Detection of selection signatures in the genome of a domestic population of anadromous rainbow trout (*Oncorhynchus mykiss*)

María I. Cadiz[1,2,7], María E. López[3], Diego Díaz-Domínguez[4], Giovanna Cáceres[1,2], Rodrigo Marin-Nahuelpi[2,7], Daniel Gomez-Uchida[5,7], Cristian B. Canales-Aguirre[6,7], Pablo Orozco-terWengel[8], José M. Yáñez[2,7]*

[1] Programa de Doctorado en Ciencias Silvoagropecuarias y Veterinarias, Campus Sur, Universidad de Chile. Santa Rosa 11315, La Pintana, Santiago, Chile. CP: 8820808.

[2] Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Avenida Santa Rosa 11735, 8820808, La Pintana, Santiago, Chile

[3] Department of Aquatic Resources, Swedish University of Agricultural Sciences, Drottningholm, Sweden.

[4] Departamento de Ciencias de la Computación, Universidad de Chile.

[5] Departamento de Zoología. Facultad de Ciencias Naturales y Oceanográficas. Universidad de Concepción

[6] Centro i~mar, Universidad de Los Lagos, Camino Chinquihue 6 km, Puerto Montt, Chile.

[7] Núcleo Milenio de Salmónidos Invasores (INVASAL), Concepción, Chile.

[8] School of Biosciences, Cardiff University, Cardiff, CF10 3AT

*jmayanez@uchile.cl +56-2 29785533 (Corresponding Author).

Abstract

Domestication processes and artificial selection are likely to leave signatures that can be detected at a molecular level in farmed rainbow trout (*Oncorhynchus mykiss*). These signatures of selection are genomic regions that contain functional genetic variants that may confer higher fitness to their bearers. We genotyped 749 rainbow trout from a commercial population using a rainbow trout Axiom 57K SNP array panel and identified putative genomic regions under selection using the *pcadap*t, Composite Likelihood Ratio (*CLR*) and Integrated Haplotype Score (*iHS*). After applying quality-control pipelines and statistical analyses, we detected 12, 96 and 16 SNPs putatively under selection, associated with 96, 781 and 115 candidate genes, respectively. Several of these candidate genes were associated with growth, early development, reproduction, behavior and immune system traits. In addition, some of the SNPs were found in relevant biological regions (O4, O5 and O20) associated to autosomal inversions localized in Omy05 and Omy020. These findings could represent a genome-wide map of selection signatures in farmed rainbow trout and could be important in explaining domestication and selection for genetic traits of commercial interest.

Keywords: *iHS*, *pcadapt*, domestication, SNPs.

1. **Introduction**

The rainbow trout (*Oncorhynchus mykiss* Walbaum 1792) is native to North America and its geographical distribution ranges from Alaska to Mexico [1,2]. The domestication of this anadromous species began in the 1870s in California [1]. Since then, due to its importance for recreational angling and aquaculture, it has been introduced on all continents except Antarctica. It is one of the main species of fish reared in cold freshwater worldwide, particularly in Europe, North America, and Chile. The species production greatly expanded in the 1950s after the development of pelleted feeds [1]. In the early 1970s, AKVAFORSK Inc. began the first genetic improvement program of *O. mykiss* aimed at increasing body growth rate [3,4]. Rainbow trout have reached a high level of domestication (e.g. the entire life cycle is controlled in captivity [5,6]), and there are at least 13 genetic improvement programs [7] including traits such as growth, disease resistance, carcass quality, and age at sexual maturity [1]. The increase in the number of genetic improvement programs for rainbow trout has led to at least 22% of production relying on improved stocks [8]. According to FAO et al. [9], 848.1 thousand tons of rainbow trout were produced in world aquaculture in 2018.

Domestication and genetic improvement programs have produced populations genetically differentiated from the wild varieties from which they derived [10]. Continuous artificial selection has shaped the domestics' genome leaving signatures of selection that are detectable using molecular techniques [11,12]. These candidate regions may be regulated features such as morphology, production performance, reproduction, behavior, adaptation to different environments, and resistance to diseases, among others [13]. Positive selection signatures are genomic regions that contain functional genetic variants that confer higher fitness to their bearers [14], and usually, exhibit (i) increased allele frequencies of favorable

