Sealed in a lake : Biology and conservation of the endangered Saimaa ringed seal

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Review

Sealed in a lake — Biology and conservation of the endangered Saimaa ringed seal: A review

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ABSTRACT

Wildlife species living in proximity with humans often suffer from various anthropogenic factors. Here, we focus on the endangered Saimaa ringed seal (*Pusa hispida saimensis*), which lives in close connection with humans in Lake Saimaa, Finland. This unique endemic population has remained landlocked since the last glacial period, and it currently consists of only ~400 individuals. In this review, we summarize the current knowledge on the Saimaa ringed seal, identify the main risk factors and discuss the efficacy of conservation actions put in place to ensure its long-term survival. The main threats for this rare subspecies are bycatch mortality, habitat destruction and increasingly mild winters. Climate change, together with small population size and an extremely impoverished gene pool, forms a new severe threat. The main conservation actions and priorities for the Saimaa ringed seal are implementation of fishing closures, land-use planning, protected areas, and reduction of pup mortality. Novel innovations, such as provisioning of artificial nest structures, may become increasingly important in the future. Although the Saimaa ringed seal still faces the risk of extinction, the current positive trend in the number of seals shows that endangered wildlife populations can recover even in regions with considerable human inhabitation, when legislative protection is combined with intensive research, engagement of local inhabitants, and innovative conservation actions. Such multifaceted conservation approaches are needed in a world with a growing human population and a rapidly changing climate.

1. Introduction

The Saimaa ringed seal (*Pusa hispida saimensis*) is a subspecies of the Holarctic ringed seal (*P. hispida*). Since the last glacial period, it has been landlocked in the freshwater lake system that eventually formed the current Lake Saimaa in southeastern Finland. This endemic population has been exploited by humans since prehistoric times, and archaeological remains of inland seals from hearths date back 6000 years (Ukkonen, 1993). For the scientific community, the Saimaa ringed seal was first described in the late 19th century by fisheries inspector Oscar Nordqvist (1892). At that time, seals were perceived as competitors due to their presumed harm to fisheries and fish stocks. Exploitation was particularly intense during the early 20th century, when Saimaa ringed seals were also hunted for bounties, with this practise continuing until 1948 (Ranta et al., 1996). While the meat was typically not consumed by humans, the blubber was utilized in various ways in rural areas (Becker, 1984; Ylimaunu, 2000). Overexploitation caused the population to decline, and even led to local extinctions in some regions of the lake. The Saimaa ringed seal was finally protected by law in 1955. Despite the ban on hunting, the population continued to decline, mainly due to environmental toxins, habitat fragmentation and by-catch mortality (Kunnasranta et al., 2016).

During the 1970s, the Saimaa ringed seal became a symbol of environmental protection and nature conservation in Finland, but more systematic monitoring and conservation efforts were started in the 1980s by environmentalists and academics (Kunnasranta et al., 2016). In the past 40 years, many threats have been identified, and science-based mitigation approaches have been developed and implemented.

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Although some academic dissertations on the Saimaa ringed seal focused on its basic biology (Käkelä, 1996; Strandberg, 2012), most of them concentrated on key factors that are essential for monitoring and protection of the subspecies (Kunnasranta, 2001; Palo, 2003; Sipilä, 2003; Niemi, 2013; Valtonen, 2014; Auttila, 2015; Koivuniemi, 2019; Liukkonen, 2020). Moreover, issues relating to socio-economical and societal acceptability of seal conservation have been highlighted (Moisseinen, 1997; Tonder, 2005). The findings of these studies have typically had direct implications for practical conservation measures. Planning of conservation actions has especially been aided by knowledge of movement patterns and habitat use obtained through telemetry studies (Hyvärinen et al., 1995; Koskela et al., 2002; Kunnasranta et al., 2002; Niemi et al., 2012, 2013a, 2013b, 2019), and recent methodological advances continue to provide new tools for monitoring and conservation (Auttila et al., 2014; Valtonen et al., 2015; Koivuniemi et al., 2016, 2019; Liukkonen et al., 2017, 2018; Jounela et al., 2019; Nepovinnykh et al., 2020; Pulkkinen et al., 2020).

The Saimaa ringed seal narrowly escaped extinction in the 1980s, and active research and conservation measures have set the population on a trajectory of slow recovery. Nevertheless, with a population estimate of barely over 400 individuals, it is still considered one of the most endangered pinnipeds in the world. Furthermore, new challenges are emerging, especially with climate change with negative effects on ice-dependent seals. This review presents the most relevant information on the Saimaa ringed seal, with the aim of improving awareness and conservation of this unique freshwater pinniped. We evaluate most of the published scientific literature available on the subspecies, whilst also including some 'grey literature' that provides valuable data and insights despite not having been published in international scientific forums. Thus, we aim, for the first time, to (1) summarize the most relevant information on the biology of the Saimaa ringed seal, (2) provide an overview of key conservation issues, (3) identify ongoing actions, and (4) propose additional conservation actions for the future.

2. Methods

2.1. Data and literature search

We searched Google Scholar, Google and ResearchGate using scientific and English and Finnish common names of ringed seals (*Pusa/Phoca hispida saimensis*, Saimaa ringed seal and saimaannorppa). Publications were also searched from the citations of research papers published by the Saimaa ringed seal research group of the University of Eastern Finland (https://www.uef.fi/en/web/norppa/publications). The most relevant publications related to conservation biology of the Saimaa ringed seal were selected. Census data were collected from the webpages of Metsähallitus (2020), which is the governmental organization in charge of monitoring and protecting the Saimaa ringed seal population. Furthermore, the Saimaa ringed seal photo-ID database maintained by the University of Eastern Finland (UEF, 2020) and the open database for environmental information (https://www.syke.fi/avoindata) were used.

