RESEARCH ARTICLE

Genomic evidence uncovers inbreeding and supports translocations in rescuing the genetic diversity of a landlocked seal population

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Abstract

Fragmentation of isolated populations increases the risk of inbreeding and loss of genetic diversity. The endemic Saimaa ringed seal (*Pusa hispida saimensis*) is one of the most endangered pinnipeds in the world with a population of only ~400 individuals. The current genetic diversity of this subspecies, isolated in Lake Saimaa in Finland for ca. 1000 generations, is alarmingly low. We performed whole-genome sequencing on Saimaa ringed seals (N = 30) and analyzed the level of homozygosity and genetic composition across the individual genomes. Our results show that the Saimaa ringed seal population has a high number of runs of homozygosity (RoH) compared with the neighboring Baltic ringed seal (*Pusa hispida botnica*) reference population ($p < 0.001$). There is also a tendency for stillborn seal pups to have more pronounced RoH. Since the population is divided into semi-isolated subpopulations within the Lake Saimaa exposing the population to deleterious genomic effects, our results support augmented gene flow as a genetic conservation action. Based on our results suggesting inbreeding depression in the population, we recommend Pihlajavesi as a potential source and Southern Saimaa as a potential recipient subpopulation for translocating individuals. The Saimaa ringed seal is a recognized subspecies and therefore translocations should be considered only within the lake to avoid an unpredictable risk of disease, the introduction of deleterious alleles, and severe ecological issues for the population.

Introduction

Preservation of genetic diversity has been recognized as essential to the conservation efforts of endangered species (Frankel 1974). High genetic diversity is positively linked to the viability and evolutionary potential of a population

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but is often compromised in endangered species. Decreasing population size and increasing isolation reduce fitness both at individual and population level via inbreeding depression (e.g., Frankham 1996, 2010, 2015; O'Grady et al. 2006; Hedrick and Garcia-Dorado 2016; Kardos et al. 2016, 2018; Weiser et al. 2016; Frankham et al. 2019; Harrisson et al. 2019; Gkafas et al. 2020; Kyriazis et al. 2021; Ning et al. 2021). Genetic rescue aims to restore, preserve, and increase current genetic diversity in semi-isolated subpopulations and thus reduce the extinction risk of endangered populations. It is largely implemented through translocations, which aim to increase the diversity by adding individuals to areas with impoverished genetic variation. The International Union for Conservation of Nature defines translocation as deliberate and mediated movement of wild individuals or populations from one part of their range to another (IUCN/SSC 2013).

The Saimaa ringed seal (*Pusa hispida saimensis*), occupying a 4400 km^2 freshwater lake in Finland, is one of the most endangered pinnipeds in the world (Kovacs et al. 2012). As a landlocked subspecies, it has suffered strongly from a variety of human-induced factors such as hunting, habitat loss, environmental toxins, incidental bycatch mortality, and wintertime water-level fluctuations related to hydropower production. Due to systematic conservation efforts since the early 1980s, the population has slowly grown from ~ 100 individuals in 1980 to ~ 400 individuals in 2020 (Kunnasranta et al. 2021). However, this endemic population is increasingly threatened by climate change, reducing the ice and snow cover, crucial for ringed seals giving birth in snow lairs (Auttila et al. 2014). To protect this unique environment, main Saimaa ringed seal habitats in the Lake Saimaa archipelago are being proposed as a new natural site on UNESCO's list of World Heritage sites (Ministry of the Environment 2020).

The deglaciation of Fennoscandia and subsequent isolation of Lake Saimaa from the Baltic Ice Lake (a proto-Baltic Sea) approximately 9500–11,000 years ago (Stroeven et al. 2016) set the stage for the founding of the Saimaa ringed seal population and for the ongoing total genetic isolation from other ringed seals. Not surprisingly, the genetic variation, as shown both by nuclear microsatellites and mitochondrial DNA markers of the current Saimaa ringed seal population is among the lowest detected in pinnipeds (Valtonen et al. 2012; Nyman et al. 2014; Stoffel et al. 2018; Peart et al. 2020). For instance, the heterozygosity at microsatellite loci ($H_E = 0.34$) is as low as observed in other endangered or genetically depauperate pinnipeds such as the Mediterranean monk seal (*Monachus monachus*, $H_E \approx 0.37$, Pastor et al. 2004; Karamanlidis et al. 2021) or northern elephant seal (*Mirounga angustirostris* $H_E \approx 0.37$, Abadía-Cardoso et al. 2017), and is notably lower than in the marine ringed seals ($H_E \geq 0.80$; Davis et al. 2008; Martinez-Bakker et al. 2013; Nyman et al. 2014). In addition to the impoverished

genetic diversity, genetic studies indicate that the Saimaa ringed seal population is divided into semi-isolated subpopulations across the lake (Valtonen et al. 2012, 2014, 2015). This division into units with only restricted gene flow among them can make the already small population even more vulnerable to stochastic environmental and genetic effects (e.g., Lacy 1987; Reed and Frankham 2003; Kardos et al. 2018; Kyriazis et al. 2021).