adaptive substitutions [15,16], (ii) an increased linkage disequilibrium (LD) that decays with the distance in base pairs from the target of selection [17], and (iii) lower genetic diversity at adjacent sites of a selective sweep than non-selected sites [18]. Vitti et al. [19] divided the methods for detection of selection signatures into three major classes: (a) those that are searching for deviations in allele frequency spectrum (e.g. *Tajima's D*, *Fay & Wu's H, CLR*), (b) those based on extended haplotype homozygosity within populations (e.g. *iHS*, *Rsb, XP-EHH*), and (c) those based on population differentiation (e.g. F_{ST}-based outlier detection and principal component analysis). However, the ability to identify the target of selection depends on many factors, including but not limited to, the number of populations surveyed, temporal scale of the selective event, strength of selection coefficient and type of selection signature [19,20]. Consequently, using more than one method to detect targets of selection is often a good option [21], with *pcadapt* [22], *CLR* [23] and *iHS* [24] being two suitable methods to identify recent positive selection.

Previous studies in salmonids have associated selection signatures to traits such as migration in brown trout (*Salmo trutta*) [25], reproductive ecotypes (i.e. shore or stream spawning) in sockeye salmon (*Oncorhynchus nerka*) [26], ecotypes with different evolutionary thermal adaptation (i.e. populations from deserts and mountains) in redband trout (*Oncorhynchus mykiss gairdneri*) [27], and economically important traits (e.g. growth, early maturation and disease resistance) in Atlantic salmon (*Salmo salar*) [11,28,29] and coho salmon (*Oncorhynchus kisutch*) [30]. Few studies have addressed signatures of selection in rainbow trout (i.e. [31–33]). Martinez et al. [31], using a set of 110 linked expressed sequence tags (EST) and 188 anonymous microsatellites identified selection signatures associated with egg development, spawning time, and life-history variation. Limborg et al. [32], using a panel of 276 SNPs, identified natural selection signatures between anadromous and resident populations at eight candidate loci associated with the adaptive immune response. Weinstein et al. [33], using 57K SNP identified

85 signatures of selection in wild F1 migratory and resident rainbow trout of Southeast Alaska associated
86 with smoltification. All previously mentioned studies focused only on wild populations, leaving a gap in
87 knowledge for the selection history related to rainbow trout domestication.
88
89 The advances in genomics allowed the development of extensive marker panels for agriculture, livestock
90 and aquaculture species. Palti et al. [34] developed a 57K SNP array with SNP distributed across the
91 rainbow trout genome on a scale of one SNP for every ~48,000 bp. Rainbow trout is an excellent model
92 species to identify selection signatures due to its well recognized recent history of domestication, its
93 intense artificial selection record, and its adaptation to different environments. The aim of this study was
94 to identify selection signatures in the genome of one domestic population of rainbow trout. A total of 749
95 individuals of a farmed population were genotyped with a panel of 57K SNP. Selection signatures were
96 searched using two statistical methods: (i) *pcadapt*, (ii) *CLR* and (iii) *iHS*.

2. Materials and Methods

2.1. Sampling

We used 749 rainbow trout from the breeding population belonging to the 2014 year-class of the EFIGEN S.A. (formerly Aguas Claras S.A.) breeding program (Puerto Montt, Chile). These fish were introduced from Denmark in 1998 to Quetroleufu, Chile, by Aguas Claras S.A. [35–37]. Prior to their introduction, there is no further information about this population. Subsequently, this population was implemented to establish a breeding nucleus that has undergone 6 generations of selection for growth (3 generations), carcass quality, and appearance (2 generations) traits [35–37]. In recent years, this strain has been developed to resistance to infectious pancreatic necrosis virus (IPNV) [35,37], sea lice (*Caligus rogercresseyi*) [38], and Salmonid rickettsial syndrome (SRS) [36]. Additionally, this anadromous population is characterized by low mortality and late maturation (3rd year) [39]. Bioethical considerations were taken for animal management following regulations of *Comité de Bioética Animal, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Chile* (certificate N°17,019-VET-UCH).

2.2. Genotyping

Total DNA was obtained from fin-clip samples using the *DNeasy Blood & Tissue* (Qiagen) kit, following the manufacturer´s recommendations. Each sample was genotyped with the commercial rainbow trout Affymetrix® Axiom® 57K SNP panel [34]. The SNP quality control was evaluated using Affymetrix's AXIOM Analysis Suite software with the default settings, removing SNPs that did not match high-quality clustering patterns [35,40]. The SNP array coordinates were updated to the latest version of the rainbow trout genome (GCA_002163495.1 Omyk_1.0) by aligning the 200bp probes of each variant to the Omyd_1.0 genome. Only variants aligned to chromosomes were kept. Furthermore, SNPs that did not

pass the following quality control filters were removed using VCFtools v.0.1.15 [41]: (i) call rate < 95%, (ii) SNPs deviated from Hardy-Weinberg Equilibrium after Bonferroni correction (HWE, p-value<$1x10^{-6}$), and (iii) minor allele frequency (MAF) < 0.05. Additionally, we applied a minimum call rate of 90% for individuals. After quality control filtering, 36,538 SNPs and all individuals were kept for further analyses. Finally, we imputed the missing genotypes and phased the haplotypes with Beagle v.3 [42] using default parameters.

