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Genetic evidence of farmed straying and introgression in Swedish wild salmon populations

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ABSTRACT: Escaped farmed Atlantic salmon represent a well-documented and ongoing threat to wild conspecific populations. In Norway, the world-leading producer of farmed salmon, annual monitoring of straying and genetic introgression by farmed escapees in wild salmon rivers has been carried out since the late 1980s. In this study, we applied molecular and statistical methods routinely used in the Norwegian monitoring programme to investigate the magnitude of escaped farmed salmon and genetic introgression in salmon rivers on the west coast of Sweden, where suspected escapees have been observed. Our results confirm that escaped farmed salmon stray, successfully spawn, and produce offspring at levels similar to those observed in neighbouring Norway. These findings raise concerns over population productivity and long-term viability and highlight the need for more permanent monitoring of the presence and consequences of escaped farmed salmon in Swedish salmon rivers. Our results further illustrate that farmed gene flow may constitute a transboundary problem with potential international implications.

KEY WORDS: Gene flow · Aquaculture · Atlantic salmon · *Salmo salar* · Single nucleotide polymorphisms · SNPs

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1. INTRODUCTION

During the last half-century, aquaculture production of Atlantic salmon *Salmo salar* Linnaeus, 1758 for the international food market has increased dramatically (Bostock et al. 2010). A vast majority of the production takes place in net pens in the sea where large-scale escape events sometimes occur. It was noted early on that escaped farmed salmon pose a threat to wild populations (e.g. Hindar et al. 1991). A growing body of scientific studies has confirmed that domesticated escapees frequently enter salmon rivers where they interact ecologically and genetically with wild conspecifics, risking population productivity and long-term persistence (e.g. Jonsson & Jonsson 2006, Forseth et al. 2017, Glover et al. 2017).

In Norway, the world's leading producer of farmed salmon, genetic homogenization among populations and widespread introgression have been documented in a large number of rivers (Glover et al. 2012, Karlsson et al. 2016). Similar reports also exist from Scotland and eastern Canada, 2 other areas where sea-based salmon farming also exists (Green et al. 2012, Coulson 2013, Keyser et al. 2018, Gilbey at al. 2021).

During the 2010s, the total average annual production of farmed salmon in Norway reached 1.2 million t (Norwegian Directorate of Fisheries 2021a). Norway has around 400 rivers with wild salmon populations of high biological and socio-economic value. In the years 2014–2020, an annual average of 154 000 salmon (range: 17 000–290 000) escaped from Norwegian facilities according to official statistics (Norwegian Directorate of Fisheries 2021b). These numbers, based on reports from the fish farms, are uncertain and expected to be underestimates, ac-

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cording to the Norwegian Directorate of Fisheries that is responsible for the collection. Many of these escapees survive and later stray into rivers with wild salmon. For comparison, the estimated total number of wild spawners returning to the Norwegian coast (prefishery abundance) has declined from around 1.0 million salmon in the mid-1980s to ca. 0.5 million in the 2010s (Glover et al. 2017 and references therein).

A programme for monitoring of escaped farmed salmon in Norwegian rivers was initiated in 1989 (Diserud et al. 2019). This programme was expanded and developed further in 2014 (Glover et al. 2019). Using a set of different methods, levels of farmed escapees are currently estimated annually in a selected network of more than 200 rivers. Field data from river catches, snorkelling surveys, etc. are complemented with scale readings and DNA analyses for the identification of escaped and wild-born individuals with different levels of farmed admixture (Glover et al. 2019, Diserud et al. 2020). Following a long-term decrease in the proportion of recorded escapees from 1989 to 2017, farmed salmon were still observed in two-thirds of the rivers monitored in 2014–2017 (Glover et al. 2019).