In addition to diversity-level estimations, modern genomic analyses have offered new tools to assess inbreeding in natural populations. Genome-level nucleotide differences between individuals are commonly known as single-nucleotide polymorphisms (SNPs). SNPs are single-nucleotide differences in genome sequence between the alleles of an individual or between two or more individuals, which implicate the genetic variability in a population. They can be used to observe slight genetic differences within a population and predict an individual's ancestry. An alternative estimator for the level of inbreeding is provided by the analysis of SNP-based contiguous lengths of homozygous areas, i.e., runs of homozygosity (RoH, Broman and Weber 1999; Ceballos et al. 2018), across the whole genome (Lencz et al. 2007; Keller et al. 2011; Pemberton et al. 2012; Grossen et al. 2017). RoH correlate positively with inbreeding and extensive RoH indicate close relatedness of individuals. RoH length also indicates how recent the observed inbreeding is: the longer the RoH the more recent the observed inbreeding (Browning and Browning 2012). The longest RoH in mammal genomes may exceed 10 million base pairs (Mbp) (Purfield et al. 2012; Grossen et al. 2017). In the Saimaa ringed seal population, a genome-wide SNP and RoH analysis in comparison to the neighboring Arctic (*P. h. hispida*), Baltic (*P. h. botnica*) and Ladoga (*P. h. ladogensis*) subspecies shows evidence of lost genetic diversity and contemporary inbreeding (Löytynoja et al. 2022).

In this study, we further examine the most recent genomic data of the Saimaa ringed seals to better understand the diversity and the level of inbreeding of this small, isolated, and fragmented population as well as to assess the potential benefit of translocations within Lake Saimaa. This is the first study to combine samples from various age groups in different Saimaa ringed seal subpopulations including samples from stillborn individuals and young pups. We analyze all single-nucleotide differences in the individual genomes and summarize the RoH and SNP compositions. We compare the homozygosity levels observed in the genomes of Saimaa ringed seals against the levels observed in the Baltic ringed seals and between the Lake Saimaa subpopulations. The specific objectives of this study are to (1) investigate differences in the RoH levels between the Baltic and Saimaa populations and between the Saimaa subpopulations, (2) compare the SNP composition between subpopulations, and (3) identify potential source and recipient subpopulations for

translocating individuals within Lake Saimaa based on the RoH levels and SNP composition. The results will be used to make recommendations for an improved genetic conservation protocol for the Saimaa ringed seal. These recommendations may be valuable in the conservation of other endangered species.

Materials and methods

Sample material

We analyzed the genomes of Saimaa ringed seal pups that were stillborn, died before weaning, or died at less than a year old (N = 30, Fig. 1, Appendix S1). We selected this rare and high-quality sample material due to its accessibility and non-invasive nature. Two of the samples were from weaned pups (To-20/A1702 and Sa-20) that were found in poor condition and taken into care in 2020. To-20 died soon in captivity, but Sa-20 was released back into the wild the

Fig. 1 Map of Lake Saimaa showing the locations of seal samples used in this study
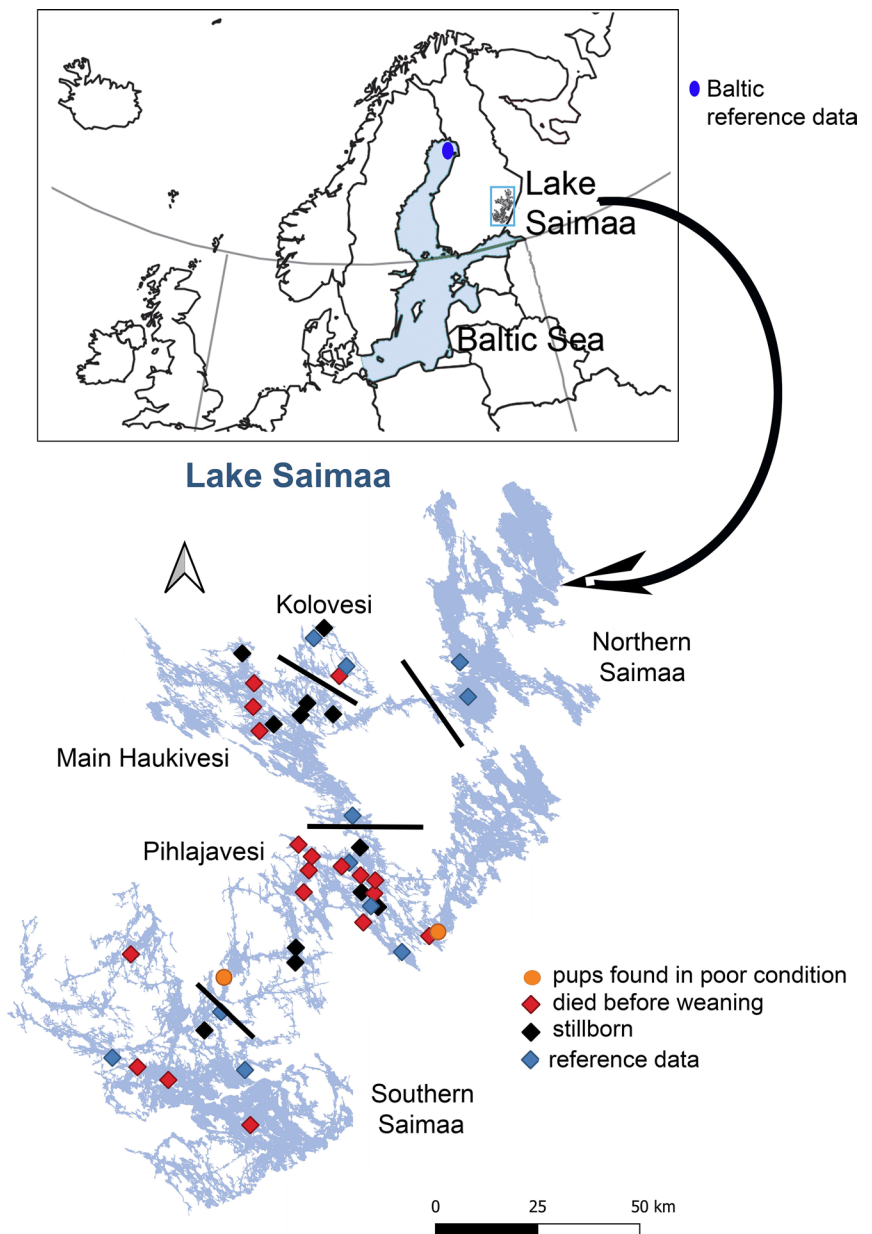
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same summer without further records of its existence. The samples were collected and examined under the Centre for Economic Development, Transport and the Environment permits VARELY/3480/2016 and VARELY/2497/2018 during 1995–2020.