2.3. Genetic variation and population structure

For the estimation of patterns of genetic variation and population structure, we further removed SNPs that presented correlations between their allele frequencies larger than the basal level of LD found in this population (0.125; described below). Our SNP set was filtered for linkage disequilibrium (LD) using PLINK v1.09 [43] with the option *–indep-pairwise* and using windows of 50 consecutive SNPs, sliding 10 SNPs at the time and removing one SNP from each pair when the Pearson's correlation coefficient r^2 was 0.125 or higher. Summary statistics of genetic diversity, such as the observed and expected heterozygosity (H_O and H_E) and inbreeding coefficient (F_{IS}), were calculated using PLINK v1.09. To examine the genetic structure, we used a principal component analysis (PCA; calculated in PLINK v1.09 and visualized in R). Finally, we implemented PLINK v1.09 to characterize the pairwise linkage disequilibrium (LD) as Pearson's squared correlation coefficient (r^2), where SNP pairs were located into 100 bins to calculate the mean values of r^2 for each bin. Additionally, we estimated the historical effective population size (N_e) across generations using SNePv1.1 [44] and an average generation length of three years [45].

2.4. Signatures of selection

We used three methods to detect signatures of selection. The first method based on principal component analysis was conducted with the *pcadapt* package v4.3.3 [22]. This method detects outlier markers based on Principal Component Analysis (PCA) while accounting for population structure [22]. This method is robust to admixture and does not assume prior knowledge of population structure [46]. The test statistic used for this method is the Mahalanobis distance (D) where a vector of the *z*-scores is derived for regressing each SNPs with K principal components [22]. To choose the K number of the principal components, we applied Cattell's rule [47]. The *p*-values were obtained from transforming Mahalanobis distance (D) based on the chi-square distribution [47]. To identify the SNPs candidates for selection, we applied the approach of Storey and Tibshirani [48] based on a False Discovery Rate (FDR) at 0.05.

The second method was the Composite Likelihood Ratio (*CLR*) analysis using the SweeD v3.3.2 software [23]. This intra-population method is based on the skewness in the site-frequency spectrum of the alleles across multiple loci along each chromosome to detect selective scan [49]. *CLR* estimates the ratio of the likelihood of a selective sweep at a given position to the likelihood of a null model [30]. We estimate the *CLR* in each chromosome using the grid size set to 100kb.

The third method was the standardized Integrated Haplotype Score (*iHS*) [24], which is included in the R package REHH v3.1.2 [50]. This method is based on extended haplotype homozygosity (*EHH*) and corresponds to the probability that two randomly chosen chromosomes carrying the core haplotype are identical by descent [50,51]. The *iHS* compares the *EHH* between alleles within the same population [51]. This method requires the information of ancestral allele identification for each SNP. We estimated the ancestral and derived alleles aligning the reference genome of rainbow trout against the *Salmo salar* (GCA_000233375.4) with BLAST using probes of our variants and then applying an in-house script to

obtain the ancestral and derived alleles. For SNPs that could not be obtained, the ancestral allele was inferred as the highest allele frequency in the total dataset, as suggested in other studies [52,53].

Identifying the causal variants of selection is laborious as frequently the markers identified to be under selection are not obvious functional elements (e.g. genes). Therefore, in such cases, it is necessary to look for neighbouring functional elements to the selection target that could explain the signature of selection [16]. Candidate regions for selection were defined as those genomic positions containing SNPs with values of *pcadapt* with an expected FDR $\alpha = 0.05$, scores of *CLR* corresponding to the 99.5th percentile to the distribution and values of *iHS* in the top 0.05% of the distribution. Based on the estimated LD decay in this population, we used a range of up to 250Kb on each side of the candidate SNP to identify candidate genes under selection. The genes intersecting the candidate regions detected by *pcadapt*, *CLR* and *iHS* approaches were considered putative candidates for selection and detected using BEDTools [54].

