis of images of ascending salmon. Here, each fish was given a specific position in the river that could vary by about 20–25 cm, but when matched with the size of known objects from the reference pictures, an estimate of the size of fish could then be made. Similar to the surveillance in fishways, estimated fish lengths determined from the array of cameras could also be incorrectly estimated by upwards of 3–8 cm. Hence, some salmon may have been under- or overestimated by a small amount, but this would not have a significant influence when partitioning the fish into the two size groups used in the analysis.

Identification of escaped farmed salmon

Farmed salmon were separated from wild fish through inspection of video camera images according to the morphological features and description provided by Fiske et al. (2005) and Jonsson & Jonsson (2011). The video camera system allows individual picture frames to be stopped, examined in detail, and if necessary to zoom in on certain features for better resolution of specific identifying characteristics. The main morphological parameters examined were the overall body shape, pigmentation, colour and shape of fins. Farmed salmon often have a short gill cover while fins are often rounded, and occasionally split. In addition, farmed fish will often differ in overall morphology that separates them from the wild fish in the rivers monitored (see Table 2).

Table 2. Main visual morphological differences observed in the video pictures used to discriminate between wild and escaped farmed salmon. Following criteria summarised by Fiske et al. (2005) and Jonsson & Jonsson (2011).

	Wild salmon	Farmed salmon
Body	Streamlined body, dark back and top of head vs. silvery body side	Rounded, reduced streamlining, thicker caudal peduncle, homogenous colour
Head	Smooth curved head silhouette, overshot jaw	Disrupted curve on upper head silhouette, snout and jaw deformations, undershot jaw
Tail	Large tail area relative to body area, with sharp outline	Small tail, rounded edges and several points with split fin
Pigment spots	Missing or very few pigment spots below lateral line	Numerous small pigment spots, especially below lateral line and on gill cover
Gill cover	Large, covering gills	Short, often exposing a stripe of white skin, or even exposing gills
Dorsal fin	Large and sharp outline, straight fin rays	Small and worn down (wavy), rounded fin rays, narrower fin base
Adipose fin	Relatively small	Relatively large
Other fins	Sharp outline, straight fin rays, relatively large	Rounded, small and worn down, wavy fin rays

Salmon that escape from cages early in life will not display the same distinguishing features as those individuals that have recently escaped, or those that have spent a long enough period of time in cages to take on farm-type characteristics. Hence, estimates of escapees identified from the video surveillance are assumed to be minimum values.

Statistical analyses

Run timing of farmed and wild salmon

The combination of year and river was highly unbalanced in the sample (Table 1). As a consequence, we were not able to disentangle the effects of year and river and decided to control for these variables by including them as a single concatenated random factor, *RiverYear*, in the analyses. Thus, *RiverYear* was defined by one unique level for each combination of river and year (Fig. 4a). The total sample comprised 55 900 observations (fish measured) in 78 *RiverYear*. To investigate how run timing of farmed and wild fish was related to fish length, the *Date of run* (days since January 1) was initially fit to a mixed linear model using the nlme library in R, ver. 2.13.0 (Pinheiro et al. 2014). *RiverYear* was included as a random effect. Fish type (farmed/wild) was included as a fixed factor, and fish length was included as covariate. It was expected that the relationship between run timing and fish size would differ between farmed and wild salmon, and therefore, the interaction between fish type and fish length was explicitly tested. The interaction term was highly significant ($P < 0.0001$), and therefore, the modelling proceeded by treating farmed and wild fish separately. To account for non-linear relationships between run timing and fish length, the date of run was fit to generalised additive mixed models (GAMs) using the mgcv library (Wood 2006) in R for wild and farmed salmon separately. Fish length was modelled with smooth functions using a thin plate regression spline as basis. To include the random effect of *RiverYear*, the term s (*RiverYear*, $bs='re'$) was included in the model, that is the random effect was treated as smooths (see the mgcv package and Wood 2008). For each model (wild and farmed), the predicted values for the average *RiverYear* are shown. Standard Errors are given for the *Fish length* – term of the models (i.e. excluding the variation due to *RiverYear*). Predicted values and standard errors were obtained from the *predict* function in *Gam*.

Proportion of farmed salmon

To model how the proportion of farmed salmon developed during the season, the proportion of farmed to wild salmon was fitted to GAMs, using a logit link function with a binomial distribution.

