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1	Estimates of autozygosity through runs of homozygosity in farmed coho salmon
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11	Abstract - The characterization of runs of homozygosity (ROH), using high-density single
12	nucleotide polymorphisms (SNPs) allows inferences to be made about the past demographic
13	history of animal populations and the genomic ROH has become a common approach to
14	characterize the inbreeding. We aimed to analyze and characterize ROH patterns and
15	compare different genomic and pedigree-based methods to estimate the inbreeding
16	coefficient in two pure lines (POP A and B) and one recently admixed line (POP C) of coho
17	salmon breeding nuclei, genotyped using a 200K Affymetrix Axiom® myDesign Custom
18	SNP Array. A large number and greater mean length of ROH were found for the two "pure"
19	lines and the recently admixed line (POP C) showed the lowest number and smaller mean
20	length of ROH. The ROH analysis for different length classes suggests that all three coho
21	salmon lines the genome is largely composed of a high number of short segments (<4 Mb),
22	and for POP C no segment >16 Mb was found. A high variable number of ROH, mean length
23	and inbreeding values across chromosomes; positively the consequence of artificial selection.
24	Pedigree-based inbreeding values tended to underestimate genomic-based inbreeding levels,

25	which in turn varied depending on the method used for estimation. The high positive
26	correlations between different genomic-based inbreeding coefficients suggest that they are
27	consistent and may be more accurate than pedigree-based methods, given that they capture
28	information from past and more recent demographic events, even when there are no pedigree
29	records available.
30	Keywords: admixture, autozygosity, inbreeding, run of homozygosity, Oncorhynchus
31	kisutch, runs of homozygosity, pedigree
32	
33	1. Introduction
34	Coho salmon (Oncorhynchus kisutch) is one of the six Pacific salmon species which
35	can be found in North America and Asia [1]. In Chile, coho salmon farming began at the end
36	of the 1970s, when about 500,000 eggs were imported from the Kitimat River (British
37	Columbia) and Oregon to start the genetic basis of the Chilean broodstocks [2,3]. The first
38	coho salmon breeding program started in 1992 with rapid growth as the main breeding
39	objective. After four generations of selection for harvest weight, genetic gains of ~10% per
40	generation were reported [2,3].
41	Genetic improvement programs for aquaculture species have been successfully
42	established for increasing the productivity, for traits like growth and resistance against
43	diseases [4,5]. However, one of the negative consequences of selective breeding is the
44	accumulation of inbreeding, due to the use of related individuals for reproductive purposes
45	[6]. As consequence, a reduction in both the additive genetic variance and diversity is
46	observed, as well as a decrease in the response to selection. Furthermore, inbreeding can

47 result in a phenomenon known as inbreeding depression, defined as a reduction in fitness48 traits, including growth, survival and reproductive ability, due to the expression of

detrimental recessive alleles given the existence of highly homozygous animals in the
population [6,7]. Thus, monitoring and managing the inbreeding levels is critical in the
operation of genetic improvement programs [8–10].

52 Inbreeding is traditionally calculated using pedigree records, the estimates might not 53 reflect the true inbreeding level due to 1) the stochastic nature of recombination, 2) the 54 assumption that there are no changes in allele frequencies in time and 3) the persistence of 55 ancestral short segments through time [11]. In addition this approach fails to capture the 56 relatedness among founder animals from the base population [12]. Furthermore, previous 57 studies agreement that errors in pedigrees and incomplete or missing information lead to 58 incorrect or biased inbreeding estimates [13]. The development of genomic technologies, 59 including dense single nucleotide polymorphism (SNP) creates opportunities to estimate 60 inbreeding from genomic-based approaches; for instance, identity by state (IBS) using a 61 genomic relationship matrix [14] or through ROH [15].

ROH are defined as continuous homozygous segments of the individuals' genome 62 63 [16], *i.e.*, genomic regions which have identical haplotypes that are identical by state (IBS), 64 which might be a consequence of not random mating or consanguineous mating [17]. 65 Therefore, ROH can be used for quantifying individual autozygosity that occurs when parents 66 have a common ancestor and pass on segments that are identical by decedent (IBD) to the 67 progeny [18]. ROH may provide a more accurate measure of inbreeding levels, compared to 68 using pedigree records [18,19]. Furthermore, the identification and characterization of ROH 69 can provide insights into population history, structure and demographics over time [18,20]. 70 Long ROH segments are indicative of recent IBD, whereas short segments indicate ancient 71 inbreeding, and the sum of all these segments are suggested to be an accurate estimation of 72 the inbreeding level of an individual [21].

73 Inbreeding studies using genome-wide data were previously reported in humans 74 [16,22,23], cattle [11,19,24–26], swine [27–29], sheep [30], and goats [31]. A recent study 75 reported ROH patterns in rainbow trout populations to show the impact on selection on the 76 genetic diversity in farmed stocks [32]. Studies aimed at ROH pattern characterization and 77 comparisons between coefficients of inbreeding using different approaches are scarce in 78 aquaculture species, due to the necessity of deep and complete pedigree information and 79 dense genomic information. The objectives of this study were: (i) to identify and characterize 80 the ROH patterns in three farmed Chilean coho salmon populations and (ii) to compare 81 estimates of inbreeding coefficients calculated from runs of homozygosity (F_{ROH}), genomic 82 relationship matrix (F_{GRM}), observed and expected number of homozygous genotypes 83 (F_{HOM}), and a pedigree-based relationship matrix (F_{PED}).

84

85 **2. Methods**

86 2.1 Coho salmon populations and genotypes

87 Two independent coho salmon populations, managed in two-year reproductive cycles 88 (POP A and POP B) were used in this study and belong to the Pesquera Antares breeding 89 program established in Chile in 1997. Both populations have undergone nine generations of 90 selection for harvest weight, since 1997 and 1998, POPA and B respectively. In addition, 91 POP C is the progeny produced by mating sires from the seventh and dams from eighth 92 generations of POP A and B, respectively. POP C was generated in 2013 to limit inbreeding 93 levels, as suggested by Yáñez et al. [8]. The reproduction system, fish tagging and selection 94 criteria of POP C were described previously [33,34].

Genomic DNA was extracted from fin clips of 88, 45 and 108 animals from POP A,
B and C, respectively. The samples were genotyped using a 200K Affymetrix Axiom®

97	myDesign Custom SNP Array developed by the EPIC4 coho salmon genome consortium
98	(http://www.epic-4.org) and built by ThermoFisher Scientific (San Diego, USA). More detail
99	about the array design was previously described by Barria et al. [35]. A genotype quality
100	control was performed in Plink v1.09 [36] using the following parameters to exclude
101	markers: Hardy-Weinberg Equilibrium (HWE) <i>p-value</i> < 1e–6, Minor Allele Frequency
102	(MAF) < 0.01 and call rate < 0.90 for genotypes and samples. Furthermore, we retained only
103	the SNP markers that commonly segregated among the three populations.
104	

104

105 2.2 Principal components and admixture analysis

We used the software Plink v1.09 [36] to evaluate the genetic differentiation among the three coho salmon populations through principal component analysis (PCA). The first two PCAs were plotted using R scripts [37]. The population structure was also examined using a hierarchical Bayesian model implemented in STRUCTURE software v.2.3.4 [38]. We used three replicates of K values ranging from 1 to 12, running of 50,000 iterations and burn-in of 20,000 iterations. To choose the best K value we used the posterior probability values [38].

