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1 # Multiple selection signatures in farmed Atlantic salmon adapted
2 # to different environments across Hemispheres

3

4 **Running title:** Selection signatures in farmed Atlantic salmon

5

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28 **1. ABSTRACT**

29 Domestication of Atlantic salmon started approximately forty years ago, using both
30 artificial and natural selection strategies. Such selection methods are likely to have imposed
31 distinctive selection signatures on the salmon genome. Therefore, identifying differences in
32 selection signatures may give insights into the mechanism of selection and candidate genes
33 of biological and productive interest. Here, we used two complementary haplotype-based
34 statistics, the within-population integrated Haplotype Score test (|iHS|) and the cross-
35 population Extended Haplotype Homozygosity test (XP-EHH) to compare selection
36 signatures in four populations of Atlantic salmon with a common genetic origin. Using
37 |iHS| we found 24, 14, 16 and 26 genomic regions under selection in Pop-A, Pop-B, Pop-C,
38 and Pop-D, respectively. While using the XP-EHH test we identified 27, 25 and 15
39 potential selection regions in Pop-A/Pop-B, Pop-A/Pop-C and Pop-A/Pop-D, respectively.
40 These genomic regions harbor important genes such *igf1r* and *sh3rf1* which have been
41 associated with growth related traits in other species. Our results contribute to the detection
42 of candidate genes of interest and help to understand the evolutionary and biological
43 mechanisms for controlling complex traits under selection in Atlantic salmon.
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47 **Keywords**

48 Selection signatures, *Salmo salar,* domestication, SNP data, artificial selection.

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57 ## 2. BACKGROUND

58 Atlantic salmon (*Salmo salar* L) were first farmed in Norway during the 1960s, and have
59 now become one of the most important aquaculture species (FAO 2016). Despite a
60 generation interval of three to four years, breeding programs have achieved rapid
61 improvement of economically important traits such as growth, sexual maturation and
62 disease resistance (GJEDREM *et al.* 2012). One of the first farmed populations named Mowi
63 strain, was established with fish from west coast rivers in Norway, with major contributions
64 from River Bolstad in the Vosso watercourse, River Årøy and possibly from the
65 Maurangerfjord area (VERSPOOR *et al.* 2007). Salmon from the Vosso and Årøy rivers are
66 characterized by large size and late maturity (VERSPOOR *et al.* 2007). Phenotypic selection
67 for growth, late maturation and fillet quality was the focus in this population until 1999
68 (GLOVER *et al.* 2009). Ova from this population were imported into Fanad Peninsula,
69 Ireland between 1982 and 1986 to establish an Irish-farmed population (NORRIS 1999).
70 Similarly, ova from this Irish farmed population were introduced to Chile in the early
71 1990s. These stocks were subsequently adapted to the biotic and abiotic factors present in
72 southern hemisphere conditions. Artificial selection and adaptation to captive environments
73 has left detectable genomic patterns in farmed Atlantic salmon populations, as evidenced
74 by differences between wild and farmed populations for several traits, such as growth rate
75 (THODESEN *et al.* 1999; GLOVER *et al.* 2009; SOLBERG *et al.* 2012), predator awareness
76 (EINUM AND FLEMING 1997) and gene transcription patterns (ROBERGE *et al.* 2006; BICSKEI
77 *et al.* 2014; CHRISTIE *et al.* 2016).
78
79 Domestication processes are likely to have exerted selection pressures on certain genomic
80 regions that underlie traits of human interest or other traits involved in adaptation to captive
81 environments. Accordingly, positive selection pressures will cause the frequency of alleles
82 underlying favorable traits to increase rapidly in these domesticated populations. Linkage
83 disequilibrium between favorable mutations and neighboring loci will increase and spread,
84 given there is little opportunity for recombination over the brief time since the onset of
85 intense selection (SABETI *et al.* 2002). Analyses of these selection signatures in domestic
86 animals can provide further insights into the genetic basis of adaptation to diverse
87 environments and genotype/phenotype relationships (OLEKSYK *et al.* 2010; ANDERSSON