3. **Results**

3.1. Genetic variation and population structure

We estimated observed and expected heterozygosities of 0.459 and 0.447 and an inbreeding coefficient of -0.026, from a subset of 2,426 SNPs, after pruning SNPs with a LD correlation coefficient (r^2) of 0.125. The genetic structure showed one major clusters based on the principal component analysis (PCA) (Figure 1), where the first two eigenvectors explained 10.82% and 8.86% of the variability, respectively.

The pattern of LD (Figure 2a) showed a quick decay of LD at small distances (less than 25,000 base pairs). Beyond that point (r^2 ~0.22), a steady decrease in LD is observed until reaching a value of ~0.125, which is roughly stable at large genomic distance scales. The average LD (r^2) values in this population was 0.1457. The pattern of LD decay within chromosomes was very similar to the overall linkage decay curve, except for chromosomes 5 and 20 that present comparatively higher LD and which also remains high at longer genomic distances, in accordance with the presence of the double inversions in chromosome 5 (21.99 and 32.83Mb) and 20 (14Mb) as previously described [55] (Supplementary Figure S1, Supplementary Table S1, Supplementary Material). This population shows a continuously decreasing N_e trend from 1,444 to 86 over the last 1,500 years (Figure 2b).

3.2. Signatures of selection

Using 36,538 SNPs, we identified several regions harboring evidence of selection signatures by three methods. Besides, we found three relevant regions previously, referred to as regions O4, O5, and O20, that were detected with the *pcadapt*, *CLR*, and *iHS* methods, respectively (Figure 3, Figure 4 and Figure

202 5). Candidate genes related to domestication processes were further labeled as: (G) growth, (E) early
203 development, (R) reproduction, (B) behavior, (I) immune system, and (A) adaptation to culture
204 environment (Supplementary Table S2, Supplementary Material).
205
206 The *pcadapt* approach identified 12 candidate after FDR adjustment at 0.05%. The 12 SNPs are associated
207 with 96 genes localized in Omy04 (11 SNPs) and Omy27 (1 SNP) (Figure 3, Supplementary Table S3,
208 Supplementary Material). The candidate region in Omy04, which be call region O4, consists of two
209 clusters of selection targets, with the first cluster including 9 SNPs with an average distance of ~651Kb,
210 while the second cluster includes only two SNPs separated by ~834Kb. In the Omy27, we found only one
211 SNP that does not appear to have been under selection. Due to the cluster of SNPs under selection in
212 Omy04 (an indicative of a reliable signature of selection) we focused on the markers on that chromosome
213 to search for genes associated with selection signatures. Among these we found genes associated with
214 growth (*Sh3rf1*, *Prkaa2*, *Dab1*, *Plpp3, Dhcr24*, *C1qtnf7*, *Slain2*, *Sgcb*, *Dse*, *Col10a1*, and *Sox8*),
215 reproduction (*Psmb5*, *Cpeb2*, *Spata18*, *Ube2j1*, *Ufl1*, *Hs3st5*, *Rasd1*, *Zar1*, and *Rpl5*), immune system
216 function (*Trim25*, *Rgs1*, *Bach2*, *Tlr13*, *Trim65*, *Trim21*, *Trim39*, and *Palld*), early development (*Gsn*,
217 *Prdm5*, *Rgs2*, *Uchl5* and *Pbx1*) and environmental adaptation (*Gadd45a*) in Omy04. Details of the
218 candidate genes related to domestication are shown in Supplementary Table S2, Supplementary Material.
219
220 The *CLR* methods reveal 96 SNPs over the threshold and associated to 781 genes distributed along the
221 genome, excluding chromosomes Omy13, Omy16, Omy21, and Omy23 (Figure 4, Supplementary Table
222 S4, Supplementary Material). We found a second relevant peak region, called region O5 (Figure 4B),
223 composed of seventeen candidates SNPs, of which a portion of markers overlapped with two adjacent
224 inversions of 22.83 and 32.94 Mb on Omy05 [55]. In O5 region and the other candidates regions, we

found several genes previoulsy linked to growth (*Zc3h3*, *Cyld*, *Smad7*, *Arl15*, *Mrap2*, *Col2a1*, *Atp2a1*, *Itga9,* and *Pax9*), reproduction (*Ptges*, *Miga2*, *Kif3b,* and *Mapk10*), immune system (*Calmodulin*, *Dolpp1*, *Gpx7* and *Adcyap1r1*), early development (*Surf1*, *Rpl7a* and *Skiv2l2*), behavior (*Dnmt3a,* and *Dpysl5*) and adaptation to culture environment (*Sema7a* and *Mafa*). Besides, several genes were detected previously in studies of salmonids species (*Isg20l2*, *Vcp*, *Purb*, *Col9a2*, *Pax9*, *Vash1*, *Pomt2*, *Iah1*, *Itgb1bp1*, *Acyp2, Ube2g1*, *Foxn3*, *Purb, Tbc1d20, Cyld, Atp2a1*, *Cyld, and Mrap2*). Details of the candidate genes related to domestication are shown in Supplementary Table S2, Supplementary Material.

