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A high-density SNP array tailored for selectively bred Arctic charr (*Salvelinus alpinus*)

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ABSTRACT

SNP arrays are indispensable tools for integrating genomic information into breeding programs. A SNP array for Nordic Arctic charr (*Salvelinus alpinus*) containing approximately 600,000 SNPs was developed from variants detected in Swedish, Norwegian and Icelandic farmed populations. In the current study, an in-depth analysis of the genetic diversity status of the Swedish population was conducted using high-quality SNPs. Animals from three non-overlapping year classes were genotyped (n = 382). Following quality control 169,873 SNPs were retained for downstream analysis. A principal components analysis (PCA) did not reveal any underlying genetic structure, in agreement with the background information of this population. A linkage disequilibrium (LD) decay analysis indicated a strong to moderate LD up to a physical distance of 300 kbp. In parallel, the LD estimates were used to estimate the effective population size (Ne), which declined from 260 (15 generations ago) to approximately 20 over the last four generations. Furthermore, runs of homozygosity (ROH) were detected, and inbreeding coefficients were estimated based on them. The median values of the inbreeding coefficients for the three year classes ranged from 14.4 % to 15.9 %. Nevertheless, those inbreeding estimates were primarily based on short ROH ($\leq$ 4Mbp), reflecting non-recent shared ancestry. The median inbreeding coefficients based on ROH longer than 4 Mbp, on the other hand, ranged between 8.3 % and 9.7 %. The produced SNP array is expected to be instrumental in the transition of the Nordic Arctic charr industry to the genomic era, allowing, among other things, for a more efficient management of the genetic diversity of captive populations.

1. Introduction

The field of aquaculture breeding has been propelled over the last decade thanks to advancements in genomic technologies (Zenger et al., 2019). High-throughput sequencing, in particular, played a key role in the development of SNP arrays for several aquaculture species, enabling genomic-based breeding evaluations (Song et al., 2023). Moreover, high-throughput sequencing has, to a large extent, democratised the usage of genomic breeding through genotyping by sequencing (GBS) methodologies (Robledo et al., 2018). As such, even aquaculture species lacking a SNP array were able to benefit from modern breeding practices (Barbanti et al., 2020; Oikonomou et al., 2025; Palaiokostas et al., 2020).

Although GBS offers some advantages over SNP arrays, such as greater flexibility, significantly lower initial costs, and, at least in theory, no SNP ascertainment bias, SNP arrays still remain the preferred tool for commercial breeding programmes (You et al., 2020). A key factor behind SNP arrays' dominant position in breeding is that the data quality is usually substantially better than that from GBS. This is no surprise, as the former have already undergone several quality control stages during development, whereas in the latter, the data are in a "raw" format. As a straightforward example from the literature, the most common upper threshold for missing data for retaining a SNP from GBS data is between 20 % and 30 % (Barría et al., 2018; Manousaki et al., 2016; Oral et al., 2017; Syaifudin et al., 2019). More strict thresholds often result in a substantial reduction in the number of available SNPs for downstream analysis. On the other hand, for SNP arrays, the corresponding threshold is usually well below 10 % without substantial loss of data (Barría et al., 2021; Garcia et al., 2018; Peñaloza et al., 2021; Zhou et al., 2020). Further, SNP arrays lead to convenient tabular data that can be routinely analyzed more straightforwardly and with less computational effort.

Aside from facilitating genomic breeding evaluations, SNP arrays can provide valuable insights into a population's genetic diversity and structure at a genome-wide level. The above are critical factors for the success of any breeding program, and even more so in aquaculture, where low effective population (N_e) sizes have been reported on several

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occasions (Saura et al., 2021). Furthermore, as most aquaculture breeding programs operate in either a closed nucleus form or allow limited gene flow at best (Gjedrem, 2010; Gjedrem and Rye, 2018), the pool of additive genetic variance, the driving force behind selective breeding, might not be particularly large. Therefore, the high-resolution insights into genetic diversity provided by SNP arrays can support its efficient management through informed matings (Gómez-Romano et al., 2013). In relation to the above, inbreeding levels can be assessed across the entire genome, rather than a basic overall measure provided by a traditional pedigree analysis. More specifically, long stretches of homozygosity can be detected, formally known as runs of homozygosity (ROH). Notably, ROH are considered nowadays the method of choice for inferring both past and recent inbreeding accumulation (Peripolli et al., 2017).

Arctic charr is a salmonid suitable for farming in the Nordics due to its inherent capacity for growth even during winter months (Sæther et al., 2013). Although the production volume never reached prior expectations, it is still considered a niche market of considerable economic value (Carlberg et al., 2018). It is worth noting that, as its harvest size usually ranges between 800 and 1500 g, it is an attractive candidate for recirculating aquaculture systems. As such, several business plans are currently underway, aiming to farm Arctic charr in recirculating aquaculture systems, which, if successful, will result in a multi-fold increase of the global production volume in the near future.

A selective breeding program for Arctic charr has been operational in Sweden for approximately 40 years (Eriksson et al., 2010; Palaiokostas et al., 2021), with a primary focus on improving growth-related traits. The animals produced are trademarked as Arctic Superior and are reared at the Aquaculture Centre North (ACN) facilities in Northern Sweden. As of 2025, the 10th generation of selection has been formed. Until very recently, the breeding program was based solely on pedigree records, as genomic resources were scarce. By applying GBS and whole-genome resequencing (WGS) to over 1500 animals from the breeding program, we generated substantial genomic resources (Palaiokostas et al., 2022; Pappas et al., 2023) that enabled the development of a high-density SNP array.

In this study, we developed a high-density SNP array for Arctic charr with the main goal of improving the performance of Swedish Arctic charr. During its development, variant information from Icelandic and Norwegian Arctic charr was also utilised, enhancing the array's broader value. Thereafter, we employed the array to assess the genetic diversity of the Swedish Arctic charr breeding nucleus. Metrics such as genetic diversity and linkage disequilibrium decay were determined, along with predictions of recent and historical *Ne*. Additionally, ROH were identified, and estimates of inbreeding coefficients and potential homozygosity islands were derived.

2. Materials and methods

2.1. Design of a high-density SNP array for Nordic Arctic charr

This SNP array was developed by our research group in collaboration with Benchmark Genetics and ThermoFisher. More specifically, the SNPs of the high-density array originated from GBS and WGS, which involved more than 1500 Arctic charr from the Swedish breeding program (Palaiokostas et al., 2022; Pappas et al., 2023), 160 broodfish from a Norwegian producer (Palaiokostas et al., 2024) and 48 broodfish from the Icelandic Arctic charr breeding program (unpublished data). The above were supplemented with RNAseq data generated from available pooled blood samples from Swedish Arctic charr. Overall, 24 pools, each containing an equal amount of blood from five different adult fish, were sequenced. RNA extraction and preparation of RNAseq libraries were performed by Novogene Co., Ltd. (Beijing., China) according to their standard protocols. SNPs were identified using previously described pipelines (Palaiokostas et al., 2024; Pappas et al., 2023) with the only difference being that we used the new Arctic charr reference genome produced by our group (GCF_045679555.1).