113

114 2.3 Runs of homozygosity

Runs of homozygosity analysis was performed separately for all animals in each population using the R package detectRUNS [39]. The following constraints were applied to ROH detected: (i) the minimum number of SNPs included in a ROH was 50, (ii) the minimum length of a ROH was set at 1 Mb, (iii) the maximum distance between adjacent SNPs was 500 Kb, (iv) maximum missing genotypes allowed were 5, (v) density was at least 1 SNP per 50 kb and (vi) sliding windows approach was used to detect ROH for each genotyped animal

121	at each marker position. ROH were classified into five length classes: 1-2, 2-4, 4-8, 8-16
122	and > 16 Mb, identified as $ROH_{1-2 Mb}$, $ROH_{2-4 Mb}$, $ROH_{4-8 Mb}$, $ROH_{8-16 Mb}$, and $ROH_{>16 Mb}$,
123	respectively.
124	
125	2.4 Inbreeding coefficient
126	We estimated inbreeding coefficients using three different genomic methods and
127	pedigree relationship matrix (FPED). Inbreeding coefficient based on runs of homozygosity
128	(F_{ROH}) was estimated for each animal based on all ROHs (ROH _{ALL}) and the ROH distribution
129	of five different lengths (ROH _{1-2 Mb} , ROH _{2-4 Mb} , ROH _{4-8 Mb} , ROH _{8-16 Mb} , and ROH _{>16 Mb}), as
130	follows [40]:
131	$F_{\rm ROH} = \frac{L_{ROH}}{L_{AUTO}} $ (eq. 1)
132	where L_{ROH} is the sum of ROH lengths and L_{AUTO} is the total length of genome covered by
133	the genome-wide SNP panel used, assumed to be 1685.79 Mb.
134	The F_{HOM} was calculated by computing the number of observed and expected
135	homozygous (hom) genotypes for each sample, as follows:
136	$F_{HOM} = \frac{\text{observed hom expected hom.}}{\text{total observations - expected hom.}} $ (eq. 2)
137	The F _{GRM} was calculated using the genomic relationship matrix (GRM) [14], as
138	follows:
139	$G = \frac{ZZ'}{2\Sigma_{i=1}^{n} p_{i}(1 - p_{i})} $ (eq. 3)
140	where Z is a genotype matrix that contains the $0 - 2p$ values for homozygotes, $1 - 2p$ for
141	heterozygotes, and $2 - 2p$ for opposite homozygotes, p is the allele frequency of SNP <i>i</i> . The

142	diagonal elements of the matrix G represent the relationship of the animal j with itself, thus,
143	the genomic inbreeding coefficient is calculated as $G_{jj} - 1$.
144	Pedigree-based inbreeding coefficients were estimated using the software
145	INBUPGF90 [41]. The pedigree information used was provided by Pesquera Antares
146	breeding program in Chile, for all animals born between 1998 and 2014, 1997 and 2013 and
147	1998 and 2013 for POP A, B and C respectively.
148	Pearson correlation between genomic- and pedigree-based inbreeding coefficients
149	was estimated within population using function cor.test in R [37].
150	
151	3. Results
152	3.1 Quality control and genomic population structure
153	The MAF < 0.01 criteria excluded higher numbers of SNPs (~29.9, 19.7 and 18.5 K
154	for POP A, B and C, respectively), and a number of markers between 3.2K to 14.9K were
155	removed to select only common markers segregating across all three populations (Table 1).
156	Thus, out of the initial 135,500 markers, a total of 102,129 markers passed all the QC filtering
157	steps and were shared among the three populations.
158	In the PCA analysis, the first two eigenvectors, together, accounted for 29.2% of the
159	total genetic variation and revealed three stratified populations (Figure 1). PCA1 included
160	22.15% of the total genetic variation and generated the principal clusters to differentiate the
161	three coho salmon populations, whereas PCA2 explained the variation present within each
162	population.
163	The best K-value for admixture analysis was selected after performing several runs
164	of MCMC for each K-value (ranging from 1 to 12), based on the posterior probability (Pr) of
165	the fitted admixture model to the data with each K-value used (Pr(K)) [38]. The best K-value

166	was suggested to be $K = 11$. These results indicate that POP A and B shared a large proportion
167	of their genome with each other, probably due to the similar origin of the base populations.
168	In addition, Figure 2 indicates a higher admixture level for POP C, due to the recent cross
169	between POP A and B to generate this population.
170	
171	3.2 Distribution of runs of homozygosity
172	We identified ROH in all animals for coho salmon POP A and B, and in 103 out of
173	108 individuals for POP C. A total of 3,250, 1,605, and 273 ROH and an average number of
174	36.93±7.13, 35.65±8.64, 2.65±1.27 ROH per animal were identified for POP A, B and C,
175	respectively. The mean ROH length was 6.47±7.38, 7.172±7.69 and 2.58±2.07 Mb for POP

176 A, B and C, respectively (Table 2) and the longest segment identified was 61.82 Mb, found 177 in chromosome 2 for POP B (Figure S1). The ROH analysis for different length classes 178 suggests that for the three coho salmon populations the genome is mostly composed of a high 179 number of short segments ($ROH_{1-2 Mb}$, $ROH_{2-4 Mb}$). No segment was found for $ROH_{>16Mb}$ in 180 POP C.

181 The number of ROH identified differs between chromosome and population. POP A 182 has the highest number of ROH per chromosome, with more than 150 for chromosomes 183 Okis5, Okis6 and Okis17. For POP B, chromosomes Okis5, Okis18 and Okis19 have more 184 than 100 ROH, whereas for POP C, with the exception of chromosome Okis5, have less than 185 50 per chromosomes (Figure 3). The average ROH length also differs between chromosomes 186 and population. POP A has two chromosomes (Okis5 and Okis11) with ROH segments 187 greater than 10 Mb. POP B has five chromosomes (Okis3, Okis4, Okis6, Okis11 and Okis14) 188 with ROH segments greater than 10 Mb; while all chromosomes in POP C have ROH 189 segments smaller than 7 Mb (Figure 4).

190 Figure 5 shows the relation between the total number of ROH and the total length of 191 ROH for each animal across the three populations. A considerable difference between POP 192 C and POP A or B was found. For POP C, all animals have a small number of ROH (<8) 193 with total length <25 Mb, whereas most individuals in POP A and B have at least 20 ROHs 194 with a total length >100 Mb, with some extreme individuals with segments covering more 195 than 300 Mb. The number of ROHs and segment length per animal and per chromosome are 196 shown in Figure S1. The high number of segments >10 Mb in Okis5, Okis6 and Okis28, 197 especially for POP A and B, suggests recent events of inbreeding, whereas the small 198 segments as in Okis20 for POP A and B, and for most of chromosomes for POP C, suggests 199 more ancient inbreeding.

200

201 *3.3 Genomic- and pedigree-based inbreeding*

202 We used four different methods to estimate the inbreeding coefficient, from the 203 information of 102K markers and pedigree data (Table 3). The average inbreeding coefficient 204 estimated using ROH was different between ROH classes, the values decreased when the 205 ROH length segments increased for all populations. The mean value for FROH_{ALL} was the 206 same for both POP A and B (0.142 and 0.152, respectively), but it was significantly different 207 (p<0.05) for POP C (0.004) when compared to POP A or B. The F_{HOM} resulted in the lowest 208 inbreeding values ranging from -0.036 to -0.105 for POP A and C, respectively. The mean 209 value for F_{GRM} was different (p<0.05) between the three populations, the highest and lowest 210 values were reported for POP B and C, respectively, whereas the F_{PED} value was not different 211 between POP A and B, but was significantly lower for POP C (0.002, p<0.05). Additionally, 212 we calculated the inbreeding coefficient based on the ROH per chromosome (Figure 6). POP 213 A and B had the most chromosomes with inbreeding values higher than 0.2, as in Okis5,

Okis6 and Okis28 for POP A, and Okis5, Okis12, Okis14, Okis18 and Okis26 for POP B,
whereas lower values were found for POP C and for most of the chromosomes the inbreeding
was equal to zero.