The *iHS* analysis revealed 16 SNPs over the 0.05% top values associated with 115 genes localized in the chromosomes 20 (Omy20) (Figure 5, Supplementary Table S5, Supplementary Material), called region O20. The average distance between SNPs in the candidate region O20 corresponds to ~547Kb, which overlapped with an inversion on Omy20 [55]. We found several genes related to growth (*Myof*, *Gdf2*, *Gdf10*, and *Ankrd1*), reproduction (*Htr7*, *Rbp4*, and *Dkk1*), immune system function (*Ch25h* and *Pten*), and early development (*Prkg1*, *P4ha1*, *Pcdh15*, *Noc3l*, *Plce1*, and *Cep55*). Details of the functions of candidate genes associated with domestication are shown in Supplementary Table S2, Supplementary Material.

4. Discussion

4.1. Genetic variation and population structure

In this study, we used a 57K SNP panel to analyze the diversity and genetic structure in one domestic population of rainbow trout to detect selection signatures. The genetic diversity found in this farmed population (H_O/H_E= 0.459/0.447) was higher than the levels found in six French domestic strains of rainbow trout, with values of H_O and H_E ranging from 0.36-0.38 and 0.35-0.37, respectively [56]. The genetic diversity values are higher than other domestic salmonids such as Atlantic salmon (H_O=0.27-0.41; H_E=0.24-0.41) [29,57] and coho salmon (H_O=0.37-0.39; H_E=0.36-0.39) [30]. Similarly, the heterozygosities found here were higher than those obtained by Weinstein et al. [33] from two wild experimental crosses (F1) of migratory and resident rainbow trout of Southeast Alaska also genotyped with the 57K SNP array [34], H_O= 0.15-0.18 and H_E= 0.14-0.17, respectively. Gross et al. [58] found higher genetic diversity in domestic rather than wild rainbow trout populations using ten microsatellites. In principle, it is expected that domestic populations that are strongly selected for production traits and are isolated from other populations, should have reduced levels of genetic diversity [59]. Conversely, natural populations should present higher genetic diversity levels, at least in their ancestral distribution range [60]. Therefore, it is possible that the selection has not resulted in a significant decline of diversity despite the continuous decline of Ne, which may be because of a possible hybrid background of this population.

The LD of this domestic population decays relatively rapidly, with LD decreasing by ~50% within the first 100Kb (r^2=0.146), which is in line with LD decay patterns previously described for French rainbow trout lines (r^2=0.23) [56] and other domestic salmonids (Atlantic salmon [61] and coho salmon [30]). The

quick decay of LD is consistent with a historical larger effective population size, which can be observed in our results (i.e. ~1,444). However, this N_e has been characterized by a continuous decline over the last 1,500 years until reaching the current strain's N_e of 86. These results are consistent with other studies in rainbow trout [56] and Atlantic salmon [61], that show the N_e has been eroded as in most domestic species in their recent history [62]. The minimal N_e to reduce inbreeding to not more than 1% per generation, and thereby maintaining appropriate levels of genetic variation (both neutral and adaptive) in a population on the long term should be at least 50 [63]. While the current N_e of this population is higher than the minimum recommended, it is important to continue to monitor the genetic variation levels, as further selection and genetic improvement may play an important role in affecting levels [56,62,64]. Furthermore, maintaining the current N_e is also necessary to secure a viable genetic background for the future, in line with the Convention on Biological Diversity Aichi target 13 that requires the maintenance of genetic variation and stopping its loss and erosion for all domestic species [65].