Following detection of genetic variants for the development of the high-density array we retained SNPs that were biallelic, with minimum minor allele (MAF) frequency of 0.1, a quality score above 30, a minimum sequence depth of 20, allelic balance at heterozygous sites ranging between 0.25 and 0.75, proportion of properly read pairs for observed reference or alternate alleles above 0.80 and call rate above 0.9. Furthermore, only SNPs for which no other polymorphic sites existed 35 bp up- and downstream were retained. Finally, aiming to maximize the number of fitted SNPs in the array, all A/T and C/G polymorphisms were excluded as those would require twice as many probes as any other SNPs. All filtering steps were performed with bcftools v1.19 (Danecek et al., 2021).

2.2. Background of the studied population - application of the high-density SNP array

Arctic charr originating from the Swedish national breeding programme were used. Wild fish from the Swedish lake Hornavan served as the base population of the breeding program. Unfortunately, no records exist regarding the number of fish that were initially used. To date, the breeding programme has operated in a closed nucleus system with a mating design of one sire for two dams and discrete generations. Overall, the number of full-sib families per generation has ranged between 45 and 125. After fertilisation, individual families are reared separately until they reach an average weight of 10 g or more, at which point they are tagged with passive integrated transponders (PIT tags). Thereafter, the fish are reared in a communal setting.

In the current study, 382 adult fish from the Swedish breeding program were used. More specifically, animals from three consecutive year classes of 2013 (n = 96), 2017 (n = 96) and 2021 (n = 190). In each year class, an equal number of males and females was used. Genomic DNA extraction from collected fin-clips and genotyping with a custom Axiom™ SNP array were performed by Identigen (Dublin, Ireland). The obtained genotypic data from the high-density SNP array were filtered using plink v1.9 (Chang et al., 2015), discarding SNPs with a call rate below 0.95, MAF below 0.05 and ones deviating from Hardy-Weinberg equilibrium ($P < 1e\text{-}06$).

2.3. Generic metrics of genetic diversity and population structure

Following SNP filtering, generic diversity metrics, such as mean observed heterozygosity (H_o), expected heterozygosity (H_E), and Wright's F statistics, i.e. individual inbreeding coefficients (F_{IS}) and the fixation index (F_{ST}) between the three year classes, were estimated using vcftools v0.1.15 (Danecek et al., 2011). A principal component analysis (PCA) was conducted using the R package adegenet v2.1.5 (Jombart, 2008) to elucidate the underlying genetic structure of the studied populations.

2.4. Linkage disequilibrium decay and estimation of effective population size

The software popLDdecay v3.40 (Zhang et al., 2019) was used to calculate linkage disequilibrium (LD) and assess its decay over physical distances up to 300 kbp for each of the three year classes. The same procedure was repeated for males and females to investigate potential recombination differences between the two sexes. Additionally, effective population sizes (N_e) were computed using the software GONE (Santiago et al., 2020) using default settings for unphased data.

For comparison, we also estimated the recent effective population size from pedigree inbreeding. We estimated inbreeding coefficients with the GeneticsPed (Gorjanc and Henderson, 2023; Meuwissen and Luo, 1992) R package. The pedigree comprised 26,624 individuals across 10 generations. We calculated the proportional change in inbreeding Δf between generations, and effective population size as:

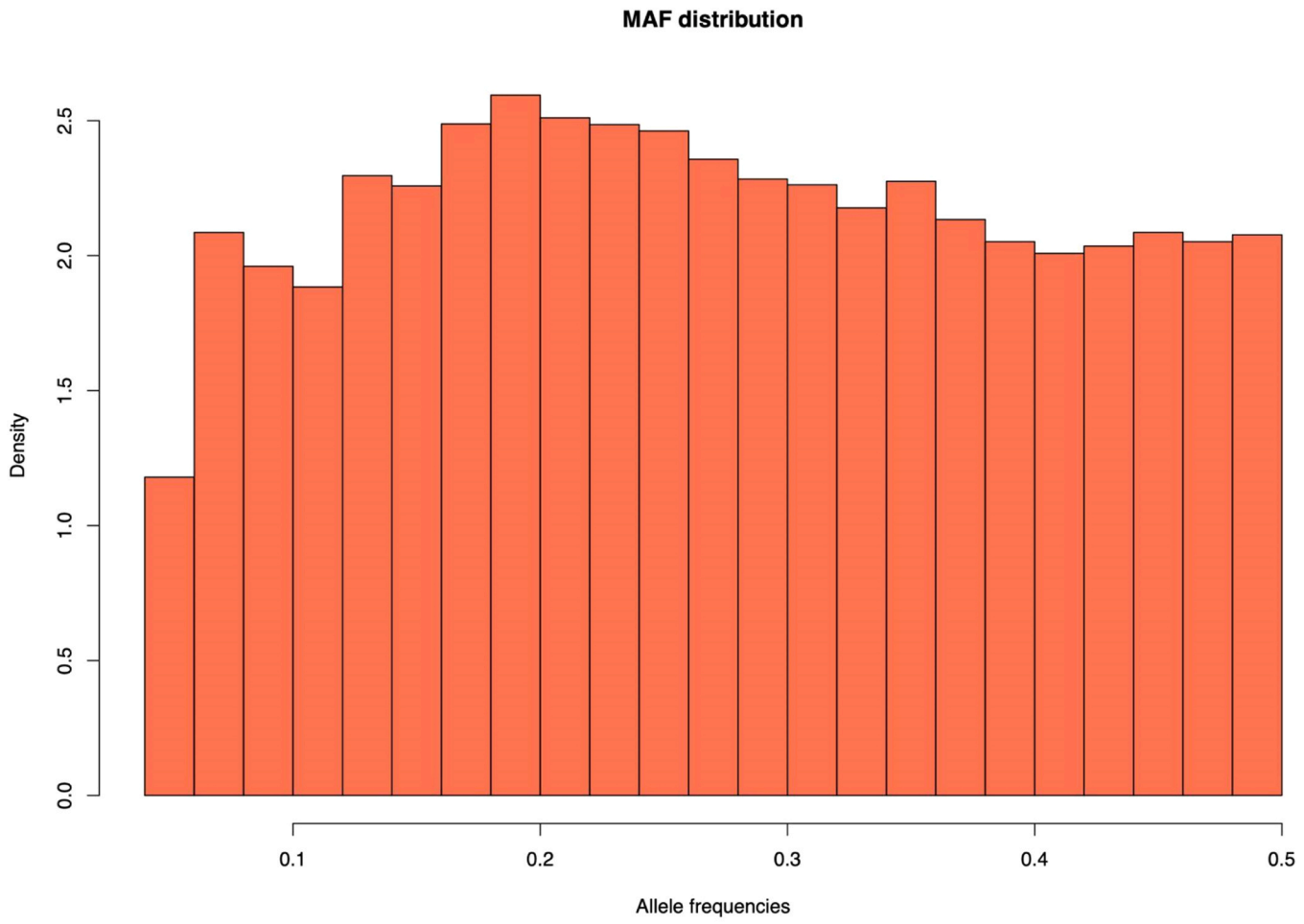

Fig. 1. Distribution of minor allele frequency of SNPs passing quality control filters.