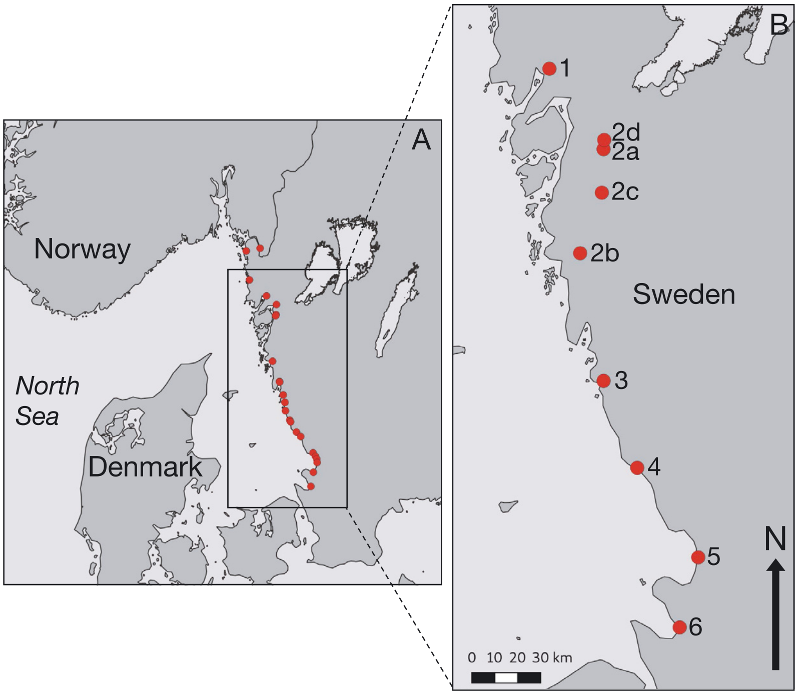

Fig. 1. (A) Locations of 23 watercourses with Atlantic salmon populations in south-western Sweden (Fiskeriverket 1999). (B) Location of sites for samples included in the present study. Numbers 1–6 depict historical (H) and contemporary (C) samples. 1 = Örekilsälven (H,C), 2 = Göta älv (C) (a = Lilla Edet, b = Säveån, c = Grönån, d = Brattorpsån), 3 = Viskan (H), 4 = Ätran (H,C), 5 = Lagan (H,C), 6 = Rönne å (C)

Despite geographical proximity (ca. 500 km by sea) to coastal areas with extensive salmon aquaculture in south-western Norway, and to Norwegian salmon rivers at an even closer distance where straying and genetic introgression by escaped farmed salmon have been detected, there is so far no conclusive scientific evidence for similar problems in south-western Sweden (Kattegat/Skagerrak area). In this part of Sweden, Atlantic salmon exist in 23 (mainly small) watercourses (Fig. 1A). At present, Sweden has no sea-based salmon farming from which adults may escape. However, reports exist of suspected escapees, recognized through their morphological appearance (fin damage, supposed vaccination scars, etc.). Non-local microsatellite genotypes have also been identified among suspected farmed escapees from the Swedish Rivers Lagan (in 2008) and Göta älv (in 2008 and 2010), although their origin could not be verified in earlier genetic analyses (Palm et al. 2011, with references).

In the present study, we applied the same set of diagnostic single nucleotide polymorphism (SNP) markers and statistical methods as routinely used in the Norwegian monitoring programme (Karlsson et al. 2011, 2014, 2016, Diserud et al. 2020) to investigate the magnitude of straying and introgression by escaped farmed salmon in Swedish rivers. Our main aims were (1) to identify potential escapees among adult salmon previously analysed with microsatellites, and (2) to provide a first assessment of levels of farmed introgression in Swedish wild salmon populations based on juvenile samples.

2. MATERIALS AND METHODS

Genetic data (diagnostic SNP markers) was compared between samples collected from 6 rivers in south-west Sweden (Fig. 1B), collected before and/or after the rapid expansion of the salmon aquaculture industry in the 1980–1990s (referred to herein as 'historical' and 'contemporary' samples, respectively). As historical references, we used adult scale samples (n = 191) from 4 rivers (Örekilsälven 1972–1974, Viskan

Table 1. Number of analysed salmon individuals per watercourse and time period. Contemporary samples are divided into adults and juveniles. Numbers in parentheses represent fish originally genotyped before omitting individuals not suitable for further statistical analyses (i.e. identified trout and salmon × trout hybrids, and salmon with too few scored SNP genotypes; see Section 3 for details). Map codes correspond to those in Fig. 1; na: data not available