Because of the detected interaction between fish length and fish type with respect to run timing, small (<65 cm) and large (≥ 65 cm) salmon were modelled separately. Run timing (*Date*) was modelled with smooth functions using a thin plate regression spline as the basis. Sample size for small salmon was 30 041 (29 857 wild and 184 farmed) in 78 *RiverYears*. Sample size for large salmon was 25 859 (24 810 wild and 1049 farmed) in 78 *RiverYears*. As above, *RiverYear* was controlled for by including the term s (*RiverYear*, $bs='re'$). For each model (large and small), the predicted values for the average *RiverYear* are shown. Standard errors are given for the *Date of run* – term of the models. Predicted values and standard errors were obtained from the *predict* function in *Gam*.

Results

Incidence of farmed fish

Of the 56 925 salmon identified by video surveillance in the 15 study rivers, nine rivers had annual runs of wild salmon of more than 1500 fish, while six had returns varying from about 100 to more than 900 fish (Table 1). The highest number of wild salmon was observed in river Roksdalselva with nearly 19 000 fish. By comparison with wild salmon, escaped farmed fish were relatively rare and averaged 4.3% across all rivers, ranging from 0.1% at Mandalselva to 16.9% at Moelva. At nine of the fifteen rivers surveyed, 20 or fewer farmed salmon were identified while more than 150 escapees were found in three rivers. Proportionally, escaped farmed salmon made up $<1\%$ of the total salmon returns in seven monitored rivers (Table 1), but more than 9% in three rivers (Moelva – 16.9%; Sagvatnan – 13.1%; Laukhella – 9.4%). In contrast to wild salmon, most of the escaped farmed fish were ≥ 65 cm (85.1%).

Variation in run timing among rivers

Run timing of wild Atlantic salmon varied among the study rivers with three groups potentially being defined based on the median date of salmon return. The earliest runs (small and large salmon combined) occurred in early July at Urvollelva, Stordalselva and Laukhella (Fig. 2). The majority of rivers were characterised with the median return date occurring in mid-July to late July (Fig. 2). Late run rivers were those where the median date of return occurred around mid-August or later, such as Mandalselva and Suldalslågen, with Arendalselva being the most extreme with median return dates in mid-September. The duration of the return migration (difference between the 10 and 90th percentiles of the run) was

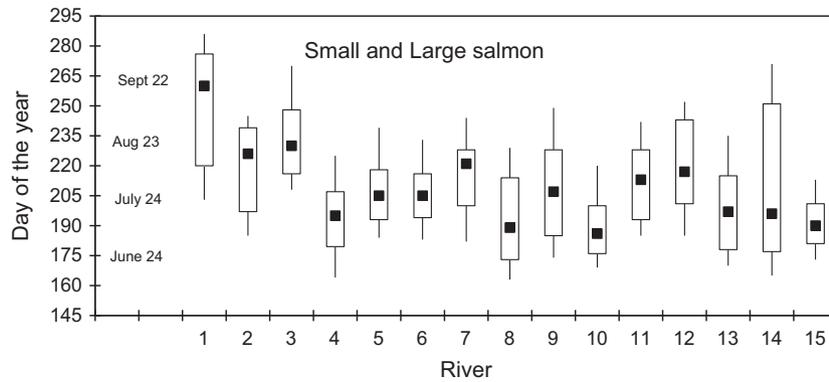


Fig. 2. Variation in wild adult Atlantic salmon run timing among various Norwegian rivers. Small and large salmon combined. River number corresponds to the rivers outlined in Table 1. Vertical lines represent the 10 and 90th percentiles of the day of the year of return migration, the rectangle encompasses the 25 and 75th percentiles, while the solid dark marker is the median (50th) run timing metric based on the overall average where multiple years of data are available (Table 2).

moderately long averaging 8.9 weeks across all rivers. However, wild salmon entered the rivers over an extended period of 12–15 weeks at the rivers Arendalselva and Roksdalselva.

Comparison of farmed and wild fish

In the linear mixed model, the relationship between run timing and fish length differed significantly between farmed and wild salmon [P (interaction term) < 0.0001 ; $N = 55\,900$; $n_{RiverYear} = 78$]. The separate models of farmed and wild salmon (Fig. 3) revealed the difference. For wild salmon larger fish generally entered the river earlier than small fish [$R^2(adj) = 0.22$; $N = 54\,667$; $n_{RiverYear} = 78$, $edf(Date) = 1.00$, $P < 0.0001$]. In contrast, run timing of farmed salmon became progressively later with increasing fish size up to a length of approximately 85 cm [$R^2(adj) = 0.29$; $N = 1233$; $n_{RiverYear} = 69$; $edf(Date) = 2.88$, $P = 0.007$]. Consequently, the difference in run timing between wild and farmed fish