2.2. Genome data analyses

The genetic properties of the Saimaa ringed seal population have hitherto been studied mainly using nuclear microsatellites and mitochondrial control-region sequences. However, as whole-genome data have recently become available (Savriama et al., 2018), we used this new information for comparing levels of within-population genetic diversity in Saimaa and Baltic ringed seals. To match the sample sizes, we selected the published sequencing reads of nine individuals with the highest sequence quality and genomic coverage from both populations. These individuals have sample accessions ERS2313526, ERS2313598, ERS2313603, ERS2313604, ERS2313606-ERS2313608, ERS2313610, ERS2313611, ERS2313693, ERS2313697-ERS2313702, ERS2313724 and ERS2313725 in the Sequence Read Archive (SRA, 2004) of the National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/sra). We then mapped the quality-filtered reads against the Weddell seal (*Leptonychotes weddellii*) reference genome (LepWed1.0, 2004; https://www.ncbi.nlm.nih.gov/assembly/GCF_000349705.1) with the Burrows-Wheeler aligner (Li and Durbin, 2010). We selected the 1000 longest nuclear DNA sequences of the reference for downstream analysis. The sequences constitute a total of 1,646,446,825 base pairs (bp) that is 52.2% of the total length of the reference. In addition, we analyzed the LepWed1.0 mitochondrial DNA sequence of 16,604 bp. Finally, we calculated both genome-wide and mitochondrial nucleotide diversity (π and π_{mt}) of the populations using POPBAM (Garrigan, 2013).

3. Distribution and habitat

Ringed seals have inhabited Fennoscandian lakes for over 9000 years, since the end of the last glacial period (Ukkonen, 2002). During prehistoric times, seals were probably present in many Finnish lakes, but stocks outside Lake Saimaa have since vanished, most likely due to anthropogenic pressures (Ukkonen, 1993). The current distribution of the Saimaa ringed seal comprises only the Lake Saimaa complex, which covers a large part of Southeast Finland (61° 05′ to 62° 36′ N, 27° 15′ to 30° 00′ E) (Fig. 1). The closest extant post-glacial sister populations are found in Lake Ladoga (*P. h. ladogensis*) and in the Baltic Sea (*P. h. botnica*). These subspecies are ecologically, morphologically and genetically distinct (Hyvärinen and Nieminen, 1990; Kunnasranta, 2001; Amano et al., 2002; Palo et al., 2003; Valtonen et al., 2012; Nyman et al., 2014; Savriama et al., 2018). Currently, the Ladoga population consists of some 5000 (Trukhanova et al., 2013) and the Baltic stock of at least 20,000 (Helcom, 2020) individuals.

Lake Saimaa is about 180 km long and 140 km wide, with a mean depth of 12 m (maximum 85 m). The highly fragmented lake system is formed by several basins connected by narrow straits, and the labyrinthine appearance is amplified by the presence of 14,000 islands (Kuusisto, 1999). Six cities, with a combined human population of over 286,000 are located around the lake, and nearly 70,000 holiday cottages (Liukkonen et al., 2017) are scattered in its archipelagos and along the shorelines. Although Lake Saimaa is the largest lake of Finland, its surface area is only 4400 km^2, which is a very limited habitat for a mobile aquatic mammal. In comparison, the annual home ranges of juvenile Baltic ringed seals can be over twice the surface area of Lake Saimaa (Oksanen et al., 2015).

Although Saimaa ringed seals can be sporadically observed all over Lake Saimaa, the current main distribution area covers only about 70% and the main breeding area about 50% of the lake (Niemi et al., 2012). Over half of the population lives in the central part of the lake, in the Pihlajavesi and Haukivesi basins (Fig. 1), where about 60% of pups are born annually. However, as the population is slowly recovering, seals are recolonising peripheral areas of Lake Saimaa (Metsähallitus, 2020).

During regular winters, Lake Saimaa has full ice cover by the end of December, and ice break-up occurs at the latest in the beginning of May. The snow cover is the thickest in February–March (Kuusisto, 1999). Ringed seals excavate lairs in snowdrifts, where they rest, give birth and nurse their young. In contrast to the habitats of marine ringed seals (e.g., Smith and Stirling, 1975), there are no open ice fields with hummocked or ridged ice in Lake Saimaa. Therefore, the breeding habitat is closely connected to shorelines of islands and islets, the only places on the lake where snow accumulates to drifts deep enough for lair construction (Helle et al., 1984; Sipilä, 1990).

4. Population size and conservation status

The Saimaa ringed seal population was originally much larger than it is today. Based on bounty statistics, Kokko et al. (1998, 1999) estimated that over 1000 seals could have inhabited Lake Saimaa some 100 years