Map code	River	Site/ tributary	Historical adults		Contemporary adults		Contemporary juveniles	
			Year(s)	n	Year(s)	n	Year(s)	n
1	Örekilsälven		1972–1974	38 (41)	2008–2009, 2011–2012	37 (40)	2009–2013	39 (40)
2a	Göta älv	Lilla Edet	na		2010	87 (87)	na	
2b	Göta älv	Säveån	na		na		2009–2010	35 (35)
2c	Göta älv	Grönån	na		na		2009–2010	40 (40)
2d	Göta älv	Brattorpsån	na		na		2012, 2014	12 (12)
3	Viskan		1936	48 (50)	na		na	
4	Ätran		1952–1954	37 (50)	2008–2011	40 (40)	2010–2011, 2013	38 (40)
5	Lagan		1952–1955	49 (50)	2008	32 (32)	na	
6	Rönne å		na		na		2011–2012	39 (40)
Totals				172 (191)		196 (199)		203 (207)

1936, Ätran 1952–1954, and Lagan 1952–1952; Table 1) archived at the Institute of Freshwater Research, Drottningholm, Sweden. These scales represent Swedish wild salmon populations before any potential impact from escaped farmed salmon (cf. Karlsson et al. 2014, 2016). As farmed references, we used the same samples as in Karlsson et al. (2016), comprising ca. 500 individuals from several year classes collected from salmon breeding kernels used by 3 leading Norwegian aquaculture companies.

Contemporary adult samples (n = 201) included dried scales or fin clips (stored in ethanol) from 4 rivers (Table 1). From 3 of these rivers, we also had historical scale samples. As a focussed search for escaped farmed salmon (or their wild-born offspring), we selected individuals from Lagan (scales, 2008) and Göta älv (fin clips, 2010), that in previous analyses had shown a large share of genotypes at microsatellite loci of non-local population origin (Palm et al. 2011 and references therein). All of these adults had an intact adipose fin, indicating that they did not belong to the local hatchery stocks used for compensatory releases in these 2 rivers (since 2004, all hatchery-reared smolts released in Sweden must have their adipose fin removed). For Ätran and Örekilsälven, we used scale samples collected by anglers throughout 4 fishing seasons (2008–2011). The aim was to screen for adult farmed genotypes using samples from 2 rivers without prior documentation of non-local genotypes.

Contemporary juvenile samples (n = 207) consisted of fin clips from parr collected by electrofishing in 4 rivers during 2009–2014 (Table 1). From 2 of these rivers, we also had historical adult scale samples. The juvenile samples were collected over several years across several fishing sites. In Göta älv, the largest Swedish river (average annual flow of 570 m^3 s^{-1}), salmon reproduces in some of the tributaries. Juvenile samples were selected from the 2 most important ones (Säveån and Grönån) that hold genetically distinct local populations (Palm et al. 2011), and from a tributary (Brattorpsån) where a more recent microsatellite survey indicated allele frequencies that tended to deviate somewhat from those in other parts of the Göta älv system (Söderberg et al. 2020).

We used the same methods for DNA extraction, PCR reactions, and SNP genotyping as in Karlsson et al. (2016). Among the SNP markers shown by Karlsson et al. (2011) to discriminate Norwegian farmed from wild salmon, we focussed on 48 loci that are routinely screened in the Norwegian monitoring programme (e.g. Diserud et al. 2020). The SNP assay employed also includes 16 SNPs with large differences in allele frequency between salmon and brown trout *Salmo trutta*; deviating multi-locus genotypes at those loci were further analysed with an additional diagnostic set of markers to differentiate between salmon, brown trout, and their hybrids (Karlsson et al. 2013). Only confirmed salmon with at least 80% scored SNP genotypes at the 48 diagnostic (farmed/wild) markers were retained for downstream data analyses.