As reference data, we used published whole-genome sequencing data from Saimaa ringed seal samples (N = 11) collected during 1995–2017 (Fig. 1, Appendix S1) and Baltic ringed seal samples (N = 9) collected during 2007–2015 (Savriama et al. 2018). Baltic ringed seals were chosen as the reference group for its neighboring northern location, population size (N ≈ 13,000, Sundqvist et al. 2012), and available high-quality whole-genome data. The Saimaa samples consisted of individuals that survived beyond weaning (9 pups, one 1-year-old and one adult: Appendix S1). The Saimaa individuals had genomic coverages between 4.2X and 21.6X and those of Baltic individuals between 9.3X and 28.9X (Appendix S1). The Baltic ringed seal samples were from the Bothnian Bay; no detailed location information for these samples was available. We assigned each Saimaa individual into five groups representing the subpopulations: Main Haukivesi (n = 10), Pihlajavesi (n = 20), Kolovesi (n = 3), Northern Saimaa (n = 2), and Southern Saimaa (n = 6), according to the sample collection basin (Fig. 1).

Sequencing

We sequenced all samples with either the Illumina Next-Seq500 or the MGI Tech Co. DNBseq-G400 sequencing platform (Appendix S1). The working principle of all platforms is essentially the same: base incorporation light color detection with a high-density camera. The main exception is that the Illumina NextSeq500 uses a bridging polymerase chain reaction (PCR) protocol to amplify the sample material whereas the DNBseq platform does not use PCR. We prepared the sequencing libraries with the standard library preparation protocols provided by Illumina and MGI.

Secondary analysis

We filtered the sequencing reads with Cutadapt (Martin 2011) version 1.9.1 and used a minimum read length of 50 base pairs and a sequencing quality threshold value of 25. This corresponds to a minimum base call correctness of 99.5% in the reads that pass the minimum length criterion. Cutadapt removed the residual sequencing library adapter sequences that may sometimes be introduced to raw sequencing reads due to the sequencing technology. We mapped the reads with the Burrows-Wheeler Aligner software (Li and Durbin 2009) against a draft reference genome produced by the Saimaa Ringed Seal Genome Project (https://www.saimaaringedseal.org/). The reference genome was built by scaffolding the 2183 contiguous sequences of the original

draft assembly (Löytynoja et al. 2022) with a novel linkage disequilibrium (LD) -based method (Kivikoski et al. 2021) into 41 super scaffolds totaling 2,33 giga base pairs (Gbp). We then performed a joint variant calling pipeline of the Genome Analysis Toolkit (Van der Auwera and O'Connor 2020), which produced Variant Call Format (VCF) files for the next stage of the analysis. The secondary analysis statistics per individual are presented as supplementary material (Appendix S1).

