



Widespread genetic introgression of escaped farmed Atlantic salmon in wild salmon populations

Journal:	<i>ICES Journal of Marine Science</i>
Manuscript ID	ICESJMS-2016-094.R2
Manuscript Types:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Karlsson, Sten; Norwegian Institute for nature research (NINA), Diserud, Ola; Norsk Institutt for Naturforskning Fiske, Peder; Norwegian Institute for nature research (NINA), Hindar, Kjetil; NINA,
Keyword:	Atlantic salmon, genetic introgression, farmed salmon, aquaculture, genetics, SNPs

SCHOLARONE™
Manuscripts

1
2
3
4 **1 Widespread genetic introgression of escaped farmed Atlantic salmon in**
5
6
7 **2 wild salmon populations**
8
9
10
11
12

13 4 Sten Karlsson^{†*}, Ola H. Diserud[†], Peder Fiske, Kjetil Hindar
14
15

16 5 *†Shared first authorship*
17

18 6 *Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Sluppen, NO-7485*
19

20 7 *Trondheim, Norway*
21
22
23

24 8
25

26 9 **Corresponding author: tel: +47 91124058; fax: +4773851401; e-mail:*
27

28
29 10 *sten.karlsson@nina.no*
30
31

32 11
33

34 12 Running headline: Farmed to wild salmon genetic introgression
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4 13 **Abstract**
5
6

7 14 Farmed Atlantic salmon (*Salmo salar*) escape from net pens and enter rivers to spawn,
8
9 15 potentially resulting in genetic introgression and reduced fitness of wild salmon. Here we
10
11 16 quantify genetic introgression of farmed to wild salmon, using molecular genetic markers, in
12
13 17 populations from 147salmon rivers, representing three quarters of the total wild salmon
14
15 18 spawning population in Norway. For 109 rivers with adult modern samples and sample sizes
16
17 19 of 20 or more, the average level of farmed genetic introgression was 6.4% (median = 2.3%),
18
19 20 with a range between 0.0 and 42.2%. Fifty-one of these rivers showed significant farmed
20
21 21 genetic introgression when compared to historical reference samples. We observed a highly
22
23 22 significant correlation between estimated farmed introgression and average proportion of
24
25 23 escaped farmed salmon. We quantify levels of introgression as unweighted averages or
26
27 24 weighted by population sizes, to compare geographical regions and to compare levels of
28
29 25 introgression in rivers and fjords designated as locations deserving a high level of protection.
30
31 26 We found a generally lower level of introgression in National Salmon Rivers and National
32
33 27 Salmon Fjords subjected to formal protection by parliament. We conclude that farmed to wild
34
35 28 genetic introgression is high in a large proportion of Norwegian salmon rivers, with the
36
37 29 highest levels found in the most intensive areas of salmon farming. The extensive genetic
38
39 30 introgression documented here poses a serious challenge to the management of farmed and
40
41 31 wild Atlantic salmon in Norway and, in all likelihood, in other regions where farmed-salmon
42
43 32 escape events occur with regularity
44
45
46
47
48
49

50 33

51
52
53 34 Key words: Atlantic salmon, genetic introgression, farmed salmon, aquaculture, genetics,
54
55 35 SNPs
56
57
58
59
60

36 Introduction

37 Farmed Atlantic salmon differ genetically from wild salmon because of a variety of causes.
38 Breeding programs of farmed Atlantic salmon were established in Norway in the early 1970s
39 based on salmon collected from several populations in Central and Western Norway
40 (Gjedrem *et al.*, 1991; Gjøen and Bentsen, 1997). The breeding program has successfully
41 changed the genetics of farmed Atlantic salmon to improve commercially important traits,
42 such as growth, utilization of feed, and filet quality (Thodesen *et al.*, 1999; Gjedrem and
43 Baranski, 2009; Solberg *et al.*, 2013). These genetic improvements have undoubtedly
44 contributed to the rapid expansion of the Atlantic salmon farming industry in Norway, with a
45 production close to 1.3 million tons in 2015.

46 Farmed Atlantic salmon also differ genetically from wild salmon because of selection to
47 captivity, and loss of genetic variation from a limited number of wild founders and
48 subsequent genetic drift (Hutchings and Fraser, 2008). Because of the reduced fitness
49 (Fleming *et al.*, 2000; McGinnity *et al.*, 2003; Skaala *et al.*, 2012; Reed *et al.*, 2015) and
50 lower genetic variation in farmed salmon (Mjølnerød *et al.*, 1997; Skaala *et al.*, 2004; Skaala
51 *et al.*, 2005; Karlsson *et al.*, 2010) compared to their wild conspecifics, there is a concern that
52 genetic introgression of escaped farmed salmon to wild salmon might reduce the viability of
53 wild Atlantic salmon. Reported numbers of escaped farmed salmon in Norway have ranged
54 from 39 000 to 920 000 since 1993, with an average of 380 000 (Norwegian Directorate of
55 Fisheries, <http://www.fiskeridir.no/English>). Inventories since 1989 have shown high
56 proportions of escaped farmed salmon in many Norwegian rivers, with large variations
57 between years (Fiske *et al.*, 2006) and rivers (Gausen and Moen, 1991; Diserud *et al.*, 2013).
58 A similar situation has been documented in eastern North America with a large number of

1
2
3
4 59 escaped farmed entering salmon rivers, in many rivers outnumbering the wild spawning
5
6 60 population and with extensive variation between rivers and years (Morris *et al.*, 2008).
7
8

9 61 Genetic introgression of escaped farmed salmon to wild salmon populations has been
10
11 62 modelled (Hindar *et al.*, 2006) based on relative fitness estimates (Fleming *et al.*, 2000;
12
13 63 McGinnity *et al.* 2003) and observed proportions of escaped farmed salmon (Fiske *et al.*,
14
15 64 2006). The spawning success of escaped farmed salmon (Fleming *et al.*, 1996; 1997) and
16
17 65 survival of their offspring (Fraser *et al.*, 2008; 2010; Skaala *et al.*, 2012; Sundt-Hansen *et al.*,
18
19 66 2015) depend on a variety of factors in wild populations, farmed escapes and the environment
20
21 67 in which they meet, and make it difficult to accurately predict farmed to wild genetic
22
23 68 introgression. The development of improved models with important and more precise
24
25 69 parameters requires quantification of the farmed to wild genetic introgression (Heino *et al.*,
26
27 70 2015).
28
29
30
31

32 71 Several molecular genetic markers for quantifying genetic introgression of farmed
33
34 72 escaped salmon in wild salmon populations have been identified (Karlsson *et al.*, 2011).
35
36 73 These markers were used to quantify genetic introgression in 20 Norwegian salmon
37
38 74 populations, based on observed temporal genetic changes and Approximate Bayesian
39
40 75 Computation (ABC) of the farmed-to-wild gene flow that is consistent with these changes
41
42 76 (Glover *et al.*, 2013). The ABC method is restricted, as it relies on the existence of historical
43
44 77 samples from each population to be analyzed. From the generic genetic differences observed
45
46 78 at the genetic markers identified by Karlsson *et al.* (2011), an alternative standardized method
47
48 79 was developed by Karlsson *et al.* (2014). This method does not rely on historical samples
49
50 80 from all populations, but uses the directional genetic change from farm-to-wild introgression,
51
52 81 and not genetic changes stemming from genetic drift and/or gene flow between wild
53
54 82 populations. In short, the method uses historical samples from many wild populations and
55
56
57
58
59
60

1
2
3
4 83 samples from the Norwegian breeding kernels for farmed salmon, and estimates for each
5
6 84 individual of interest the proportion of membership to these two groups, using STRUCTURE
7
8 85 (Pritchard et al., 2000).
9

10
11 86 The objective of the present study was to obtain an extensive coverage of farmed to wild
12
13 87 Atlantic salmon genetic introgression using the new molecular genetic and analytical
14
15 88 methods. We analysed 21 562 Atlantic salmon hatched in the wild in 147 Norwegian rivers,
16
17 89 including 16 407 adults and 5 155 juveniles. Here, we first present a comprehensive
18
19 90 geographical coverage of status with respect to farmed to wild introgression. Second, we
20
21 91 compare estimates of introgression in samples based on juveniles with samples based on
22
23 92 returning adults from the same population. Third, we assess the relationship between long-
24
25 93 term proportions of escaped farmed salmon and genetic introgression. Finally, we assess to
26
27 94 what extent a major conservation policy decision in Norway, designating 52 rivers as National
28
29 95 Salmon Rivers and 29 fjords as National Salmon Fjords where important salmon populations
30
31 96 receive extra protection (e.g. Vøllestad *et al.*, 2014), has an effect on the levels of
32
33 97 introgression.
34
35
36
37
38
39
40
41

42 99 **Material and Methods**

43
44
45 100 To quantify genetic introgression resulting from spawning of escaped farmed salmon in the
46
47 101 wild, we analysed only fish hatched in the wild. We excluded fish classified as escaped
48
49 102 farmed salmon, or with uncertain classification, based on their growth patterns in the scales
50
51 103 (Lund and Hansen, 1991; Fiske *et al.*, 2005). Samples of juvenile, pre-smolt salmon can
52
53 104 safely be regarded as hatched in the wild, because the escape of juvenile farmed salmon from
54
55 105 land-based facilities to rivers in this study is unlikely.
56
57
58
59
60

1
2
3
4 106 We extracted total genomic DNA from scales of adult salmon and from fin-clips of
5
6 107 juvenile salmon using DNEASY tissue kit (QIAGEN). Initially, we used the Sequenom SNP-
7
8 108 genotyping platform for genotyping of 5897 individuals at 99 SNP loci, with PCR
9
10 109 amplifications in 4 multiplexes. Primer extension reactions followed recommendations from
11
12 110 Sequenom (www.sequenom.com) and fragments were separated and identified using
13
14 111 Sequenom Mass ARRAY™ analyzer (Autoflex mass spectrometer). We conducted
15
16 112 genotyping in real time depending on the presence or absence of a mass peak in expected
17
18 113 mass range for each locus (Tang *et al.*, 1999) using the MassARRAY™ RT 3.4 software. We
19
20 114 obtained reliable genotypes from 59 SNPs described as being collectively diagnostic in
21
22 115 differentiating between wild and farm salmon (Karlsson *et al.*, 2011; Jensen *et al.*, 2013). For
23
24 116 the remaining 15 293 individuals, we used the EPI™ 96.96 Dynamic array IFCs genotyping
25
26 117 platform (Fluidigm, San Francisco, CA). Reliable genotypes were obtained for 48 of the same
27
28 118 SNPs genotyped by the Sequenom platform (Karlsson *et al.*, 2011). The SNP genotypes from
29
30 119 the Sequenom and the Fluidigm SNP-genotypes were merged for the 48 common SNP loci
31
32 120 (Table S1).
33
34
35
36