Standardized levels of farmed individual introgression were calculated following Karlsson et al. (2014), and we refer to that paper for further details. In brief, wild and farmed idealized *in silico* populations were first created based on genotypic data for historical Swedish wild and contemporary Norwegian farmed reference samples, respectively, from which wild and farmed 'centre points' were created and illustrated graphically using principal coordinates analysis and GeneAlEx 6.5 (Peakall & Smouse 2006; Fig. 2). For each fish, the probability of belonging to the wild versus the farmed centre point was calculated using the Structure software (Pritchard et al. 2000). This probability is hereafter referred to as *P*(Wild) (= 1 − *P*(Farm)).

The 4 historical Swedish wild samples were genetically similar to each other and to historic Norwegian samples from the wild 'Atlantic population group', but markedly distinct from the farmed references (Fig. 2). Therefore, we concluded that levels of introgression could also be safely estimated for Swedish rivers without a local historical reference.

When testing for farmed introgression in contemporary samples, we used the 2-sample test by Karlsson et al. (2016) based on logit-transformed *P*(Wild). Estimates and tests of farmed introgression were performed by using the average *P*(Wild) estimates of all 4 historical reference samples combined and by using the local historical sample when available. Resampling was used in so-called 'tail-tests' for the detection of admixed genotypes by evaluating if the lower 5%-percentile for *P*(Wild) was lower than expected in a pure wild sample (cf. Karlsson et al. 2016).

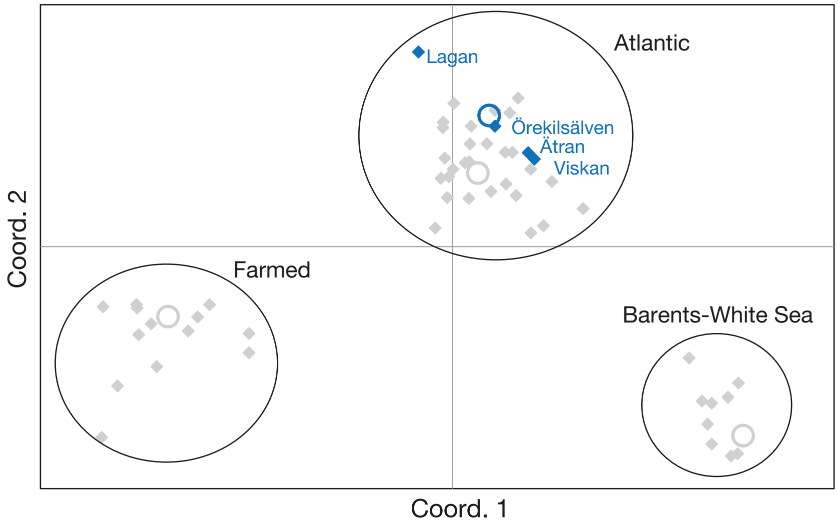

Fig. 2. Principal coordinates analysis plot based on pairwise F_{ST} estimates (48 diagnostic single nucleotide polymorphism markers) between 4 historical Swedish salmon populations (blue diamonds) combined with historical wild and farmed Norwegian reference samples (grey diamonds; data from Karlsson et al. 2016). Wild salmon populations are divided into 2 distinct groups (Atlantic and Barents−White Sea). Open circles represent 'centre points' for *in silico* generated populations based on allele frequencies for pooled samples within each cluster

3. RESULTS

Following SNP genotyping, 26 out of 597 individuals were omitted from further statistical analyses. Most of these removed fish (18 historical adults, 3 contemporary adults, 1 juvenile) were salmon with too few scored genotypes, but 2 (1 historical adult and 1 contemporary juvenile) were identified as brown trout and 2 juveniles were found to be salmon × trout hybrids. Thus, the remaining total material comprised 571 individuals (Table 1).

Estimated proportions of wild/farmed ancestry and associated significance tests are presented in Table 2, with corresponding probability distributions shown in Figs. 3 & 4. Because results based on local historical references (where available) and the common average reference for Swedish salmon populations were markedly similar (Table 2), we focus only on results based on the common reference.