217 The Pearson correlation between different genomic methods to estimate the 218 inbreeding coefficient suggested a high positive correlation (>0.82, p<0.001) for POP A and 219 POP B (Figure 7 and 8, respectively). Correlation between different ROH length classes 220 decreased in function with the comparison between shorter and longer segments, e.g. highest 221 correlation between $ROH_{1-2 Mb}$ and $ROH_{2-4 Mb}$ and lowest between $ROH_{1-2 Mb}$ and $ROH_{>16Mb}$. 222 The lowest correlation values among genomic methods was reported between $ROH_{>16Mb}$ and 223 both ROH_{HOM} and ROH_{GRM}. In addition, for POP A and POP B correlation low correlation 224 values were found, respectively, ranging from 0.35 to 0.39 (p<0.01), between genomic 225 methods and FPED.

Different patterns of correlations were observed for POP C, compared to POP A and B, probably due to the low inbreeding level of this recently admixed population. Medium to high positive correlation was reported between the ROH classes (0.54 to 0.94, p<0.001), and a correlation equal to unity was observed between ROH_{HOM} and ROH_{GRM}. For other correlations, small values (ranged from 0.28 to 0.34) or not different from zero were observed (Figure 9).

- 232
- **4. Discussion**
- 234 *4.1 Genomic population structure*

The first two principal components explained more than 29% of the total genetic variation for the three populations studied, which were separated into three different clusters (Figure 1). The admixture results are in agreement with the recent event of hybridization of

POP A and B to generate POP C, where the genetic differentiation between POP A and B may have been be partly generated by differences in the base population, which can have a pronounced effect on allele frequencies [42]. In addition, considering that POP A and B have been independently selected by at least eight generations each, differences in the selection processes, as well as the environmental conditions and drift, may have influenced the differences observed in Figure 2.

244

245 4.2 Runs of homozygosity characterization

246 Figure 3 and 4 show that independent of the population, the ROH patterns seem to be 247 differentially distributed within specific genomic regions, same as the inbreeding values 248 between chromosomes (Figure 6). The highest autozygosity, e.g. in chromosome Okis5 and 249 Okis6 for POP A and B, is likely the consequence of artificial selection [26], considering that 250 these populations have been under genetic selection for harvest weight for at least eight 251 generations. A ROH study in humans [43] suggested that the homozygosity segments are 252 more common in regions with high linkage disequilibrium (LD) and low recombination rates. 253 Thus the highest mean levels of LD found in Okis5 and Okis6 in animals from the same 254 populations [35] are in accordance with the two chromosomes with the highest number of 255 ROH in the present study.

Differences in the number of ROH and segment length was observed within and across populations (Figure 5 and Additional file 1). The higher number of ROH in POP A compared to POP B is most likely due to higher sample size in the former, whereas the differences in ROH length between the three populations may be due to differences in the effective population size, selection intensities, or threshold of inbreeding allowed for the matings, suggesting that artificial selection commonly increases the autozygosity across the

262 genome and creates long ROH in specific regions of the genomes [26]. In contrast, the shorter 263 segments and smaller number of ROH in POP C when compared against both POP A and B 264 may be the result of recent population admixture between these populations. Furthermore, 265 animals from the same population might have the same total ROH lengths but a variable 266 number of segments, which is probably the result of different distances from common 267 ancestors [25]. Interestingly, for both POP A and B, the length class ROH_{2-4 Mb} has more 268 ROH than ROH_{1-2 Mb} (Table 2), which is different than what is commonly found in other 269 species [15,44,45]. These differences can be due to the criteria adopted to identify ROH or 270 an inherent characteristic of these populations. There is no consensus on the best parameters 271 to characterize ROH patterns [32]; thus, here we used the minimum number of 50 SNPs and 272 the length of 1 Mb to define a ROH segment. We chose the current parameters due to the 273 historical demographics of coho salmon in Chile. The ROH_{2-4 Mb} should date from about 20 274 generations ago (approximately 40 years considering the generation interval of 2 years), 275 which corresponds to the introduction of coho salmon in Chile at the end of the 1970s, to 276 begin the establishment of Chilean brood stocks [2,35].

277

278 *4.3 Genomics- and pedigree-based inbreeding*

Based on information of ROH length it is possible to infer the number of generations for inbreeding events [46]. The ROH due to ancient origin tend to be shorter, e.g. $ROH_{1-2 Mb}$, ROH_{2-4 Mb} and ROH_{4-8 Mb} date from 50, 20 and 12.5 generations ago, respectively. In contrast, recent ROH are longer, due to the small probability of breaking down the segments that are identical-by-descent (IBD) by means of recombination events. Thus, the ROH_{8-16 Mb} and ROH_{>16 Mb} are dated to 6 and 3 generations ago, respectively [22,46]. For both POP A and B

285 it was possible to identify short and long segments in most of the animals analyzed, whereas 286 in the POP C a small number of animals (n = 7) presented ROH_{8-16 Mb} and none ROH_{>16 Mb}. 287 In recent years, some studies have investigated different genomic methods to estimate 288 inbreeding coefficients in cattle [12,25,26,45,47,48], pigs [27,28,49,50], goats [51–53] and 289 rainbow trout [32]. However, this is the first study aimed at characterizing the ROH patterns 290 and comparing different genomic- and pedigree-based methods to estimate inbreeding 291 coefficients in farmed coho salmon populations. Both genomic- and pedigree-based 292 strategies have some advantages and disadvantages. The pedigree inbreeding coefficient, is 293 a simple method that requires recording genealogy information, but does not account for the 294 autozygosity differences among animals with the same inbreeding history. In contrast, 295 genomic inbreeding can measure the realized inbreeding of an individual and incorporate the 296 breeding history of the animal, including new mutations, ancient and contemporary 297 inbreeding [27].

298 A comparison of inbreeding coefficients, showed F_{GRM} gave the highest values, 299 especially for B and C, probably because the alleles IBD and identical by state (IBS) are not 300 differentiated for F_{GRM} [12]. This result is in agreement with results previously found in 301 humans, cattle, and simulation studies [12,15,16]. F_{HOM} resulted in negative inbreeding 302 values for all populations (Table 3), suggesting that the individuals have lower levels of 303 homozygosity than expected in the reference population under Hardy-Weinberg equilibrium 304 [54] and underestimated values should be expected [55]. The FPED for POP A and POP B 305 were smaller than values estimated using FROH_{ALL} and F_{GRM}, but are in accordance with the 306 values estimated for the same populations using previous generations [8,10]. The F_{PED} can 307 be easily underestimated when pedigree information of less than 20 generations is used [55]. 308 The difference between F_{ROH} and F_{PED} could be also due to the unknown pedigree

information before recording, which in practical terms means that inbreeding levels forfounding animals were not zero.

- 311
- 312 4.4 Inbreeding coefficients correlations

ROH can be identified for each animal, and the inbreeding coefficient will reflect the direct level of homozygosity, not influenced by allele frequencies [19]. Also with regard to information about recent and remote inbreeding [56]. High correlations (>0.80) were found between FROH and other genomic inbreeding estimates for POP A and B (Figure 7 and 8). Some authors have also reported a strong or moderate correlation between genomics methods used to calculate inbreeding coefficients for different species [11,27,57,58].