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88 2012). Access to genomic data through next-generation sequencing and high-throughput
89 genotyping technologies have made the comparison of genomic patterns of SNP variation
90 between different livestock breeds possible, allowing for the identification of putative
91 genomic regions and genes under selection in various species including cattle (FLORI *et al.*
92 2009), horses (PETERSEN *et al.* 2013; FRISCHKNECHT *et al.* 2016), sheep (KIJAS *et al.* 2012;
93 FARIELLO *et al.* 2014), pigs (AMARAL *et al.* 2011), Atlantic salmon (VASEMÄGI *et al.* 2005;
94 VASEMÄGI *et al.* 2012; MÄKINEN *et al.* 2014; GUTIERREZ *et al.* 2015; LÓPEZ *et al.* 2018)
95 and tilapia (HONG XIA *et al.* 2015).
96
97 There are several approaches for detecting selection signatures in the genome, one of which
98 relies on the length or variability of haplotypes. Directional selection acting on a new
99 beneficial mutation results in the haplotype harboring the mutation to increase in frequency
100 and to be longer than average. In order to exploit this, Sabeti et al (2002), proposed the
101 extended haplotype homozygosity (EHH) statistic to detect of positive selection in a
102 population, which is specifically the probability that two randomly selected haplotypes are
103 identical-by-descent over their entire length around a core SNP (Sabeti et al 2002). This
104 concept forms the basis for other haplotype homozygosity based metrics, such as the
105 relative EHH (REHH) (SABETI *et al.* 2002) and the widely-used integrated Haplotype Score
106 (|iHS|) (VOIGHT *et al.* 2006). |iHS| compares EHH between derived and ancestral alleles
107 within a population and has the most power to detect selection when the selected allele is at
108 intermediate frequencies in the population (SABETI *et al.* 2006; VOIGHT *et al.* 2006). To
109 detect selection signatures between populations, the cross-population Extended Haplotype
110 Homozygosity test (XP-EHH) compares the integrated EHH profiles between two
111 populations at the same SNP. It was designed to detect ongoing or nearly fixed sites
112 harboring selection in one population (SABETI *et al.* 2007).

113 Although previous studies have already been carried out to detect selection signatures in
114 Atlantic salmon (MÄKINEN *et al.* 2014; GUTIERREZ *et al.* 2015; LIU *et al.* 2016; LÓPEZ *et al.*
115 2018) exploration of selection signatures in additional populations will illuminate how
116 genetic variation among the different strains, adapted to different culture conditions, across
117 hemispheres has not been assessed yet. Herein we used an Affymetrix 200K SNP array
118 dataset to investigate selection signatures in farmed Atlantic salmon populations from the

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119 same origin, cultivated in Ireland and Chile. We identified several selection signatures
120 using two haplotype-based approaches (|iHS| and XPEHH) at the whole genome level in
121 four Atlantic salmon populations. These findings are important as they highlight regions of
122 the genome that might benefit economically relevant attributes, such as growth, resistance
123 to local diseases and adaptation to specific environmental conditions.

124

125 3. MATERIALS AND METHODS

126 Samples, genotyping and quality control.

127

128 We used a total of 270 individuals from four farmed Atlantic salmon populations of
129 Norwegian origin (Pop-A, n = 40; Pop-B, n = 71; Pop-C, n = 85; Pop-D, n = 74). Pop-A
130 fish are from the Irish strain (Fanad) originating from the west coast Rivers of Norway, as
131 described in the Introduction section. Artificial selection for improving growth, maturity
132 and fillet quality was applied from the beginning in this population (GLOVER *et al.* 2009).
133 We estimated that this population had been under artificial selection for at least ten
134 generations. Pop-B and Pop-C are two different Chilean populations, established with fish
135 from two different year classes of the same Irish strain (Fanad) in the 1990s. Pop-B and
136 Pop-C have been farmed and adapted to the Los Lagos Region, Chile (42°S 72°O). Pop-D
137 is another Chilean population founded with fish from the same Irish farmed strain but
138 adapted to the XIInd Region, Magallanes, Chile (53°S 70°O). Pop-B, Pop-C and Pop-D
139 populations experienced four generations of selective breeding for growth in Chilean
140 farming conditions at the time of sampling.

141

142 Genotyping of all populations was performed using Affymetrix's Atlantic salmon 200K
143 SNP Chip described in YÁÑEZ *et al.* (2016). We assessed SNP quality control using Axiom
144 Genotyping Console (GTC, Affymetrix) and SNPolisher (an R package developed by
145 Affymetrix) *i*) removing SNPs that did not match with high quality clustering patterns,
146 according to the best practices recommended by Affymetrix, *ii*) removing SNPs with call
147 rate lower than 95% and iii) we discarded individuals with genotyping call rate under 90%.
148 We used only SNPs that mapped to chromosomes in the newest version of the Atlantic

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149 salmon reference genome, ICSAG_v2 (GenBank: GCA_000233375.4). After quality
150 control filtering, 146,102 SNPs remained for downstream analyses.
151
152 **Genetic diversity and population structure**
153
154 We evaluated genetic diversity in terms of the observed heterozygosity (H_O) and expected
155 heterozygosity (H_E) calculated with PLINK v1.07 (PURCELL *et al.* 2007). To investigate
156 population structure based on individual ancestry proportions, we performed model-based
157 clustering assuming no prior knowledge about strain origins in ADMIXTURE 1.2.2
158 (ALEXANDER *et al.* 2009). We performed 10 separate randomly seeded runs for each
159 number K of ancestral populations ($1<K<20$) and selected the optimum K according to the
160 lowest value of the cross-validation error. The aforementioned analyses were conducted
161 using a total of 20,000 SNPs after retaining only those with linkage disequilibrium (LD)
162 values of at most 0.2 to minimize possible confounding effects of LD on the underlying
163 patterns of genetic structure.
164
165 **Selection signatures, gene annotation and functional analyses**
166
167 To detect potentially regions harboring selection signatures, two complementary haplotype-
168 based detection methods, iHS and *XPEHH,* were used for within and between population
169 analyses, respectively.
170 **Detection of within-population selection signatures using *iHS*.** The iHS score is based
171 on the ratio of extended haplotype homozygosity (EHH) for haplotypes anchored with the
172 ancestral versus derived allele. The ancestral allele state for salmon is unknown and so to
173 avoid losing SNPs by trying to polarize them from publicly available outgroup references,
174 we assumed that the major allele represented the ancestral state as used by Bahbahani *et al*
175 (2015). We phased the haplotypes using Beagle (BROWNING AND BROWNING 2009). Single-
176 site iHS values were calculated across the genome for each population. |iHS| scores were
177 calculated using the REHH package (GAUTIER AND VITALIS 2012) and a score threshold of
178 3.0 was used to infer candidate genomic regions under selection.
179