4.2. Signatures of selection

In this study, we applied three different tests to identify selection signatures and studied the effect of domestication and genetic improvement on this rainbow trout population's genome. These methods detect different regions of positive selection in rainbow trout. *CLR* analysis detected the most candidates regions followed by *iHS* and *pcadapt* methods. No overlap was observed among the three methods; yet, *CLR* and *iHS* methods recorded overlapping regions on Omy20, spanning a total of 2.8 Mb that contains 10 shared genes. These patterns of discrepancies between different methods have been observed in previous studies in salmonid species [30]. Besides, we found several genes detected previously in studies about selection signatures in different species, including Atlantic salmon (domestic population: *Isg20l2*, *Vcp*, *Col9a2*,

288 *Pax9*, *Vash1*, *Pomt2*, *Iah1*, *Itgb1bp1*, *Mocs, Trim39* [29]; *Acyp2, Ube2g1, Psmb5, Cpeb2, Palld, Dhcr24,*
289 *C1qtnf7, Slain2, Sgcb, Prdm5* [57]; *Foxn3* [66]; wild population: *Purb and Fbxl5* [67]; domestic-wild
290 populations: *Zip1* [11]); Coho salmon: *Tbc1d20* [30]); *Oreochromis niloticus* (*Trim16* [68]); livestock
291 species (chicken, *Med22* [69], *Ahcyl1* [70]; llama and alcapa, *Pmd8* and *Antxr2* [71]; cattle, *Strip1* [72],
292 *Slc6a117, Hs3st5, Pbx1* [73], *Tgfbi* [74] and *Dym* [75]) and humans (*Itga9* [76]).
293
294 We found three relevant segments on the genome of functional interest, O4, O5, and O20, localized on
295 the Omy04, Omy05, and Omy20, respectively. In region O4, we found 9 candidate SNPs in Omy04, which
296 overlapped with a paralogous region of the Omy05, which contain two inversions (Figure 3B, dashed red
297 line corresponds to the paralogous regions shared by both chromosomes; Omy05: 58,931,000-86,873,922
298 - Omy04: 13,224,448-40,450,364 [55]). In region O5, we found seventeen candidate SNPs, of which a
299 portion of them (7 SNPs) intersected with two adjacent inversions of 22.83 and 32.94 Mb localized on
300 Omy05 [55] (Figure 4B, dashed blue line corresponds to the probable localization of the two chromosomal
301 inversions). We also identified region O20 in Omy20, which contains 16 SNPs putatively under selection,
302 which overlap with a smaller inversion of 14 Mb that contains multiple rearrangements [55] (Figure 5B,
303 dashed blue line corresponds to the probable localization of the chromosomal inversion).
304
305 Inversion regions are relevant structural variants and play a major role in local adaptation and
306 diversification [77]. They protect inverted sequences from recombination during meiosis, enabling
307 favorable alleles to be maintained over generations by balancing selection [77]. Recently, Pearse et al.
308 [55] described two inversions on Omy05 and Omy20 on Rainbow trout's genome. Omy05 is composed of
309 two adjacent inversions spanning ~55Mb [55], which contains a supergene that mediates sexual conflict
310 over migratory tendencies via sex-dependent dominance reversal. They found genes associated with key

311 photosensory, circadian rhythm/entrainment, adiposity, and sex-specific effect (gonad/sex steroid). The
312 Omy20 contains a mulptiple small inversion without major description. Homeologous regions for this
313 inversion (Omy05) in Omy01 and Omy12 have previously been associated with migratory phenotypes in
314 northern populations [78,79]. In this study, based on homologous regions between Omy4 and Omy5, we
315 found genes with putative functions associated with domestication that we explain below (*Dab1*, *Prkaa2*,
316 *Plpp3*, *Psmb5*, *Prdm5*, *Sh3rf1*, *Palld*, *Sgcb*, *Gsn*, *Gadd45a*). Here we found that O4, O5, and O20 regions
317 and the other regions harbor candidate genes linked to growth, early development, reproduction, immune
318 system, behavior, and adaptation to the environment (Supplementary Table S2, Supplementary Material).
319 These traits are typically modified in domestic species since they have been direct targets of artificial
320 selection and have been under the effect of inadvertent selection.
321
322 **Growth** has been the principal target in genetic improvement programs in rainbow trout [80]. The
323 population used in this study has been improved for growth for at least three generations. Therefore,
324 findings of genomic regions under selection harbouring genes related to growth were expected. As
325 described in Supplementary Table S2, several genes, including *Cyld, Smad7*, *Atp2a1*, *Dab1*, *Prkaa2*,
326 *Plpp3, Mrap2*, *Col2a1, Col10a1*, *Ankrd1*, *Myof*, and *Sox8* have been previously associated with growth-
327 related traits in some teleost fishes, such as *O. mykiss*, *Salmo salar*, *Danio rerio, Sparus aurata* and
328 *Lepisosteus oculatus* [80–87]. In rainbow trout, we found genes putative involve on body weight (*Cyld*
329 [85]*, Dab1*, *Prkaa2*, *Plpp3* [88]), promyogenic role (*Smad7* [86]) and growth trait (*Atp2a1* [80]). In
330 Atlantic salmon, we found genes associated to body weight and jaw deformity (*Mrap2* [81] and
331 *Col2a1*[87]). In addition, we also detected nine genes which have been related to growth in studies
332 performed in livestock species, including chicken (*Dhcr24* [89]; *Slain2* and *Sgcb* [91]), sheep (*C1qtnf7*
333 [92]), pigs (*Arl15* [93]) and cattle (*Gdf10* [94] and *Zn3h3* [95]). We also identified ten candidate genes

linked with early development in other teleost fish. This trait may influence the growth because the muscles first arise in early embryonic life of teleost fish, unlike other amniotes [96].