319 The genomic-based inbreeding method correlated moderately or poorly with pedigree 320 data, showing values lower than 0.39 (Figure 7 to 9). Similary weak or no correlation was 321 reported for cattle [24,45,47], whereas a moderate to strong positive correlation was 322 described by some authors [15,40,48,59]. An increase in the correlation between genomic-323 and pedigree-based inbreeding as the pedigree depth increases is expected [24]. Here we used 324 the complete pedigree information of nine generations for both POP A and POP B, whereas 325 for POC C a pedigree depth of eight generations was used. In a previous pedigree-based inbreeding study using the same broodstock population of POP A (7th generation) and POP 326 327 B (8th generation), an increasing tendency for inbreeding values in the last four generations 328 was reported for both populations [8] and a continued inbreeding accumulation until 9th 329 generation used in our study is well-known. Thus, we expected a higher correlation between 330 long ROH segments (ROH_{8-16 Mb}, and ROH_{>16 Mb}) and F_{PED} values. The weak or no 331 correlation may be explained by the depth of pedigree records [55], incorrect or incomplete 332 pedigree information [47], the F_{PED} that assumed the founder individuals are unrelated [12],

333 and the fact that FPED does not consider the stochastic nature of recombination and the 334 persistence of ancestral short segments through time, due to the lack of recombination in 335 specific regions [11]. These facts suggest that the F_{PED} may not reflect true inbreeding values. 336 Additionally, the population sample size must be representative to avoid population 337 stratification [15,24] and to improve the correlation between genomic- and pedigree-based 338 inbreeding However, in our case, POP B is the population with the smallest sample size (n = 1)339 45), but was the only one that resulted in significant correlations (Figure 8). Various studies 340 of ROH used similar or smaller sample size in livestock species and rainbow-trout 341 [19,32,44,48].

342 A relatively large effective population size (Ne) is recommended to maintain the 343 control of inbreeding in the medium-term. However, decline in the historical Ne was reported 344 for animals from the same population as POP A [35]. The reduction may be due to the 345 prioritization of genetic gain using high selection pressure without putting strong control on 346 the family contribution for each generation [8]. Consequently, mating close relatives is more 347 probable, which results in a high level of inbreeding and the creation of long ROH segments 348 for both POP A and B. Therefore, to increase the effective population size and to limit the 349 inbreeding level [8], POP C was generated. According to our results, this strategy was 350 effective in reducing the inbreeding levels and changing the patterns of ROH, clearly 351 differentiating from POP A and B. These results are in accordance with some studies 352 [15,48,60,61] that suggest that high heterogeneity populations due admixture or 353 crossbreeding lines contributed to the breakdown of long homozygous segments and reduced 354 the inbreeding levels in captive populations.

355

5. Conclusion

357	In this study, we found different numbers and lengths of runs of homozygosity in
358	three coho salmon populations farmed in Chile. Moreover, the inbreeding coefficient
359	estimated using genomic- or pedigree-based methods have varied among populations and the
360	high correlations between genomic inbreeding methods suggest that these are the more
361	accurate methods to estimate autozygosity levels and thus must be used as an alternative
362	when pedigree information is inaccurate, incomplete or unavailable.
0.40	

363

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- 368

369 Authors' contributions

GMY performed the analysis and wrote the initial version of the manuscript. PC and RMN
contribute with writing. BK develop the chip array. JMY conceived and designed the study;
contributed to the discussion and writing. All authors have reviewed and approved the
manuscript.

374

375 Competing interests

376 The authors declare that the research was conducted in the absence of any commercial377 or financial relationships that could be construed as a potential conflict of interest.

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References

- Groot, C. (Cornelis); Margolis, L. *Pacific salmon life histories*; UBC Press, 1991; ISBN 9780774803595.
- Neira, R.; Lhorente, J.P.; Yáñez, J.M.; Araneda, M.; Filp, M. Evolution of Coho Salmon (Oncorhynchus kisutch) Breeding Programs. In Proceedings of the 10th World Congress of Genetics Applied to Livestock Production; Vancouver, 2010; pp. 1–6.
- Lhorente, J.P.; Araneda, M.; Neira, R.; Yáñez, J.M. Advances in genetic improvement for salmon and trout aquaculture: the Chilean situation and prospects. *Rev. Aquac.* 2019, *11*, 340–353.
- 4. Gjedrem, T. Genetic improvement of cold-water fish species. *Aquac. Res.* **2000**, *31*, 25–33.
- Gjedrem, T.; Robinson, N.; Rye, M. The importance of selective breeding in aquaculture to meet future demands for animal protein: A review. *Aquaculture* 2012, 350–353, 117–129.
- Howard, J.T.; Pryce, J.E.; Baes, C.; Maltecca, C. Invited review: Inbreeding in the genomics era: Inbreeding, inbreeding depression, and management of genomic variability. *J. Dairy Sci.* 2017, *100*, 6009–6024.
- Gallardo, A.; Garcı, X.; Paul, J.; Neira, R. Inbreeding and inbreeding depression of female reproductive traits in two populations of Coho salmon selected using BLUP predictors of breeding values. 2004, 234, 111–122.
- Yáñez, J.M.; Bassini, L.N.; Filp, M.; Lhorente, J.P.; Ponzoni, R.W.; Neira, R. Inbreeding and effective population size in a coho salmon (Oncorhynchus kisutch) breeding nucleus in Chile. *Aquaculture* 2014, 420–421, S15–S19.

- Ponzoni, R.W.; Khaw, H.L.; Nguyen, N.H.; Hamzah, A. Inbreeding and effective population size in the Malaysian nucleus of the GIFT strain of Nile tilapia (Oreochromis niloticus). *Aquaculture* 2010, 302, 42–48.
- Yoshida, G.M.; Yáñez, J.M.; de Oliveira, C.A.L.; Ribeiro, R.P.; Lhorente, J.P.; de Queiroz, S.A.; Carvalheiro, R. Mate selection in aquaculture breeding using differential evolution algorithm. *Aquac. Res.* 2017, 48.
- Ferenčaković, M.; Hamzić, E.; Gredler, B.; Solberg, T.R.; Klemetsdal, G.; Curik, I.;
 Sölkner, J. Estimates of autozygosity derived from runs of homozygosity: empirical evidence from selected cattle populations. *J. Anim. Breed. Genet.* 2013, *130*, 286–293.
- Forutan, M.; Ansari Mahyari, S.; Baes, C.; Melzer, N.; Schenkel, F.S.; Sargolzaei, M. Inbreeding and runs of homozygosity before and after genomic selection in North American Holstein cattle. *BMC Genomics* 2018, *19*, 98.
- Cassell, B.G.; Adamec, V.; Pearson, R.E. Effect of Incomplete Pedigrees on Estimates of Inbreeding and Inbreeding Depression for Days to First Service and Summit Milk Yield in Holsteins and Jerseys. *J. Dairy Sci.* 2003, 86, 2967–2976.
- VanRaden, P.M. Efficient Methods to Compute Genomic Predictions. J. Dairy Sci.
 2008, 91, 4414–4423.
- Marras, G.; Gaspa, G.; Sorbolini, S.; Dimauro, C.; Ajmone-Marsan, P.; Valentini, A.;
 Williams, J.L.; Macciotta, N.P.P. Analysis of runs of homozygosity and their relationship with inbreeding in five cattle breeds farmed in Italy. *Anim. Genet.* 2015, 46, 110–121.
- McQuillan, R.; Leutenegger, A.-L.; Abdel-Rahman, R.; Franklin, C.S.; Pericic, M.; Barac-Lauc, L.; Smolej-Narancic, N.; Janicijevic, B.; Polasek, O.; Tenesa, A.; et al. Runs of Homozygosity in European Populations. *Am. J. Hum. Genet.* 2008, *83*, 359–

372.