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Detection of between-population selection signatures using *XP-EHH*. The XP-EHH statistic compares the integrated EHH between two populations at the same SNP, in order to identify selection based on overrepresented haplotypes in one of the populations, detecting entirely or approximately fixed sites (SABETI *et al.* 2007). The direction of selection can be determined from the sign of XP-EHH scores, whereby negative XP-EHH scores suggest selection in the 'reference' population, whereas positive scores suggest selection in the 'observed' population. Pop-A was used as the reference population to the other three populations, hence there were three pairs of comparisons.

Gene functional annotation

Genomic regions harboring SNPs showing evidence of selection were annotated based on the ICSAG_v2 reference genome (LIEN *et al.* 2016) using SnpEff (CINGOLANI *et al.* 2012). Gene transcripts from these candidate regions were aligned (using blastx) (ALTSCHUL *et al.* 1990) to the zebra fish (*Danio rerio*) peptide reference database (downloaded from http://www.ensembl.org/) to determine gene identify. As evidence of homology we used an e-value □ 0 and then retrieved the zebra fish gene identifiers and gene ontology (GO) information from the ensembl biomart database (http://www.ensembl.org/biomart).

4. RESULTS

Genetic diversity and structure.

We investigated genetic diversity within each population using SNPs filtered for missing data per individual (max 10%), missing data per marker (max 5%) and allele frequency (min 5%) as described in the Materials and Methods section. A total of 146,103 SNPs were retained for analyses after these quality control steps. Observed heterozygosity levels were similar across the four domestic populations. And was slightly higher than expected for populations A, B and C, and even higher in population D (See Table 1).

Admixture analysis was used to determine the composition of ancestral lineages among individuals to offer insight into the observed genetic variation. We found K=12 ancestral lineages to be optimal in describing the ancestry of the individuals across the 4 populations (Figure 1).

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212 **Candidate regions under selection - |iHS|**

213 We used the haplotype-based |iHS| test to look for selection within populations. For each
214 population we defined candidate selection regions using the thresholds of |iHS| > 3 (Figure
215 2 and Table 2). Candidate regions were retained if two SNPs separated by ≤ 500 Kb passed
216 this threshold and were annotated using the positions of the first and last SNP as
217 boundaries, extending 500 Kb to each side. In Pop-A we identified 120 markers putatively
218 under selection among ten chromosomes, Ssa02 and Ssa10 combined had approximately 60
219 SNPs. The highest score (-log(p-value) = 5.04) was found in Ssa05 in a region of 6,7 Kb,
220 associated with the CR762469.1 gene; other high scores were found in Ssa10 and Ssa01,
221 nearby to *mipol1*, *furinb*, *csnk1g2a* and *rs17*. Other candidate genes undergoing selection
222 for this population are shown in Supplementary Table S1.

223

224 In Pop-B fourteen regions passed the threshold, distributed among eight chromosomes
225 (Ssa1, 6, 10, 12, 13, 14, 16, and 27). The highest score was in Ssa06, harboring the SASH1
226 gene. Ssa01 and Ssa13 encompassed 4 and 3 regions under selection, respectively,
227 spanning from 11 Kb to 228 Kb. A total of 24 genes were located in these regions
228 (Supplementary Table S1).

229

230 In Pop-C |iHS| detected 121 SNPs passing the threshold and we annotated sixteen genomic
231 regions. Ssa22 showed the highest scores and larger regions under selection, harboring
232 genes such kcnkf, *sc61a*, *mapk3*, *f264* and *cdh2*. Ssa16 and Ssa19 also exhibited high |iHS|
233 scores spanning regions 3 Kb to 1788 Kb.

234

235 Finally, Pop-D presented the highest number of SNPs (134 SNPs) above the threshold
236 compared with other populations, distributed across 11 chromosomes. We defined 25
237 genomic regions under selection, most of them located in Ssa26, where the highest |iHS|
238 scores were also found. Genes such as uqcrfs1, neto1, itfg1 and phkb were found in these
239 regions. Ssa24 also presented higher |iHS| values in one of its regions associated with tchp,
240 ube3b and myo1ha among others. Details of genes and regions can be found in
241 Supplementary Table S1.