In fish farming, maturation is often delayed by exposing fish to different light regimes to those in natural conditions, affecting the perception of seasonality and circannual rhythms [97]. Additionally, the population used in the present study has been selected for anadromous maturity at three years. In this regard, we expect that genes related to reproductive traits may show evidence of selection. We found sixteen genes involved in **reproduction** under positive selection in this population, of which seven genes (*Rbp4, Mapk10, Zar1*, *Rpl5, Dkk1, Ptges and Kif3b*) are specifically associated with reproduction in teleost fish. The *Rbp4* gene was related to retinoid metabolism in the rainbow trout ovarian follicle, and is expressed in theca and granulosa cells surrounding the oocytes in trout ovaries [98]. The *Mapk10* gene was localized previously in an important chromosomal inversion in Omy05, and it was implicated with circadian rhythm and migratory phenotypes in rainbow trout [55]. *Zar1* gene is a maternal-effect gene crucial for the oocyte-to-embryo turn [99]. In rainbow trout, it might play a role in oocyte/embryo development [100], while in zebrafish, its loss causes early oogenesis arrest and female-to-male sex reversal [101]. *Pteges* gene was linked with gonad differentiation in zebrafish [102]. *Rpl5* gene seems to play a crucial role in the development of ovaries and oogenesis in Nile tilapia [103]. In primitive fish species, the high expression of *Dkk1* has been associated with the gonadal development of sturgeons (*Acipenser ruthenus* [104] and *Scaphirhynchus platorynchus* [105]). In contrast, in zebrafish, the increased expression of *Dkk1* can result in male-biased sex ratios [106]. We also found other groups of candidate genes previously associated with reproduction in other mammals (cattle, *Psmb5* [90,107] and *Ufl1* [108]; sheep *Hs3st5* [109]; mouse, *Spata18* [110], *Ube2j1* [111] and *Miga2* [112]) and birds (chicken, *Rasd1* [113]; goose, *Htr7* [114]).

It is well known that host-pathogen interactions lead to strong selection in the genome of host species [115–117]. In this study, we found several genes that are involved in the immune system and specifically with host-pathogen interaction in a cultured environment. For example, in *Salmo salar*, we found several genes previously associated with response against Amoebic Gill Disease (*Trim39* [118]), hematopoietic necrosis (IHN) virus (*Pten* [119]), sea lice (*Lepeophtheirus salmonis*) (*Calmodulin* [122]) and parasite-driven selection (*Purb and Fbxl5* [67]). In Coho salmon, the *Sh3rf1* gene was associated with disease resistance against *Piscirickettsia salmonis* [123]. *Palld* gene is related to the molecular mechanism against Koi herpesvirus resistance (KHVR) in *Cyprinus carpio* [124]. Finally, *Tlr13* was involved in the immune response against bacteria and viruses in *Acipenser dabryanus* [125]. We suggest that these genes may be involved in traits related to response to diseases in rainbow trout as part of the adaptation to continuous outbreaks of infectious and parasitic diseases in farming conditions. These results may be relevant because the success and sustainability of salmonid aquaculture depend on the control of diseases [126]. Development of more resistant fish strains has been one of the primary purposes of research and development in genetic improvement programs of salmonids in Chile and worldwide [127]. Finally, we detected genes associated with the adaptation to the culture environment (*Gadd45a*) and behavior (*Dpysl5*) in rainbow trout. The *Gadd45a* gene is a putative biomarker for cold shock [128] and water quality stress [129]. *Dpysl5* gene has been associated with intergenerational impacts on offspring behavior behind thermal maternal stress [130].