- Brüniche-Olsen, A.; Kellner, K.F.; Anderson, C.J.; DeWoody, J.A. Runs of homozygosity have utility in mammalian conservation and evolutionary studies. *Conserv. Genet.* 2018, 19, 1295–1307.
- Peripolli, E.; Munari, D.P.; Silva, M.V.G.B.; Lima, A.L.F.; Irgang, R.; Baldi, F. Runs of homozygosity: current knowledge and applications in livestock. *Anim. Genet.* 2017, 48, 255–271.
- Signer-Hasler, H.; Burren, A.; Neuditschko, M.; Frischknecht, M.; Garrick, D.;
 Stricker, C.; Gredler, B.; Bapst, B.; Flury, C. Population structure and genomic inbreeding in nine Swiss dairy cattle populations. *Genet. Sel. Evol.* 2017, 49, 83.
- MacLeod, I.M.; Larkin, D.M.; Lewin, H.A.; Hayes, B.J.; Goddard, M.E. Inferring demography from runs of homozygosity in whole-genome sequence, with correction for sequence errors. *Mol. Biol. Evol.* 2013, *30*, 2209–23.
- Sams, A.J.; Boyko, A.R. Fine-Scale Resolution of Runs of Homozygosity Reveal Patterns of Inbreeding and Substantial Overlap with Recessive Disease Genotypes in Domestic Dogs. *G3 (Bethesda)*. 2019, *9*, 117–123.
- Kirin, M.; McQuillan, R.; Franklin, C.S.; Campbell, H.; McKeigue, P.M.; Wilson, J.F. Genomic Runs of Homozygosity Record Population History and Consanguinity. *PLoS One* 2010, *5*, e13996.
- Nothnagel, M.; Lu, T.T.; Kayser, M.; Krawczak, M. Genomic and geographic distribution of SNP-defined runs of homozygosity in Europeans. *Hum. Mol. Genet.* 2010, 19, 2927–35.
- 24. Gurgul, A.; Szmatoła, T.; Topolski, P.; Jasielczuk, I.; Żukowski, K.; Bugno-Poniewierska, M. The use of runs of homozygosity for estimation of recent inbreeding

in Holstein cattle. J. Appl. Genet. 2016, 57, 527-530.

- Mészáros, G.; Boison, S.A.; Pérez O'Brien, A.M.; Ferenčaković, M.; Curik, I.; Da Silva, M.V.B.; Utsunomiya, Y.T.; Garcia, J.F.; Sölkner, J. Genomic analysis for managing small and endangered populations: a case study in Tyrol Grey cattle. *Front. Genet.* 2015, 6, 173.
- Kim, E.-S.; Cole, J.B.; Huson, H.; Wiggans, G.R.; Van Tassell, C.P.; Crooker, B.A.;
 Liu, G.; Da, Y.; Sonstegard, T.S. Effect of Artificial Selection on Runs of Homozygosity in U.S. Holstein Cattle. *PLoS One* 2013, *8*, e80813.
- 27. Gomez-Raya, L.; Rodríguez, C.; Barragán, C.; Silió, L. Genomic inbreeding coefficients based on the distribution of the length of runs of homozygosity in a closed line of Iberian pigs. *Genet. Sel. Evol.* **2015**, *47*, 81.
- Xu, Z.; Sun, H.; Zhang, Z.; Zhao, Q.; Olasege, B.S.; Li, Q.; Yue, Y.; Ma, P.; Zhang, X.; Wang, Q.; et al. Assessment of Autozygosity Derived From Runs of Homozygosity in Jinhua Pigs Disclosed by Sequencing Data. *Front. Genet.* 2019, *10*, 274.
- Ai, H.; Huang, L.; Ren, J. Genetic Diversity, Linkage Disequilibrium and Selection Signatures in Chinese and Western Pigs Revealed by Genome-Wide SNP Markers. *PLoS One* 2013, 8, e56001.
- Beynon, S.E.; Slavov, G.T.; Farré, M.; Sunduimijid, B.; Waddams, K.; Davies, B.; Haresign, W.; Kijas, J.; MacLeod, I.M.; Newbold, C.J.; et al. Population structure and history of the Welsh sheep breeds determined by whole genome genotyping. *BMC Genet.* 2015, 16.
- 31. Manunza, A.; Noce, A.; Serradilla, J.M.; Goyache, F.; Martínez, A.; Capote, J.; Delgado, J.V.; Jordana, J.; Muñoz, E.; Molina, A.; et al. A genome-wide perspective

about the diversity and demographic history of seven Spanish goat breeds. *Genet. Sel. Evol.* **2016**, *48*.

- 32. D'Ambrosio, J.; Phocas, F.; Haffray, P.; Bestin, A.; Brard-Fudulea, S.; Poncet, C.; Quillet, E.; Dechamp, N.; Fraslin, C.; Charles, M.; et al. Genome-wide estimates of genetic diversity, inbreeding and effective size of experimental and commercial rainbow trout lines undergoing selective breeding. *Genet. Sel. Evol.* **2019**, *51*, 26.
- Yañez, J.M.; Bangera, R.; Lhorente, J.P.; Oyarzún, M.; Neira, R. Quantitative genetic variation of resistance against Piscirickettsia salmonis in Atlantic salmon (Salmo salar). *Aquaculture* 2013, 414–415, 155–159.
- 34. Yáñez, J.M.; Lhorente, J.P.; Bassini, L.N.; Oyarzún, M.; Neira, R.; Newman, S. Genetic co-variation between resistance against both Caligus rogercresseyi and Piscirickettsia salmonis, and body weight in Atlantic salmon (Salmo salar). *Aquaculture* 2014, 433, 295–298.
- 35. Barria, A.; Christensen, K.A.; Yoshida, G.; Jedlicki, A.; Leong, J.S.; Rondeau, E.B.; Lhorente, J.P.; Koop, B.F.; Davidson, W.S.; Yáñez, J.M. Whole genome linkage disequilibrium and effective population size in a coho salmon (Oncorhynchus kisutch) breeding population using a high density SNP array. *Front. Genet.* **2019**, *10*, 498.
- Purcell, S.; Neale, B.; Todd-Brown, K.; Thomas, L.; Ferreira, M.A.R.; Bender, D.; Maller, J.; Sklar, P.; de Bakker, P.I.W.; Daly, M.J.; et al. PLINK: A tool set for wholegenome association and population-based linkage analyses. *Am. J. Hum. Genet.* 2007, *81*, 559–575.
- R Core Team R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2015. 2016.
- 38. Pritchard, J.K.; Stephens, M.; Rosenberg, N.A.; Donnelly, P. Association Mapping in

Structured Populations. Am. J. Hum. Genet. 2000, 67, 170-181.