$Ne = \frac{1}{2\Delta f}$.

2.5. Runs of homozygosity and inbreeding estimates

ROH were identified by the R package detectRUNS v0.9.6 (Biscarini et al., 2019) using a sliding window approach. The window length was set to 100 SNPs, the maximum gap at 250 kbp and the minimum ROH length was set to 1Mbp. In addition, the maximum number of allowed "opposite" genotypes was 2 per window (accounting for 2 % of the window), while the minimum number of SNPs was set equal to the window size. Overall, the detected runs were assigned to four different length classes: 1–2 Mbp, 2–4 Mbp, 4–8 Mbp and 8–16 Mbp in order to derive inbreeding related information due to common ancestry in recent generations as well as before the onset of the breeding program. The identified ROH were used to calculate inbreeding coefficients (F_{ROH}) for each individual using the *Froh_inbreeding* function of detectRUNS. Further, the ROH in different length classes were used to calculate inbreeding coefficients based on ROH of minimum length of 2 Mbp, 4 Mbp, 8 Mbp and 16 Mbp using the *Froh_inbreedingClass* function of detectRUNS. Finally, mean inbreeding coefficients were estimated for each year class.

2.6. Islands of homozygosity

The ROH were used to detect islands of homozygosity, i.e. regions of the genome that are enriched in ROH. We divided the genome into 1 Mbp windows and calculated the frequency of individuals that had a run of homozygosity overlapping each window using the GenomicRanges (Lawrence et al., 2013) R package. To set a threshold for detecting islands of homozygosity with a frequency higher than expected under genetic drift, we simulated neutral evolution with msprime (Baumdicker et al., 2022). The simulations consisted of 100 replicates of chromosome 1, using the effective population sizes estimated by GONE for the last 200 generations, and assuming a constant population size before that. The mutation rate and recombination rate per basepair were both set to 10^{-8}. In order to avoid known biases from using coalescent simulation in small population sizes, we used discrete time Wright-Fisher simulation for the last 200 generations (Nelson et al., 2020). Simulated data were analysed for ROH detection the same way as real data, and the maximum simulated ROH frequency in each replicate was recorded. The threshold was set so that the probability of finding a ROH frequency above the threshold under neutral evolution was 5 %.

3. Results

3.1. SNP selection for the high-density array

Approximately 11.5 million putative biallelic SNPs were initially detected. Following quality control filtering ~ 600,000 SNPs from the Swedish population were retained, out of which ~ 150,000 originated from RNAseq. Similarly, ~ 430,000 SNPs and ~ 950,000 SNPs from the Norwegian and Icelandic populations respectively, passed the aforementioned quality control filtering. Thereafter, 638,741 unique SNPs assayed by 702,278 probes were selected to populate the array following in silico prediction conducted by ThermoFisher. Overall, the array design comprised 262,080 SNPs from the Swedish population, of which

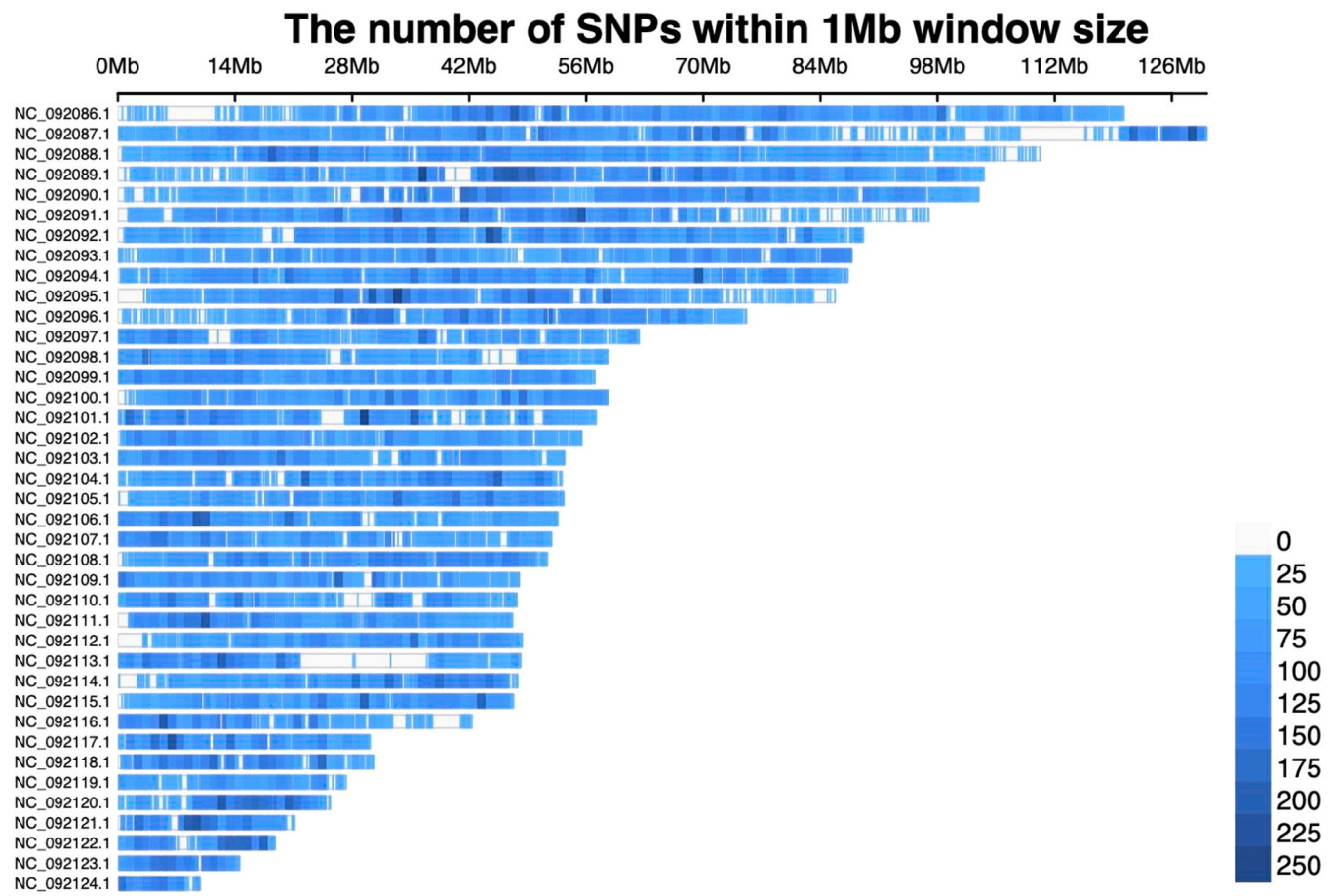

Fig. 2. Distribution of SNPs across the Arctic charr reference genome (GCF_045679555.1) that passed quality control filters. The plot was constructed using the R package CMplot (Yin et al., 2021).