Analysis of runs of homozygosity

RoH in the genomes were analyzed using the BCFtools/RoH pipeline (Narasimhan et al. 2016) which detects RoH based on the emission probabilities of a hidden Markov model. BCFtools is an open-source genome analysis software toolkit that is part of the SAMtools software (Li et al. 2009). It is common to use a cutoff length that discards short homozygous areas that appear quite frequently in animal genomes, for example, due to linkage disequilibrium (Purfield et al. 2012). Accordingly, we used a cutoff length of 500,000 base pairs (500 kbp) for RoH. We defined RoH exceeding 2 Mbp as long and RoH between 500 kbp and 2 Mbp as short. We used full coverage read data up to 28.9X to analyze the subpopulation level differences in RoH lengths. To investigate individual differences in long RoH, we also downsampled the mapped read data to 5X for all individuals to balance the sequencing coverages. We compared RoH longer than 3Mbp, 4Mbp and 5Mbp between stillborn individuals and those that died later.

Analysis of genetic composition

The number of SNPs and the SNP density across the genome (e.g., per 1 Mbp) are indicators of genetic diversity. SNP information of the samples was acquired from the VCF files produced in the secondary analysis. First, we identified the number of raw SNPs and the SNP density per individual (Appendix S1). Second, we filtered the raw VCF data using a minimum genomic position sample depth of 10, i.e., at least 10 out of 50 samples must have a SNP in the genomic position for the position to pass the filter. Third, we required a minor alternate variant frequency (= minor allele frequency) of 0.05 for the variant in the position and a minimum variant call quality, Q = 20, which translates to a 99% probability that the variant call in the position is correct. Finally, we counted the numbers of group-specific and shared positions with single-nucleotide variance between the Lake Saimaa groups.

We performed a Mann–Whitney U test for the selected indices of diversity: the (1) number of RoH, (2) number of long RoH, (3) percentage of RoH, and (4) median RoH length across the individual genomes. First, we tested the

differences in the observed diversity between the within-lake groups and the Saimaa reference group. The observed non-significant differences between the within-lake and reference individuals (Appendix S2) allowed us to pool all Saimaa individuals into their respective groups within Lake Saimaa. Second, we tested the differences in observed diversity between the Saimaa (n = 41) and Baltic ringed seal reference group (n = 9) individuals. We then performed a Kruskal–Wallis analysis of variance (ANOVA) test for the Lake Saimaa groups to test whether the areas within Lake Saimaa were differentiated. Finally, we performed a pairwise Mann–Whitney U test for the Lake Saimaa groups with Bonferroni adjusted p-values.

Results

We discovered considerable differences in the levels of homozygosity between Saimaa and Baltic individuals (Fig. 2, Appendices S2–S5). The Saimaa individuals had a significantly higher number and percentage of RoH compared with the Baltic ringed seals ($p < 0.001$, Fig. 2a–c and Appendix S2). The median RoH length was short, less than 1,000,000 base pairs in all individuals (Figs. 2d and 3d and Appendix S5). There were no significant differences in the

median RoH lengths between Saimaa and Baltic individuals ($p > 0.1$, Fig. 2d, Appendix S2). Within Lake Saimaa, Pihlajavesi individuals showed the highest variation in their RoH levels (Fig. 3).

Of the stillborn samples, individual 2402 (Pihlajavesi) had the highest number of RoH of all samples, 907 (Appendix S3). Individuals 2377 (Main Haukivesi) and 2402 had the highest overall percentage of RoH across the genome, 39.7% and 37.1%, respectively (Appendix S4).

Overall, the number of RoH was highly variable among different individuals (Fig. 4a). When comparing the stillborns with pups that died under the age of 12 months, the difference was statistically significant ($p = 0.0496$, Fig. 4b, Appendix S2). However, as the sequencing coverage can affect RoH lengths and number, we made a more detailed comparison of RoH lengths after downsampling the data to 5X coverage. Differences in sequencing depth could be a concern in our data since stillborn samples tended to have lower quality DNA and sequencing coverage (Appendix S1). After downsampling, stillborns showed tendency for longer RoH with 58% (7/12) of stillborn and 28% (8/29) of pups born alive having RoH lengths exceeding 4 Mbp (Fig. 4c). In addition, the number of long RoH tended to be higher in the stillborn samples (Fig. 4d), but the differences were not significant (smallest $p = 0.088$ for the RoH greater than 3
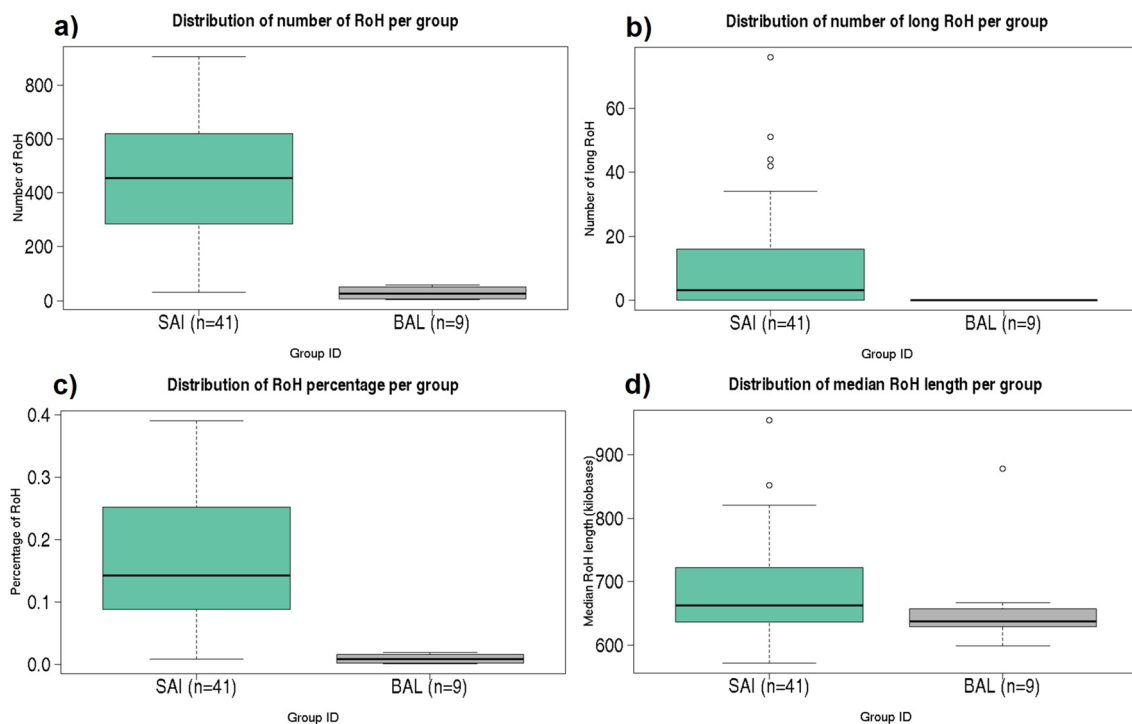