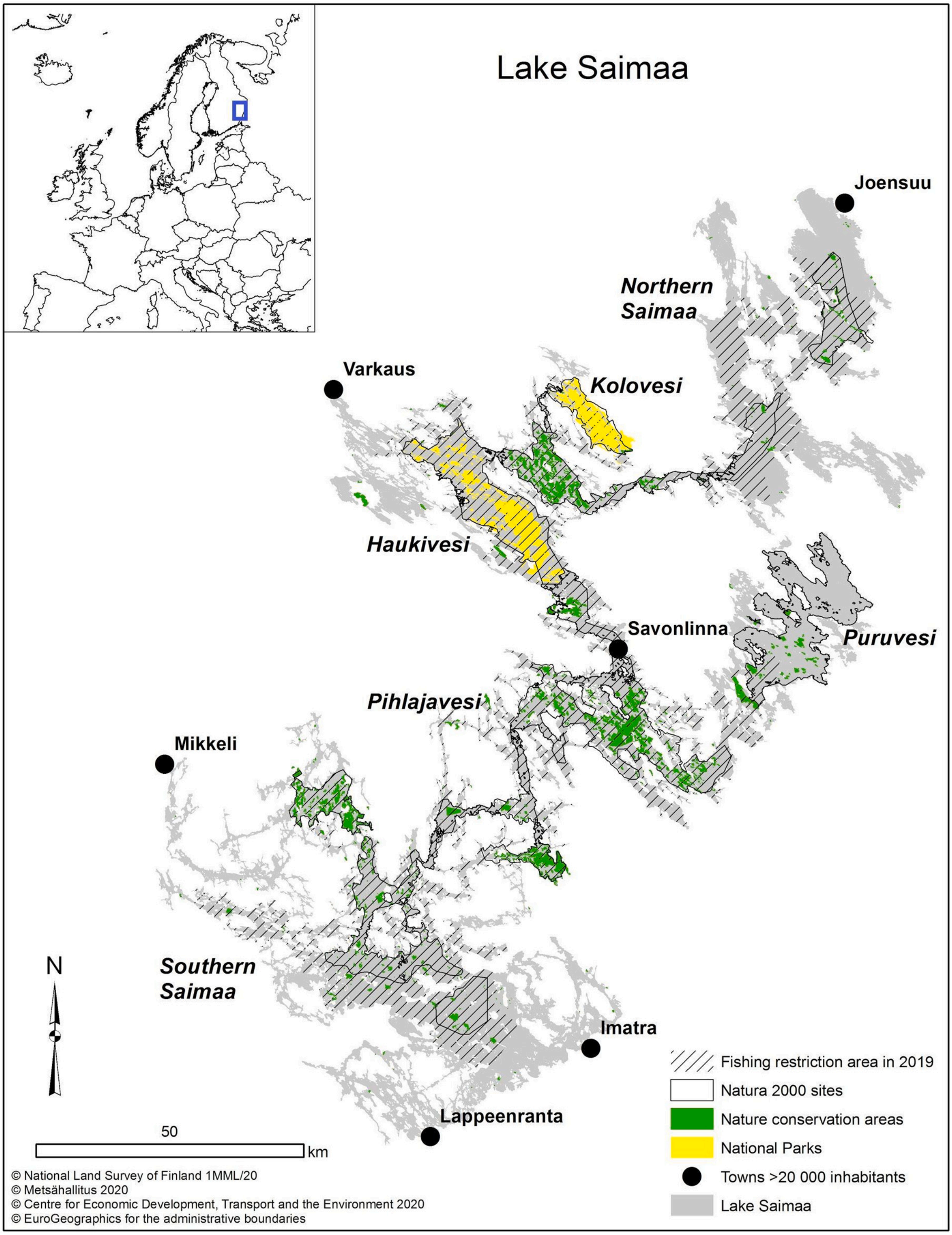

Fig. 1. Map of Lake Saimaa showing the locations of the main basins and largest towns, and the extent of various types of conservation areas designated for seal conservation.

ago, but population sizes of a few thousands have also been suggested (Hyvärinen and Sipilä, 1992; Sipilä, 2003). Based on their breeding habitat requirements, it has been estimated that up to 4000 seals could potentially inhabit the lake (Niemi et al., 2019). Between 1950 and 1980, uncertain estimates of the population size ranged from 60 to 400 individuals, but the first systematic census at the beginning of the 1980s indicated 100–160 seals (Sipilä, 1991; Hyvärinen et al., 1998; Kunnasranta et al., 2016). Subsequently, the population has slowly recovered due to focused conservation measures and improved water quality. The latest population estimate is slightly over 400 individuals, with some 80–90 pups born annually (Metsähallitus, 2020).

Since the 1980s, the Saimaa ringed seal population-size estimates have been based on annual counting of snow lairs during the late nursing season in April. Numbers of pups born (=birth lairs) during three consecutive years of specified breeding areas provide the main data for each annual estimate of population size (individuals over one year old).

In addition, regional estimates for areas where pups are not regularly born are based on numbers of haul-out lairs and observations of seal individuals (Sipilä, 2003). Details of the census method have not been published, but they largely rely on expert opinion (Koivuniemi et al., 2019). Based on these annual estimates (Metsähallitus, 2020), the population has increased, on average, by ca 3% per year since 2000. During the same period, the estimated number of pups has increased from around 50 to over 80 (Fig. 2). Although the census method may include unknown biases and uncertainty, it is likely that the population is increasing (Koivuniemi et al., 2019). However, the increase is not as fast as it theoretically could be, as the potential annual growth rate of seal populations is estimated as ~10% (Harding et al., 2007).

The Saimaa ringed seal was included as the first subspecies in the IUCN Red list of threatened species in 1966 (Wilson et al., 2001). In the 1980s, WWF Finland established a working group that focused on developing methods for population monitoring and on providing recommendations for conservation actions (Sipilä, 1991). In 2010, the Saimaa ringed seal was listed as critically endangered (CR) both in the Red List of Finnish species (Rassi et al., 2010) and by the IUCN (Kovacs et al., 2012). At present, its conservation status is regarded as endangered (EN) due to active conservation measures leading to an increasing population trend (Sipilä, 2016; Hyvärinen et al., 2019). Under European legislation, the Saimaa ringed seal is listed in Annexes II and IV of the Council directive (1992) Habitats Directive (Council Directive 92/43/EEC), which requires that "Special Areas of Conservation (SACs)" are designated to ensure its strict protection. The first official strategy and action plan, which was published in 2011 (Ministry of the Environment, Finland, 2011), describes the national guidelines regarding the key conservation measures.

5. Biology

5.1. Size and morphology

The knowledge on morphology as well as monitoring mortality and health of the Saimaa ringed seal population is mostly based on individuals found dead. Stranded and by-caught animals are systematically collected, and carcasses that remain in a reasonably good condition are necropsied by a veterinarian (Sipilä, 2003). Seals are aged by counting the cementum layers in the lower canine teeth (Stewart et al., 1996). Whenever possible, the skull, baculum and tissue samples (muscle, kidney, liver and blubber) are taken and deposited in the Saimaa ringed seal tissue bank, which includes frozen samples from nearly 700 seals collected since the end of the 1970s.

The Saimaa ringed seal is a medium-sized and sexually slightly dimorphic seal, with only small differences in age-specific skull size

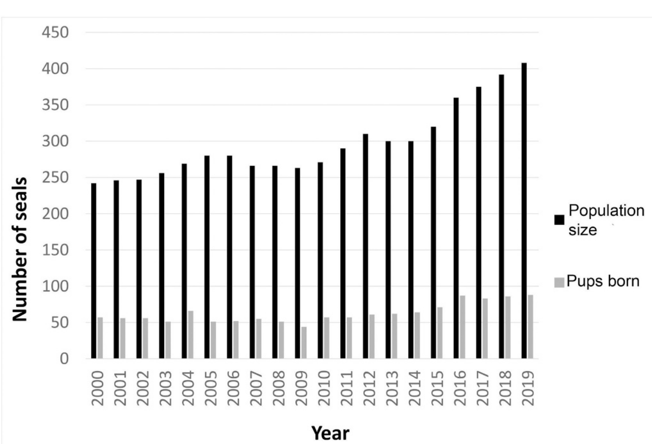

Fig. 2. Estimated population size of Saimaa ringed seals >1 yr and pups born during 2000–2019 (Sipilä and Kokkonen, 2009; Metsähallitus, 2020).