37 121 As a reference for farmed salmon, we used genotypes from 503 individuals from the three
38
39 122 leading breeding companies (Marine Harvest, Salmobreed and AquaGen) from the year
40
41 123 classes 2004–2009 (MH), 2004–2007 (SB) and 1998–2001, 2008 (AG). Each yearclass
42
43 124 represented one of four different breeding kernels from each breeding company. In 2005,
44
45 125 AquaGen pooled the four breeding kernels into one big kernel, represented by the 2008
46
47 126 sample. To investigate historical genetic signatures of farmed salmon, we used 129 samples
48
49 127 from 1982–1988 from the four AquaGen breeding kernels. As references for non-admixed
50
51 128 wild salmon, we used historical samples of 2187 wild individuals from 39 populations,
52
53 129 geographically distributed in rivers from southern to northern Norway. In agreement with
54
55 130 previous studies (Bourret *et al.*, 2013; Jensen *et al.*, 2014), the Norwegian populations
56
57
58
59
60

1
2
3
4 131 clustered into an Atlantic and a Barents-White Sea phylogenetic group, with the latter
5
6 132 including populations from Finnmark County and the former including populations south of
7
8 133 Finnmark (Figure 1). All founder populations for the farm strains are from the Atlantic Sea
9
10 134 phylogenetic group, as judged from the genetic contributions from source populations in the
11
12 135 third generation of the breeding program (Gjøen and Bentsen, 1997). Although the Atlantic
13
14 136 and the Barents-White Sea phylogenetic groups are well separated, some populations in
15
16 137 Troms County represent a transition between them. We analysed samples from 147
17
18 138 Norwegian rivers, including 5155 juvenile individuals and 16 407 adult individuals. From 109
19
20 139 of these populations, we had adult modern samples with sample sizes of more than 20. For the
21
22 140 remaining 38 populations we had only juveniles, historical samples, sample sizes less than 20
23
24 141 (for detailed information see Table S2). Scale samples of adult salmon were obtained from
25
26 142 sport fishing, and from catches of broodfish for stocking or during autumn monitoring, while
27
28 143 juvenile samples were obtained by electrofishing.
29
30
31
32
33
34

35 145 **Statistical analyses**

36
37 146 We applied the method by Karlsson *et al.* (2014) to estimate the level of farmed to wild
38
39 147 genetic introgression. This method uses the STRUCTURE program (Pritchard *et al.*, 2000) in
40
41 148 a manner that avoids bias from the level of heterogeneity and different sample sizes as
42
43 149 described by Kalinowski (2011) and standardizes the estimates of admixture when
44
45 150 introgression occurs from several farmed populations. We generated an idealized wild and
46
47 151 farmed population in Hardy-Weinberg proportions from a pool of reference individuals of
48
49 152 wild and farmed salmon using the HybridLab program (Nielsen *et al.*, 2006). For the farmed
50
51 153 salmon, we used all modern samples from the three breeding companies. For the wild salmon,
52
53 154 we generated one population for the Atlantic phylogenetic group and one for the Barents-
54
55 155 White Sea group. Samples used for creating these wild center points are indicated in Table
56
57
58
59
60

1
2
3
4 156 S2, column “REF Year”. These ideal populations ($n = 100$) represented center points for the
5
6 157 three groups to which the probability of belonging was estimated (Figure 1). In an analysis of
7
8 158 molecular variance (AMOVA), including the farmed reference samples and the historical wild
9
10 159 reference samples from the Barents-White-Sea group, 18.01% of the variance was ascribed to
11
12 160 variations between these groups ($P < 0.001$), and 4.08% to variance among populations within
13
14 161 the groups ($P < 0.001$). In a comparison between farmed populations and the historical wild
15
16 162 reference population from the Atlantic group, 7.19% of the variance was ascribed to
17
18 163 variations between these groups ($P < 0.001$) and 3.48% to variance among populations within
19
20 164 groups ($P < 0.001$). Single individuals were analysed with the farmed center point and the two
21
22 165 wild center points representing the correct phylogenetic group for that individual, using an
23
24 166 admixed model, 50 000 repetitions as burn in and 100 000 repetitions after burn in as
25
26 167 implemented in STRUCTURE (Pritchard *et al.*, 2000). For each fish, the probability of
27
28 168 belonging to the wild center point, hereafter $P(Wild)$, was recorded.
29
30
31

32
33 169 For statistical analyses of farmed introgression, we generated probability distributions of
34
35 170 belonging to the wild center point for historical wild salmon (all samples in column “REF
36
37 171 Year” in Table S2) and for modern farmed salmon. Four populations (rivers Skibotnelva
38
39 172 [river ID 205.Z], Signaldalselva [204.Z], Målselv [196.Z], and Skipsfjordelva [202.11Z])
40
41 173 represented genetic transitions between the Atlantic and the Barents-White Sea phylogenetic
42
43 174 groups and could not be analysed using the Atlantic or the Barents-White Sea center points.
44
45 175 Instead, they were analysed by generating in silico populations from historical samples for
46
47 176 each of these populations, except for Signaldalselva for which we did not have historical
48
49 177 samples. Samples from the nearby River Skibotnelva were used as the analytical center point
50
51 178 for the Signaldalselva population.
52
53

54
55 179 From the distribution of individual probabilities of belonging to the wild center point
56
57 180 $P(Wild)$ for a given sample (population and year), we estimated genetic introgression from
58
59
60

1
2
3
4 181 escaped farmed salmon into this year's wild Atlantic salmon populations (Karlsson *et al.*,
5
6 182 2014). $P(Wild)$ was logit-transformed before the statistical inference (Warton and Hui, 2011).
7
8
9 183 For each contemporary sample with a historical reference from the same river, we tested
10
11 184 whether this population was introgressed with a two-sample test for comparing means,
12
13 185 assuming random sampling and equal variances for contemporary and reference samples.
14
15 186 Further, we assumed that all wild populations had the same variance, estimated as the
16
17 187 weighted average of the historical wild reference sample variances. Although the distributions
18
19 188 for logit-transformed $P(Wild)$ for wild reference samples are relatively symmetric (see
20
21 189 example in Figure 2), they depart too much from normality to perform standard tests for
22
23 190 homogeneity of variances. By resampling squared deviations from all wild references, we
24
25 191 found that 8.6% (3 of 35) of the wild population variances were significantly different from
26
27 192 the pooled variance with a 5% significance level and were close to what we expected under
28
29 193 the homogeneity assumption. Several of the wild reference populations have significantly
30
31 194 different averages, so when testing whether a population without historical reference is
32
33 195 introgressed we needed to consider this variance in wild population average values within a
34
35 196 phylogenetic group. For populations without a historical reference from the same river, the
36
37 197 contemporary average was therefore compared to the overall wild average for this
38
39 198 phylogenetic group with this additional variance component included in the sampling
40
41 199 distribution. For both tests, the null hypothesis states no genetic introgression; that is, mean
42
43 200 $P(Wild)$ from the contemporary population equals the mean $P(Wild)$ from the historical
44
45 201 reference population. The alternative hypothesis states that the contemporary mean $P(Wild)$ is
46
47 202 smaller than the historical mean.
48
49
50
51

52
53 203 The distributions for individual $P(Wild)$ values for the samples are illustrated for the River
54
55 204 Eira (104.Z) in Figure 2. Notable is the distinctiveness of the distribution for the farm
56
57 205 references (red line). The distribution for the contemporary sample (pooled sample for the
58
59
60

1
2
3
4 206 years 2012–2015; dashed black line) has a mean value significantly smaller than both the
5
6 207 historical distribution for the River Eira population (solid black line) and the distribution for
7
8 208 the whole Atlantic phylogenetic group (solid blue line).
9

10
11 209 For many samples, the observed change in mean value may not be significant, even if the
12
13 210 populations show signs of genetic introgression. As in Figure 2, the contemporary distribution
14
15 211 can indicate that a proportion of the population is introgressed by having a heavy left tail
16
17 212 while the majority of the population is still mostly wild-like. Genetic introgression into a
18
19 213 subpopulation can be tested by, for example, inspecting the lower 5-percentile of the
20
21 214 distributions. Expected tail properties will be sensitive to distribution assumptions, so we
22
23 215 opted for a randomization test approach. If the 5-percentile of a contemporary sample of a
24
25 216 given size is much lower than expected from a sample of the same size from the historical
26
27 217 distribution, it indicates that this sample has a too large proportion of individuals that
28
29 218 genetically are admixed with farmed salmon. This effect was evaluated by simulating $n =$
30
31 219 10 000 samples of the same size as the contemporary sample from the historical reference for
32
33 220 the whole phylogenetic group, and registering the 5 percentiles of each simulated sample. The
34
35 221 proportion of simulated 5-percentiles that was lower than the 5-percentile of the historical
36
37 222 reference is the P -value of the test.
38
39
40

41
42 223 Juveniles of farmed and admixed origin show lower survival to adulthood than juveniles
43
44 224 of pure wild origin (Fleming *et al.*, 2000; McGinnity *et al.*, 2003). We expected therefore to
45
46 225 find a higher level of introgression in juveniles than in adults in the same cohorts. To explore
47
48 226 this in our data, we compared juvenile samples with adult samples from the same river, using
49
50 227 a quasi-cohort comparison. Specifically, we compared farmed introgression between juvenile
51
52 228 and adult samples in 26 rivers, where sampling of juveniles occurred 3–5 years earlier than
53
54 229 sampling of adults. Even though this is not a formal cohort analysis, at least some of the same
55
56 230 year classes are likely represented in both the juvenile and adult samples.
57
58
59
60

1
2
3
4 231 Regional averages of introgression were constructed as unweighted averages and as
5
6 232 averages weighted by spawning population size in each river studied (Forseth *et al.*, 2013).
7
8 233 We defined regions as counties from the northernmost, Finnmark County, to the southernmost
9
10 234 in western Norway, Rogaland County, whereas the counties from southernmost Norway to the
11
12 235 south-eastern border with Sweden, were treated as one region (Fiske *et al.*, 2006) denoted
13
14 236 Southeast.

15
16
17 237 A major conservation policy for wild Atlantic salmon in Norway, National Salmon Rivers
18
19 238 and National Salmon Fjords, was established by the Norwegian Parliament in 2003
20
21 239 (completed 2007) to increase the level of protection of Atlantic salmon, including protection
22
23 240 from fish farming. By the final decision in 2007, 52 rivers were designated as National
24
25 241 Salmon Rivers (of which we studied 48, cf. Vøllestad *et al.*, 2014) and 29 coastal areas were
26
27 242 designated National Salmon Fjords (all are represented by our samples). We calculated
28
29 243 unweighted and weighted averages for these groups of rivers in the same manner as for
30
31 244 counties.