Fig. 2 Distributions of **a** number of runs of homozygosity (RoH), **b** number of long RoH, **c** percentage of RoH and **d** median RoH length in kilobases per sample group. The IDs are: SAI = Saimaa, BAL = Baltic reference. The boxplots represent the first quartile (box base), the median (horizontal black line at the box center), and the third quartile (box top) in the sample. The box whiskers extend to 1.5*interquartile range. Round dots are considered outliers with respect to the rest of the data points in the dataset
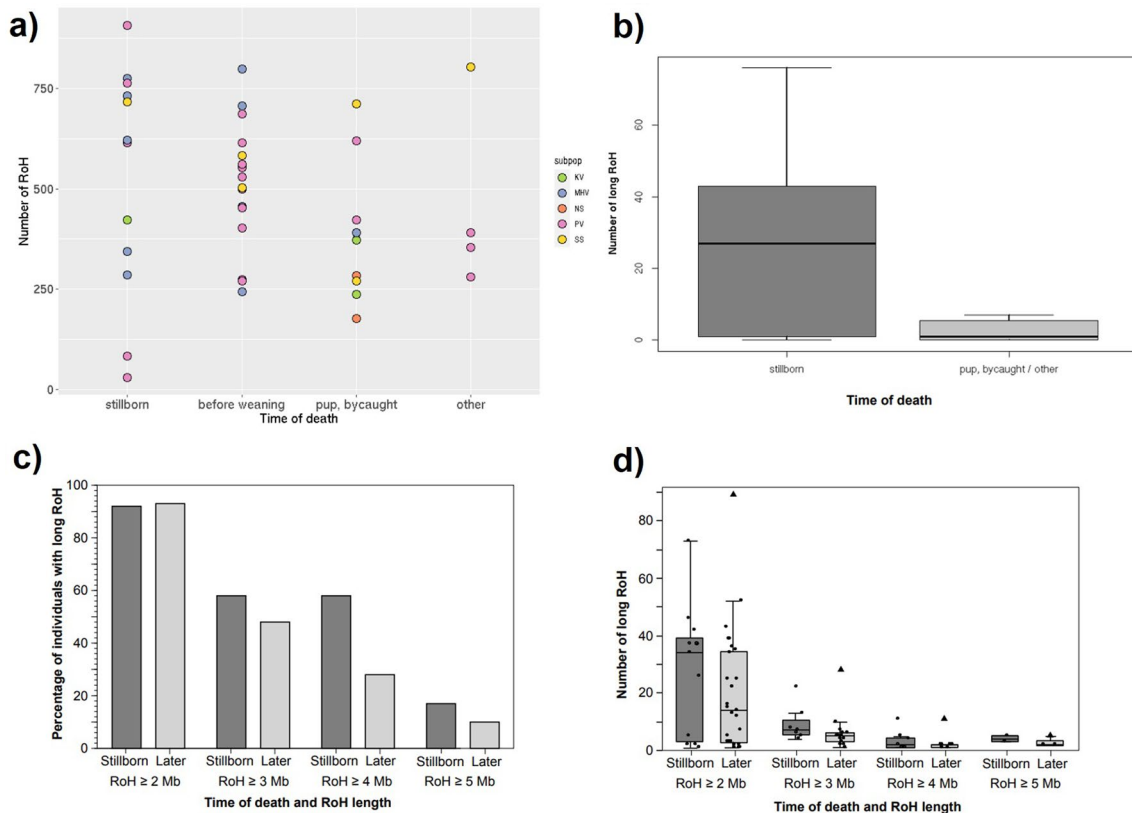
Fig. 3 Distributions of **a** number of runs of homozygosity (RoH), **b** number of long RoH, **c** percentage of RoH and **d** median RoH length in kilobases, per group within Lake Saimaa. The group IDs are: *MHV* Main Haukivesi, *PV* Pihlajavesi, *SS* Southern Saimaa, *KV* Kolovesi, *NS* Northern Saimaa