57,080 originated from RNAseq. In terms of the remaining SNPs 160,166 and 216,485 were from the Norwegian and the Icelandic population, respectively.

3.2. SNP array implementation - quality control and filtering of the obtained genotypes

The array was used to genotype 382 adult Swedish Arctic charr. During quality control, 142,755 variants were removed due to low call rate (< 90 %). Additionally, 322,900 and 3213 SNPs were removed because they did not meet the MAF and Hardy-Weinberg thresholds, respectively. Overall, 169,873 SNPs passed all quality control filters and were retained for downstream analysis. Out of the retained SNPs, ~ 67 % had a MAF equal to or above 0.2 (Fig. 1). All 382 genotyped fish had an average call rate above 99 % and, as such, were all retained for downstream analysis.

The retained SNPs span the Arctic charr reference genome (GCF_045679555.1), with their number per chromosome ranging from 991 (NC_092124.1) to 8379 (NC_092087.1). The average SNP density per Mbp was approximately 60, although genomic regions with large gaps were also apparent, with the most prominent located in chromosome NC_092113.1 (Fig. 2).

3.3. Generic metrics of genetic diversity and population structure

The observed heterozygosity ranged from 0.28 to 0.42. The mean observed heterozygosity was equal to 0.37 (SE 0.01), while the expected heterozygosity was slightly lower and equal to 0.36 (Table S1). The F_{IS} coefficient ranged from −0.16 and 0.22 with a mean value of −0.019 (SE 0.003). No distinct differences were observed between the year classes for any of the aforementioned metrics.

This was further supported by the estimated F_{ST} values, which ranged from 0.002 to 0.006. The minimum was observed between year classes 2017 and 2021, while the maximum was between 2013 and 2021. The results from PCA also indicated minimal differentiation amongst the year classes. The first two PCs from PCA accounted for 3.2 % and 3 % of the explained variance, respectively (Fig. 3). Overall, no apparent distinct clusters were observed between the year classes.

3.4. Linkage disequilibrium decay and estimation of effective population size

As expected, LD decreased with the physical distance between SNP pairs. LD estimated by the mean r^2 reached a plateau at approximately 0.2 at a physical distance of 300 kbp. This pattern was the same amongst all year classes (Fig. 4). No differences in terms of LD decay were observed between the males and females.

The estimated N_e decayed from 260 (15 generations ago) to approximately 20 in the last four generations. According to the obtained estimates, a substantial drop in N_e from 110 to 20 occurred five generations ago (Fig. 5A). For comparison, we estimated N_e based on pedigree, which shows a higher current N_e of 83 as well as recent fluctuations not captured by the GONE estimates. For earlier population history (Fig. 5B), the estimates suggest that N_e has gradually decreased from around 1000 over the last 100 generations.

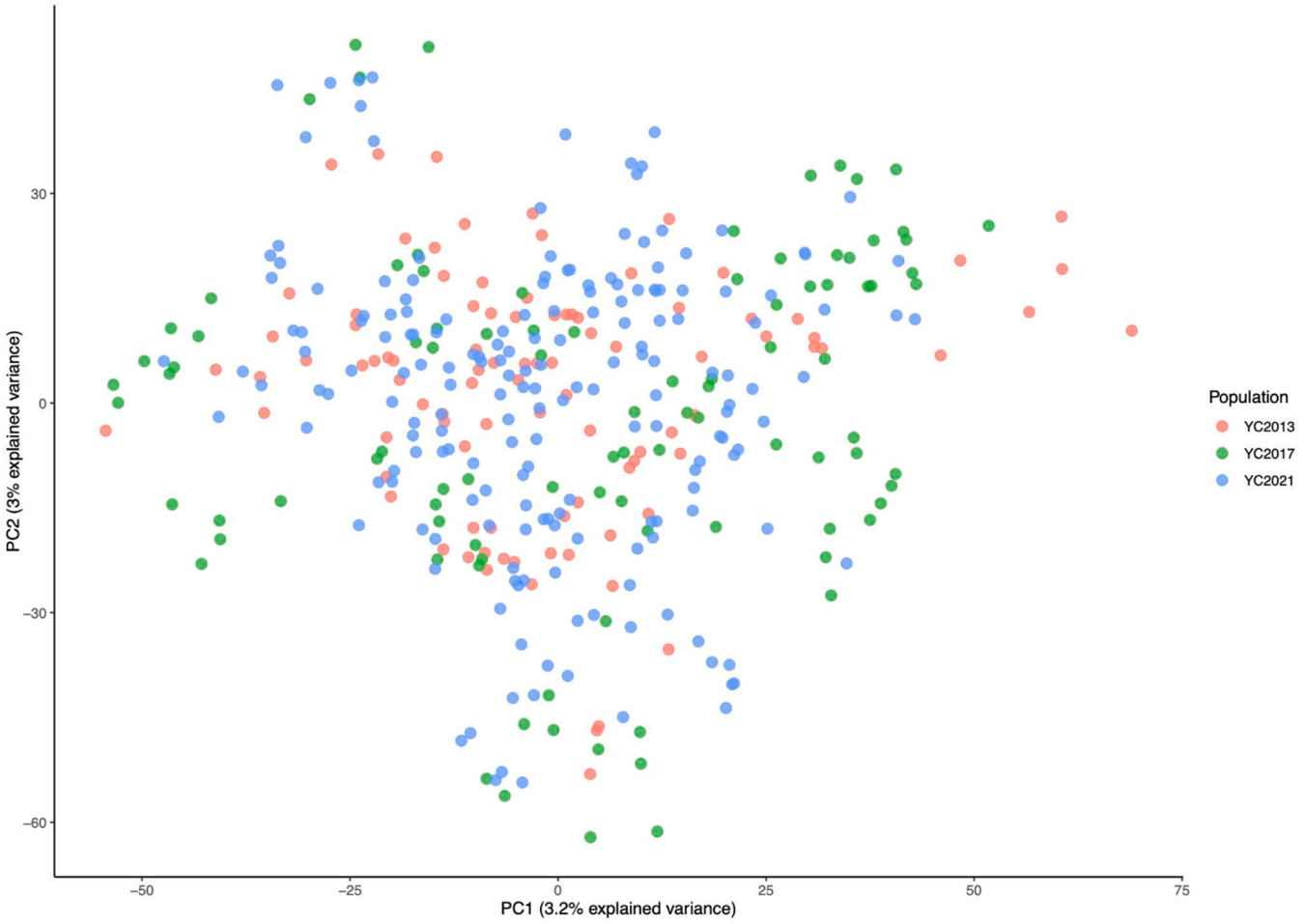

Fig. 3. Principal component analysis (PCA) of the three studied year classes of the Swedish Arctic charr breeding program. A unique colour is used to represent individuals belonging to the same year class.