32
33
34
35 245 To study associations between group levels of introgression and average proportions of
36
37 246 escaped farmed salmon, we used the method developed by Fiske *et al.* (2006) and Diserud *et*
38
39 247 *al.* (2010) to calculate an ‘annual incidence’ of escaped farmed salmon, by averaging
40
41 248 proportions of escaped farmed salmon in anglers’ catches in summer and in organized surveys
42
43 249 in autumn and by calculating a weighted average by river catches. At the individual river
44
45 250 level, Diserud *et al.* (2012, 2013) developed a long-term ‘average annual incidence’ for the
46
47 251 years 1989–2012 for all rivers that were represented by four or more years in the time series.
48
49
50

51 252

52 53 253 **Results**

54
55
56
57
58
59
60

1
2
3
4 254 Based on adult modern samples from 109 salmon rivers with a sample size of 20 or more, we
5
6 255 observed significant genetic introgression from escaped farmed salmon in 51 wild salmon
7
8 256 populations (47%) and an estimated level of introgression >10% in 27 populations, between
9
10 257 4–10% in 19 populations and < 4% in 63 populations (Table S2, Figure 3). When all samples
11
12 258 were considered, significant genetic introgression was observed in 77 of 147 rivers (Table
13
14 259 S2).

15
16
17
18 260 Comparisons in 26 rivers of juvenile samples with adult samples taken 3–5 years later,
19
20 261 presumably representing the same cohorts, showed an average reduction of 2.5 percentage
21
22 262 points between estimates of introgression in juvenile and adult life stages. Variation between
23
24 263 rivers was high ranging from a 13% increase to a 17% reduction in farmed introgression from
25
26 264 juvenile to adult samples.
27
28
29

30 265

31 32 266 **Geographical distribution of farmed to wild genetic introgression**

33
34
35 267 In the following, the presentation of level of introgression is based on pooled adult samples
36
37 268 from recent sampling years in 109 rivers with a sample size of at least 20 individuals.

38
39 269 National Salmon Rivers with special protection against anthropogenic impacts, including
40
41 270 salmon farming, had on average lower levels of farmed genetic introgression (unweighted
42
43 271 average, 4.5%) than salmon rivers without protection (unweighted average, 7.8%). The
44
45 272 protecting effect of National Salmon Fjords appeared to be smaller as salmon rivers in and
46
47 273 outside these fjords had similar (average, 6.4%) levels of farmed genetic introgression (Table
48
49 274 1). When considering population size (weighted averages), rivers within the National Salmon
50
51 275 Fjords had however a lower level of introgression (1.8%) than other rivers (3.5%).
52
53
54
55
56
57
58
59
60

1
2
3
4 276 Genetic introgression has occurred in all regions of Norway, and the highest genetic
5
6 277 introgression is found in the most intensive salmon farming regions (Figure 3). Unweighted
7
8 278 averages of genetic introgression were largest in Troms County (14.5%) and Hordaland
9
10 279 County (13.9%) and smallest in Nord-Trøndelag County (0%) and Rogaland County (1.8%)
11
12 280 (Table 2). However, four regional averages were based on less than 10 rivers, Troms and
13
14 281 Nord-Trøndelag being two of them. We also found significant introgression in samples
15
16 282 excluded because of sample sizes less than 20, including adult samples (Byaelva [128.Z] and
17
18 283 Salvassdraget [140.Z]) from Nord-Trøndelag (Table S2). Hence, no region in Norway is
19
20 284 without farmed introgression.
21
22
23

24
25 285 Weighted averages by wild population size in the sampled rivers within each county were
26
27 286 largely determined by status of the largest rivers and illustrate the geographical distribution of
28
29 287 farmed introgression relative to the number of genes of farmed origin (proportion of farmed
30
31 288 genomes). Hordaland County had the largest proportion of genomes with farmed origin
32
33 289 (11.1%), and Nord-Trøndelag County the smallest (0%). In the two phylogenetic groups of
34
35 290 Norway, we found more introgression in the Atlantic group (unweighted average = 6.9%,
36
37 291 weighted average = 2.6%) than in the Barents-White Sea group (unweighted average = 2.6%,
38
39 292 weighted average = 1.0%). Nationally, unweighted and weighted estimated proportions of
40
41 293 farmed genomes were 6.4%, and 2.1%, respectively (Table 2).
42
43
44
45

46 294

47 48 295 **Genetic introgression relative to farmed escapees**

49
50
51 296 We observed a highly significant relationship between accumulated genetic introgression and
52
53 297 average annual proportion of escaped farmed salmon, explaining 24% of the variance in
54
55 298 introgression between rivers (Figure 4). The relationship was stronger at the region level, with
56
57 299 proportion of escaped farmed salmon explaining 56% of the variance when weighted by
58
59
60

1
2
3
4 300 population size (open diamonds in Figure 4). For populations in the Atlantic Sea phylogenetic
5
6 301 group, the relationship was highly significant (red solid diamonds and dashed red line in
7
8 302 Figure 4; $P < 0.01$, $R^2 = 0.19$, gradient = 0.3), while for populations in the Barents-White Sea
9
10 303 phylogenetic group the relationship was weak and not significant (blue solid diamonds and
11
12 304 dashed line, Figure 4; $P > 0.05$, $R^2 = 0.05$, gradient = 0.05).

15 305 **Temporal trends**

16
17
18 306 We had samples from different periods (decades) in 27 populations, allowing us to examine
19
20 307 temporal trends in the level of genetic introgression. Twelve of the populations showed an
21
22 308 increase in genetic introgression, seven a decrease and six showing no introgression over
23
24 309 time. In three populations for which we had more than two samples in time, there were
25
26 310 increases followed by decreases in genetic introgression. Populations with downward trends
27
28 311 had initial levels of genetic introgression between 1.8% and 6.1%, and in a more recent
29
30 312 sample levels of introgression were between 0.0% and 3.8% (median = 0.2%). River Kinso
31
32 313 (050.1Z) showed a decrease from a high of 24.7% in the 2000s to 12.7% in the 2010's.
33
34 314 However, the trend in River Kinso is uncertain because there was only one sampling year
35
36 315 representing the 2010s period and only 15 fish were analysed. A sample of juveniles from
37
38 316 2011 showed 29.4% introgression. A majority of the populations with an upward trend in
39
40 317 genetic introgression had initial levels of genetic introgression between 0.0% and 7.5%, but
41
42 318 showed large increases in genetic introgression with temporal differences in genetic
43
44 319 introgression ranging from 1.5% to 23.7% (median = 11.2%).
45
46
47
48
49

50 320

51 52 53 321 **Detecting early genetic introgression**

1
2
3
4 322 We tested to what extent our set of SNP markers and the standardized method for detecting
5
6 323 introgression (Karlsson *et al.*, 2014) worked for characterizing earlier generations of farmed
7
8 324 salmon than those used for selecting SNPs differentiating between farmed (breeding kernel
9
10 325 year classes 1998–2009) and historical wild salmon (Karlsson *et al.*, 2011). A comparison of
11
12 326 distributions of *P(Wild)* between historical (1982–1988) and contemporary AquaGen samples
13
14 327 indicated that the historical farmed populations appeared to be more wild than modern
15
16 328 samples of farmed salmon (Figure 5).

329 **Discussion**

330 We quantified genetic introgression of farmed Atlantic salmon into 21 562 wild salmon from
331 147 populations. Levels of introgression above 10% can now be found in any part of Norway
332 in juveniles, as well as in adult salmon that have completed a life cycle in the wild. As
333 expected, the level of introgression in wild populations is significantly associated with the
334 average proportion of escaped farmed salmon in the river over the last 25 years.

335 Our method allows quantification of introgression from the individual level to
336 populations, regions and the national level, and in rivers with and without a historical
337 baseline. We found the highest levels of introgression in the counties of Norway where
338 escaped farmed salmon have been present in highest proportions.

339 In Hordaland County, western Norway, one of the two cradles of fish farming, several
340 populations show high levels of introgression, with the rivers Opo (048.Z), Granvin (052.1Z;
341 juveniles) and Dale (061.Z) showing recent levels of introgression above 40% and three other
342 rivers (Vosso (062.Z), Kinso (050.1Z), and Etne (041.Z)) showing introgression above 10%.
343 Affected rivers are found both along the coast and within the major (Hardangerfjord) and
344 minor fjords in the county. Highly affected rivers in this county were also found in a study of
345 20 Norwegian rivers by Glover *et al.* (2013).

1
2
3
4 346 Other rivers with high levels of introgression are found in Troms County in northern
5
6 347 Norway, Sogn og Fjordane County and Møre og Romsdal County in western Norway. Rivers
7
8 348 with low levels of introgression are most common in south-eastern Norway, Rogaland County
9
10 349 in the southwest and Finnmark County in the northeast. The river holding Norway's largest
11
12 350 Atlantic salmon population, River Tana (234.Z) on the border with Finland, has a low level of
13
14 351 introgression (0 in our Table S2). The spawning population (or rather, populations, see Vähä
15
16 352 *et al.*, 2008) of the Tana is so large (> 40 000 fish), compared the other salmon rivers (average
17
18 353 = 1 900, range: 100-18 000), that it strongly affects regional weighted averages in Finnmark,
19
20 354 the Barents-White Sea phylogenetic group and even the national average.
21
22
23

24 355 **Current levels of introgression are likely underestimated**

25
26
27 356 The farmed references in the present study are representative for introgression that occurred
28
29 357 between the 1990s and present. They cover a large part of this period (year classes hatched
30
31 358 1998 to 2009) and may be representative of more years, as a previous study showed no
32
33 359 significant change in allele frequencies at microsatellites in two breeding kernels sampled one
34
35 360 generation (Karlsson *et al.*, 2010).
36
37
38

39 361 Intrusion of farmed Atlantic salmon on the spawning grounds of wild salmon was
40
41 362 detected on a large scale from 1986 onwards (Gausen and Moen 1991). Introgression during
42
43 363 this early time period is, however, likely underestimated, because we found a weaker genetic
44
45 364 contrast between historical wild salmon and farmed salmon samples from the 1982–1988 than
46
47 365 in the farmed salmon samples from 1998–2009 used as farmed references. Our statistical
48
49 366 method has been tested against simulated data sets and has been shown to give precise
50
51 367 estimates of introgression at the population level (Karlsson *et al.*, 2014). Precaution is
52
53 368 therefore warranted in our evaluation of the status of populations with no or only weak levels
54
55 369 of farmed introgression detected in the present study.
56
57
58
59
60

370

371 **Introgression varies by farmed intrusion and phylogeographic origin**

372 Geographical variation in levels of introgression may have several explanations, the most
373 immediate being that the proportion of escaped farmed salmon in spawning populations also
374 varies. On both local (river) and regional (county) levels, we found a significant, positive
375 correlation between average annual proportions of escaped farmed salmon 1989–2012
376 (Diserud *et al.*, 2013) and introgression in recent samples.