(Hyvärinen and Nieminen, 1990; Auttila et al., 2015a) and three-dimensional shape (Kurki, 2020) between the sexes. The average weight and length of newborn pups is 5 kg and 68 cm, respectively, while the average weight at three months of age is around 20 kg (Hyvärinen et al., 1998; Auttila et al., 2015a). The adult length from nose to the tip of tail is 132 cm and weight 59 kg. The maximum weights observed in springtime are 124 kg for males (Niemi et al., 2012) and 95 kg for females (Kunnasranta et al., 2002). Seasonal changes in body mass are mostly due to changes in blubber content. In winter, 50% of the body volume can consist of blubber (Usenius et al., 2007). The blubber content is lowest in late spring after the breeding and moulting seasons. The Saimaa ringed seal achieves maximum body length around the age of four years, and asymptotic body mass around two years later (Auttila et al., 2015a).

The Saimaa ringed seal is a morphologically distinct subspecies of *P. hispida* (Hyvärinen and Nieminen, 1990; Berta and Churchill, 2012). Based on skull measurements, Saimaa ringed seals differ clearly from all other ringed seal populations (Amano et al., 2002). The auditory bulla is particularly high in the Saimaa ringed seal, suggesting a better sense of hearing (Hyvärinen and Nieminen, 1990). Moreover, the location of the bulla in relation to the temporomandibular joint differs from marine ringed seals (Laakkonen and Jernvall, 2020). Recent anatomical studies have also found minor differences in the branching of the bronchi in the lungs (Laakkonen and Jernvall, 2016), and have suggested a lower number of lobes (reniculi) in the kidneys (Nihtilä, 2019) of the Saimaa ringed seal in comparison to its marine counterparts.

As in ringed seals in general (Stewart et al., 1998), the primary teeth of the Saimaa ringed seal are reabsorbed during gestation or soon after birth. The permanent teeth (I 3/2, C1/1, PC 5/5) are fully formed and erupting at the time of birth. Due to lack of tight occlusion, pinnipeds tend to have greater variability in their tooth shape than most mammals (Jernvall, 2000; Cruwys and Friday, 2006; Miller et al., 2007). However, the Saimaa ringed seal shows clearly lower dental variation than other ringed seal subspecies (Valtonen et al., 2019).

5.2. Lifespan

Saimaa ringed seals can live over 40 years, but mortality data suggest that the natural lifespan is 19–23 years (Sipilä, 2003). The generation time of the subspecies is 11 years (Palo et al., 2001). Females become sexually mature at the age of four years, males a couple of years later. The sex ratio is 1:1 at birth (Auttila et al., 2015a). Juvenile survival rates are lowest and negatively influenced by perinatal and by-catch mortality. Causes of mortality that are not directly connected to human factors are not systematically monitored due to the poor condition of most stranded carcasses. Nevertheless, there are a few observations of volvulus, swine erysipelas and cancer, and starving is often observed in weaned pups (Sipilä, 2003; Ministry of the Environment, Finland, 2011).

5.3. Annual cycle

Soon after ice formation in early winter, Saimaa ringed seals begin to maintain breathing holes, which they create using the claws of their front flippers. When snow accumulates, they dig subnivean snow lairs for resting (haul-out lair) and for giving birth and nursing (birth lair) (Helle et al., 1984; Sipilä, 1990). Lairs are located in snowdrifts along shorelines of islands, and the number of lairs used by an individual seal may vary between 0 and 10 (Niemi et al., 2019). Pups are born in mid-February to mid-March in snow lairs, which offer shelter against harsh weather conditions and predators (Helle et al., 1984, Sipilä, 1990). Unlike most mammals (Kristal et al., 2012), female seals do not eat the placenta and, thus, placentas found at lair sites provide an opportunity for non-invasive genetic monitoring of the population (Valtonen et al., 2015). Typically, a single pup is born, but twins have occasionally been observed. The nursing period lasts 7–12 weeks (Sipilä and Hyvärinen, 1998; Niemi, 2013). Pups have silky grey lanugo hair, which is moulted to short and bristly adult hair typically in late April (Niemi et al., 2013a). Females come into oestrus during the nursing season. Mating of ringed seals occurs in the water (McLaren, 1993), which is probably the case also in the Saimaa ringed seal. Gestation lasts 11 months, including delayed implantation of three months. Females give birth in successive years, but older individuals presumably take gap years (Sipilä, 2003). Weaning occurs typically in mid-May, and pups begin to disperse soon thereafter (Niemi et al., 2013b).

Following the breeding season, adult and juvenile seals over one year of age start to moult. Moulting begins after ice break-up, peaking from May to mid-June. During the moult, the seals haul out for extended time periods on rocks along shorelines (Hyvärinen et al., 1995; Kunnasranta et al., 2002), and undergo replacement of hair and top layers of skin. The typically dark pelage has light, irregularly ring-shaped patterns that are unique to each individual. The patterns remain constant from weaning to adulthood (Fig. 3), allowing reliable identification of individuals over their whole lifespan (Koivuniemi et al., 2016). Saimaa ringed seals exhibit a circadian pattern of haul-out behaviour that shifts seasonally. During the moulting season, the seals haul out both at day and night, but later in the summer more frequently at night (Kunnasranta et al., 2002; Niemi et al., 2013a).

5.4. Spatial movements

The Saimaa ringed seal is very sedentary, and adults exhibit a high degree of site fidelity across years (Hyvärinen et al., 1995; Koskela et al., 2002; Kunnasranta, 2001; Niemi et al., 2013a; Koivuniemi et al., 2016; Liukkonen et al., 2018). Due to the limited lake habitat, home ranges are small in comparison to those of their marine relatives (e.g., Oksanen et al., 2015). The mean open water home-range size is around 90 km^2, but the most intensively used regions (core areas) cover only some 5 km^2 (Niemi, 2013). However, adults may sporadically exhibit extended trips. In winter, movements are more restricted, and average home ranges are around 8% of those during the open-water season (Niemi et al., 2012, 2019). Juveniles are mobile particularly during their first summer. Dispersing pups have been observed to move up to 15 km in one day, and can be found up to 25 km away from their natal site soon after weaning (Niemi et al., 2013b). Home ranges of pups at the age of 3–4 months are highly variable in size, ranging from three to 162 km^2. However, although juveniles can initially disperse far from their natal sites, individuals seem to return to or stay near their natal sites as adults (Koivuniemi et al., 2016), and especially females are highly philopatric (Valtonen et al., 2012).