Previous suspicions of farmed genotypes among the adult salmon from Göta älv (2010) and Lagan (2008) could be confirmed. Both of these samples showed large and significant levels of introgression, estimated at 75 and 59%, respectively (Table 2). However, their density distributions for logit-transformed *P*(Wild) estimates differed clearly; whereas the Göta älv sample showed a clear bi-modal pattern with a majority of seemingly pure farmed and some pure wild genotypes, the corresponding distribution for the Lagan sample was more unimodal and dominated by intermediate genotypes (Fig. 3). A lower but still significant introgression (9%) and genotypes of farmed ancestry were also detected among adults from Ätran, whereas no significant introgression (2%) or farmed genotypes were detected in the adult sample from Örekilsälven (Table 2, Fig. 3).

Corresponding analyses of wild-born juveniles revealed similar and statistically significant levels of farmed introgression in Rönne å (5%), Ätran (6%), and Örekilsälven (6%). Tail-tests (Table 2) and associated density distributions (Fig. 4) also indicated presence of some genotypes of farmed ancestry with intermediate *P*(Wild) estimates (significant proportion in Örekilsälven and nearly significant in Rönne å and Ätran; Table 2). No indications of farmed introgression or genotypes could be detected among

Table 2. Results from statistical analyses of contemporary samples (cf. Table 1): n: number of individuals; average *P*(Wild): the estimated proportion of wild genes (*P*[Wild] [= 1 − *P*(Farm)]) calculated using the common average and a local historical reference sample ('ref.'), respectively, with levels of significance from tests for farmed introgression. The 'tail-test' evaluates the null hypothesis that all genotypes are of wild genetic origin (the sample from Göta älv/Brattorpsån, n = 12, was too small for performing the test; indicated by 'na'). Note that juvenile samples from the Göta älv tributaries Grönån and Säveån were grouped according to both tributary and year of sampling. $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Sample (sampling year)	n	*P*(Wild)	Proportion wild genes Average ref.	 Local ref.	Tail-test (prob.)
Adults					
Göta älv (2010)	87	0.18	0.25***		0.00***
Lagan (2008)	32	0.42	0.41***	0.41***	0.00***
Ätran (2008–2011)	40	0.95	0.91***	0.90***	0.00***
Örekilsälven (2008–2011)	37	0.97	0.98	1.00	0.30
Juveniles					
Göta älv/Brattorpsån (2012–2014)	12	0.93	0.86***		na
Göta älv/Grönån (2009–2010)	40	0.98	0.98		0.03*
Göta älv/Säveån (2009–2010)	35	0.98	1.02		0.90
Göta älv/Grönån & Säveån (2009)	39	0.98	1.00		0.84
Göta älv/Grönån & Säveån (2010)	36	0.98	1.00		0.76
Rönne å (2011–2012)	39	0.96	0.95**		0.08
Ätran (2010–2013)	38	0.95	0.94***	0.93***	0.07
Örekilsälven (2009–2013)	39	0.97	0.94*	0.96	0.02*