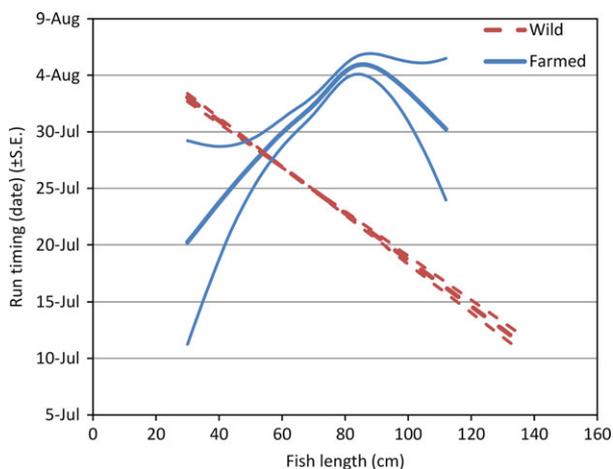


Fig. 3. GAM models relating the river entry date to the size of fish for wild and farmed salmon respectively. River and year were controlled for in the models, and the figure shows the average estimates from all rivers and years \pm SE (dashed line) for the fish length term.

increased with increasing fish length. While both farmed and wild small salmon returned to the river at about the same time, wild salmon of 70–90 cm appeared on average nearly 2 weeks earlier than similarly sized farmed salmon.

Proportion of farmed fish

The model for large fish (≥ 65 cm) indicated that the proportion of farmed salmon increased until late August and decreased thereafter [Fig. 4b, $R^2(adj) = 0.27$; $N = 25\,859$; $n_{RiverYear} = 78$; $edf(Date) = 5.28$, $P < 0.0001$]. The model for small salmon (< 65 cm) revealed lower and relatively constant proportions of farmed fish throughout the season [Fig. 4b, $R^2(adj) = 0.03$; $n_{RiverYear} = 78$; $N = 30\,041$; $edf(Date) = 3.16$, $P = 0.181$]. It should be noted that the sample size of the concatenated *RiverYear* variable was low, particularly during periods both later in the season (after late September) and early (i.e. before mid-June) (Fig. 4a) such that the standard errors during these times were moderately wide.

Discussion

Video camera surveillance was used to examine the incidence and timing of wild and escaped farmed salmon returning to various Norwegian rivers. The incidence of escaped farmed salmon averaged $< 5\%$ across the 15 video monitored rivers with large-sized escaped farmed salmon returning up to 2 weeks later than similar sized wild fish indicating that the general pattern for size- and age-dependent ascendance differs among wild and farmed fish. Differential migration times between wild and escaped farmed salmon could ultimately influence management strategies designed to ensure conservation of the wild population. In the present study, wild and escaped farmed salmon were identified using morphological differences as observed in video surveillance pictures (see Table 2). This method is appropriate for detecting recently escaped adult salmon, but is questionable for