5.5. Diving

The Saimaa ringed seal is well adapted to aquatic life, and pups enter the water already during the early nursing season (Rautio et al., 2009). Individuals may spend around 80% of their time in water, and are able to sleep under water during extended diving bouts. The mean dive duration of adults ranges from 2.8 to 6.5 min, with a maximum of over 20 min (Hyvärinen et al., 1995, Kunnasranta et al., 2002). The typical dive depth ranges from 10 to 16 m, and the maximum depth is limited by the maximum depth of Lake Saimaa. Kunnasranta et al. (2002) defined five dive types falling into three main categories (travelling, feeding, and resting) based on dive depth and time characteristics. Dive depths are positively correlated with dive duration and body mass of the seal. Saimaa ringed seals have well-developed mystacial vibrissae, which play an important role in orientation in murky waters (Hyvärinen and Katajisto, 1984; Hyvärinen, 1989; Hyvärinen et al., 2009).

5.6. Feeding

Analyses of both digestive tract contents and stable isotopes show that Saimaa ringed seals feed almost exclusively on small schooling fish. The most important prey, which comprise over 90% of the diet, are perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), vendace (*Coregonus albula*), smelt (*Osmerus eperlanus*) and ruff (*Acerina cernua*) (Kunnasranta et al., 1999; Auttila et al., 2015b). These species are the most abundant fish species of Lake Saimaa, and food availability is suggested not to be a limiting factor for the seal population (Auvinen et al., 2005). Reflecting the low crustacean diversity of the freshwater habitat, only one species, *Mysis relicta*, is consumed by the seals (Kunnasranta et al., 1999). The lacustrine diet is clearly seen also in the fatty acid composition of the Saimaa ringed seal, when compared to its marine relatives (Käkelä, 1996; Käkelä and Hyvärinen, 1997, 1998; Käkelä et al., 1997; Strandberg et al., 2011). The size of most consumed fish is about 10 cm, so the seals use their teeth only to capture the prey before swallowing it whole. An individual consumes on average 3.5 kg fish per day, but there is seasonal variation in feeding, consumption being highest in late summer and fall and lowest in spring, when the seals are moulting (Kunnasranta et al., 1999).

5.7. Social behaviour and vocalization

Saimaa ringed seals have long been considered to be solitary. However, recent photo-ID studies indicate that there may be long-lasting social interactions among individuals (Kunnasranta et al., 2017). They also produce a repertoire of underwater vocalizations, which are mostly connected to breeding activities and mother–pup recognition (Rautio et al., 2009). Some sound types, such as knocking-sounds, resemble those found in the vocal repertoire of the more social Ladoga ringed seals (Kunnasranta et al., 1996). Airborne vocalizations consist of high-pitched whines of pups (Rautio et al., 2009) and growls of adults in social interactions during haul-out. Furthermore, capacity for some degree of echolocation has been speculated (Hyvärinen, 1989).

5.8. Parasites and pathogens

Rates of parasitism and diseases in the Saimaa ringed seal population are mainly monitored through necropsies conducted by the Finnish Food Safety Authority. In comparison to marine seals (Sonne et al., 2020), the

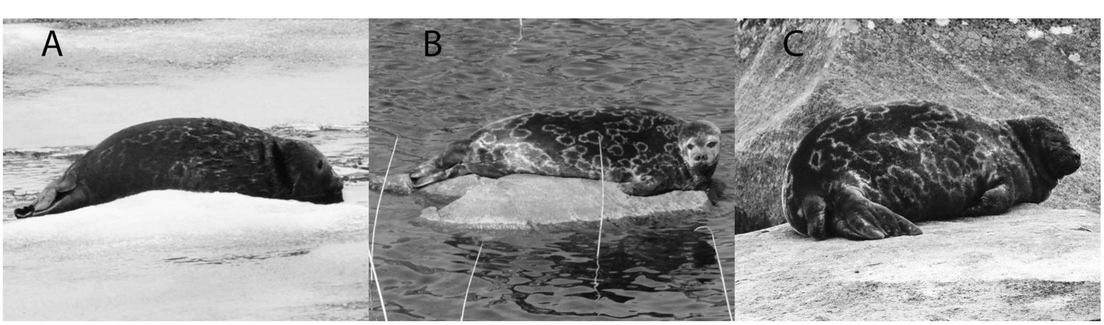

Fig. 3. A Saimaa ringed seal male (Phs033), which has been identified based on fur patterns as A) a pup in 2011, B) juvenile in 2014, and C) an adult in 2019. ©UEF, 2020.

parasite community of the Saimaa ringed seal is species-poor. While 3–4 species of helminth worms (*Corynosoma* spp.) are known to infest intestines of Baltic ringed seals, only one of them, *C. magdaleni*, occurs in Lake Saimaa (Valtonen and Helle, 1988; Sinisalo et al., 2003, 2004; Nyman et al., 2019). Numbers of *C. magdaleni* worms increase with seal age but vary widely across individual seals (Sinisalo et al., 2003). Cestode helminths are only occasionally found in the intestines of Saimaa ringed seals. Sinisalo et al. (2003) identified immature cestodes as *Diphyllobothrium ditretum* and *Schistocephalus* sp., but recent genetic barcoding results suggest that the species may have been misidentified (Nyman et al., 2019).

Saimaa ringed seals host only a single ectoparasite species, the seal louse (*Echinophthirius horridus*) (Leidenberger et al., 2007). Seal lice are presumed to act as vectors of the seal heartworm (*Acanthocheilonema spirocauda*) among marine seals (Leidenberger et al., 2007; Lehnert et al., 2016). Heartworms have not yet been found in necropsies of Saimaa ringed seals, but small nematodes, most likely representing *Parafilarioides gymnurus*, are found in histological slide preparations of the lungs of many individuals (M. Isomursu, pers. comm. 6.7.2020). Microbial diseases are encountered, but swine erysipelas caused by the bacterium *Erysipelothrix rhusiopathiae* has been observed, and *Streptococcus* and *Staphylococcus* species have been found in infected joints (M. Isomursu, pers. comm. 6.7.2020).

5.9. Genetics

The Saimaa ringed seal is genetically distinct from other subspecies of the ringed seal (Fig. 4) (Nyman et al., 2014; Peart et al., 2020). The main difference to other subspecies is that its genetic diversity is very low (Palo, 2003; Palo et al., 2003; Valtonen et al., 2012; Martinez-Bakker et al., 2013; Nyman et al., 2014). In fact, heterozygosity estimated on the basis of nuclear microsatellite variation ($H_E = 0.36$) is among the lowest detected in pinnipeds (Valtonen et al., 2014). The lack of diversity seems to be reflected also in phenotypic variation: the Saimaa ringed seal shows clearly lower dental variation than other ringed seal subspecies (Valtonen et al., 2019).