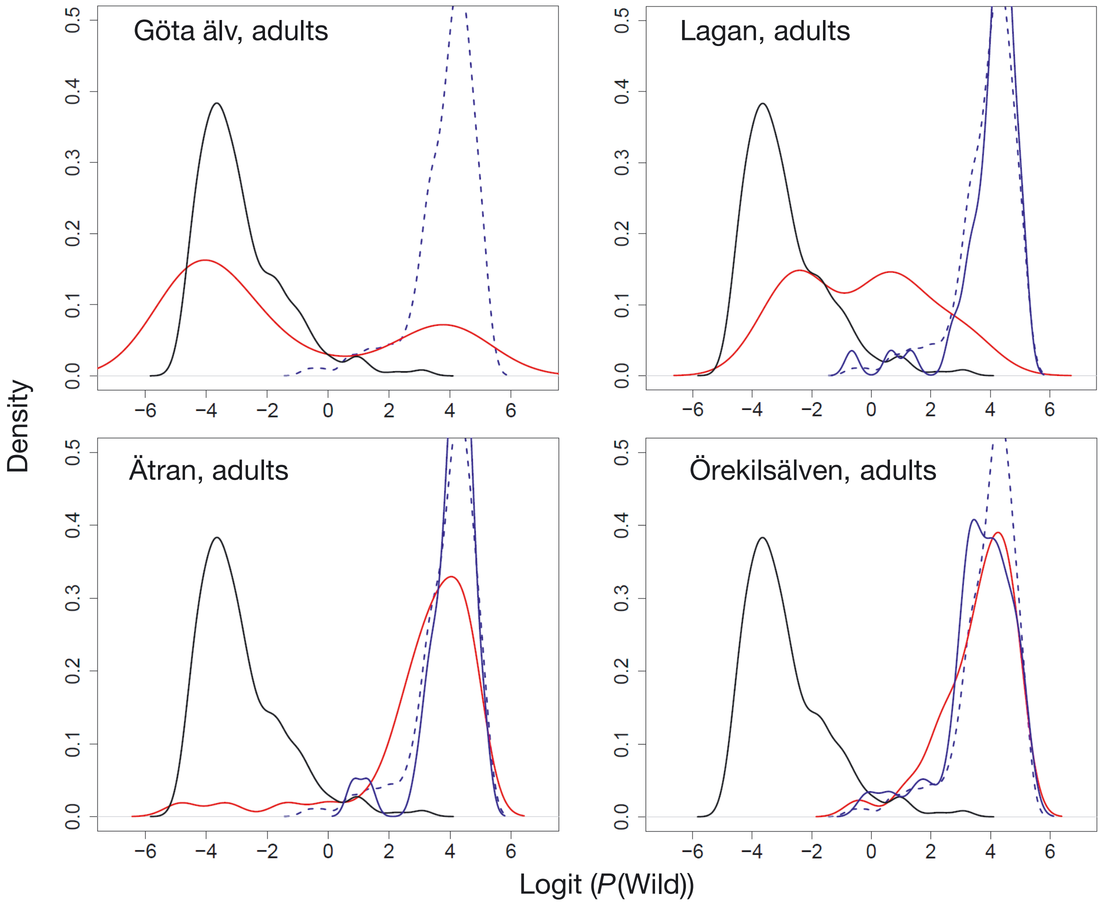

Fig. 3. Density distributions (red lines) based on logit-transformed individual estimates of the probability of wild origin (*P*(Wild)) for adult salmon samples (cf. Table 2). Also shown are corresponding distributions for farmed (solid black) and local wild (solid blue; where available) reference samples and the average historical wild Swedish reference (dashed blue). On the *x*-axis, logit(p) = 0 equals p = 0.5, logit(p) = 4.6 equals p = 0.99, etc