Conclusion

Here we present a genome-wide analysis of the genetic diversity of a Chilean domestic population of steelhead rainbow trout *Oncorhynchus mykiss*. We identified that this lineage presented a historically large

effective population size, which is consistent with a relatively high level of genetic variation and low range of high linkage disequilibrium. However, the current effective population size has reduced to ~86, which in within the range of values recommended by FAO to minimize inbreeding and contribute to the maintenance of the current genetic diversity in captive populations. We also found evidence for selection signatures across the genome of this population. Part of these regions are confined to inversion polymorphisms, facilitating selection to occur within these regions and safekeeping of beneficial alleles from the rest of the recombination landscape across the genome and their loss through other selective processes or genetic drift. Within these inversions and in the rest of the candidates regions detected across the genome of rainbow trout, we found genes mainly associated with growth, reproduction, immune system, behavior and early development; traits which are related to domestication and artificial selection in this species. Lastly, the results presented here provide a background of standing genetic variation and adaptive signals in a farmed rainbow trout population, which provides further knowledge on the effects of domestication and intense directional selection in salmonids. In further research, we suggest including ancestral wild populations of rainbow trout, as a pairwise comparison with their genetic variation may help further elucidating the targest of selection in the domestic strains including details such as which allele was selected for in the domestic lineages. Such analysis would also increase the knowledge about the effect of domestication by exploring the nonparallel and parallel genomic footprints between wild/domestic populations.

Ethics approval and consent to participate

Nile tilapia sampling procedures were approved by the Comité de Bioética Animal from the Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile (certificate Nº17,019-VET-UCH).

Consent for publication

Not applicable.

Availability of data and material

Genotypes from this article have been deposited on FigShare: https://doi.org/10.6084/m9.figshare.7725668.v1.

Conflict of Interest Statement

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

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Authors' contributions

MIC performed the analysis and wrote the initial version of the manuscript. MEL, DD contributed with analysis, discussion, and writing. GC and RM contributed with data recopilation on functional

characterization. JMY, MIC, and MEL conceived, designed the study. MIC, MEL, DGU, CC, POTW, and JMY contributed to discussion and writing. All authors have reviewed and approved the manuscript.

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Appendix A.

Supplementary Material

Table S1. Values of LD decay in each chromosome.

Table S2. Candidate genes under selection on rainbow trout detected by *iHS*, *pcadapt* and *CLR* methods.

Table S3. List of all genes detected by *pcadapt* method.

Table S4. List of all genes detected by *CLR* method.

Table S5. List of all genes detected by *iHS* method.

FigureS1. LD decay in each chromosome.

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Figure 1. Principal component analysis (PCA) of genetic differentiation among 749 individuals of one domestic population of rainbow trout based on 57K SNPs. Each dot represents one individual.

Figure 2. Results of genetic variations: a) Linkage disequilibrium (r^2) decay over the distance between variants across the genome; b) Historical effective population sizes (N_e) over generations of one domestic population of rainbow trout.

Figure 3. Results of signatures of selection by the *pcadapt* method in one domestic population of rainbow trout based on 57K SNPs. A) Manhattan plot illustrates the distribution of *pcadapt* scores (-log(*p*-value)) across the genome of rainbow trout. Orange spots represent outliers. B) Manhattan plot shows the distribution of *pcadapt* scores (-log(*p*-value)) in region A across chromosome 4; red spots represent outliers and box represent the genes that intersect this region, and colors represent the putative function (blue, reproduction; green, inmmune system; light-magenta, growth, dark-magenta, early development, grey, adaptation to culture enviroment). Dashed blue line represents the approximate ubication of the chromosomal inversion of the Omy20 [55].

Figure 4. Results of signatures of selection by the *CLR* method in one domestic population of rainbow trout based on 57K SNPs. A) Manhattan plot illustrates the distribution of *CLR* scores across the genome of rainbow trout. Orange spots represent outliers. B) Manhattan plot shows the distribution of *CLR* scores across chromosome 5; red spots represent outliers; box represents the genes that intersect this region, and colors represent the putative function (blue, reproduction; green, inmmune system; light-magenta, growth, dark-magenta, early development). Dashed blue line represents the approximate localization of the two chromosomal inversions on the Omy05 [55].

Figure 5. Results of signatures of selection by the *iHS* method in one domestic population of rainbow trout based on 57K SNPs. A) Manhattan plot illustrates the distribution of *iHS* scores (-log(*p*-value)) across the genome of rainbow trout. Orange spots represent outliers. B) Manhattan plot shows the distribution of *iHS* scores (-log(*p*-value)) in region B across chromosome 20; red spots represent outliers; box represents the genes that intersect this region, and colors represent the putative function (blue, reproduction; green, inmmune system; light-magenta, growth, dark-magenta, early development). Dashed red line represents overlapped homeologous region of the Omy04 with Omy05 [55].