Since the Saimaa population has never been very large, most of its genetic diversity was undoubtedly lost gradually during the nearly 10,000 years of isolation (e.g., Nyman et al., 2014). Nevertheless, even the recent human-induced bottleneck has been shown to have an effect (Stoffel et al., 2018; Peart et al., 2020), and the present effective population-size estimate based on microsatellites ($N_e = 11–114$; Nyman et al., 2014, Valtonen et al., 2014) indicates that the population is too small to maintain its current genetic diversity. The small effective population size is seen in the significant changes in mtDNA haplotype frequencies during the past few decades (Valtonen et al., 2012) and continuing loss of heterozygosity (Valtonen et al., 2014). Based on genome-wide ddRADseq data, Peart et al. (2020) recently estimated the long-term coalescent effective population size to be 247-fold in comparison with the current number of mature individuals in the population, suggesting that the Saimaa population retains more ancestral variation than would be expected based on its current population size.

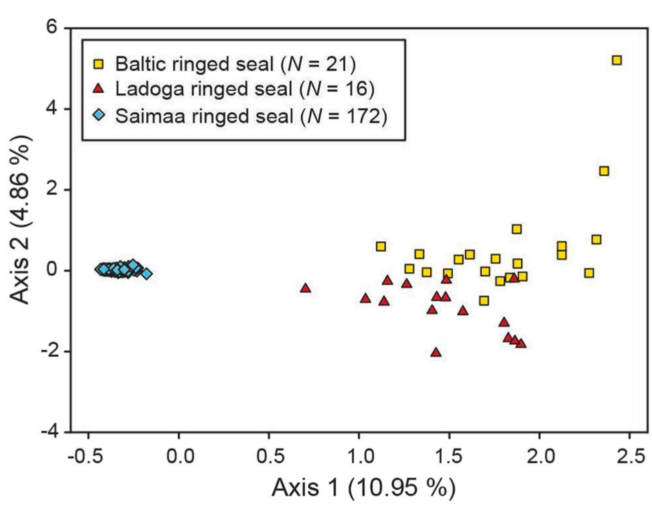

Fig. 4. Factorial correspondence analysis plot of individual ringed seals from the Baltic Sea, Lake Ladoga and Lake Saimaa based on microsatellite data (modified from Nyman et al., 2014).

Genome-wide nucleotide diversity (π) appears lower in Saimaa than in the Baltic population (Table 1). Although the difference in the mean diversities observed here is not statistically significant ($p = 0.1035$), the observed mitochondrial nucleotide diversity (π_{mt}) in the Saimaa population (0.0023) is only about half of that of the Baltic population (0.0043) (Table 1). The publication of the Saimaa ringed seal genome is forthcoming (https://saimaaringedseal.org/), whereupon this analysis can be targeted, for example, to the coding regions of the genome.

The microsatellite-based study by Valtonen et al. (2014) demonstrated fine-scale spatial genetic structuring in the Saimaa population. The results indicated that the population is divided into five regional subpopulations with limited gene flow. These findings were somewhat surprising, because marine ringed seals exhibit weak or no population structure across very large distances (Palo et al., 2001; Martinez-Bakker et al., 2013). This phenomenon is most likely due to the fragmented topography of the lake and the philopatric tendencies of Saimaa ringed seals (Valtonen et al., 2014).

6. Threats and key conservation measures

6.1. Intentional killing and public attitude

After being warranted national protection in 1955, Saimaa ringed seals were occasionally poached. However, since active conservation and monitoring started, major deliberate killings have not been observed. The last verified intentional shooting is from the year 1982 (Becker, 1984).

In earlier days, Saimaa ringed seals were disliked due to the economic losses that they supposedly caused to fisheries (Ylimaunu, 2000). Later, negative attitudes have mostly focused on conservation schemes, which have occasionally faced strong local criticism (Salmi et al., 2000; Tonder and Jurvelius, 2004; Tonder and Salmi, 2004; Bell et al., 2008; Ratamäki and Salmi, 2015). However, in recent questionnaire surveys, Finnish citizens have shown clear positive attitudes towards conservation of the Saimaa ringed seal, on both national and local levels (LIFE Saimaa Seal, 2019). Nevertheless, local opposition to restrictions on fishing and land use still occurs (Jaakkola et al., 2019), mainly by landowners and recreational gill net fishermen. Ensuring local support is therefore still an important element of sustainable seal conservation. Locals participate in seal monitoring and conservation actions, for example by collecting photo-ID data for abundance estimation. Besides, awareness campaigns among fishermen and tourists have improved knowledge on seal safe-fishing methods (LIFE Saimaa Seal, 2019). The increase in nature tourism has also helped locals to secure economic benefits from seal conservation.

Table 1
Summary statistics of nucleotide diversity (π) in Saimaa and Baltic ringed seals based on mapping of quality-filtered sequencing reads (after Savriama et al., 2018) against the 1000 longest sequences (52.2%) of LepWed1.0 (2004). The right-most column shows the mitochondrial nucleotide diversity (π_{mt}).

Population	Mean π (min–max)	Median π	π_{mt}
Saimaa	0.05837 (0.00515–0.21452)	0.05930	0.00229
Baltic	0.06062 (0.00519–0.21778)	0.06524	0.00430

6.2. Fishing

Fishing forms one of the major conservation concerns. It has been a threat to the Saimaa ringed seal since the 1970s, when the gill net material changed from fragile cotton to durable synthetic fibre (Becker, 1984). By-catch mortality explained almost half of the deaths for the 230 seals for which it was possible to determine the cause of death during 2000–2014 (Ministry of the Agriculture and Forestry, Finland, 2015). By-catch mortality predominantly occurs in gill nets and is focused especially on pups during the post-weaning period (Sipilä, 2003), but juveniles younger than two years are still vulnerable (Jounela et al., 2019). Only some 30 commercial fishermen operate on Lake Saimaa, while the estimated number of recreational fisher households is 80,000, 30,000 of which use gill nets (Ratamäki and Salmi, 2015). Seal–fishery conflict is therefore more related to subsistence or recreational fishing than to commercial operations. Most of the lake area and associated fishing rights are privately owned, but visitors can buy fishing licences from the owners.