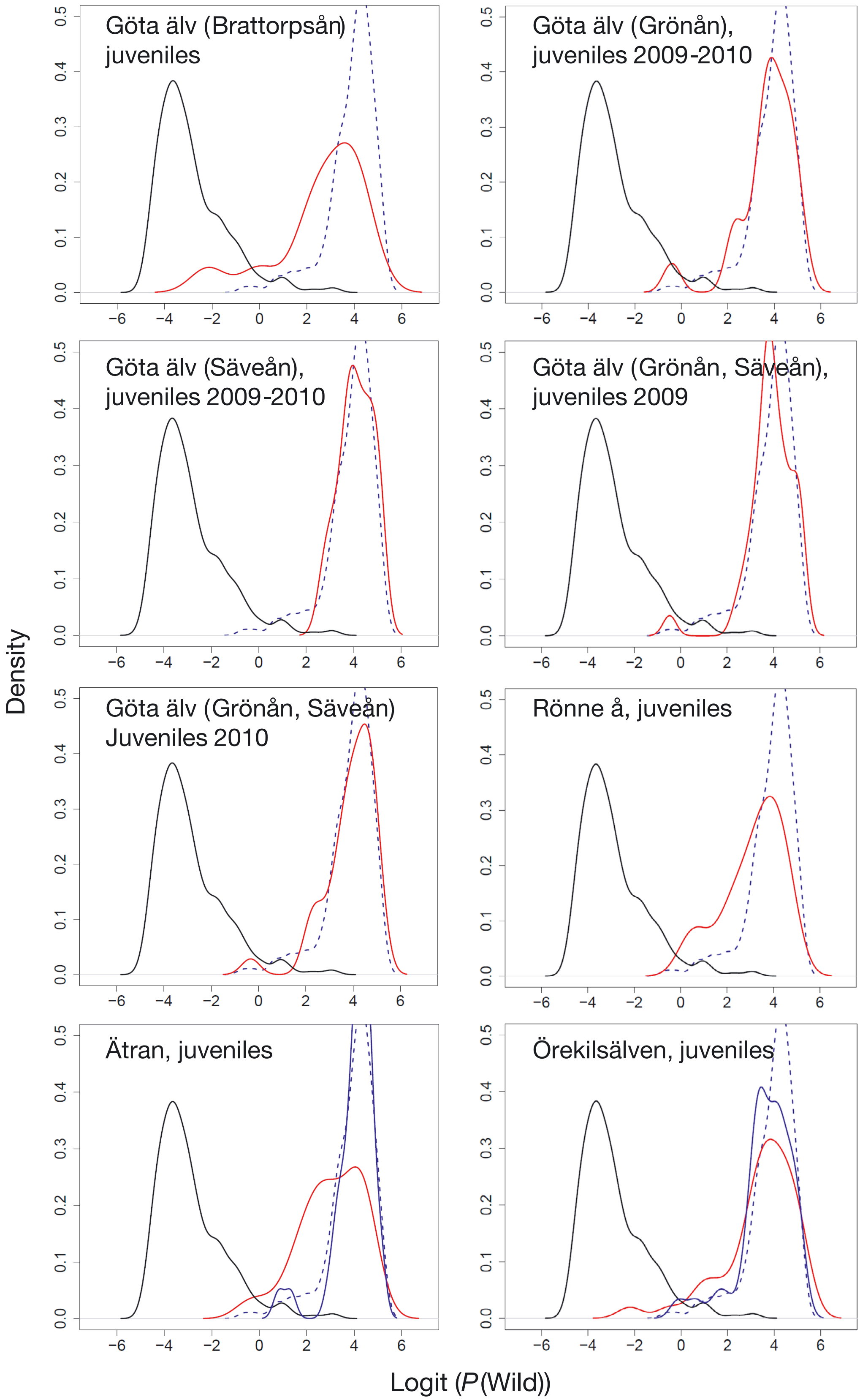

Fig. 4. As in Fig. 3, but for juvenile salmon samples (cf. Table 2)

juveniles from the Grönån and Säveån tributaries in Göta älv, but a significant and large level (14%) of introgression was estimated for the juvenile sample from the small Brattorpsån tributary.

4. DISCUSSION

Using well-established methods routinely applied in the ongoing Norwegian monitoring programme, we provide the first scientific evidence for straying of adult salmon of farmed origin (escapees and putative wild/farmed-hybrids) into Swedish rivers. Analyses of naturally spawned juveniles further revealed that escaped farmed salmon have successfully reproduced in several watercourses. Although being a fairly limited study in terms of numbers of rivers and years, these results are important as they confirm the well-documented problem of long-distance dispersal of escaped farmed salmon (Skilbrei 2010, Jensen et al. 2013), and further, illustrate that genetic introgression may also occur in countries without their own farmed production.

Genetic introgression was detected among juveniles from all 4 watercourses investigated, with estimates ranging from 0 to 14% in Göta älv, whereas intermediate values (5–6%) were found in Rönne å, Ätran, and Örekilsälven. As a comparison, Karlsson et al. (2016), in their comprehensive study, reported significant introgression in 51 out of 109 (47%) screened Norwegian populations with an average of 6.4% introgression. Their findings and the present results are of major conservation concern, as farmed introgression is expected to affect population productivity negatively via demonstrated alterations in life-history traits and reduced fitness in wild/farmed hybrids (McGinnity et al. 2003, Bolstad et al. 2017, Skaala et al. 2019).

The difference in introgression levels between the watercourses in this study may relate to factors such as discharge, population size and vulnerability, and other geographical and local ecological settings. In addition, levels of introgression within watercourses may vary substantially among cohorts and year of sampling. However, given the limited scope of the present study, it is too early to draw any further conclusions. Additional studies of spatial and temporal variation in genetic admixture rates are warranted, which may be achieved via a Swedish monitoring programme (see below).