Run timing of wild and escaped farmed salmon

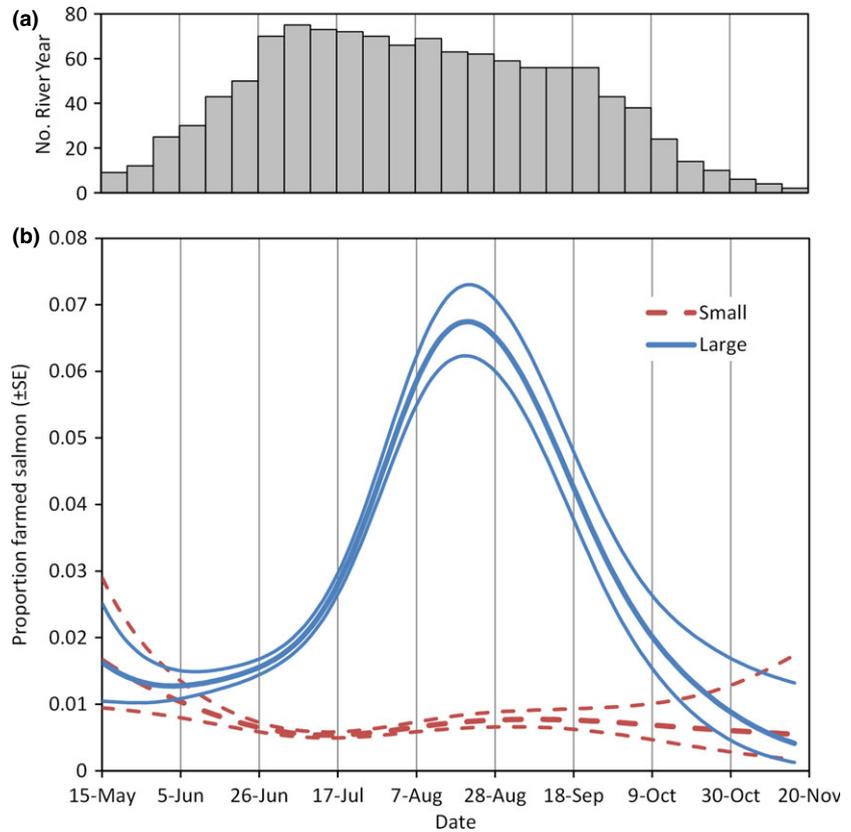


Fig. 4. (a) (top) Number of RiverYear included during the video surveillance period, and (b) (bottom) binary GAM models relating the proportion of farmed salmon to river entry date for large (≥ 65 cm) and small (< 65 cm), respectively. River and year were controlled for in the model, and the figure shows the average estimates from all rivers and years \pm SE (dashed line) for the Date term.

farmed fish that may have escaped early in life, for example, as smolts, subsequently returning to rivers as mature salmon after staying one or more years at sea.

Continued farming through adulthood greatly increases environmentally induced phenotypic divergence between farmed and wild salmon (Fleming et al. 1994). Escaped fish that have spent a longer period of time at sea do not necessarily share the morphological characteristics of adult farmed salmon listed in Table 2; thus, especially salmon escaping as smolts can be misclassified as wild salmon by anglers when they return to spawn. Hence, an unknown number of farmed fish were likely misclassified as wild fish when viewing the video surveillance images. Accordingly, the estimated proportion of farmed fish reported in the current study most likely represents minimum values of those fish that escaped later in life. Indeed, no methods are without some level of uncertainty (Friedland et al. 1994; Youngson et al. 1997), including genetic techniques (Glover 2010), and that a combination of approaches has often been recommended to identify escaped farmed salmon (Lund & Hansen 1991).

While escapees were observed in all systems, they were generally few in number totalling 20 or less across all years from 13 of the 15 sites/rivers. The greatest numbers were reported at three rivers

(Moelva, Laukhella and Gaula) where the average annual occurrence was 73.7, 67.4 and 17.3 fish, respectively, while the greatest proportions of escaped farmed fish occurred at Sagvatnan (13.1%) and Moelva (16.9%). The average percentage of escapees among rivers was 4.3%, while the percentage of farmed salmon based on the grand total of all fish was 2.2%. The sample of fish was highly unbalanced between river and year resulting in very small samples of farmed fish in certain rivers and years (Table 1). Hence, we were unable to disentangle the effect of river and year in the analyses, and in order to control for the variation caused by these factors, we included the unique combinations of river and year (*riveryear*) as a random factor in the analyses. Although this procedure controls for systematic differences, it should be noted that the relationship between river entry date and size for farmed salmon was based on a relatively small sample dominated by a few rivers, resulting in relatively high confidence intervals, especially for small fish (Fig. 3). Similarly, sampling was generally concentrated in the period from mid-June to late September (Table 1, Fig. 4a), resulting in relatively uncertain estimates of the proportion of farmed salmon before June 1 and after October 1 (Fig. 4b).

The phenomenon of finding numerous rivers with escapees present, but generally with relatively few

fish in number, appears common throughout much of the distributional area where salmonid aquaculture occurs. Morris et al. (2008) reported escaped farmed salmon occurring in 56 of 62 eastern North American rivers that were within 300 km of aquaculture operations. The average proportion of farmed fish among all rivers was 9.2%, but only 3.0% when using the grand total. These figures are within the same range as those observed in the current study. An escapee incident in Northern Ireland resulted in farmed fish subsequently being found in English and Welsh rivers, where the estimated proportion reported in spawning escapements was 3.2% (Milner & Evans 2003). In the River Bush, Crozier (1998) also reported a relatively low incidence of escapees averaging <1% annually and similar to that reported for the River Tana (Teno in Finnish) determined on samples obtained during the summer fishing season (Erkinaro et al. 2010).

Based on estimates largely from rod captures in Norwegian rivers, Lund et al. (1991) reported that 5.8% of fish angled during the fishing season were of reared origin although with substantial differences among rivers. Similarly, the prevalence of escaped farmed salmon estimated from fisheries in Scottish rivers averaged <5% (Walker et al. 2006). Other studies found that estimates of escapees in rivers could be influenced by seasonal differences, that is, whether angled samples were taken during the summer or autumn, usually with escapees more prevalent in the autumn samples (Fiske et al. 2006; Erkinaro et al. 2010). Fiske et al. (2006) used a blended approach where estimates from both autumn spawning site surveys were combined with escapees estimated from summer angling catches. In a later study, Glover et al. (2012) found that the contribution of escapees was >15% in 8 of 21 rivers, but <10% in 11 rivers.