242

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243 **Candidate regions under selection – *XPEHH***

244 We also looked for selection signatures using the XPEHH test between the following
245 populations pairs: A/B; A/C and A/D (Figure 3). We detected, 437 (A/B), 764 (A/C) and
246 262 (A/D) XPEHH scores outlier SNPs indicative of selection (Table 3). We considered
247 potential genomic regions under selection as those containing two or more consecutive
248 SNPs less than 500 Kb apart and that had XPEHH score > 3. After merging overlapping
249 regions 27, 25 and 15 candidate regions were identified for A/B, A/C and A/D comparisons
250 respectively. The total length of the candidate regions was 10.13 Mb for A/B, 12.11 Mb for
251 A/C and 4.05 Mb for A/D. Comparison between A/C yielded negative results in
252 chromosome Ssa14 and Ssa16, furthermore comparison A/D yielded negative results in
253 Ssa14, Ssa24 and Ssa26, suggesting selection in the reference population (A). The gene
254 annotation revealed in A/B the *plecb* gene on Ssa02 and *myo1cb*, *slc43a2a* and *ywhae1*
255 genes on Ssa09, associated with the highest values of XPEHH. In A/C the chromosome
256 Ssa10 presented a large number of SNPs and regions putatively under selection. Also this
257 chromosome presented the highest scores; genes such as *fnbp1l*, *bcar3*, slc5a9 and *fryl* were
258 associated with these values. The highest values for A/D were also located on Ssa10 with
259 *lhx4*, *shr3rf1* and *ftr33* genes. The negative values of XPEHH harboring genes such *agla*,
260 *kcmf1*, *cds1* and *tshz3b* suggest selection on population A.

261

262 **Gene ontology for candidate genes under selection.**

263 To further explore the functions of the candidate genes nearby markers showing evidence
264 of selection signatures, we annotated the candidate genes detected by both methods using
265 DAVID browser (https://david-d.ncifcrf.gov). These candidate genes were enriched in 14
266 gene ontology terms. None of these categories were common across all four populations,
267 but Developmental process and Multicellular organismal process were common on Pop B-
268 C and D. Regulation of biological process was shared for Pop A –B and D; Single-
269 organism process was common for Pop A –B and C; Biological regulation was found in
270 Pop-B and Pop-D; and Growth and Locomotion were common for Pop-B and Pop-C.
271 Anatomical structure development, Biosynthetic process, Cell growth and Single-
272 multicellular organism process were present only in Pop-A; while Localization and
273 Signaling were found only in Pop-B (4).

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274 **5. DISCUSSION**

275 In this study two complementary tests were used to detect genome wide selection
276 signatures within and between four Atlantic salmon populations with Norwegian origin.
277 We used |iHS| test to evaluate selection signatures within populations and XPEHH to
278 evaluate across populations. We used the oldest population as the reference population
279 when using XPEHH to evaluate the effect of domestication and artificial selection in three
280 different locations in Chile.

281 **Structure and diversity**

282 To examine genetic population structure and relationships among the major groups of
283 salmon, we conducted an ADMIXTURE analyses based on high-quality SNP data. This
284 analysis revealed twelve clusters, which was expected considering the admixed origin of
285 these populations (VERSPOOR *et al.* 2007). The four populations used in this study come
286 from the Mowi strain, which was created, using samples from several rivers along the west
287 coast of Norway (NORRIS *et al.* 1999). The population with the lowest level of admixture
288 was Pop-A, which was also the population with the lowest genetic diversity, a condition
289 that could reflect a higher intensity of artificial selection in this population. Intense artificial
290 selection causes loss of genetic variation as a consequence of the mating of related
291 individuals (GJEDREM 2005). Pop-B and Pop-C showed very similar patterns of
292 heterozygosity and admixture level, which was expected due to the similar breeding
293 practices and environmental conditions to which they have been subjected. Pop-D,
294 however, showed the highest level of heterozygosity and a more complex pattern of
295 admixture, likely produced by a lower pressure of artificial selection on this population.
296 Recent genetic introgression cannot be discarded for Pop-D given the potential of crosses
297 with a different strain for management issues. The results presented here also reinforce the
298 notion that a few generations (at least four in this particular case) are sufficient to generate
299 large changes in terms of genetic structure in farmed Atlantic salmon populations, with the
300 same genetic origin, which have been subjected to different management and
301 environmental conditions. Estimates of inbreeding coefficient (F_{IS}) showed the lowest
302 value in Pop-D, which is consistent with the heterozygosity level in this population. Pop-A
303 presented the second lowest value, despite the fact that this population has been subjected

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304 to the most intense selection pressure probably due to a better inbreeding management with
305 the use of DNA fingerprinting technology to know relatedness among individuals in order
306 to avoid inbreeding.
307