3.5. Runs of homozygosity and inbreeding estimates

The number of long homozygous genomic regions per individual ranged between 58 and 128. Those genomic regions were classified into five categories based on their physical length (0–2, 2–4, 4–8, 8–16, > 16 Mbp) in order to derive inbreeding related information both due to common ancestry in recent generations as well as before the onset of the breeding program. More than 70 % of the identified runs involved stretches of up to 4 Mbp, while those above 16 Mbp accounted for ~2 % of all runs. Similarly, inbreeding coefficients based on ROH for each of the studied animals ranged between 0.05 and 0.29. Overall, the median values of the inbreeding coefficients for each of the three year classes ranged from 14.4 % to 15.9 %. When inbreeding coefficients were calculated from different size categories of ROH, the median inbreeding coefficients based on ROH longer than 4 Mbp were 8.3 %, 9.7 %, and 8.8 % (Fig. 6).

3.6. Islands of homozygosity

The frequency of ROH was estimated in windows across the genome to highlight regions where many individuals have ROH, i.e. islands of homozygosity. ROH frequency varied across the genome, with the highest values observed in a window on chromosome 8 (Fig. 7). This window, from 38000001 to 39000000 bp, reached above the ROH frequency threshold derived by simulation, which corresponds to 5 % probability of obtaining such a high frequency by genetic drift. The window contains 23 annotated genes of diverse functions (Table 1).

4. Discussion

In the current study, we developed a high-density SNP array for Arctic charr, marking the passage of the Swedish breeding program to the genomics era. As previously mentioned, the landscape of aquaculture breeding has undergone a significant transformation over the past 15 years, largely driven by advances in genomics. SNP arrays are the tools of choice in commercial aquaculture breeding programs, boosting the accuracy of breeding evaluations and allowing for a more efficient management of genetic diversity compared to traditional pedigree approaches (Yáñez et al., 2023).

Although it is unclear how many fish were initially used to establish the Swedish breeding programme, it is likely that this number was not particularly large, as is typical for the base population of most farmed fish. In fact, it has been reported on several occasions that base populations in farmed fish are notably low in both census and effective population sizes (Sonesson et al., 2023). As fish fecundity is orders of magnitude higher than that of terrestrial livestock, the farmer has considerable flexibility in terms of meeting production targets by using a small number of broodfish. Clearly, this has been fundamental and highly beneficial for the entire aquaculture industry. However, in hindsight, the long-term progress of a breeding programme can be seriously hindered unless genetic diversity is managed with care.

As the Swedish Arctic charr breeding program has been operating for approximately 40 years under a closed breeding nucleus scheme, it was deemed beneficial to conduct an in-depth evaluation of the genetic diversity status. Although we have conducted similar studies in the same

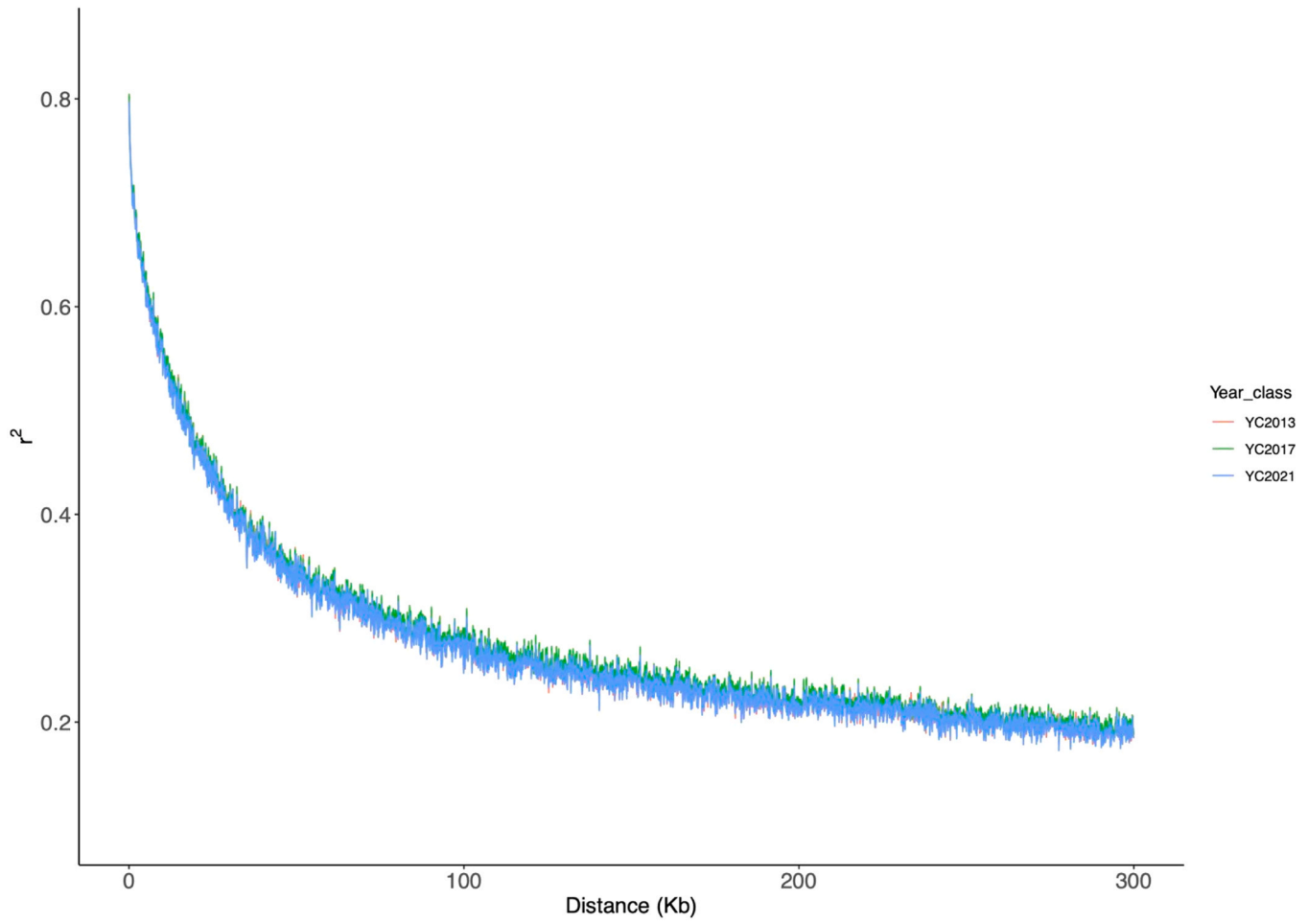

Fig. 4. Linkage disequilibrium decay by physical distance (in kbp) estimated using the mean recombination rate (r^2) for three year classes of the Swedish Arctic charr breeding program.