Mbp, Mann–Whitney *U* test). We note that the individual having the largest number of long RoH in the downsampled data was the seal pup To-20 that was found in poor condition, and which then died in captivity (triangle in Fig. 4d). The high level of RoH could have contributed to the death of To-20. The use of DNBseq-G400 and high sequencing coverage for this individual may also have exaggerated the RoH values in the downsampled data. If To-20 is excluded from the analyses, the number of long RoH in stillborns is significantly greater compared to pups born alive ($p = 0.035$ for the RoH greater than 3 Mbp). Although these results should be considered tentative because of the limited sample size, they are suggestive of inbreeding depression in the Saimaa ringed seals shown especially in the stillborn individuals.

Of the Lake Saimaa groups, Southern Saimaa showed the highest and Northern Saimaa the lowest median level of homozygosity (Fig. 3). The Kruskal–Wallis ANOVA test of the groups indicated significant differences in number, percentage, and median length of RoH within Lake Saimaa ($p < 0.05$ for all diversity indices, Appendix S2). While this is a general signal of significant within-lake differentiation, the pairwise Mann–Whitney *U* test for the within-lake groups did not find significant differences between the

subpopulations for any of the four diversity indices after applying Bonferroni correction (Appendix S2).

After filtering, there were 731,209 genomic positions with single-nucleotide variance at the population level. Altogether, 292,302 (40.0%) of the positions were shared between all Lake Saimaa groups (Fig. 5). Notably, there were a total of 39,986 group-specific positions between the groups. Pihlajavesi had the highest number of these, 19,943, i.e., 2.7% of all positions and 49.9% of group-specific positions found between the groups (Fig. 5).

Discussion

This is the first study to investigate RoH and single-nucleotide variation at whole-genome level on the Saimaa ringed seal, a small landlocked population that has lived in total isolation for ca. 1000 generations. Our results are in line with earlier studies showing low genetic diversity in the population (Palo et al. 2003; Valtonen et al. 2012; Martinez-Bakker et al. 2013; Nyman et al. 2014; Savriama et al. 2018; Stoffel et al. 2018; Peart et al. 2020; Löytynoja et al. 2022). The diversity loss has been attributed to either a founder event
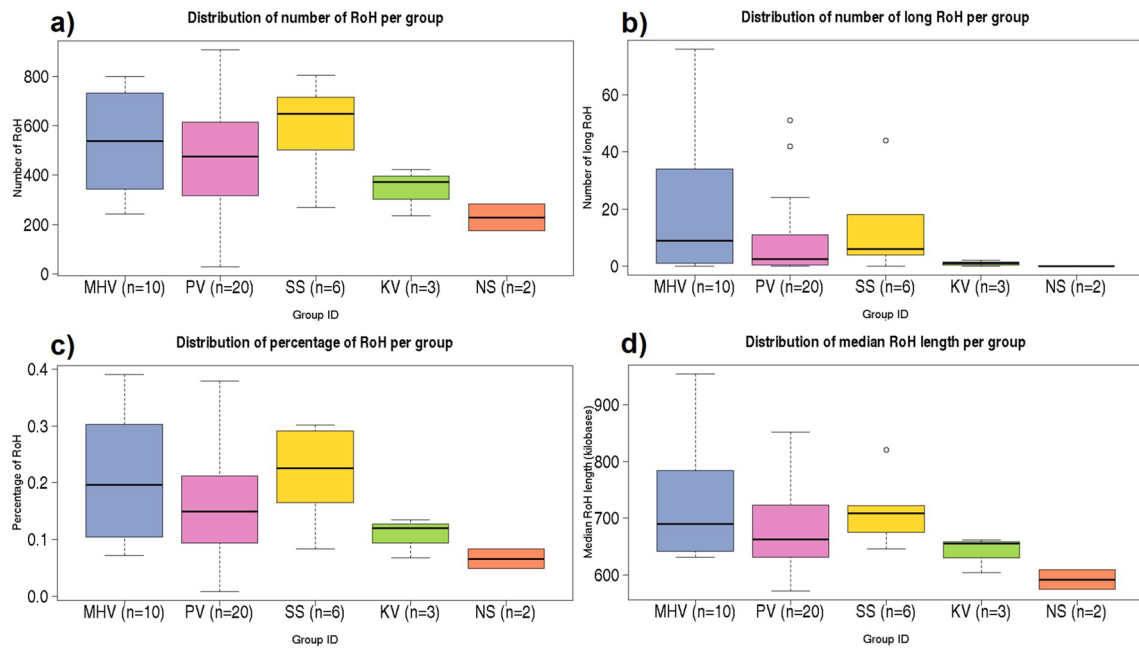
Fig. 4 Examining inbreeding depression in Saimaa ringed seals between stillborns and pups aged under 12 months. Distributions of **a** number of RoH per individual across subpopulations, **b** distributions of the number of long RoH, **c** percentages of individuals with RoH exceeding 2–5 megabase-pairs (Mbp) and **d** distributions of the number of long RoH. In subplots b-d, the boxplots represent the