377 The most impacted rivers, with respect to long-term average proportions of escaped
378 farmed salmon, are found in the counties of Hordaland (Opo [048.Z], Kinso [050.1Z], Eio
379 [050.Z] and Frugardselva [044.3Z]) being highest among those studied genetically, all with
380 average proportions 1989–2012 of escaped farmed salmon above 50% according to Diserud *et*
381 *al.*, 2013) and Troms (River Salangselva [191.Z] with 65%, Diserud *et al.*, 2013).

382 Our samples of wild Atlantic salmon are represented by two phylogenetic groups, the
383 Atlantic group and the Barents-White Sea group (Bourret *et al.*, 2013). Even though wild
384 populations from both phylogenetic groups were represented among the source populations
385 (Gjedrem *et al.*, 1991), only the Atlantic group was represented in the third generation of
386 farmed salmon in the breeding programme (cf. Gjøen and Bentsen 1997). Interestingly, we
387 found a significant association between proportions of escaped farmed salmon and
388 introgression for the Atlantic group and not for the Barents-White Sea group, and a steeper
389 gradient in the Atlantic group (Figure 4). This might reflect differences in genomic
390 architecture between the two phylogenetic groups and a higher barrier to introgression in the
391 Barents-White Sea group. The barrier is not absolute, as we found significant introgression in
392 several of the Barents-White Sea populations, even in numerically strong populations like
393 River Alta (212.Z) and Vestre Jakobselv (240.Z). The number of samples from the Barents-

1
2
3
4 394 White Sea group is however limited, and a conclusion about barriers to introgression in
5
6 395 relation to phylogenetic origin must await further study.
7
8

9 396

11 397 **Additional explanations of variation in introgression**

12
13
14 398 A large proportion of the variance in the level of introgression could not be explained by
15
16
17 399 proportions of escaped farmed salmon (Figure 4). This is not unexpected, as one of the main
18
19 400 conclusions from a review of genetic effects following releases was the wide variety of
20
21 401 outcomes, ranging from no detectable effect to complete introgression or displacement of the
22
23 402 native population (Hindar *et al.*, 1991). Experimental studies of farmed and wild salmon,
24
25 403 however, point to some general findings about causes of variation.
26
27

28
29 404 It has been shown experimentally that farmed salmon escaping early from captivity have
30
31 405 higher reproductive success in competition with wild salmon than later escaping farmed
32
33 406 salmon, i.e. comparing hatchery-released smolts with farmed adults (Fleming *et al.*, 1996;
34
35 407 1997). So far, this has not been accounted for in analyses of how escaped farmed salmon
36
37 408 leads to introgression, but will be possible in the future as scale reading advances to include
38
39 409 the likely size at which farmed salmon escape.
40
41

42
43 410 The density of wild Atlantic salmon on the spawning ground may also be important. The
44
45 411 breeding behavior of Atlantic salmon involves female-to-female competition for access to
46
47 412 high-quality spawning sites to excavate the nests, and male-to-male competition for access to
48
49 413 females (Fleming and Einum, 2011). Lura (1995) suggested that the spawning success of
50
51 414 escaped farmed females was density dependent because the contributions of eyed eggs,
52
53 415 relative to their proportion among the spawners, were lower in rivers and years with high
54
55 416 densities of spawners. Likely explanations may be that farmed females are outcompeted from
56
57
58
59
60

1
2
3
4 417 the most favourable nest sites at high densities (Lura, 1995), and there may be a larger
5
6 418 proportion of unspawned eggs in farmed than in wild salmon at high densities (Jonsson *et al.*,
7
8 419 1990; Fleming *et al.*, 1996; 2000). For males, Fleming *et al.* (1997) showed density-
9
10 420 dependent spawning success in an experimental study of hatchery-reared vs. wild River Imsa
11
12 421 males. In contrast, late-escaping farmed males showed poor reproductive success regardless
13
14 422 of density in the same spawning arenas (Fleming *et al.*, 1996). We do not yet know whether
15
16 423 there are differences in reproductive success among the various selected strains of farmed
17
18 424 salmon, but we know that farmed fish vary in their genetic relationships with wild salmon
19
20 425 (Karlsson *et al.*, 2011, 2010, 2014).

21
22
23
24
25 426 Lower average introgression is found in National Salmon Rivers and to a lesser extent in
26
27 427 rivers within a National Salmon Fjord. This indicates that national salmon fjords and rivers
28
29 428 provide increased protection from farmed introgression. One common factor among these
30
31 429 populations is that emphasis was put on the numerically strongest populations when rivers
32
33 430 were chosen for designation as National Salmon Rivers. Population size in itself may be a
34
35 431 protective measure from introgression (Heino *et al.*, 2015), which is also supported by the
36
37 432 difference between unweighted and weighted averages found here (Table 2). Another type of
38
39 433 protection is the increased distance between aquaculture operations and wild salmon rivers,
40
41 434 which makes it less likely for a salmon river in a National Salmon Fjords to receive escaped
42
43 435 farmed salmon, than outside of such a fjord, other things being equal (Fiske *et al.*, 2013).

44
45
46
47 436 However, we do not see low introgression levels in all salmon populations with this
48
49 437 protective regime. For example, River Daleelva (061.Z), River Vosso (062.Z), River Vikja
50
51 438 (070.Z), River Årøyelva (077.Z), River Jølstra (084.Z), River Olden (088.1Z), River Røssåga
52
53 439 (155.Z) and River Beiarelva (161.Z) are National Salmon Rivers or are situated in a National
54
55 440 Salmon Fjord and have > 10% farmed genetic introgression. One explanation for the variation
56
57
58
59
60

1
2
3
4 441 in the protecting effect of National salmon rivers and fjords might be the size of the protected
5
6 442 region, exemplified by the large Trondheimsfjord. The entire Trondheimsfjord is a National
7
8 443 Salmon Fjord in a highly intensive farming region, where a high level of introgression was
9
10 444 found in a coastal population (River Teksdalselva [134.Z]), but consistently lower levels were
11
12 445 found in rivers inside the major Trondheimsfjord. In the Hardangerfjord system, on the other
13
14 446 hand, only a small part (less than 5 % of the fjord area) is designated as a National Salmon
15
16 447 Fjord, Etnefjorden. Most rivers in the Hardangerfjord show high levels of introgression, as
17
18 448 does River Etne (041.Z). Another explanation for high levels of introgression in salmon
19
20 449 populations within National Salmon Fjords is that some of these rivers have occasionally had
21
22 450 low levels of wild spawners, because of the parasite *Gyrodactylus salaris* (Vikja, Røssåga,
23
24 451 Beiarelva; Johnsen and Jensen, 1991), or of other anthropogenic factors. A likely mechanism
25
26 452 is easier access to spawning opportunities when wild population size is low (Sægrov *et al.*,
27
28 453 1997).

29
30
31
32
33 454 An explanation for the variable effect of National Salmon Rivers and Fjords not yet
34
35 455 highlighted is the possibility that an introgressed population may impact neighbouring
36
37 456 populations through straying of wild offspring of cultured fish (Felsenstein, 1997). An
38
39 457 important question in this regard is a potentially weaker homing of offspring from escaped
40
41 458 farmed salmon compared to the locally adapted wild salmon, because of different genetic
42
43 459 (Jonsson *et al.* 2003) or epigenetic origins (Christie *et al.*, 2016). In experiments with wild
44
45 460 and farmed Atlantic salmon, hatchery-produced smolts of farmed origin showed a higher
46
47 461 straying rate than hatchery-produced Imsa salmon released into the Imsa (Jonsson *et al.*,
48
49 462 2003).

50
51
52
53
54 463

55
56
57 464 **Differential survival of introgressed individuals**
58
59
60

1
2
3
4 465 Levels of introgression were similar between juvenile and adult salmon samples in our study.
5
6 466 Experimental studies generally show a lower lifetime survival of farmed offspring than wild
7
8 467 offspring, with hybrid groups being intermediate (McGinnity *et al.*, 1997, 2003; Fleming *et*
9
10 468 *al.*, 2000; Skaala *et al.*, 2012). It is therefore expected that within the same cohort, a general
11
12 469 reduction in mean $P(Wild)$ should be observed across life stages from alevin, to parr, to smolt,
13
14 470 to returning adults. In our material, we could not make a formal cohort analysis, but some
15
16 471 populations could be compared between juvenile and adult samples that likely showed some
17
18 472 year-class overlap. The average reduction was estimated at 2.5 percentage points, with a large
19
20 473 variation between populations, including some where the level of introgression was higher
21
22 474 among adults than among juveniles. Observational studies that control for year class (cohort)
23
24 475 are needed before the effect of viability selection on introgression can be quantified more
25
26 476 precisely.
27
28
29
30
31
32
33

34 478 **What do the levels of introgression found in this study mean?**

35
36
37 479 This question may be discussed at several different levels: genetics, fitness and viability,
38
39 480 ecology and life-history, management, and conservation. With respect to genetics, three
40
41 481 concerns are important: loss of genetic variation within populations, loss of genetic variation
42
43 482 between populations and loss of fitness (Waples *et al.*, 2012). Farmed Atlantic salmon have in
44
45 483 general lower genetic variation than wild Atlantic salmon (Mjølnerød *et al.*, 1997; Skaala *et*
46
47 484 *al.*, 2004; Skaala *et al.*, 2005; Karlsson *et al.*, 2010), and the long-term prediction from
48
49 485 escapes is that lower genetic diversity will eventually lead to a drop in diversity in recipient
50
51 486 wild populations (Tufto and Hindar, 2003), even though in the short-term, genetic variation
52
53 487 may increase from interbreeding with farmed salmon. Loss of genetic variation between
54
55 488 populations as a result of introgression from farmed Atlantic salmon has been demonstrated
56
57
58
59
60

1
2
3
4 489 both theoretically (Mork, 1991) and empirically (Skaala *et al.*, 2006; Glover *et al.*, 2012;
5
6 490 2013). Loss of fitness has been demonstrated in controlled rivers in Ireland (McGinnity *et al.*,
7
8 491 1997; 2003) and Norway (Fleming *et al.*, 2000; Skaala *et al.*, 2012) and in large-scale
9
10 492 experiments in Canada (Fraser *et al.*, 2010). The loss of viability is also indicated by these
11
12 493 same studies, as well as in meta-analysis of the population dynamics of salmon populations
13
14 494 near or far from aquaculture operations (Ford and Myers, 2008; Vøllestad *et al.*, 2009). For
15
16 495 the latter studies, however, several mechanisms in addition to introgression may be at work,
17
18 496 such as increased mortality caused by parasites associated with fish farming activities (e.g.
19
20 497 Krkosek *et al.*, 2012).