- Biscarini, F.; Cozzi, P.; Gaspa, G.; Marras, G. Detect Runs of Homozygosity and Runs of Heterozygosity in Diploid Genomes 2018.
- McQuillan, R.; Leutenegger, A.-L.; Abdel-Rahman, R.; Franklin, C.S.; Pericic, M.;
 Barac-Lauc, L.; Smolej-Narancic, N.; Janicijevic, B.; Polasek, O.; Tenesa, A.; et al.
 Runs of Homozygosity in European Populations. *Am. J. Hum. Genet.* 2008, *83*, 359–372.
- 41. Legarra, A.; Aguilar, I.; Misztal, I. A relationship matrix including full pedigree and genomic information. *J. Dairy Sci.* **2009**, *92*, 4656–4663.
- 42. Allendorf, F.W.; Phelps, S.R. Loss of Genetic Variation in a Hatchery Stock of Cutthroat Trout. *Trans. Am. Fish. Soc.* **1980**, *109*, 537–543.
- 43. Gibson, J.; Morton, N.E.; Collins, A. Extended tracts of homozygosity in outbred human populations. *Hum. Mol. Genet.* **2006**, *15*, 789–795.
- 44. Goszczynski, D.; Molina, A.; Terán, E.; Morales-Durand, H.; Ross, P.; Cheng, H.; Giovambattista, G.; Demyda-Peyrás, S. Runs of homozygosity in a selected cattle population with extremely inbred bulls: Descriptive and functional analyses revealed highly variable patterns. *PLoS One* **2018**, *13*, e0200069.
- 45. Peripolli, E.; Stafuzza, N.B.; Munari, D.P.; Lima, A.L.F.; Irgang, R.; Machado, M.A.; Panetto, J.C. do C.; Ventura, R.V.; Baldi, F.; da Silva, M.V.G.B. Assessment of runs of homozygosity islands and estimates of genomic inbreeding in Gyr (Bos indicus) dairy cattle. *BMC Genomics* 2018, 19, 34.
- 46. Broman, K.W.; Weber, J.L. Long Homozygous Chromosomal Segments in Reference Families from the Centre d'Étude du Polymorphisme Humain. *Am. J. Hum. Genet.* 1999, 65, 1493–1500.

- 47. Zhang, Q.; Calus, M.P.; Guldbrandtsen, B.; Lund, M.S.; Sahana, G. Estimation of inbreeding using pedigree, 50k SNP chip genotypes and full sequence data in three cattle breeds. *BMC Genet.* **2015**, *16*, 88.
- 48. Purfield, D.C.; Berry, D.P.; McParland, S.; Bradley, D.G. Runs of homozygosity and population history in cattle. *BMC Genet.* **2012**, *13*, 70.
- Zhang, Z.; Zhang, Q.; Xiao, Q.; Sun, H.; Gao, H.; Yang, Y.; Chen, J.; Li, Z.; Xue, M.;
 Ma, P.; et al. Distribution of runs of homozygosity in Chinese and Western pig breeds evaluated by reduced-representation sequencing data. *Anim. Genet.* 2018, 49, 579– 591.
- 50. Howard, J.T.; Tiezzi, F.; Huang, Y.; Gray, K.A.; Maltecca, C. Characterization and management of long runs of homozygosity in parental nucleus lines and their associated crossbred progeny. *Genet. Sel. Evol.* **2016**, *48*, 91.
- Cardoso, T.F.; Amills, M.; Bertolini, F.; Rothschild, M.; Marras, G.; Boink, G.; Jordana, J.; Capote, J.; Carolan, S.; Hallsson, J.H.; et al. Patterns of homozygosity in insular and continental goat breeds. *Genet. Sel. Evol.* 2018, *50*, 56.
- 52. Bertolini, F.; Cardoso, T.F.; Marras, G.; Nicolazzi, E.L.; Rothschild, M.F.; Amills, M. Genome-wide patterns of homozygosity provide clues about the population history and adaptation of goats. *Genet. Sel. Evol.* **2018**, *50*, 59.
- Onzima, R.B.; Upadhyay, M.R.; Doekes, H.P.; Brito, L.F.; Bosse, M.; Kanis, E.; Groenen, M.A.M.; Crooijmans, R.P.M.A. Genome-Wide Characterization of Selection Signatures and Runs of Homozygosity in Ugandan Goat Breeds. *Front. Genet.* 2018, 9, 318.
- 54. Wang, J. Marker-based estimates of relatedness and inbreeding coefficients: an assessment of current methods. *J. Evol. Biol.* **2014**, *27*, 518–530.

- 55. Kardos, M.; Luikart, G.; Allendorf, F.W. Measuring individual inbreeding in the age of genomics: marker-based measures are better than pedigrees. *Heredity (Edinb)*.
 2015, 115, 63–72.
- 56. Curik, I.; Ferenčaković, M.; Sölkner, J. Inbreeding and runs of homozygosity: A possible solution to an old problem. *Livest. Sci.* **2014**, *166*, 26–34.
- 57. Mastrangelo, S.; Tolone, M.; Di Gerlando, R.; Fontanesi, L.; Sardina, M.T.; Portolano,
 B. Genomic inbreeding estimation in small populations: evaluation of runs of homozygosity in three local dairy cattle breeds. *animal* 2016, *10*, 746–754.
- Sumreddee, P.; Toghiani, S.; Hay, E.H.; Roberts, A.; Agrrey, S.E.; Rekaya, R. Inbreeding depression in line Hereford cattle population using pedigree and genomic information. *J. Anim. Sci.* 2019, 97, 1–18.
- Zavarez, L.B.; Utsunomiya, Y.T.; Carmo, A.S.; Neves, H.H.R.; Brien, A.M.P.O.; Curik, I.; Cole, J.B.; Carvalheiro, R.; Feren, M.; Tassell, V.; et al. Assessment of autozygosity in Nellore cows (Bos indicus) through high-density SNP genotypes. 2015, 6, 1–8.
- 60. Howard, J.T.; Tiezzi, F.; Huang, Y.; Gray, K.A.; Maltecca, C. Characterization and management of long runs of homozygosity in parental nucleus lines and their associated crossbred progeny. *Genet. Sel. Evol.* **2016**, *48*, 91.
- 61. Bertolini, F.; Cardoso, T.F.; Marras, G.; Nicolazzi, E.L.; Rothschild, M.F.; Amills, M. Genome-wide patterns of homozygosity provide clues about the population history and adaptation of goats. *Genet. Sel. Evol.* **2018**, *50*, 59.

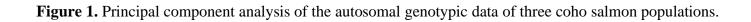
 Table 1. Number of runs of homozygosity (nROH), length (Mb) and standard deviation (SD in Mb) considered all ROH and by classes

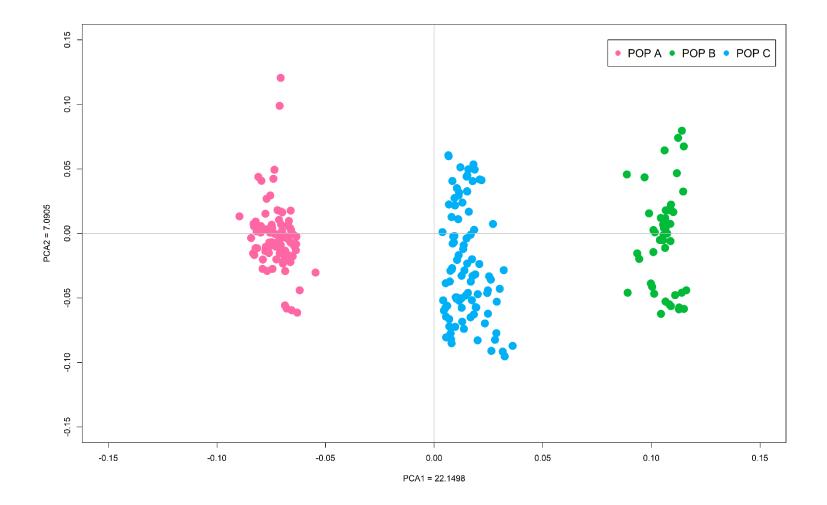
 and for each salmon coho population.