Although seal-safe methods have recently been developed in collaboration with fishermen (LIFE Saimaa Seal, 2019), the key conservation measure for reducing by-catch mortality has been restrictions of fishing (Jounela et al., 2019). The annual ban on gill netting from 15 April to 30 June is especially aimed to reduce the mortality of weaned pups, since 75% of the observed entanglements occurred during that period in the 1990s (Sipilä, 2003). In addition, use of the most dangerous types of fishing gear for all age classes (e.g., certain fish traps, hooks baited with fish, strong-mesh gill nets, multifilament nets and trammel nets) has been completely forbidden under local regulations since 1999. Nowadays, fishing restrictions are specified in a governmental Decree (259/2016) based on the Fishing Act (379/2015), and financial compensation is paid to water area owners.

The recent growth of the Saimaa ringed seal population is partly explained by spatial expansion of fishing restrictions. Since 1982, the area of temporal fishing restrictions has gradually increased from 1.5% to over 60% of the lake (Fig. 1). The enlargement of the restriction area has been justified by research-based knowledge on the movements of the seals (Niemi et al., 2012, 2013a) and on statistics showing that fishing restrictions improve the survival of weaned pups. Indeed, Jounela et al. (2019) showed that the restrictions resulted in a 20% increase in population size during 1991–2013. Nevertheless, the observed growth rate of the population is lower than expected, suggesting that there is hidden mortality that remains undetected. Moreover, the observed by-catch mortality seems to have switched from early summer to July and February. Due to the high mobility of pups, adequate spatial and temporal coverage of the fishing restrictions is important for effective conservation, but also seal-safe alternatives to gill nets are being further developed.

6.3. Fluctuations in lake water level

The water level of Lake Saimaa fluctuates seasonally and annually due to natural causes and water resource management. Rapid changes in water level during the breeding season significantly increase the mortality of pups due to lair collapse. In the 1980s, around 40% of the lanugo pups died in some winters due to water-level changes. The weaning mass of pups was also lowered, which increased their vulnerability for by-catch mortality (Sipilä, 2003). Therefore, the Act (1331/1991) governing the regulation of the outflow of water from Lake Saimaa was renewed in 1991, so that the water surface level must be stabilized within a range of 20 cm from the beginning of the ice-covered season until late March (Ministry of the Environment, Finland, 2011). Nevertheless, water-level fluctuations still exceed this range during mild winters due to increased runoff (Veijalainen et al., 2010).

6.4. Pollution

After protection from hunting in 1955, environmental toxins accelerated the decline of the population (Helle et al., 1983, 1985; Hyvärinen and Sipilä, 1984; Sipilä et al., 1990; Hyvärinen et al., 1998; Kostamo et al., 2002). Especially mercury, which was widely used as a slimicide in the pulp and paper industry, had a significant role in the population decline during the 1960s and 1970s. During that time, concentrations of phenyl mercury in tissues of Saimaa ringed seals were the highest ever measured in pinnipeds worldwide (Kari and Kauranen, 1978). Due to a shortage of selenium in the lake environment, the detoxification mechanism of the Saimaa ringed seals was not effective enough to eliminate the mercury load (Hyvärinen et al., 1998). After the use of mercury in the pulp and paper industry was banned in the early 1970s, mercury in the lake originates mainly through runoff from soil. Current levels are clearly lower than before, but still elevated in the seals (Lyytikäinen et al., 2015).

6.5. Human-caused disturbance and habitat loss

High site fidelity makes Saimaa ringed seals especially vulnerable to changes in their habitat (Kunnasranta, 2001). Seals are suggested to be most sensitive to disturbance during the breeding season (Sipilä, 2003). At present, the lairs are on average located closer to potential sources of human disturbance than they were in the past, and Liukkonen et al. (2017) showed that perinatal mortality increases significantly in areas in which the nearest building is within 800 m of a birth lair. This distance is consistent with the radius of the home ranges of females and pups during the nursing season (Niemi et al., 2012, 2019). Based on these studies, it has been possible to determine minimum buffer zones for birth sites, within which human activities should be limited by land-use planning (LIFE Saimaa Seal, 2019). In addition to juvenile survival, human-caused disturbance may influence the body condition of seals. Boat traffic may cause prolonged moult and energetic costs for seals (Paterson et al., 2012). Niemi et al. (2013b) showed that hauled-out Saimaa ringed seals react to humans by increasing vigilance levels. This, together with increasing tourism in Lake Saimaa, highlights the need for common codes of conduct in seal-related tourism.

Habitat protection has been identified as one of the most important conservation priorities. Significant advances in protecting seal habitats were the establishment of two national parks (Fig. 1). Besides, core breeding and resting sites have been protected on 11 areas (total of 1893 km^2) that belong to the Natura 2000 network for rare and threatened species (European Commission, 2020). In addition, some state-owned land and water areas and privately-owned conservation areas have been established for the protection of the Saimaa ringed seal. Land-use planning will continue to have an important conservation role also in the future, as ca 30% of the shoreline is already too intensively used to be suitable for seal breeding (Liukkonen et al., 2017).

6.6. Climate change

The Saimaa ringed seal is strongly dependent on snow and ice as a breeding habitat, which makes it extremely vulnerable to climate change. The measured increase in temperature in Finland since 1847 has been almost twice as high as the global increase (Mikkonen et al., 2015). During mild winters, perinatal mortality has increased from ca. 10% to almost 30% (Sipilä, 2003; Auttila et al., 2014; Auttila, 2015), so the predicted declines in the duration and thickness of snow and ice cover in the future (Luomaranta et al., 2019; Korhonen, 2006) are likely to have negative effects on pup survival. Without protection offered by snow lairs, pups on bare ice are exposed to thermoregulatory stress, human-caused disturbance and predation. There are no specialized predators for Saimaa ringed seals, but during mild winters with insufficient snow cover for lair construction, middle-sized carnivores such as red fox (*Vulpes vulpes*) and the invasive raccoon dog (*Nyctereutes procyonoides*), as well as large birds such as herring gulls (*Larus argentatus*) and ravens (*Corvus corax*), pose a threat for pups (Auttila et al., 2014). Especially foxes successfully prey on small pups on open ice. Disturbed nursing due to unfavourable conditions also hamper the growth of pups and lead to lowered mass at weaning (Auttila, 2015), which correlates with reduced survival rates (Sipilä and Hyvärinen, 1998).