21
22
23
24 498 Ecological change in introgressed individuals was evident from experiments in controlled,
25
26 499 natural rivers showing changes in growth rate, condition factor (length-weight relationship)
27
28 500 and age at smoltification and maturation (Fleming *et al.*, 2000; McGinnity *et al.*, 2003). This
29
30 501 was also true in a large-scale observational study that tested whether *P(Wild)* had an impact
31
32 502 on ecological key traits (Geir Bolstad, NINA, *et al.* in prep.). This change in ecological traits
33
34 503 also likely has a negative effect on fitness (Tufto, 2001; Huisman and Tufto, 2012; Baskett *et*
35
36 504 *al.*, 2013).

37
38
39
40
41 505

42 43 44 506 **Implications for management and conservation**

45
46 507 In a management and conservation context, a pertinent question is how much introgression
47
48 508 can be allowed (Ryman *et al.*, 1995). While there is no simple answer to this question, it is
49
50 509 clear that near-zero limits need to be set in order not to compromise the genetic integrity of
51
52 510 wild populations. Ryman *et al.* (1995) suggested that a defensible strategy, based on
53
54 511 population genetic considerations, could be to allow gene flow at a rate that matched
55
56 512 equilibrium levels of gene flow between semi-isolated populations, as quantified by Wright's
57
58
59
60

1
2
3
4 513 fixation index, F_{ST} . This would allow only a small number of reproductively capable escaped
5
6 514 farmed salmon spawning in wild populations every generation.
7
8

9 515 In considerations of the Endangered Species Act listing of populations of westslope
10
11 516 cutthroat trout (*Oncorhynchus clarki lewisi*) in danger of hybridization with rainbow trout (*O.*
12
13 517 *mykiss*) and Yellowstone cutthroat trout (*O. c. bouvieri*), Allendorf *et al.* (2004) suggested
14
15 518 that listing only nonhybridized populations was the only alternative that could be defended
16
17 519 from the perspective of possessing local adaptations important for long-term persistence of
18
19 520 this sub-species. An alternative criterion, allowing 10% introgression from the other taxa, was
20
21 521 discarded because it could lead to hybridized populations acting as a source for further
22
23 522 introgression. These considerations deal with sub-species and species differences, and may be
24
25 523 too conservative for our Atlantic salmon study that deals with farmed and wild population
26
27 524 differentiation and introgression. The developmental and evolutionary forces acting on
28
29 525 farmed Atlantic salmon are so unlike those in the wild that two distinct biologies are being
30
31 526 created within the Atlantic salmon species (Gross, 1998; see also Roberge *et al.*, 2006 and
32
33 527 Christie *et al.*, 2016). Gross (1998) even suggested that farmed and wild Atlantic Salmon be
34
35 528 recognized as different “species”, and that farmed salmon be treated as “exotic” when they
36
37 529 escaped to the wild, as a measure to prevent further impact from aquaculture. The calculation
38
39 530 of $P(Wild)$ at the level of individuals has an immediate use in practical management and
40
41 531 conservation. In many rivers, hydropower companies have to compensate for the reduction in
42
43 532 natural productivity of a river by releasing hatchery-produced fish. In other rivers, releases of
44
45 533 offspring from local brood stock is practiced on a voluntary basis. Regardless of purpose, a
46
47 534 genetic test compulsory for all brood stock being used was introduced in 2014 by the
48
49 535 Norwegian Environment Agency to limit the likelihood of spreading farmed salmon
50
51 536 genotypes through stock enhancement. In autumn 2014, the calculation of individual $P(Wild)$
52
53 537 led to 14% of potential broodstock in Norway being discarded for genetic reasons, and in
54
55
56
57
58
59
60

1
2
3
4 538 2015, 18% of potential brood stock was discarded (Karlsson *et al.*, 2015, 2016). In the highly
5
6 539 impacted Hardangerfjord rivers (average introgression 13.2%), calculations of $P(Wild)$ during
7
8 540 autumn 2015 showed that only 83 of 141 fish (escaped farmed salmon excluded) qualified as
9
10 541 wild-origin brood stock to create a live gene bank for the most impacted populations.

11
12
13 542 The probability distribution of $P(Wild)$ may help characterize the stage reached in an
14
15 543 accumulation of farmed introgression. In some populations, the probability distribution for
16
17 544 being wild shows distinct modes with fish at several stages of introgression, including “pure
18
19 545 wild”, “hybrid” and “farmed” (Tufto, 2000). At later stages of introgression, with a wide
20
21 546 range of admixed groups in the population, we expect a smoother distribution of individual
22
23 547 $P(Wild)$ values without distinct modes. At this time, the proportion of individuals with pure
24
25 548 wild origin is low, and management has to be cautious to preserve all ecotypes (e.g. late-
26
27 549 spawning fish; upper river spawners) in the remaining historically wild populations (Hansen
28
29 550 *et al.*, 2006).

30
31
32
33
34 551 To protect the genetic integrity of wild Atlantic salmon populations, only low levels of
35
36 552 introgression from escaped farmed salmon can be allowed into wild populations. We found
37
38 553 significant introgression in half of the populations studied, and levels of introgression above
39
40 554 10% in nearly one quarter of the populations. The rivers we studied represent three quarters of
41
42 555 the entire Norwegian wild salmon spawning population. Further introgression is likely, unless
43
44 556 substantial reduction of escaped farmed salmon in the wild, or sterilization of farmed salmon,
45
46 557 can be achieved.

47
48
49
50 558

51
52
53 559 **Acknowledgements**
54
55
56
57
58
59
60

1
2
3
4 560 We are grateful to Torveig Balstad, Line Eriksen, Merethe Spets for conducting the
5
6 561 genotyping at NINA, Sigbjørn Lien, Matthew Peter Kent, Arne Roseth, and Kristil Sundsasen
7
8 562 for conducting the genotyping at CIGENE, Thomas Moen at AquaGen for providing script for
9
10 563 creating input files and running structure in batch mode, Rådgivande Biologer, the Veterinary
11
12 564 Institute, UNI Research Miljø, Kunnskapscenter for Laks og Vannmiljø, LUKE Finland,
13
14 565 Marine Harvest, Salmobreed, AquaGen, and a number of colleagues for providing samples.
15
16 566 This study was financed by the Research Council of Norway (QuantEscape, project 216105),
17
18 567 the Norwegian Environment Agency, and by Norwegian hydropower companies and county
19
20 568 fishery offices. The analysis was also partially funded by the NINA Strategic Institute
21
22 569 Initiative “Interactions between aquaculture and wild salmonids”.

23
24
25
26
27 57028
29
30 571 **References**

- 31
32
33 572 Allendorf, F. W., Leary, R. F., Hitt, N. P., Knudsen, K. L., Lundquist, L. L., and Spruell, P.
34
35 573 2004. Intercrosses and the U.S. Endangered Species Act: should hybridized
36
37 574 populations be included as westslope cutthroat trout? *Conservation Biology*, 18:
38
39 575 1203–1213.
- 40
41
42 576 Baskett, M. L., Burgess, S. C., and Waples, R. S. 2013. Assessing strategies to minimize
43
44 577 unintended fitness consequences of aquaculture on wild populations. *Evolutionary*
45
46 578 *Applications*, 6: 1090–1108.
- 47
48
49 579 Bourret, V., Kent, M. P., Primmer, C. R., Vasemägi, A., Karlsson, S., Hindar, K., McGinnity,
50
51 580 P., Verspoor, E., Bernatchez, L., and Lien, S. 2012. SNP-array reveals genome-wide
52
53 581 patterns of geographical and potential adaptive divergence across the natural range of
54
55 582 Atlantic salmon (*Salmo salar*). *Molecular Ecology*, 22: 532–551.

- 1
2
3
4 583 Christie, M. R., Marine, M. L., Fox, S. E., French, R. A., and Blouin, M. S. 2016. A single
5
6 584 generation of domestication heritably alters the expression of hundreds of genes.
7
8 585 Nature Communications, 7:10676 doi: 10.10378/ncomms10676.
9
10 586 Diserud, O. H., Fiske, P., and Hindar, K. 2010. Regional impact of escaped farm salmon on
11
12 587 wildsalmon populations in Norway. NINA Report, 622: 1–40.(In Norwegian, English
13
14 588 summary)
15
16 589 Diserud, O.H., Fiske, P., and Hindar, K. 2012. Forslag til kategorisering av laksebestander
17
18 590 som er påvirket av rømt oppdrettslaks. NINA Rapport, 782: 1–32. [In Norwegian]
19
20 591 Diserud, O. H., Fiske, P., and Hindar, K. 2013. Forslag til kategorisering av laksebestander
21
22 592 som er påvirket av rømt oppdrettslaks – Oppdatering for perioden 1989–2012. NINA
23
24 593 Rapport, 976: 1–22. (In Norwegian)
25
26 594 Felsenstein, J. 1997. Population differentiation and evolutionary processes, *In Genetic effects*
27
28 595 of straying of non-native hatchery fish into natural populations: proceedings of the
29
30 596 workshop. Ed. by W. S. Grant. U.S. Department of Commerce, NOAA Technical
31
32 597 Memorandum, NMFS-NWFSC-30, 130 pp.
33
34 598 Fiske, P., Lund, R. A., and Hansen, L. P. 2005. Identifying fish farm escapees. In: Cadrin SX,
35
36 599 Friedland KD, Waldman JR (eds) Stock Identification Methods; Applications in
37
38 600 Fishery Science. Elsevier Academic Press, Amsterdam, pp 659–680.
39
40 601 Fiske, P., Lund, R. A., and Hansen, L. P. 2006. Relationships between the frequency of
41
42 602 farmed Atlantic salmon, *Salmo salar* L, in wild salmon populations and fish farming
43
44 603 activity in Norway, 1989–2004. ICES Journal of Marine Science, 63: 1182–1189.
45
46 604 Fiske, P., Diserud, O. H., Robertsen, G., Foldvik, A., Skilbrei, O., Heino, M., Helland, I. P.,
47
48 605 and Hindar, K. 2013. Midtveisvurdering av nasjonale laksevassdrag og nasjonale
49
50 606 laksefjorder. Rømt oppdrettslaks og bestandsstatus. NINA Minirapport 470, 24 pp. (In
51
52 607 Norwegian)
53
54
55
56
57
58
59
60