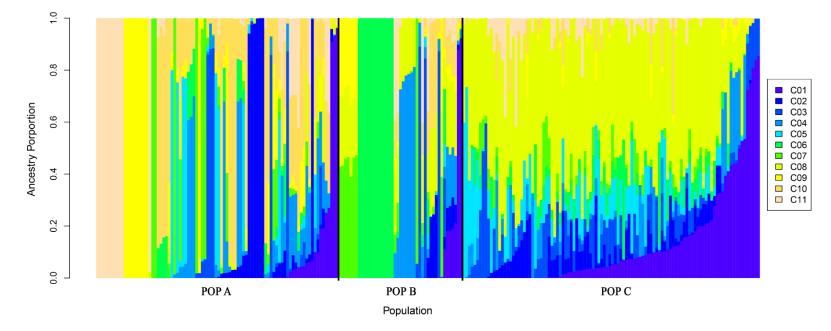
Class	POP A			POP B			POP C		
Class	nROH	Mean length	SD	nROH	Mean length	SD	nROH	Mean length	SD
ROHALL	3568	5.965	7.23	1624	6.695	7.668	495	3.319	3.921
ROH _{1-2 Mb}	1165	1.284	0.389	468	1.286	0.370	298	1.193	0.360
ROH _{2-4 Mb}	937	2.886	0.577	400	2.831	0.530	86	2.869	0.550
ROH _{4-8 Mb}	680	5.585	1.069	310	5.547	1.015	74	5.337	1.170
ROH _{8-16 Mb}	463	11.308	2.323	260	11.427	2.248	24	11.722	1.884
ROH>16 Mb	323	24.925	7.676	186	23.916	8.249	13	20.443	4.056

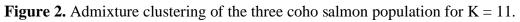
Table 2. Number of individuals (n), estimated of mean and standard deviation (SD) of inbreeding coefficient using runs of homozygosity (ROH) for different ROH length, based on excess of homozygosity (F_{HOM}), genomic relationship matrix (F_{GRM}) and pedigree-based relationship matrix (F_{PED}),

Class	POP A			POP B				POP C		
Class	n	Mean	SD	n	Mean	SD	n	Mean	SD	
ROHALL	88	0.143	0.038	45	0.143	0.062	108	0.009	0.002	
ROH _{1-2 Mb}	88	0.120	0.143	45	0.143	0.061	102	0.009	0.022	
ROH _{2-4 Mb}	88	0.113	0.133	41	0.142	0.053	51	0.009	0.024	
ROH _{4-8 Mb}	88	0.100	0.115	43	0.126	0.050	42	0.011	0.026	
ROH _{8-16 Mb}	86	0.081	0.090	41	0.107	0.042	11	0.030	0.035	
ROH>16 Mb	88	0.051	0.056	41	0.064	0.036	4	0.039	0.025	
F _{HOM}	88	-0.036	0.048	41	-0.058	0.082	108	-0.106	0.028	
F _{GRM}	88	0.145 ^b	0.037	45	0.193 ^a	0.040	108	0.051 ^c	0.009	
F _{PED}	88	0.071	0.021	45	0.081	0.014	108	0.000	0.000	









Each vertical line represent an animal and the black vertical lines were used to separate different populations.

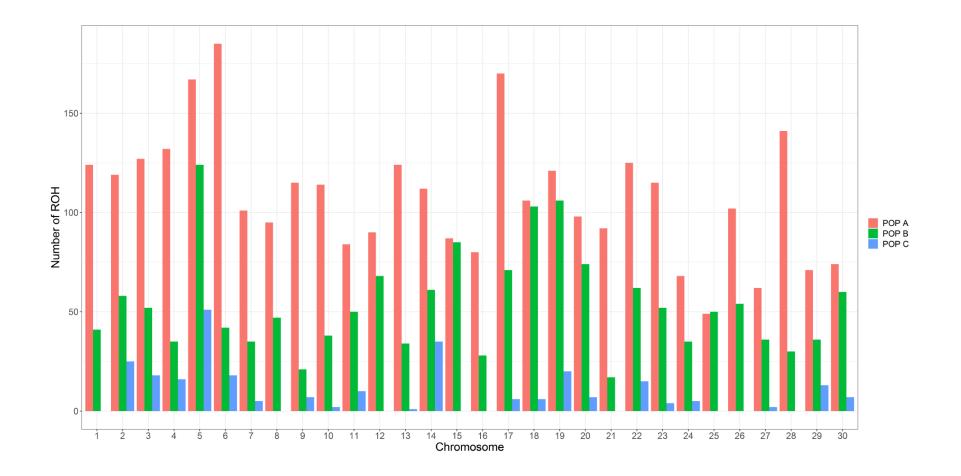


Figure 3. Distribution of number of runs of homozygosity (ROH) for each chromosome in three coho salmon populations.

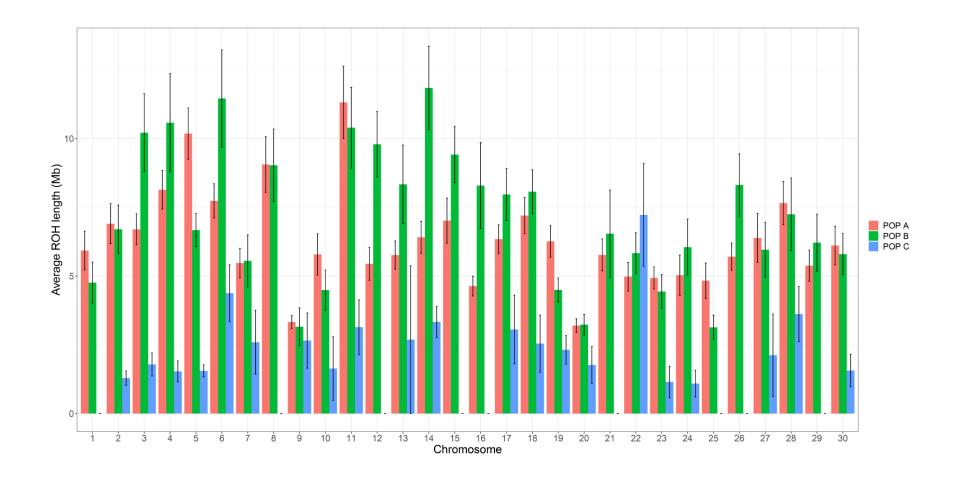
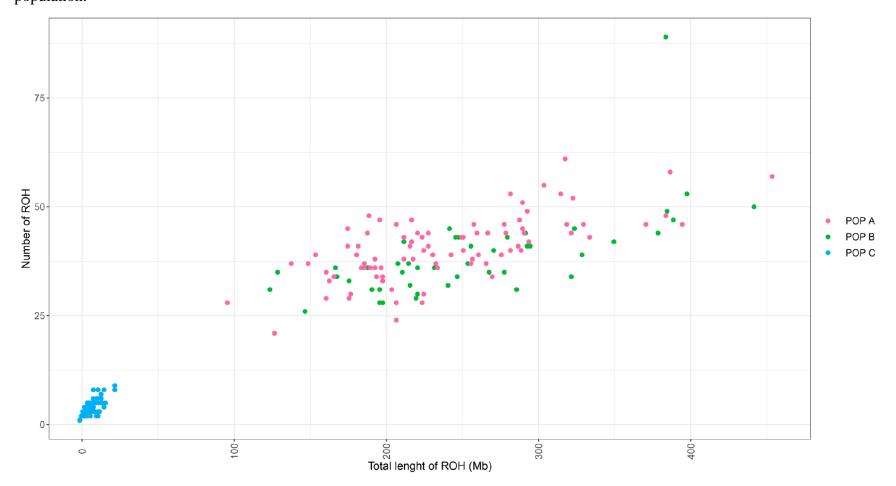


Figure 4. Average runs of homozygosity (ROH) length and standard error bars for each chromosome in three coho salmon populations.

Figure 5. Relationship between the number of runs of homozygosity (ROH) and total length of ROH (Mb) per individual from each population.