Exceptions occur to the generalisations of escapees being found in many rivers, but being relatively few in numbers. In the Magaguadavic River, New Brunswick, Canada, not only has there been a consistent decline in the numbers of wild salmon returning to the river, but also the contribution of escaped farmed salmon has risen, and in some years, they have dominated the run (Carr et al. 1997). Moreover, in the River Vosso, Norway, escaped farmed salmon may have partly replaced the natural wild population of fish (Sægrov et al. 1997; Glover et al. 2013). However, with more than 3 million escapees occurring in Norway alone over the 10-year period 2005–2014, relatively low numbers of escapees were observed or reported in rivers. This could be due to low survival at sea, especially for salmon escaping in late autumn or early winter, or the lack of propensity for immature fish to return to freshwater (Hansen 2006; Hansen & Youngson 2010; Skilbrei et al. 2014).

However, it could also be related to the relatively stable number of escapees being reported each year, which if correct, would mean the proportion of escapees has also been declining.

Part of the reason for the absence of large numbers of escapees in rivers may stem from the period of time escaped farmed salmon return to rivers and the methods used to quantify these incidences. Many studies have reported that escapees often enter rivers later in the autumn compared with wild fish (e.g. Gudjonsson 1991; Carr et al. 1997; Crozier 1998; Erkinaro et al. 2010). Hence, estimates of escapees derived from sampling the recreational catch during the summer angling season could be biased (Walker et al. 2006). Also differential catchability between wild and farmed fish could influence the results (Fiske et al. 2006), particularly if there are differences in catchability between small and large fish for either of the two groups.

Video surveillance systems can provide an alternate means to monitor escapees provided that cameras are installed early enough in the spring and remain in place long enough into the fall. In the current study, cameras were installed and operational in some rivers from late April to mid-November, although most rivers were monitored from late May to mid-October. Still, based on the statistical model used, the relationship between run timing and fish length differed significantly between farmed and wild salmon. Wild large salmon had a tendency to return earlier than small fish, whereas for escapees, run timing became progressively later for fish up to a length of about 85 cm. Consequently, the difference in run timing between wild and farmed fish increased with increasing fish length. While small fish appeared at about the same time for both groups, wild salmon of 70–90 cm appeared on average nearly 2 weeks earlier than farmed fish of the same size (see Fig. 3).

While large-sized escaped farmed salmon were found to migrate later than wild fish, there was no evidence from the rivers where monitoring continued until mid-October to mid-November of any exceptionally late autumn runs of farmed fish. Thus, the proportion of farmed fish generally increased until mid-August to late August and decreased thereafter. Although sample sizes were limited for small-sized farmed fish (<65 cm), modelling revealed a low and fairly consistent proportion of farmed fish throughout the season, at least from late May to early October, providing support, in part, for the hypothesis that size-dependent difference in the timing of ascendance of escaped fish was less prevalent in small vs. large individuals in several rivers. This may also be dependent on sex and maturity status of the farmed fish.

Based upon catch reports (June–August) from anglers in Norwegian rivers, the incidence of farmed

fish in river sport fisheries has been rather stable during the last 10 years, with an average around 7%, although only 3.2% were reported in 2013 (Anon 2015). However, during the annual monitoring fishery in a selection of Norwegian rivers, conducted just before spawning (September–October), farmed fish have averaged nearly 15% of fish sampled during the past 10 years and 17.7% in 2013 (Fiske et al. 2014). The difference between the two estimates may be explained by a later ascendance of farmed fish as partly corroborated by the current study, and also observed in the River Etne, where around 9% of farmed fish may enter the river after October 15 (Skaala et al. 2014). Studies that report a high incidence of farmed salmon in the late autumn may, however, also be biased if wild and farmed salmon utilise different habitats or if there is differential catchability of wild and farmed salmon (Svenning et al. 2015). Clearly, additional research is needed to clarify and resolve discrepancies among estimates of farmed escapees in Norwegian rivers. In particular, when using video surveillance, the accuracy of visual identification of farmed fish should be validated, and the surveillance period should ideally be extended until long after the spawning season. Also the potential bias of differential catchability between wild and farmed fish should be investigated more thoroughly.

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