- 1
2
3
4 608 Fleming, I. A., and Einum, S. 2011. Reproductive ecology: a tale of two sexes. *In* Atlantic
5
6 609 Salmon Ecology, pp. 33–65. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal
7
8 610 Wiley-Blackwell, Chichester, U.K.
9
10
11 611 Fleming, I. A., Hindar, K., Mjølnerød, I. B., Jonsson, B., Balstad, T., and Lamberg, A. 2000.
12
13 612 Lifetime success and interactions of farm salmon invading a native population.
14
15 613 Proceedings of the Royal Society of London B, 267: 1517–1523.
16
17 614 Fleming, I. A., Jonsson, B., Gross, M. R., and Lamberg, A. 1996. An experimental study of
18
19 615 the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo*
20
21 616 *salar*). *Journal of Applied Ecology*, 33: 893–905.
22
23
24 617 Fleming, I. A., Lamberg, A., and Jonsson, B. 1997. Effects of early experience on
25
26 618 reproductive performance of Atlantic salmon. *Behavioural Ecology*, 8: 470–480.
27
28 619 Forseth, T., Fiske, P., Barlaup, B., Gjørseter, H., Hindar, K., and Diserud, O. H. 2013.
29
30 620 Reference point based management of Norwegian Atlantic salmon populations.
31
32 621 *Environmental Conservation* 40: 356–366.
33
34
35 622 Fraser, D. J., Cook, A. M., Eddington, J. D., Bentzen, P., and Hutchings, J. A. 2008. Mixed
36
37 623 evidence for reduced local adaptation in wild salmon resulting from interbreeding with
38
39 624 escaped farmed salmon: complexities in hybrid fitness. *Evolutionary Applications* 1,
40
41 625 501–512.
42
43
44 626 Fraser, D. J., Minto, C., Calvert, A. M., Eddington, J. D., and Hutchings, J. A. 2010. Potential
45
46 627 for domesticated-wild interbreeding to induce maladaptive phenology across multiple
47
48 628 populations of wild Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and*
49
50 629 *Aquatic Sciences*, 67 1768–1775.
51
52
53 630 Gausen, D., and Moen, V. 1991. Large scale escapes of farmed Atlantic salmon (*Salmo salar*)
54
55 631 into Norwegian rivers threaten natural populations. *Canadian Journal of Fisheries and*
56
57 632 *Aquatic Sciences*, 48: 426–428.
58
59
60

- 1
2
3
4 633 Gjedrem, T., and Baranski, M. 2009. Selective Breeding in Aquaculture: An Introduction.
5
6 634 Springer, London, U.K.
7
8 635 Gjedrem, T., Gjøen, H. M., and Gjerde, B. 1991. Genetic origin of Norwegian farmed salmon.
9
10 636 Aquaculture, 98: 41–50.
11
12 637 Gjøen, H. M., and Bentsen, H. B. 1997. Past, present, and future of genetic improvement in
13
14 638 salmon aquaculture. ICES Journal of Marine Science, 54: 1009–1014.
15
16
17 639 Grant, W. S. (ed.). 1997. Genetic effects of straying of non-native hatchery fish into natural
18
19 640 populations: proceedings of the workshop. U.S. Department of Commerce, NOAA
20
21 641 Technical Memorandum, NMFS-NWFSC-30, 130 pp.
22
23
24 642 Gross, M. R. 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild
25
26 643 and in aquaculture. Canadian Journal of Fisheries and Aquatic Sciences, 55(Suppl. 1):
27
28 644 131–144.
29
30
31 645 Hansen, M. M., Bekkevold, D., Jensen, L. F., Mensberg, K-L. D., and Nielsen, E. E. 2006.
32
33 646 Genetic restoration of stocked brown trout *Salmo trutta* population using microsatellite
34
35 647 DNA analysis of historical and contemporary samples. Journal of Applied Ecology,
36
37 648 43: 669–679.
38
39
40 649 Heino, M., Svåsand, T., Wennevik, V., and Glover, K. A. 2015. Genetic introgression of
41
42 650 farmed salmon in native populations: quantifying the relative influence of population
43
44 651 size and frequency of escapees. Aquaculture Environment Interactions, 6: 185–190.
45
46
47 652 Huisman, J., and Tufto, J. 2012. Comparison of non-Gaussian quantitative genetic models for
48
49 653 migration and stabilizing selection. Evolution, 66: 3444–3461.
50
51 654 Hutchings, J. A., and Fraser, D. J. 2008. The nature of fisheries- and farming-induced
52
53 655 evolution. Molecular Ecology, 17: 294–313.
54
55
56
57
58
59
60

- 1
2
3
4 656 Jensen, A. J., Karlsson, S., Fiske, P., Hansen, L. P., Hindar, K., and Østborg, G. 2013.
5
6 657 Escaped farmed Atlantic salmon in the Arctic Ocean. *Aquaculture Environment*
7
8 658 *Interactions*, 3: 223–229.
- 9
10
11 659 Jensen, A. J., Karlsson, S., Fiske, P., Hansen, L. P., Østborg, G., and Hindar, K. 2014. Origin
12
13 660 and life history of Atlantic salmon *Salmo salar* near the northernmost oceanic
14
15 661 limit. *Canadian Journal of Fisheries and Aquatic Sciences*, 71: 1740–1746.
- 16
17
18 662 Johnsen, B. O., and Jensen, A. J. 1991. The Gyrodactylus story in Norway. *Aquaculture*, 98:
19
20 663 289–302.
- 21
22
23 664 Jonsson, B., Jonsson, N., and Hansen, L. P. 1990. Does juvenile experience affect migration
24
25 665 and spawning of adult Atlantic salmon? *Behavioral Ecology and Sociobiology*, 26:
26
27 666 225–230.
- 28
29
30
31 667 Jonsson, B., Jonsson, N., and Hansen, L. P. 2003. Straying in Atlantic salmon. *Journal of Fish*
32
33 668 *Biology*, 62: 641–657.
- 34
35
36 669 Kalinowski, S.T. 2011. The computer program STRUCTURE does not reliably identify the
37
38 670 main genetic clusters within species: simulation and implications for human
39
40 671 population structure. *Heredity*, 106: 625–632.
- 41
42
43 672 Karlsson, S., Thomas, M., and Hindar, K. 2010. Contrasting patterns of gene diversity
44
45 673 between microsatellites and mitochondrial SNPs in farm and wild Atlantic salmon
46
47 674 *Conservation Genetics*, 11: 571–582.
- 48
49
50
51 675 Karlsson, S., Moen, T., Lien, S., Glover, K.A., and Hindar, K. 2011. Generic genetic
52
53 676 differences between farmed and wild Atlantic salmon identified from a 7K SNP-chip.
54
55 677 *Molecular Ecology Resources*, 11 (Suppl. 1): 247–253.
- 56
57
58
59
60

- 1
2
3
4 678 Karlsson, S., Diserud, O. H., Moen, T., and Hindar, K. 2014. A standardized method for
5
6 679 quantifying unidirectional genetic introgression, *Ecology and Evolution*, 4: 3256–
7
8 680 3263.
9
10
11 681 Karlsson, S., Florø-Larsen, B., Balstad, T., and Eriksen, L. 2015. Stamlakskontroll
12
13 682 2014.NINA rapport 1143. 13 pp. (In Norwegian)
14
15
16 683 Karlsson, S., Florø-Larsen, B., Balstad, T., Eriksen, L., and Spets, M. H. 2015.
17
18 684 Stamlakskontroll 2015. NINA rapport 1266. 14 pp. (In Norwegian)
19
20
21 685 Lund, R. A., and Hansen, L. P. 1991. Identification of wild and reared Atlantic salmon, *Salmo*
22
23 686 *salar* L., using scale characters. *Aquaculture and Fisheries Management*, 22:499–508.
24
25
26 687 Lura, H. 1995. Domesticated female Atlantic salmon in the wild: spawning success and
27
28 688 contribution to local populations. Dr. scient. thesis, University of Bergen.
29
30 689 McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., Ó Maoiléidigh, N., Rogan, G., Taggart,
31
32 690 J., and Cross, T. 2003. Fitness reduction and potential extinction of wild populations
33
34 691 of Atlantic salmon, *Salmo salar*, as a result of interaction with escaped farm salmon.
35
36 692 *Proceedings of the Royal Society London B*, 270: 2443–2520.
37
38
39 693 McGinnity, P., Stone, C., Taggart, J. B., Cooke, D., Cotter, D., Hynes, R., McCamley, C.,
40
41 694 Cross, T., and Ferguson, A. 1997. Genetic impact of escaped farmed Atlantic salmon
42
43 695 (*Salmo salar* L.) on native populations: use of DNA profiling to assess freshwater
44
45 696 performance of wild, farmed, and hybrid progeny in a natural river environment. *ICES*
46
47 697 *Journal of Marine Science*, 54: 998–1008.
48
49
50
51 698 Mjølnerød, I. B., Refseth, U. H., Karlsen, E., Balstad, T., Jakobsen, K. S., and Hindar, K.
52
53 699 1997. Genetic differences between two wild and one farmed population of Atlantic
54
55
56
57
58
59
60

- 1
2
3
4 700 salmon (*Salmo salar*) revealed by three classes of genetic markers. *Hereditas*, 127:
5
6 701 239–248.
7
8
9 702 Mork, J. 1991. One generation effects of farmed fish immigration on the genetic
10
11 703 differentiation of wild Atlantic salmon in Norway. *Aquaculture*, 98: 267-276.
12
13
14 704 Morris, M. R. J., Fraser, D. J., Heggelin, A. J., Whoriskey, F. G., Carr, J W., O’Niel, S. F.,
15
16 705 and Hutchings, J. A. 2008. Prevalence and recurrence of escaped farmed Atlantic
17
18 706 salmon (*Salmo salar*) in eastern North American rivers. *Canadian Journal of Fisheries*
19
20 707 and Aquatic Sciences, 65: 2807–2826.
21
22
23 708 Nielsen, E. E., Bach, L. A., and Kotlicki, P. 2006. HYBRIDLAB (version 1.9): a program for
24
25 709 generating simulated hybrids from population samples. *Molecular Ecology Notes*, 6:
26
27 710 971–973.
28
29
30
31 711 Pritchard, J. K., Stephens, M., and Donnelly, P. 2000. Inference of population structure using
32
33 712 multilocus genotype data. *Genetics*, 155: 945–959.
34
35
36 713 Reed, T. E., Prodöhl, P., Hynes, R., Cross, T., Ferguson, A., and McGinnity, P. 2015.
37
38 714 Quantifying heritable variation in fitness-related traits of wild, farmed and hybrid
39
40 715 Atlantic salmon families in a wild river environment. *Heredity*, 115: 173–184
41
42
43 716 Roberge, C., Einum, S., Guderley, H., and Bernatchez, L. 2006. Rapid parallel evolutionary
44
45 717 changes of gene transcription profiles in farmed Atlantic salmon. *Molecular Ecology*,
46
47 718 15: 9–20.
48
49
50
51 719 Ryman, N., Utter, F., and Hindar, K. 1995. Introgression, supportive breeding, and genetic
52
53 720 conservation, pp. 341–365. *In Population Management for Survival and Recovery:*
54
55 721 *Analytical Methods and Strategies in Small Population Conservation*. Ed. by J. D.
56
57 722 Ballou, M. Gilpin and T. J. Foose. Columbia University Press, New York.
58
59
60