308 **Selection signatures**

309 As expected the highest |iHS| scores were found in Pop-A because this population has been
310 subjected to more intense artificial selection pressures for a longer time. The number of
311 SNPs under selection detected by this method was similar in Pop-A, Pop-C and Pop-D, but
312 lower in Pop-B. We suggest that this difference is due to the fact that the |iHS| test has little
313 power to detect signals near fixation (SABETI *et al.* 2007; SIMIANER *et al.* 2010). XPEHH,
314 which is more powerful at detecting selection signatures at or near fixation (Sabeti 2007),
315 detected a similar number of regions putatively under selection in Pop-B and Pop-C, but
316 lower in Pop-D. Conversely, |iHS| detected more SNP in this population, suggesting loci
317 under selection in Pop-D have experienced weaker pressure of artificial selection and a
318 greater impact of natural selection, which has prevented allele fixation. Overlaps among
319 regions detected by |iHS| method, were found only when using pairs of populations, that is,
320 a common region was found between Pop-A/B, Pop-A/C, Pop-A/D, Pop-B/C, Pop-B/D and
321 Pop-C/D. No overlap was found among four populations or when using any combination of
322 three. XPEHH detected a higher number of shared regions among populations, specifically
323 in Ssa02, which was common to all 3 tested populations. In addition, shared regions were
324 found in population pairs B/C and Pop-D/C. A greater number of shared regions detected
325 by XPEHH could be explained by a greater power to detect regions that have experienced
326 older selection events (SABETI *et al.* 2007; KLIMENTIDIS *et al.* 2011) than those detectable
327 by |iHS|. Therefore, these regions may be explaining selection signatures that originated
328 before these populations were brought to Chile.

329 **Domestication traits in salmon**

330 Selection signatures found in this study may be involved in some desirable economic traits
331 in salmon production as well as traits that are typically under the effect of domestication.
332 All populations used in this study have been subjected to artificial selection to improve
333 growth rate. According to the functional annotations of the candidate genes, several

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334 biological processes were found to be involved with growth and development, such as the
335 Development process and Regulation of Biological/metabolic processes. Additionally,
336 some of the genes identified have been associated with growth traits in other species; such
337 *sh3rf1* in chicken and cattle (HANOTTE *et al.* 2003; RUBIN *et al.* 2010) or *igf1r*, which was
338 previously found to be a size locus of large effect in dogs (SUTTER *et al.* 2007; HOOPES *et*
339 *al.* 2012). We suggest that these genes may be under selection for improving growth related
340 traits in salmon. On the other hand, we also identified genes such *scaper*, *clstn3* and *pex5*
341 related to mental disorders in humans (GLATT *et al.* 2005; PETTEM *et al.* 2013). Other genes
342 related to behavioral traits have be found in other Atlantic salmon strains, as well (Lopez et
343 al, 2018), suggesting that artificial selection acts on behavioral traits in salmon as in other
344 domestic animals (Clutton-Brock 1999).

345

346 **6. CONCLUSIONS**

347 In the present study, several candidate genomic regions with selection signatures were
348 identified using two haplotype based methods, |iHS| and XPEHH in four populations of
349 Atlantic salmon. These genomic regions harbored important genes that enriched G terms
350 including growth, developmental processes, and have been associated with growth and
351 behavior in other species. These finding improve our understanding of genomic variants
352 undergoing selection in domestic populations of Atlantic salmon.

353

354 **Ethics approval and consent to participate**

355 The sampling protocol was previously approved by The Comité de Bioética Animal,
356 Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile (Certificate N° 29–
357 2014).

358

359 **Consent for publication**

360 Not applicable

361

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362 **Availability of data and material**

363 Genotype data for each population is available from the online digital repository *figshare*
364 https://figshare.com/s/83efa70722ed5ada023a

365

366 **Competing Interest**

367 The authors have no conflicts of interest to declare

368

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372 **Author´s contributions**

373 MEL and JMY conceived the research idea. MEL drafted the manuscript and carried out
374 the analyses. TL supervised the data analyses and contributed to discussion and writing.
375 TL, AN, JPL, RN, and JMY reviewed the manuscript. All authors read and approved the
376 final manuscript.

377

378

379

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Table 1. Mean genetic diversity (Observed heterozygosity and expected heterozygosity) of four Atlantic salmon populations

Population	H_o	H_e
Pop-A	0.38±0.16	0.37±0.15
Pop-B	0.40±0.15	0.39±0.14
Pop-C	0.40±0.14	0.39±0.13
Pop-D	0.46±0.22	0.37±0.16

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Table 2. Number of SNPs identified by |iHS| among populations and chromosomes.