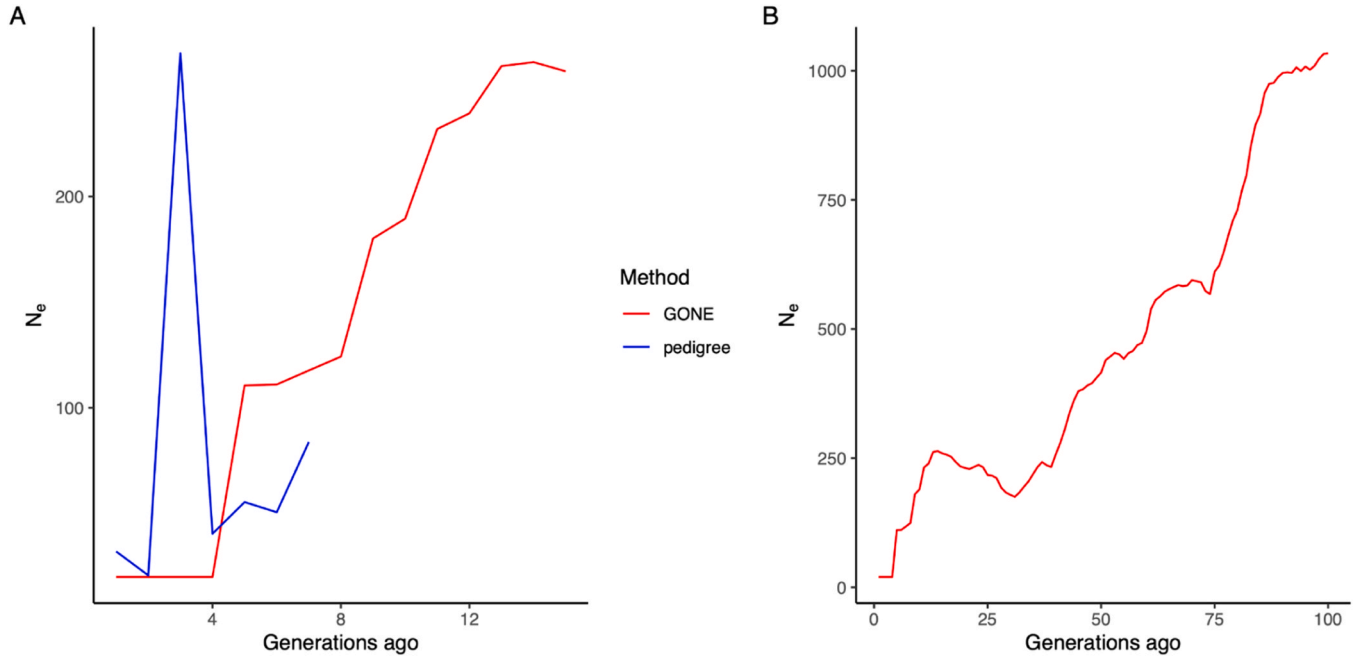

Fig. 5. Historical effective population size (N_e) estimates for the Swedish Arctic charr breeding program. **A**) Depicting N_e spanning up to 15 generations ago using either GONE or pedigree. **B)** Predicted N_e fluctuations over the last 100 generations using GONE.

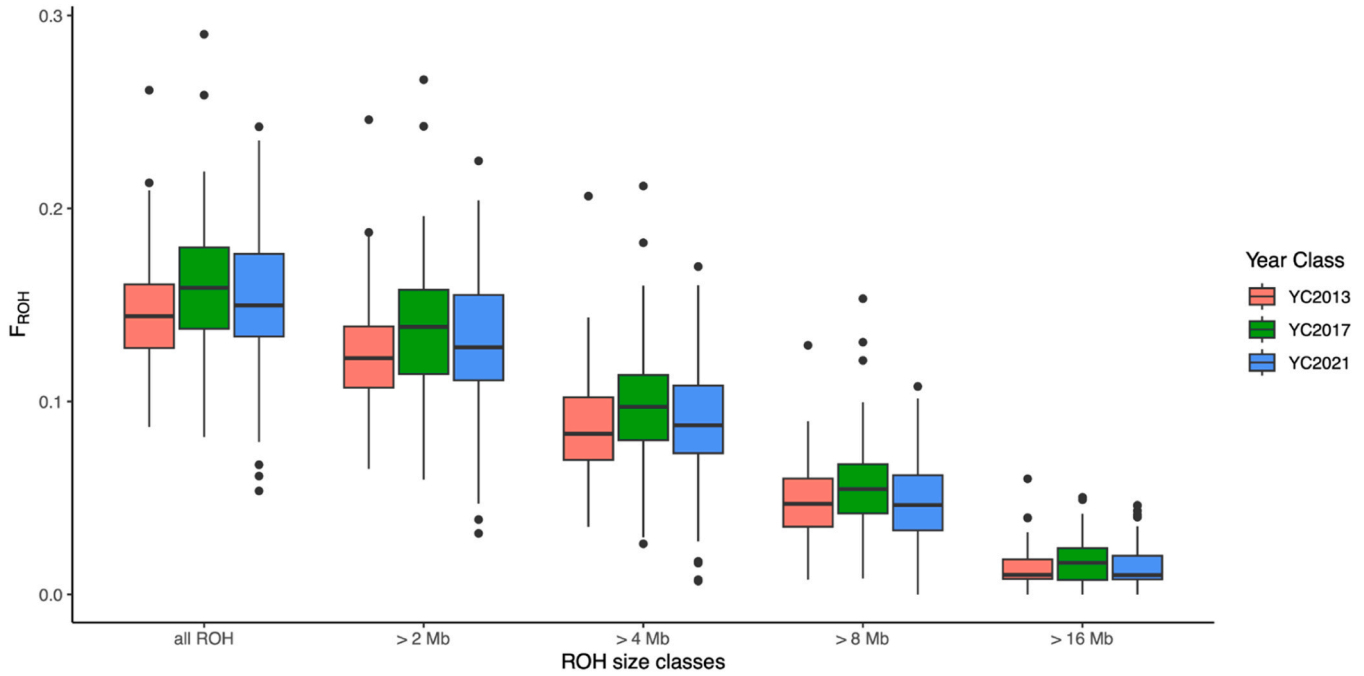

Fig. 6. Boxplots depicting the range of F_{ROH} for the three year classes based on runs of homozygosity (ROH) of different size classes. The solid horizontal line within each boxplot depicts the median value. The horizontal axis shows F_{ROH} based on all ROH, then F_{ROH} were calculated with progressively greater size restrictions on ROH, up to F_{ROH} based only on runs longer than 16 Mbp.

population over recent years (e.g., Palaiokostas et al., 2024), utilising high-quality genotypes, as is typical with SNP arrays, could offer advantages. More specifically, SNPs used in the current study are more informative than the ones previously used from GBS (Pappas and Palaiokostas, 2021), as it can be clearly seen from the MAF distribution (Fig. 2). This finding is in line with results from other SNP arrays as ones for Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss*) and barramundi (*Lates calcarifer*), where the SNP majority was highly informative in terms of MAF (Gao et al., 2023; Houston et al., 2014; Jerry et al., 2022; Palti et al., 2015). In contrast, the corresponding MAF from GBS typically resembles a geometric distribution, where the majority of markers have low values, and towards the larger MAF values, one observes a rapid decline in the number of markers. Studying markers with low MAF can unveil interesting information, and such markers have often been suggested as playing a role in complex diseases (Kido et al., 2018). However, for a population like the current one, where the focus is on applying genomic selection (Meuwissen et al., 2001) and maintaining genetic diversity, having a dataset with more balanced allele frequencies for most SNPs is beneficial. In addition, since our SNP array was developed for this same population, we automatically circumvented one of the most highlighted drawbacks of such tools. More specifically, the SNP ascertainment bias that arises when a SNP is developed in one population and used in others (Lachance and Tishkoff, 2013).