- 1
2
3
4 723 Sægrov, H., Hindar, K., Kålås, S., and Lura, H. 1997. Escaped farmed Atlantic salmon
5
6 724 replaces the original salmon stock in the River Vosso. ICES Journal of Marine
7
8 725 Science, 54: 1166–1172.
9
10
11 726 Skaala, Ø., Høyheim, B., Glover, K., and Dahle, G. 2004. Microsatellite analysis in
12
13 727 domesticated and wild Atlantic salmon (*Salmo salar* L.) allelic diversity and
14
15 728 identification of individuals. Aquaculture, 240: 131–143.
16
17
18 729 Skaala, Ø., Taggart, J. B., and Gunnes, K. 2005. Genetic differences between five major
19
20 730 domesticated strains of Atlantic salmon and wild salmon. Journal of Fish Biology, 67:
21
22 731 118–128.
23
24
25 732 Skaala, Ø., Wennevik, V., and Glover, K.A. 2006. Evidence of temporal genetic change in
26
27 733 wild Atlantic salmon (*Salmo salar* L.) populations affected by farmed escapees. ICES
28
29 734 Journal of Marine Science, 63: 1224–1233.
30
31
32
33 735 Skaala, Ø., Glover, K. A., Barlaup, B. T., Svåsand, T., Besnier, F., Hansen, M. M., and
34
35 736 Borgstrøm, R. 2012. Performance of farmed, hybrids, and wild Atlantic salmon
36
37 737 (*Salmo salar*) families in a natural river environment. Canadian Journal of Fisheries
38
39 738 and Aquatic Science, 69: 1994–2006.
40
41
42
43 739 Solberg, M. F., Skaala, Ø., Nilsen, F., and Glover, K. A. 2013. Does domestication cause
44
45 740 changes in growth reaction norms? A study of farmed, wild and hybrid Atlantic
46
47 741 salmon families exposed to environmental stress. PLoS ONE, 8(1): e54469, doi:
48
49 742 10.1371/journal.pone.0054469.
50
51
52 743 Sundt-Hansen, L., Huisman, J., Skoglund, H., and Hindar, K. 2015. Farmed Atlantic salmon
53
54 744 *Salmo salar* L. parr may reduce early survival of wild fish. Journal of Fish Biology,
55
56 745 86: 1699–1712. doi: 10.1111/jfb.12677
57
58
59
60

- 1
2
3
4 746 Tang, K., Fu, D. J., Julien, D., Braun, A., Cantor, C. R., and Kösner, H.1999. Chip-based
5
6 747 genotyping by mass spectrometry. Proceedings of the National Academy of Sciences
7
8 748 of the United States of America, 96:10016–10020
9
10
11 749 Thodesen, J., Grisdale-Helland, B., Helland, S. J., and Gjerde, B.1999. Feed intake, growth
12
13 750 and feed utilization of offspring from wild and selected Atlantic salmon (*Salmo salar*).
14
15 751 Aquaculture, 180: 237–246.
16
17
18 752 Tufto, J. 2000. Quantitative genetic models for the balance between migration and stabilizing
19
20 753 selection. Genetical Research, 76:285–293.
21
22
23 754 Tufto, J. 2001. Effects of releasing maladapted individuals: A demographic-evolutionary
24
25 755 model. American Naturalist, 158: 331–340.
26
27
28 756 Tufto, J., and Hindar, K. 2003. Effective size in management and conservation of subdivided
29
30 757 populations. Journal of Theoretical Biology, 222: 273–281.
31
32
33 758 Vähä, J. P., Erkonaro, J., Niemelä, E., and Primmer, C. R. 2008. Temporally stable genetic
34
35 759 structure and low migration in an Atlantic salmon population complex: implications
36
37 760 for conservation and management. Evolutionary Applications, 1: 137–154.
38
39
40 761 Vøllestad, L. A., Hirst, D., L'Abée-Lund, J. H., et al. 2009. Divergent trends in anadromous
41
42 762 salmonid populations in Norwegian and Scottish rivers. Proceedings of the Royal
43
44 763 Society B, 276: 1021–1027.
45
46
47 764 Vøllestad, L. A., Skurdal, J., and L'Abée-Lund, J. H. 2014. Evaluation of a new management
48
49 765 scheme for Norwegian Atlantic salmon *Salmo salar*. Fisheries Management and
50
51 766 Ecology, 21: 133–139.
52
53
54 767 Warton, D. I., and Hui, F. K. C. 2011. The arcsine is asinine: the analysis of proportions in
55
56 768 ecology. Ecology, 92:3–10.
57
58
59
60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

769

For Review Only

770 **Table 1.** Farmed genetic introgression for Norwegian Atlantic salmon rivers with and without
 771 the protection status of being National Salmon Rivers, and for salmon rivers in and not in fjor
 772 ds with the a protection status of being National Salmon Fjords. Farm introgression values are
 773 given as averages and medians, both unweighted and weighted with estimated population size
 774 .

Group	<i>N</i> Ind	<i>N</i> pop	Farm introgression - unweighted average / median	Farm introgression – weighted average / m edian
National Rivers	4347	47	0.045 / 0.016	0.016 / 0.000
Not National Rivers	4741	62	0.078 / 0.028	0.048 / 0.014
National Fjords	5337	59	0.064 / 0.018	0.018 / 0.000
Not National Fjords	3751	50	0.064 / 0.026	0.035 / 0.025

775

776

777 **Table 2.** Farmed genetic introgression in Norwegian geographical regions. Regions are set as
 778 counties (Figure 3), except for region Southeast which includes the south and the southeastern
 779 counties (Østfold, Akershus, Buskerud, Vestfold, Telemark, Aust-Agder and Vest-Agder).. R
 780 egional farm introgression values are given as averages and medians, both unweighted and we
 781 ighted with estimated population size.

Region	<i>N</i> Ind	<i>N</i> pop	Farm introgression, u nweighted	Farm introgression, weighted
Southeast	899	11	0.038 / 0.000	0.015 / 0.000
Rogaland	1070	9	0.018 / 0.008	0.007 / 0.000
Hordaland	922	10	0.139 / 0.108	0.114 / 0.108
Sogn og Fjordane	1992	21	0.068 / 0.042	0.064 / 0.000
Møre og Romsdal	1946	16	0.062 / 0.044	0.039 / 0.014
Sør-Trøndelag	365	6	0.047 / 0.020	0.013 / 0.012
Nord-Trøndelag	162	4	0.000 / 0.000	0.000 / 0.000
Nordland	556	12	0.079 / 0.028	0.077 / 0.078
Troms	324	7	0.145 / 0.083	0.067 / 0.083
Finnmark	852	13	0.026 / 0.021	0.010 / 0.000
National	9088	109	0.064 / 0.023	0.021 / 0.000

782

783

784

785

786

787

788

789 **Figure captions**

1
2
3
4 790
5
6

7 791 **Figure 1.** PCoA plot of pairwise F_{ST} estimates between historical samples from 39 Atlantic
8 salmon populations and 13 farmed strain populations (diamonds), clustered into one farmed
9 group (Farmed), one wild Atlantic salmon group from Finnmark (Barents-White Sea), and
10 792 one wild Atlantic salmon group from South of Finnmark (Atlantic). Grey diamonds are
11 793 populations (River Skibotnelva, River Målselva, and River Skipsfjordelva) outside the
12 794 clusters and genetic introgression is analysed by using the local historical samples. Open
13 795 circles are in silico generated populations from a pool of the historical samples within each
14 796 cluster.
15 797
16 798
17 799

18 800 **Figure 2.** Distribution of logit-transformed probabilities of being of wild origin $P(Wild)$, for
19 801 farmed reference (red line; mean value indicated by the red diamond), wild references for the
20 802 whole Atlantic phylogenetic group (blue line and diamond), wild reference for River Eira
21 803 (black line and diamond) and contemporary sample for River Eira (dashed black line and
22 804 open black diamond; $n = 786$ for years 2012, 2013, 2014, 2015 pooled).
23 805
24 806
25 807
26 808
27 809
28 810
29 811

30 806 **Figure 3.** Map of Norway showing estimated farmed genetic introgression in 109 Norwegian
31 807 salmon rivers from contemporary adult samples. Codes used for counties: FI = Finnmark, TR
32 808 = Troms, NO = Nordland, NT = Nord-Trøndelag, ST = Sør-Trøndelag, MR = Møre og
33 809 Romsdal, SF = Sogn og Fjordane, HO = Hordaland, RO = Rogaland, and SOUTHEAST is the
34 810 southeasternmost counties pooled into one region.
35 811

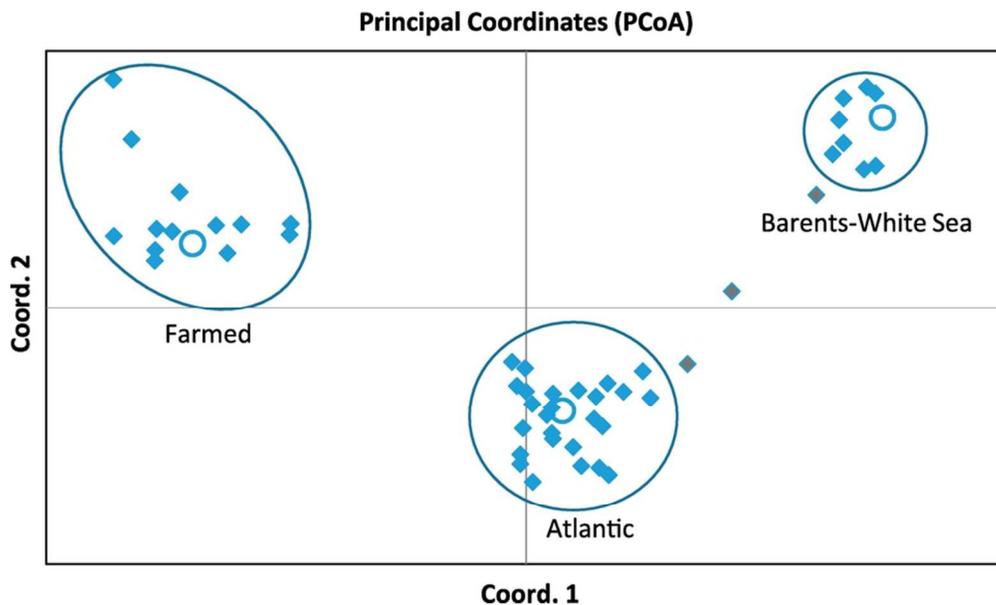
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3
4 812 **Figure 4.** Relationship between mean annual proportions of escaped farmed salmon between
5
6 813 1989 and 2012 and estimated proportion of farmed genetic introgression from molecular
7
8 814 genetic markers for 77 salmon populations (solid diamonds and dashed lines), and averaged
9
10 815 for populations within geographical regions (open diamonds). Observations from the Atlantic
11
12 816 Sea phylogenetic group are shown in red, from the Barents-White Sea phylogenetic group
13
14
15 817 shown in blue, and two populations from the transition area are shown in grey.