	Pop-A	Pop-B	Pop-C	Pop-D
Ssa01	14	11	2	15
Ssa02	31			
Ssa03				9
Ssa04				1
Ssa05	2	1	5	
Ssa06	1	6		
Ssa07	3			
Ssa08				
Ssa09	6		2	
Ssa10	43	3	6	14
Ssa11			2	
Ssa12	3	7		1
Ssa13	4	16	3	2
Ssa14	4	3	4	4
Ssa15	6	2	1	
Ssa16	1	5	32	
Ssa17				1
Ssa18				
Ssa19		2	15	
Ssa20				18
Ssa21				
Ssa22	2		49	
Ssa23				
Ssa24				15
Ssa25				
Ssa26				54
Ssa27		2		
Ssa28				
Ssa29				
Total	120	58	121	134

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Table 3. SNPs and regions under selection identified by *XPEHH* among population pairs and chromosomes.

	Pop-A/Pop-B		Pop-A/Pop-C		Pop-A/Pop-D	
	SNPs	Regions	SNPs	Regions	SNPs	Regions
Ssa01						
Ssa02	68	3	82	5	17	2
Ssa03						
Ssa04						
Ssa05	11	1			26	3
Ssa06						
Ssa07						
Ssa08						
Ssa09	289	17	71	3	6	1
Ssa10	16	2	571	13	154	4
Ssa11					10	2
Ssa12						
Ssa13						
Ssa14			1		8	1
Ssa15			7	1		
Ssa16			25	1		
Ssa17						
Ssa18						
Ssa19						
Ssa20						
Ssa21						
Ssa22						
Ssa23						
Ssa24	53	4			8	1
Ssa25						
Ssa26					32	1
Ssa27						
Ssa28						
Ssa29			7	2	1	
Total	437	27	764	25	262	15

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Figure legends

Figure 1. Individual assignment probabilities generated with ADMIXTURE (1•K•12). Each color represents a cluster, and the ratio of vertical lines is proportional to assignment probability of and individual to each cluster.

Figure 2. Genome-wide distribution of -log10(p-value) of standardized Integrated Haplotype Score |iHS| among Atlantic salmon populations.

Figure 3. Genome-wide distribution of -log10(p-value) of standardized cross-population extended haplotype homozygosity (XP-EHH) scores in pairwise Atlantic salmon populations.

Figure 4. GO enrichment analysis of genes with evidence of selection in Atlantic salmon. GO functional classification was performed using the DAVID browser.

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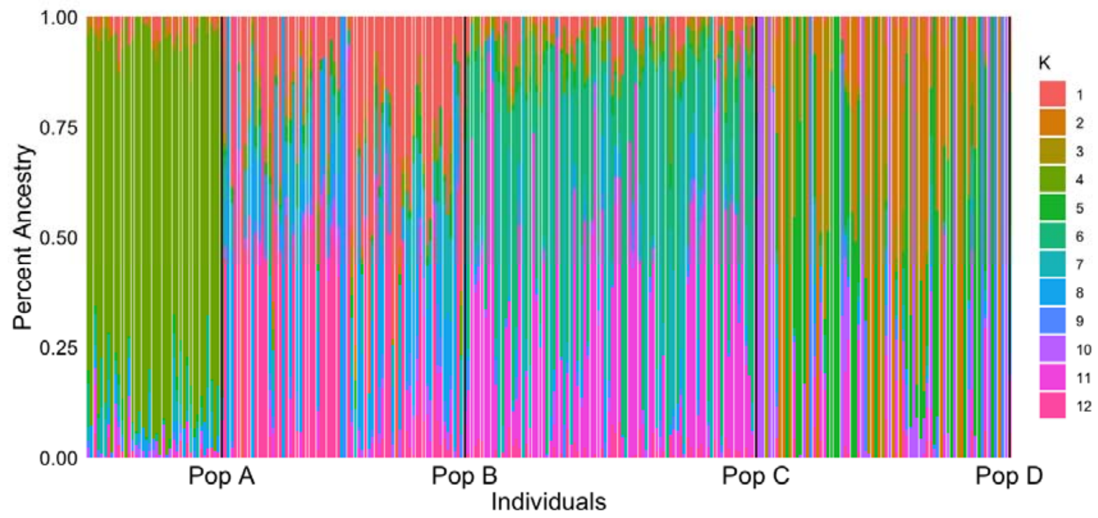
679 **Figure 1**