first quartile (box base), the median (horizontal black line at the box center), and the third quartile (box top) in the sample. The box whiskers extend to 1.5*interquartile range. The black dots are data points, and black triangles mark the To-20/A1702 seal pup that was found in poor condition and died in captivity
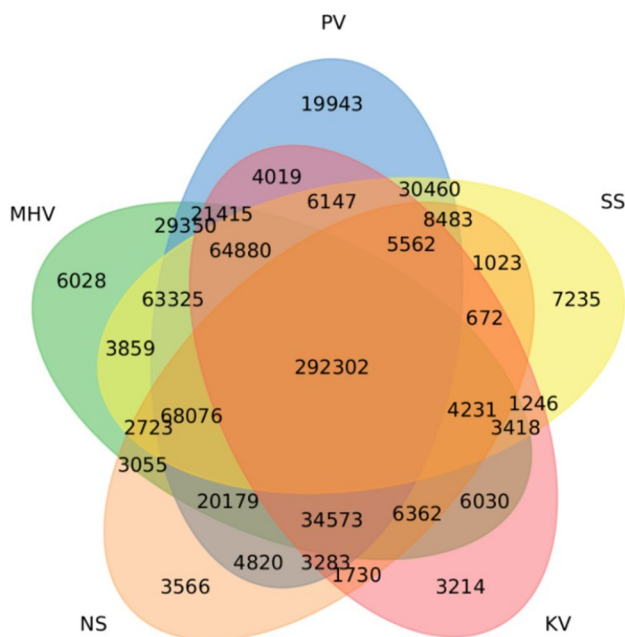
Fig. 5 Overlaps of the 731,209 genomic positions with single-nucleotide variance between the Lake Saimaa groups. The group IDs are: *MHV* Main Haukivesi (n=10), *PV* Pihlajavesi (n=20), *KV* Kolovesi (n=3), *SS* Southern Saimaa (n=6), *NS* Northern Saimaa (n=2)

after the colonization bottleneck, gradual erosion of diversity over a long isolation, or a more recent anthropogenic bottleneck caused by targeted hunting in the 1900s (Palo et al. 2003; Nyman et al. 2014; Stoffel et al. 2018; Peart et al. 2020). Populations experiencing an abrupt loss of diversity and increase of inbreeding suffer inbreeding depression more acutely (Hedrick and Kalinowski 2000; Kardos at al. 2018; Kyriazis et al. 2021). Nyman et al. (2014) suggested that low diversity of the Saimaa ringed seal largely results from a founder event by a small number of colonizers. However, Valtonen et al. (2014) found evidence for a slow decline in individual heterozygosity occurring over the past 50 years, and recent analyses by Stoffel et al. (2018) and Peart et al. (2020) likewise suggest that the human-induced population crash in the latter half of the 20th century (Sipilä 2003; Kunnasranta et al. 2021) has played a role in shaping the genetic variation of the Saimaa ringed seals.

Differences in runs of homozygosity levels between Baltic and Saimaa populations and between Saimaa subpopulations

The higher number and percentage of RoH in Saimaa ringed seals compared to the Baltic population suggest high and relatively recent inbreeding in the Saimaa ringed seals, which varies among the subpopulations in Lake Saimaa. Furthermore,

some stillborn seals showed the highest percentage and number of long RoH (Appendices S4 and S5). Although limited by sample size, we observed a tendency for stillborn individuals to have higher numbers of long RoH when compared with pups that died of other causes. The difference was further emphasized when comparing RoH with lengths exceeding several megabase-pairs. While obviously only individual cases, they suggest that inbreeding in Saimaa ringed seals directly affects fitness in individuals. The long RoH results further indicate that the parents of the stillborn individuals are more likely to be closely related.

The results are in line with several previous studies documenting reduced genetic diversity and significant population sub structuring in Saimaa ringed seals (Palo et al. 2003; Valtonen et al. 2012, 2014; Löytynoja et al. 2022). Mitochondrial diversity patterns in the Saimaa population suggest that female seals are highly philopatric, staying and reproducing in their natal regions (Valtonen et al. 2012). Furthermore, nuclear markers show highly significant population structure (Valtonen et al. 2014; Löytynoja et al. 2022), indicating that sporadic trips made by single individuals between water basins (Biard et al. 2022) do not translate to effective gene flow (cf. Virrueta Herrera et al. 2022).