Commonly, the SNP array design follows a two-stage process. In the first stage, a high-density array is produced (the number of probes can range substantially; e.g 150,000 - 800,000) that acts also as quality control for further identifying the most reproducible and informative markers that in the second step are used for a production (or low density) array usually containing ~ 57,000–60,000 probes. As a rule of thumb, an LD level above 0.2 extending through hundreds of kilobases would be suitable for genomic prediction (Calus et al., 2008). Even though deviations from the above are likely to depend on species and the targeted trait(s) for selection, the LD pattern in our study suggests that developing a lower-density array would be a pragmatic strategy. That would allow the efficient implementation of genomic breeding with reduced genotyping costs. Notably, when comparing the LD decay in our study with that of other farmed salmonids (Barría et al., 2019; Bernard et al., 2022), our results appear towards the upper end in both magnitude and persistence over physical distance. This finding appears to be in line with our population's history, as the Swedish Arctic charr breeding program is one of the oldest breeding programs for any aquaculture species, operating to date in a closed nucleus format.

Assessing the genetic diversity is a continuous process and therefore, the current study benefits from genotyping animals from three consecutive and discrete year classes. This part is especially important, as in the past we lacked this option and either concentrated on studying a single year's class (Palaiokostas et al., 2024) or, when multiple year classes were involved either a limited number of animals (n = 12) was genotyped (Pappas et al., 2023), or the genotyping density was sparse (Palaiokostas et al., 2022). Regarding genetic diversity metrics like heterozygosity, the obtained values here are in agreement with our previous studies, where the observed and expected heterozygosity ranged between 0.34 and 0.37 and 0.34–0.35, respectively (Palaiokostas et al., 2022). Furthermore, as previously mentioned, no distinct genetic groups were identified by the PCA, a result to be expected given that a closed breeding nucleus has been maintained for 10 generations of selection. Similarly, the F_{ST} metric suggested minimal genetic differentiation (0.002–0.06) among the studied year classes. It is worth noting that these are generally considerably lower than those reported for other selectively bred salmonids, except for two selected lines of rainbow trout from France where similar values (~0.02) were reported (D'Ambrosio et al., 2019).

Our estimates of the effective population size based on linkage disequilibrium and pedigree both suggest a relatively low effective population size. The pedigree-based estimates show generation-to-generation variation due to the number of families formed that is not recovered by the LD-based estimates, demonstrating some of its inherent uncertainty. The LD-based estimates also suggest a decline in effective population size prior to the onset of systematic breeding. Notably, this could be because the population that founded the breeding program was already in decline. However, one should keep in mind that these estimates are based solely on LD patterns and that accuracy declines at earlier timepoints. Moreover, the GONE method of N_e estimation is also

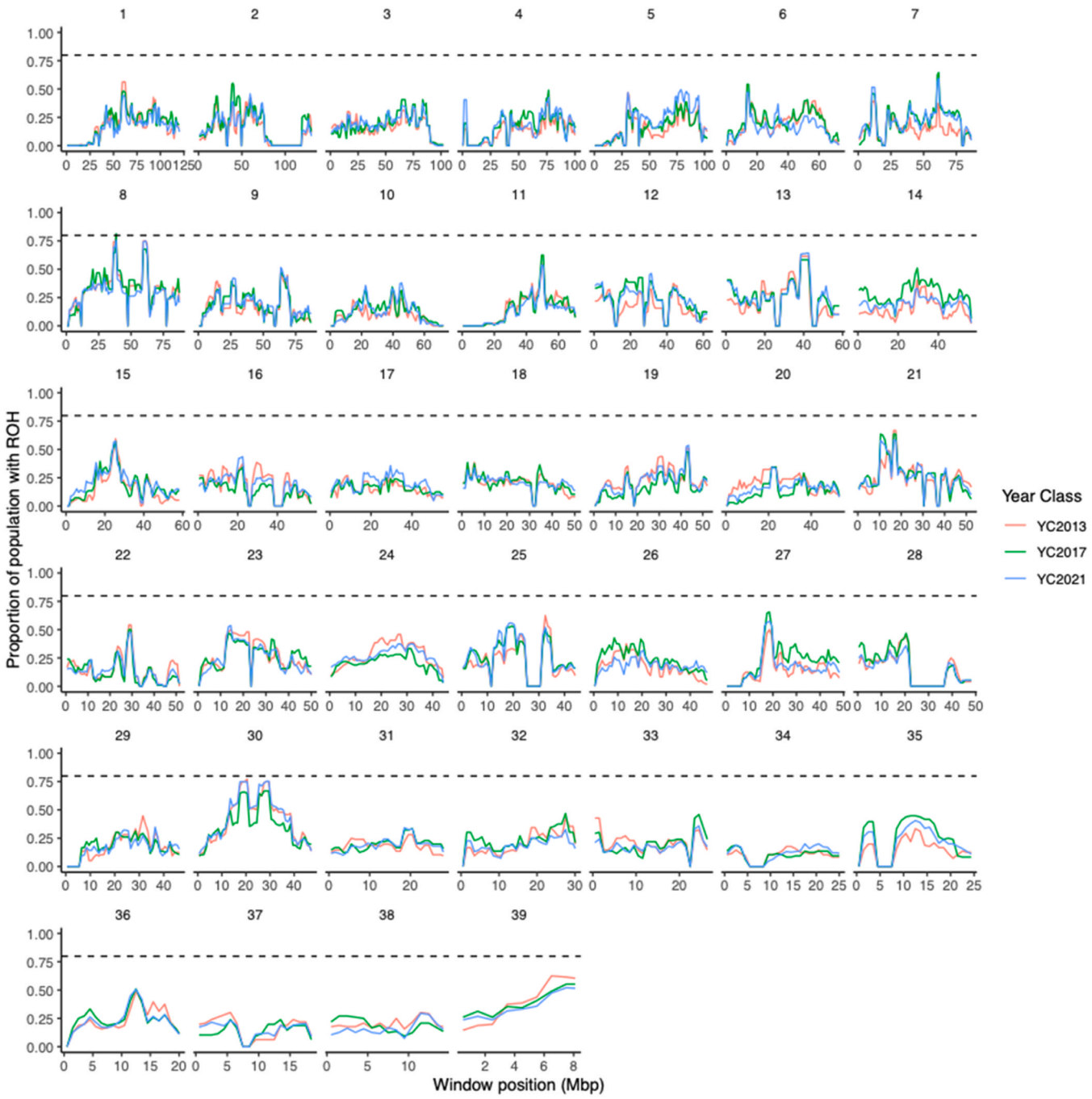

Fig. 7. Plot of ROH frequency in 1-Mbp windows along the genome. The panels show different chromosomes. The horizontal dashed line represents the ROH frequency threshold that was derived by simulation.

sensitive to population structure and admixture, meaning that the ancestral population structure before the onset of breeding may have led to an overestimation of the historical effective population size (Novo et al., 2023).