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709 **Figure 2**
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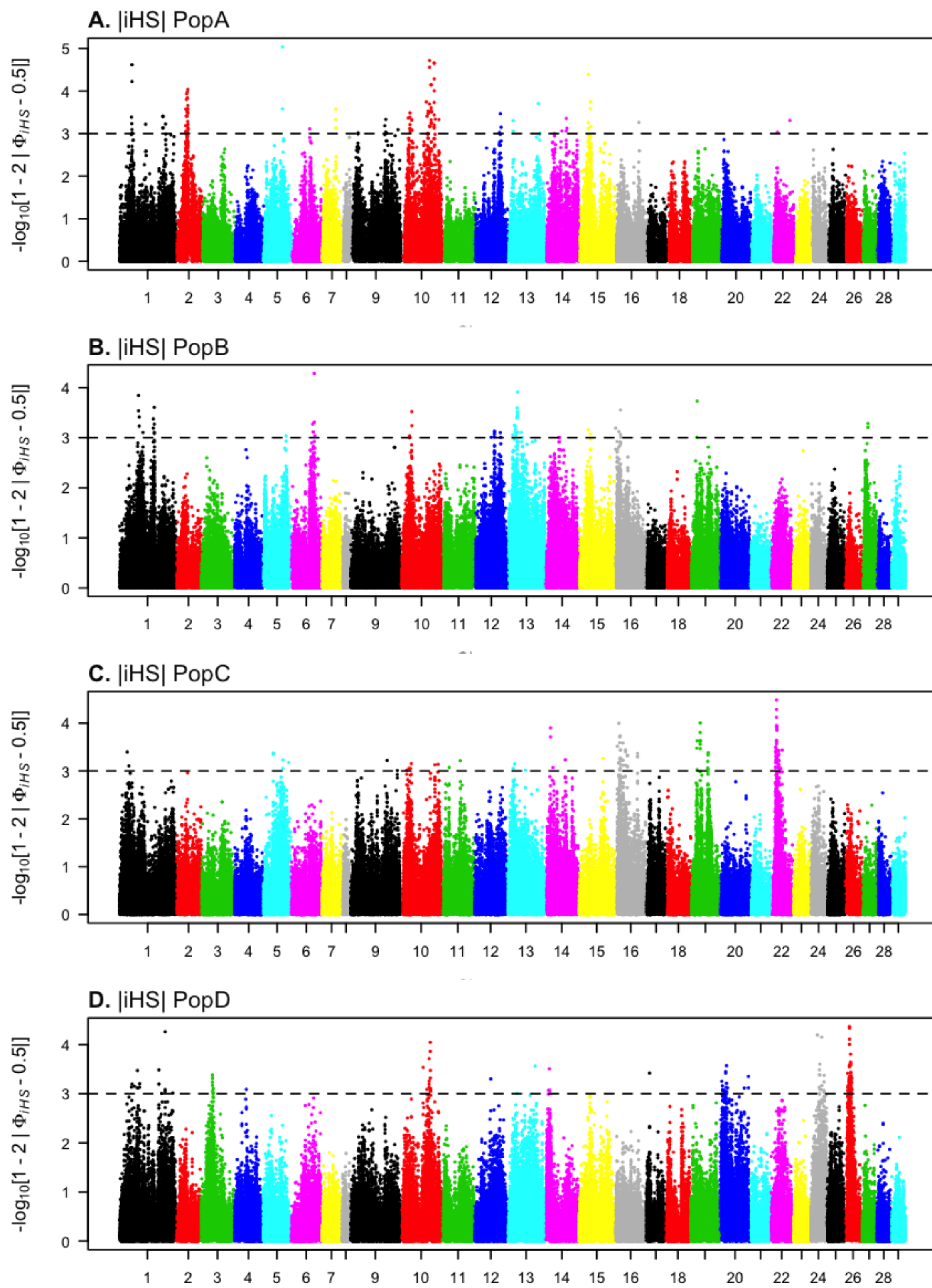