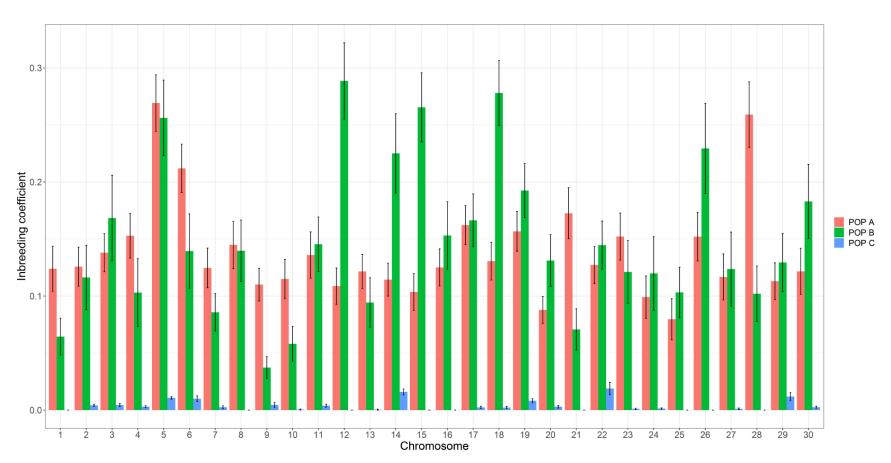


Figure 6. Distribution of inbreeding coefficients estimated using runs of homozygosity (ROH) for each chromosome in three coho salmon populations. Standard error bars were computed among individuals from the same population.

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Figure 7. Scatterplots (lower panel) and Pearson correlations (upper panel) of genomic inbreeding coefficients using runs of homozygosity (ROH) for different ROH length, based on excess of homozygosity (F_{HOM}), genomic relationship matrix (F_{GRM}) and pedigree-based relationship matrix (F_{PED}) for POP A.

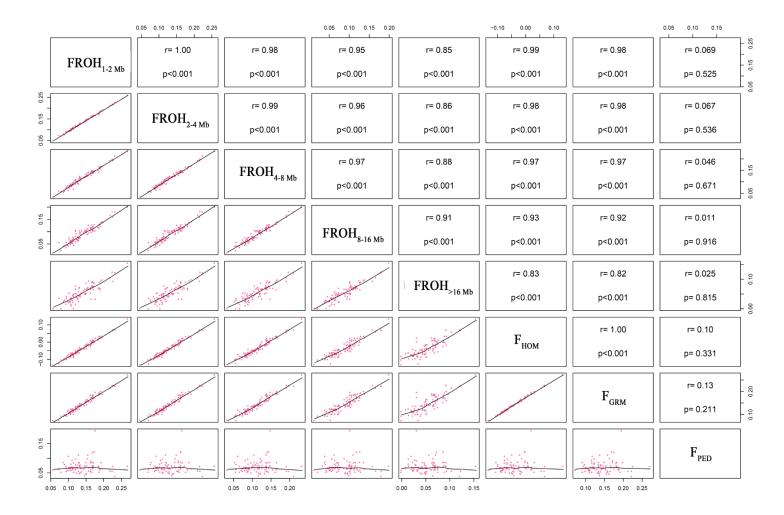


Figure 8. Scatterplots (lower panel) and Pearson correlations (upper panel) of genomic inbreeding coefficients using runs of homozygosity (ROH) for different ROH length, based on excess of homozygosity (F_{HOM}), genomic relationship matrix (F_{GRM}) and pedigree-based relationship matrix (F_{PED}) for POP B.

		0.10 0.15 0.20 0.25		0.05 0.10 0.15 0.20		-0.15 -0.05 0.05		0.00 0.04 0.08	_
	r= 1		r= 0.99	r= 0.94	r= 0.83	r= 0.98	r= 0.99	r= 0.37	0.20
	FROH _{1-2 Mb}	p<0.001	p<0.001	p<0.001	p<0.001	p<0.001	p<0.001	p= 0.012	0.10
0.20	and the second second	FROH _{2-4 Mb}	r= 0.99	r= 0.95	r= 0.84	r= 0.98	r= 0.98	r= 0.36	
0.10		1 KOI1 _{2-4 Mb}	p<0.001	p<0.001	p<0.001	p<0.001	p<0.001	p= 0.014	
	at the second	and with the second sec	FROH _{4-8 Mb}	r= 0.97	r= 0.87	r= 0.98	r= 0.98	r= 0.34	0.15
		- service it can	1 KOI1 _{4-8 Mb}	p<0.001	p<0.001	p<0.001	p<0.001	p= 0.022	0.05
0.15		and the second second	in the second se	FROH	r= 0.92	r= 0.93	r= 0.93	r= 0.36	
0.05	in the second second		- meritist the second	FROH _{8-16 Mb}	p<0.001	p<0.001	p<0.001	p= 0.014	
	·· ·· ·· ··				FROH _{>16 Mb}	r= 0.83	r= 0.83	r= 0.35	0.15
	ward wards .	minani .		······································	>16 Mb	p<0.001	p<0.001	p= 0.018	0.05
0.00	W	in the second	· · · · · ·	i i i i i i i i i i i i i i i i i i i		F _{HOM}	r= 1.00	r= 0.35	
-0.15	, marked and the second second		· · · ································	in the second	A A A A A A A A A A A A A A A A A A A	- ном	p<0.001	p= 0.018	
	New York			i .:.			F	r= 0.39	0.25
	1 marine	1 marine the start	1 Ale and a second and a second		· · · · · · · · · · · · · · · · · · ·		F _{GRM}	p= 0.008	0.15
\$ 0.08		· · · · · · · · · · · · · · · · · · ·	·····	· · · · · · · · ·	· · · · · · · · · · · · · · · · · · ·		· · · · · · · · ·	F _{PED}	
0.00 0.04	<u></u>		[<u>,</u> ,,]						
	0.10 0.15 0.20 0.25		0.05 0.10 0.15 0.20		0.05 0.10 0.15		0.15 0.20 0.25 0.3	0	

Figure 9. Scatterplots (lower panel) and Pearson correlations (upper panel) of genomic inbreeding coefficients using runs of homozygosity (ROH) for different ROH length, based on excess of homozygosity (F_{HOM}), genomic relationship matrix (F_{GRM}) and pedigree-based relationship matrix (F_{PED}) for POP C.

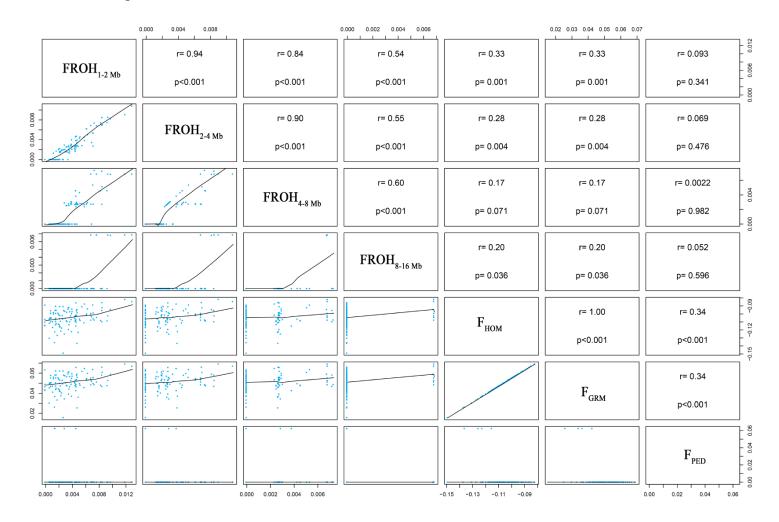


Figure S1. Runs of homozygosity patterns for all chromosome (Okis1 to Okis30) in three coho salmon population.

Each row represents one individual and each bar a ROH segment.