Inbreeding accumulation is a topic of concern for any breeding program. Naturally, a certain level of inbreeding increase is desirable and intertwined with the very core of selective breeding. Nevertheless, surpassing a threshold of inbreeding can lead to inbreeding depression that could jeopardize the future of a breeding program. As the above threshold can vary between populations and species, the generic guidelines are to retain inbreeding accumulation below 1 % per generation, corresponding to an inbreeding effective population size of 50 (Meuwissen and Woolliams, 1994). Before the genomic era, inbreeding accumulation was monitored through pedigree information by implementing classic quantitative genetics methodology. However, in this case only a crude and generic estimate of inbreeding is allowed. At the same time, the inbreeding levels of the animals in the base population must be assumed to be zero. On the other hand, genomic information can circumvent the above limitations, providing more accurate estimates (Keller et al., 2011). The genomic estimates of inbreeding from F_{ROH} together with those from N_e suggest that the population may be accumulating inbreeding above the target, even as pedigree inbreeding rates are below 1 %. Therefore, we propose that management of inbreeding with genomics, which will be made possible by a medium-density SNP chip for routine use.

In our study, inbreeding estimates were based on the detection of

Table 1
Candidate genes located in the window of high ROH frequency on chromosome 8.

Start	End	Gene	Accession	Description
38024602	38077699	*LOC139583076*	139583076	meiosis-specific protein MEI4-like
38082869	38087776	*LOC139583077*	139583077	5-hydroxytryptamine receptor 1B-like
38119886	38121214	*LOC139582367*	139582367	uncharacterized LOC139582367
38189777	38222437	*LOC139582255*	139582255	interphotoreceptor matrix proteoglycan 2-like
38221902	38317618	*LOC139582257*	139582257	unconventional myosin-VI-like
38293240	38311010	*LOC139582268*	139582268	uncharacterized LOC139582268
38322338	38341736	*LOC139582259*	139582259	sentrin-specific protease 6-like
38345406	38395647	*LOC139582258*	139582258	filamin-A-interacting protein 1-like
38388171	38399777	*LOC139582267*	139582267	uncharacterized LOC139582267
38396632	38406732	*LOC139582264*	139582264	cell cycle control protein 50A-like
38406889	38408732	*LOC139582265*	139582265	cytochrome c oxidase subunit 7A2, mitochondrial-like
38410701	38508551	*LOC139583078*	139583078	collagen alpha-1(XII) chain-like
38523242	38524236	*LOC139583079*	139583079	uncharacterized LOC139583079
38696500	38717133	*cd109*	139582294	CD109 molecule
38718866	38720799	*LOC139583081*	139583081	N-alpha-acetyltransferase 20-like
38720795	38727084	*LOC139583080*	139583080	crooked neck-like protein 1
38727547	38762696	*LOC139582295*	139582295	cilia- and flagella-associated protein 61-like
38765307	38767904	*LOC139583082*	139583082	insulinoma-associated protein 1a pseudogene
38829659	38856191	*LOC139583083*	139583083	bifunctional protein GlmU-like
38883202	38915860	*LOC139583084*	139583084	5'-3′ exoribonuclease 2-like
38915581	38917424	*LOC139583085*	139583085	homeobox protein Nkx-2.4-like
38930275	38932279	*LOC139583086*	139583086	homeobox protein Nkx-2.2a-like
38948919	38959854	*LOC139583087*	139583087	paired box protein Pax-1-like

runs of homozygosity, a previously demonstrated robust tool in aquaculture species (Yoshida et al., 2020). Notably, the estimated inbreeding coefficients of the current study are substantially larger compared to the ones estimated from whole genome-resequencing (WGS) data (Pappas et al., 2023). In both cases, the same methodology was used to estimate inbreeding coefficients, with the difference lying in the number of used SNPs. In particular, as the WGS study was based on approximately 5 million SNPs, this could suggest that those inbreeding estimates are more accurate. However, only 24 samples were used in the WGS study, compared to 382 in the current one. Furthermore, it is worth mentioning that inbreeding coefficients exceeding 15 % are not unique in the current study. In studies of rainbow trout populations in captivity for a similar time period to the Swedish Arctic charr, inbreeding coefficients based on ROH were close to 20 % without a direct connection to potential inbreeding depression (D'Ambrosio et al., 2019; Paul et al., 2024).

The frequency of the identified ROH enabled us to screen the genome for islands of homozygosity. Our analysis identified a region on chromosome 8 of potential interest regarding the identification of genes that may have been subject to selection. However, this megabasepair region contains genes with diverse functions, making it difficult to speculate which genes may have been under selection. Candidate genes include ones potentially involved in gametogenesis and meiosis, neurotransmission, visual perception, auditory perception, the cell cycle, energy metabolism and gene regulation.

Notably, the partitioning of F_{ROH} into contributions from ROH of different lengths suggests that only a small proportion of the inbreeding (ROH $>$ 4Mbp) is caused by common ancestors in the most recent generations (as expected in a managed breeding program), and rather likely goes back to shared ancestors during or before the founding of the breeding program. For context, the expected length of a ROH originating from a shared ancestor 10 generations ago is approximately 6 Mbp (Thompson, 2013). Inbreeding contributed by such early shared ancestors cannot be managed via pedigree, but can be captured by F_{ROH}. On the other hand, studies from both wild (Stoffel et al., 2021) and domestic animals (Makanjuola et al., 2020) suggest that inbreeding from ancient shared ancestors is less harmful than inbreeding due to more recent shared ancestors. This can be explained by short ROH containing a lower density of deleterious variants and a reduced mutation load in older haplotypes due to purifying selection (Stoffel et al., 2021).

Even though no direct signs of inbreeding depression are apparent in the Swedish Arctic charr, and the proportion contributed by ancient inbreeding may be less of a problem than recent inbreeding, it is fair to say that such high estimates could raise concerns. Continuous monitoring of the genetic diversity status of this population is warranted. In addition, it is likely that in the near future, the breeding program management team should explore the possibility of widening the genetic diversity pool by including animals outside the breeding nucleus. Such introductions would reduce inbreeding, as new animals would be only distantly related to the nucleus animals, thereby increasing genetic diversity. However, they would also likely reduce short-term genetic gain in selected traits unless the introduced animals have undergone selection practices as well.

CRediT authorship contribution statement

Christos Palaiokostas: Writing – original draft, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Martin Johnsson:** Writing – review & editing, Funding acquisition, Formal analysis, Data curation.

Ethical statement

The current study was performed in accordance with the Swedish and European Union's legislation described in the Animal Welfare Act 2018:1192 (ethics permit: 5.2.18 – 09859/2019).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2026.103369.

Data Availability

Data will be made available on request.

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