Single-nucleotide polymorphism composition between subpopulations

Our results show that the SNPs are unevenly distributed in the Saimaa ringed seal population. Thousands of group-specific positions of genomic single-nucleotide variance were found in all within-lake groups, the Pihlajavesi group alone containing half of the positions. The Southern Saimaa group had the second highest number of unique positions, but it also had the highest number of overlapping positions with all the other Lake Saimaa groups. Investigating the consequences, for example, whether the variants cause amino-acid changes or how the variants are distributed between the individuals in the group, will be the target of future research.

Preserving genetic variation is one way to increase the long-term survival of a population. Translocating individuals between subpopulations decreases the risk of losing useful SNPs, and in some cases, the whole population. SNPs that are unique will disappear if any of the subpopulations becomes extinct. While the significance of individual SNPs is often impossible to determine, in the case of a genetically depauperate population, such as the Saimaa ringed seals, all measures safeguarding the existing variation can be considered valuable.

Identifying potential source and recipient subpopulations

The results obtained in this study, combined with ecological information regarding the subpopulations, can be used to identify potential source and recipient regions in Lake Saimaa. Pihlajavesi and Main Haukivesi individuals showed the most variable RoH levels among the Lake Saimaa subpopulations. This is an expected result: the Pihlajavesi basin is estimated to have around 130 individuals and the Main Haukivesi basin 90 (Metsähallitus 2021), i.e., more than half of the whole population.

We observed a lower level of homozygosity in the Northern Saimaa subpopulation compared with the other Lake Saimaa subpopulations. The difference was not statistically significant but was biased toward the lower end for the RoH number, RoH percentage, and median RoH length. However, due to a small sample size (n = 2) we cannot be conclusive on the level of inbreeding in the Northern Saimaa population. Moreover, with a total population of only 20–30 individuals, Northern Saimaa looks less suitable as a source population for translocations. Conversely, at least the Southern Saimaa subpopulation and possibly Main Haukivesi subpopulation show relatively high numbers, percentages, and median lengths of RoH (Fig. 3). Despite the high variation in number, percentage, and median length of RoH, Pihlajavesi shows low median values of the diversity indices and has the highest subpopulation size, making it the most suitable source population.

Although the differences in the pairwise diversity indices within Lake Saimaa were found to be non-significant, we suggest Southern Saimaa as the potential recipient subpopulation for translocating individuals. We further identify the Kolovesi basin as a region of high concern due to its genetic isolation from the other Saimaa basins (Valtonen et al. 2014) and reduced pup production (Metsähallitus 2021). Since 2005, the population has decreased from 35 individuals to 12. The Kolovesi basin has conservation status as a national park and therefore the habitat would be favorable for translocation due to strict protection restrictions.

Saimaa ringed seal conservation perspectives

Ongoing climate change, which is estimated to be extreme in northern latitudes, increases the probability of winters without ice cover on Lake Saimaa. This would be highly detrimental to pup production as females give birth in snow lairs on icy lakeshores. Reducing the losses caused by climate change and other human-induced effects is vital for reaching favorable population size and strengthening the genetic diversity of the Saimaa ringed seal population. In addition to translocations, several actions are being carried out to improve seal survival into adulthood: fishing restrictions, water-level regulation, land use planning, building artificial nest boxes, and improving snow conditions by piling snow, are key conservation elements (see e.g., Kunnasranta et al. 2021, 2022).

A common concern with genetic rescue is that augmented gene flow may also lead to outbreeding depression and decrease fitness when source and recipient populations are genetically distant (Bell et al. 2019; Robinson et al. 2021). Within Saimaa, this risk can be ignored as the source and recipient populations originate from the same lake and have low population divergence, but the risk of outbreeding depression prevents translocations from other ringed seal populations e.g., from Like Ladoga. One within-lake translocation was successfully piloted in 1992 with an adult female which, based on the photo-identification database, was still alive 25 years later in the same region (Kunnasranta et al. 2021). Captive-reared individuals are used in many translocations (Griffiths and Pavajeau 2008; Attard et al. 2016; Landa et al. 2017), but actions are known to be more successful when wild-born individuals are used (Griffith et al. 1989).

Currently, the population size of the Saimaa ringed seals is highly dependent on the direct and indirect consequences of human activity. Since the alarmingly low numbers of 100–150 individuals in the 1980s, the population has slowly grown to ~ 400 individuals. Despite the gradual increase in population size, a few consecutive years with poor reproductive success could cause the population size to decline again. Based on a previous study on breeding habitat requirements of Saimaa ringed seals, it has been estimated that the carrying capacity of Lake Saimaa could be as high as 4,000 seals in favorable conditions (Niemi et al. 2019).

Our study shows that genomic approaches involving the analysis of RoH and SNPs are powerful in detecting differences in the genetic composition between populations, sub-populations, and individuals. Based on our results, we argue that within-lake translocations would have a positive effect on preserving the genetic diversity and population dynamics of the Saimaa ringed seal. Nevertheless, the effect of translocations will only be beneficial when performed along with other conservation actions.

Declarations

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