The 2 adult samples with remarkable proportions of farmed introgression (Lagan 2008, 59%, and Göta älv 2010, 75%) were selected to confirm previous suspicions regarding presumed escapees in 2 years with a very high share of such individuals being observed. Hence, they likely represent extreme cases, although they demonstrate that large numbers of escaped farmed salmon (in comparison to the occurrence of native salmon) may occasionally stray into larger Swedish rivers. Notably, a lower but significant level of introgression (9%) was also detected among the randomly selected adults from Ätran, whereas the adult sample from Örekilsälven seemed to consist entirely of genetically wild salmon. The adults from Ätran with low or intermediate estimates of *P*(Wild) most likely represent a mixture of escaped fish and offspring from crosses in the previous generation between such salmon and wild conspecifics (in nature and/or captivity).

It should be stressed that our data cannot be used to say with certainty from where the salmon with a shown farmed genetic ancestry originates. Given the geographical proximity and scale of aquaculture production, escapees from Norwegian facilities appear most likely, but sea-based salmon aquaculture is also practiced in Scotland, where most farmed salmon are of Norwegian genetic origin (Munro 2020). In contrast, a putative stray origin from the adjacent Baltic Sea can be dismissed, as all adults from Lagan and Göta älv in this study have been shown not to represent Baltic salmon according to microsatellite data (Palm et al. 2011 and references therein). Such salmon strays from large experiments with 'delayed-release' in the southern Baltic have previously been identified in rivers along the Swedish west coast (Pedersen et al. 2007). Regardless of the origin of the escapees, however, a genetic monitoring programme appears warranted to evaluate the scale of farmed salmon straying and reproducing in Swedish rivers with wild populations.

How such a monitoring programme should be designed in further detail goes beyond the scope of the present study, but we recommend that it be based on adult scale samples from rivers, as practised in Norway (Diserud et al. 2020). From combined diagnostic DNA analyses and readings of adult scales, it is possible to distinguish escapees from wild-born salmon with farmed genotypes (Karlsson et al. 2016). For instance, the dominance of intermediate *P*(Wild) estimates in the Lagan sample seems to indicate widespread wild/farmed hybridization in the previous generation(s), although the number of scales remaining is too sparse to allow a more thorough investigation of the origin of these fish.

Because differences in lifetime fitness have been demonstrated between wild and farmed genotypes

(Skaala et al. 2019), analysis of returning adults is expected to give a more accurate picture of the accumulated genetic introgression than analysis of juveniles. This may be exemplified by the results of Karlsson et al. (2016), who estimated that levels of farmed introgression within cohorts from 26 rivers decreased with on average 2.5 percentage points from the juvenile to the adult stage, most likely reflecting stronger natural selection acting on farmed genotypes during the entire lifespan. Likewise, Wacker et al. (2021) followed juveniles in 2 cohorts from a wild salmon population subject to long-term introgression, and showed that from age 0+ to 2+ the average levels of farmed introgression decreased by 64 and 37%, respectively. These examples of a demonstrated lower survival rate for salmon of farmed ancestry illustrate how straying and introgression pose a potent threat to the productivity and long-term viability of wild salmon populations.

In addition to monitoring of wild Swedish salmon, we also recommend analysis with diagnostic markers of hatchery salmon used for compensatory smolt releases in the Rivers Göta älv and Lagan. In these sea-ranched stocks of local origin, farmed introgression may have occurred, especially before adipose fin clipping of released smolts became obligatory some 15 yr ago. In Norway, genetic analyses aimed at identifying and excluding escaped farmed salmon and their offspring as brood fish have been mandatory since 2014 (Hagen et al. 2019, Karlsson et al. 2021).

In this study, we have demonstrated that genetic introgression of escaped farmed salmon occurs in wild populations beyond national borders. Given the long-distance straying of escaped farmed salmon (Jensen et al. 2013), this is not surprising, and it demonstrates the need for common forces across national borders to prevent further negative impacts on wild salmon. Recently, Glover et al. (2020) conducted a risk assessment for further genetic introgression from escaped farmed salmon in Norwegian salmon populations. We recommend such work to be extended to include the whole distribution range of Atlantic salmon.

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