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713 **Figure 3**
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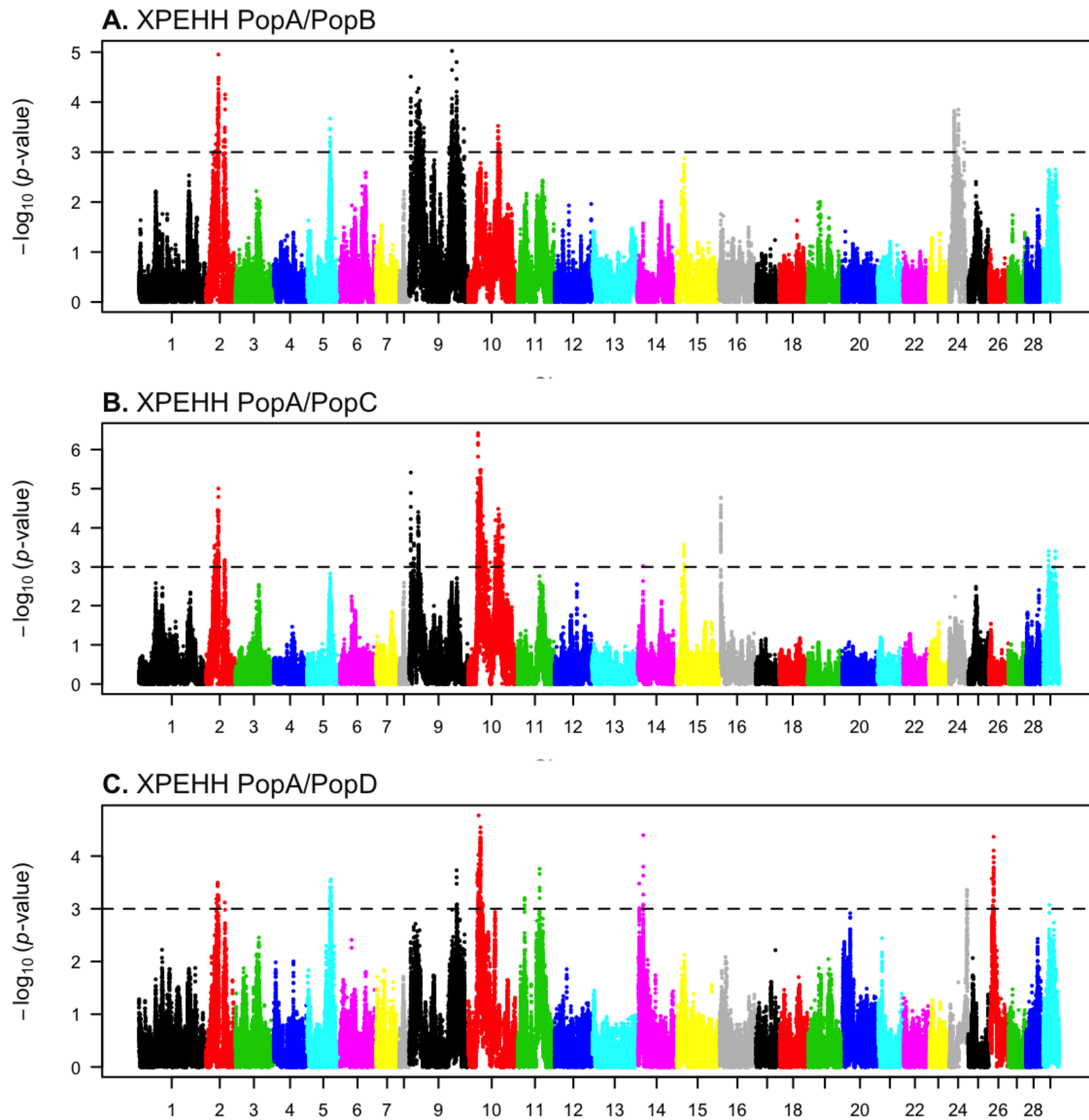

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729 **Figure 4**
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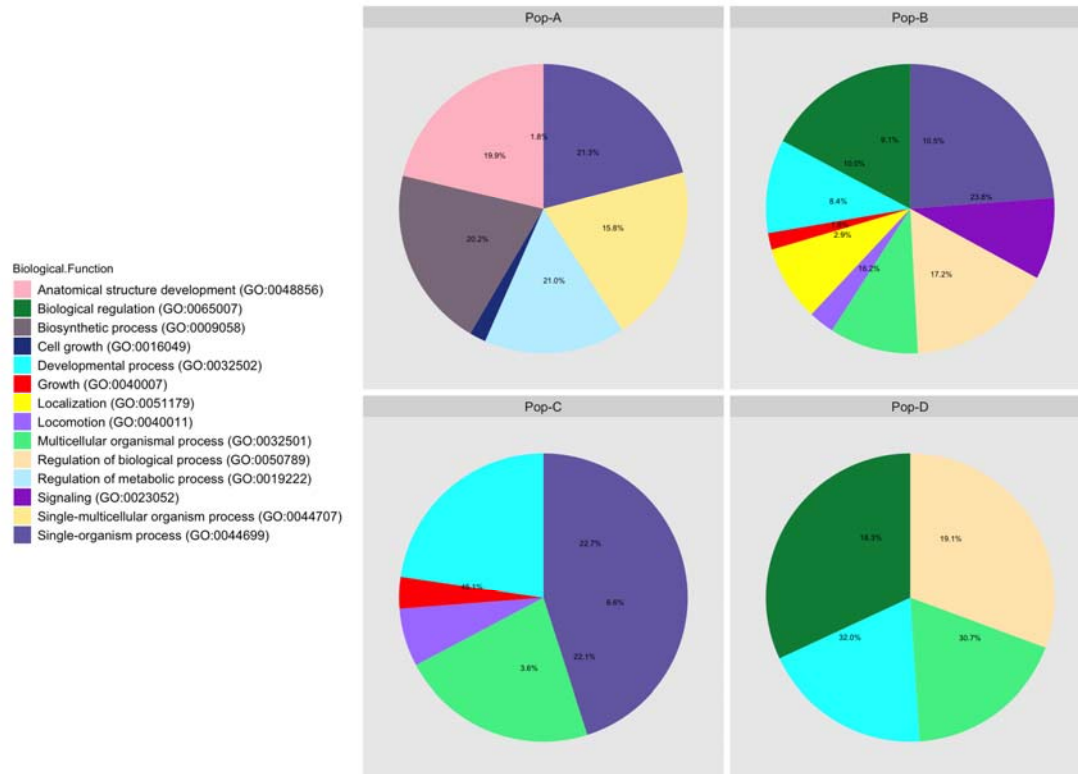

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