16
17
18 818 **Figure 5.** Distribution of STRUCTURE-generated probabilities of being of wild origin
19
20 819 $P(wild)$ for modern (red line) and historical (orange line) samples from the AquaGen farmed
21
22 820 strains.
23
24

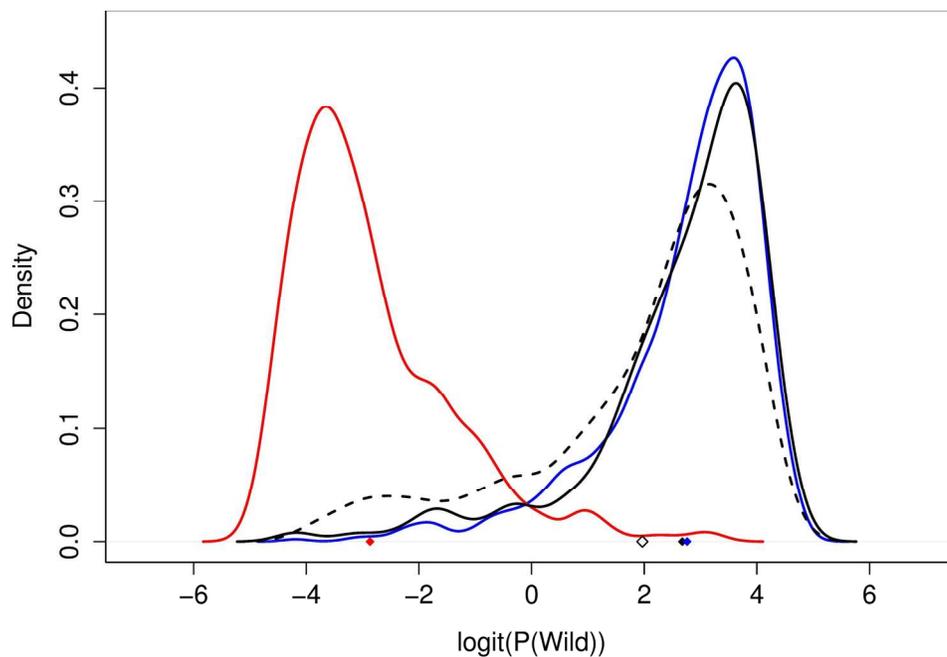
25 821

26
27
28 822
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



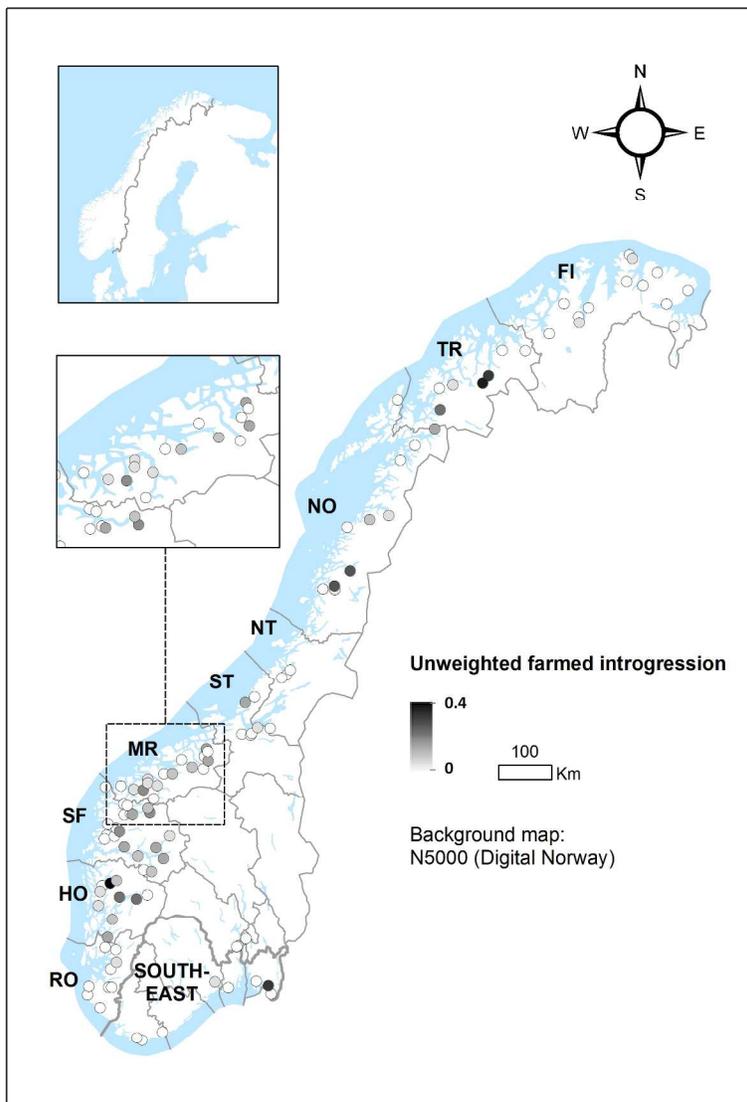
PCoA plot of pairwise F_{ST} estimates between historical samples from 39 Atlantic salmon populations and 13 farmed strains populations (diamonds), clustered into one farmed group (Farmed), one wild Atlantic salmon group from Finnmark (Barents-White Sea), and one wild Atlantic salmon group from South of Finnmark (Atlantic). Grey diamonds are populations (River Skibotnelva, River Målselva, and River Skipsfjordelva) outside the clusters and genetic introgression is analysed by using the local historical samples. Open circles are in silico generated populations from a pool of the historical samples within each cluster.
81x48mm (300 x 300 DPI)

Manuscript Only



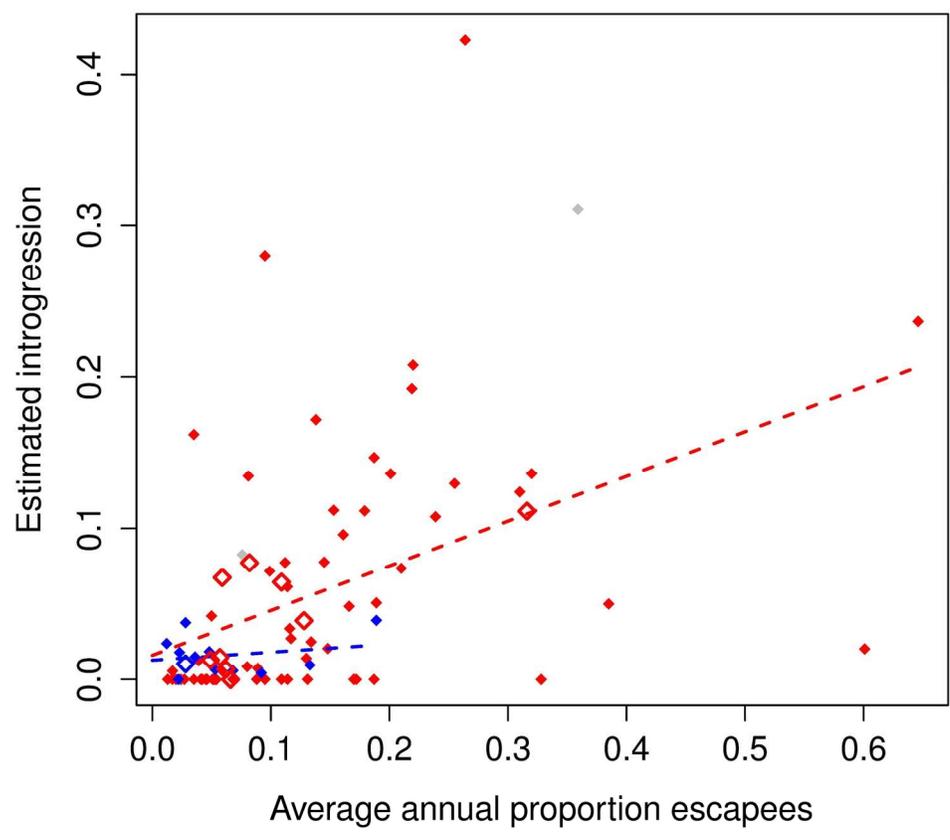
Distribution of probabilities of being of wild origin ($P(\text{Wild})$), logit-transformed for Farm reference (red line; mean value indicated by the red diamond), wild references for the whole Atlantic phylogenetic group (blue line and diamond), wild reference for River Eira (black line and diamond) and contemporary sample for River Eira (dashed black line and open black diamond; $n=786$ for years 2012, 2013, 2014, 2015 pooled).
167x128mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



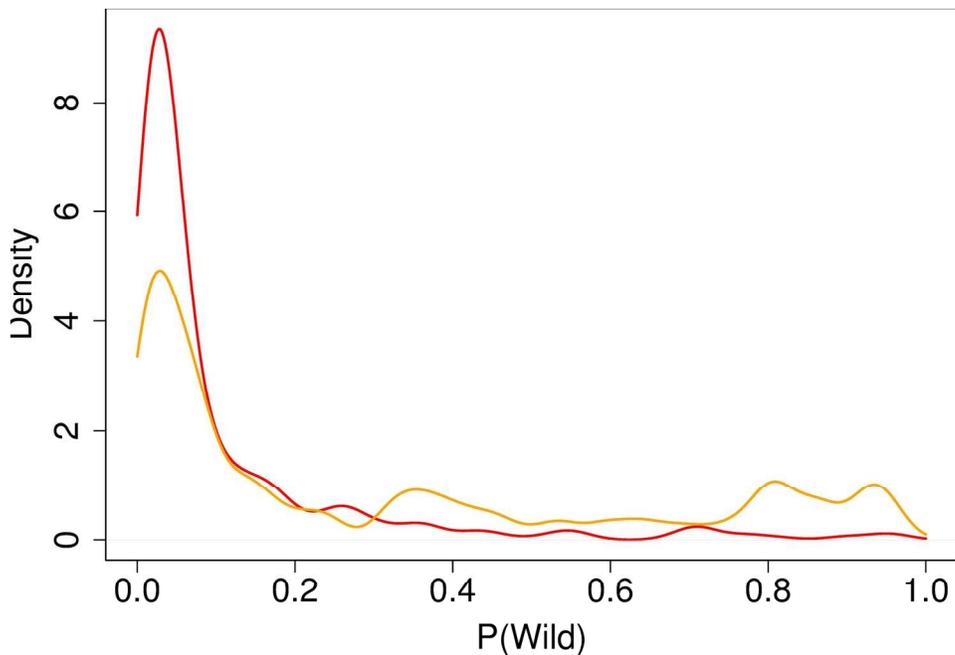
209x297mm (300 x 300 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



163x158mm (300 x 300 DPI)





Distribution of STRUCTURE-generated probabilities of being of wild origin (P(wild)) for modern (red line) and historical (orange line) samples from the AquaGen farmed strains.
167x128mm (300 x 300 DPI)

Only