Predicted climate-induced changes in the lake habitat may also have indirect negative effects on the seals. In the long term, climate change will increase the runoff and bioavailability of mercury (Lyytikäinen et al., 2015). Moreover, the expected shift in fish communities towards energetically poorer species may lower the quality of the diet of the Saimaa ringed seal (Auttila, 2015). In a warmer climate, new pathogens such as *Toxoplasma gondii* (Barbieri et al., 2016) and *Leptospira interrogans* (Higgins, 2000) may also become a threat. Canine distemper virus has caused mass die-offs in landlocked Baikal seals (*Phoca sibirica*) (Mamaev et al., 1996) and Caspian seals (*P. caspica*) (Kennedy et al., 2000), and the latter outbreak has been connected to the unusually warm winter (Kuiken et al., 2006). At worst, similar outbreaks could seal the fate of the small and isolated Saimaa population.

Restoration of breeding habitats has been carried out on Lake Saimaa through land-use planning and active restoration efforts. The most successful and globally unique conservation invention so far has been man-made snowdrifts (Auttila et al., 2014; Platt, 2015), when people have piled up snowdrifts in order to improve pup survival when the snow cover is otherwise not thick enough for lair construction. Man-made snowdrifts, mimicking natural circumstances, are piled up on known and potential lair sites using snow pushers and shovels (Fig. 5). When needed, >100 volunteers have participated in this action during the recent years. For example, in 2014 over 95% of observed pups were born in man-made snowdrifts, and perinatal mortality remained significantly lower than during previous winters with equally poor snow conditions (Auttila, 2015).

The winter 2019–2020 was the first time in the conservation history when the southern part of Lake Saimaa did not freeze over at all, and the rest of the lake lacked sufficient snow cover for seal breeding (Syke, 2020). Foreseeing a future when mild winters are frequent, the second ambitious step for breeding habitat restoration is the building of artificial nest structures or shelters. Development of floating 'nest boxes' for winters with no ice has already been started (Auttila et al., 2017) and, while artificial nest structures still require refinement with regard to shape, material and texture, two pups have already been born in an 'Art-nest'.

6.7. Stochastic effects and inbreeding

Small populations have reduced resilience to both demographic and environmental stochasticity. Although the population trend of the Saimaa ringed seal is currently increasing, the number of seals remains worryingly low (~400), considering that the population is completely isolated with no immigration from other populations. For example, sequential mild winters resulting in poor breeding success could cause the population to decline. In addition, inbreeding is inevitable in small populations with possible negative effects on fitness of individuals (Reed and Frankham, 2003).

Genetic diversity reflects the population-level evolutionary potential and the ability to respond to environmental changes. The smaller the population, the more rapidly it loses genetic diversity through genetic drift. Therefore, the small size of the Saimaa ringed seal population and the fact that it continues to lose its already low genetic diversity are causes of concern. The population is also divided into several semi-isolated subpopulations (Valtonen et al., 2014), which may intensify genetic drift and inbreeding, and thereby increase the risk of inbreeding depression and accumulation of deleterious alleles. No evident signs of inbreeding depression have yet been detected in the Saimaa ringed seal, and the increasing population trend suggests that the subspecies is relatively healthy. Nevertheless, the low level of genetic variation may slow down adaptation to new climatic conditions and increase vulnerability to accidentally introduced parasites and pathogens.

6.8. Translocations, rehabilitation, and captive breeding

Conservation of genetic diversity in the Saimaa ringed seal population should concentrate on maintaining the current level of diversity and on minimizing inbreeding (Valtonen, 2014). This can best be done by strengthening population growth and by increasing gene flow among lake regions, which will most likely increase along with population density. However, as the population of a slowly reproducing seal cannot be expected to grow very rapidly, translocations and other active conservation measures are being considered. Translocation and rehabilitation programs have been successfully implemented in some endangered pinniped species, for example, Hawaiian monk seals (*Neomonachus schauinslandi*) (Baker et al., 2011; Gilmartin et al., 2011). Within-lake translocation was successfully piloted in 1992 in Lake Saimaa with one female (Phs152) (Kunnasranta and Hyvärinen, 1996), which was still alive in spring 2020 (UEF, 2020). In addition, assisted translocations

Fig. 5. Snow piles (ca. 8 m × 3 m × 1 m) shovelled by researchers and volunteers facilitate construction of subnivean lairs by Saimaa ringed seals.

to other lakes in Finland have also occasionally been proposed, since the landlocked Saimaa ringed seal cannot respond to climate change by shifting its range northward. Such drastic measures, however, do not seem realistic in the foreseeable future. Translocating ringed seals from sister populations to Lake Saimaa (e.g., from Lake Ladoga, as suggested by Saarnisto, 2011) is also highly risky due to the risk of outbreeding depression and accidental introduction of new diseases and parasites. A captive breeding program for the Saimaa ringed seal was initiated with a few individuals during the lowest point of population size in the 1980s (Becker, 1984). The program was, however, unsuccessful, and was terminated after most of the seals died in captivity. Recently, the establishment of Saimaa ringed seal rehabilitation centers and captive breeding programs have been highlighted in the public as a means for aiding the recovery and survival of the population in a changing climate.

7. Conclusions and future perspectives

A rapid population collapse in the mid-20th century made the Saimaa ringed seal one of the most endangered pinnipeds. Fortunately, the population has recovered from the severest phase of the bottleneck in the 1980s and, according to the most recent census data, slightly over 400 individuals inhabit the lake. Despite the recent positive trend in population size, the Saimaa ringed seal is still considered to be at a significant risk of extinction, because the small size of the population makes it vulnerable to stochastic effects such as variation in mortality and birth rates, in addition to inevitable threats such as inbreeding and climate change. Therefore, the key factor to the long-term survival of the Saimaa ringed seal is to increase the population size.

We recommend that in situ actions should still be the prioritized conservation strategy for the Saimaa ringed seal. Actions should include land-use planning and targeted habitat protection, limiting variation in lake water level during the breeding season, spatial and temporal expansion of fishing closures, mitigation of the negative effects of climate change, and campaigns for raising public awareness. Translocations of seals among different regions of the lake should be considered as a means for maintaining the current genetic diversity and reducing inbreeding in local subpopulations. While rescue and rehabilitation of seals that are in weak condition could be integrated in conservation efforts, we think that viability of the population rather than individuals should be the main focus. Ex situ options such as captive breeding programs should likewise be discussed, even though the approach does not seem cost-effective or even feasible based on current knowledge.

During the last decade, conservation research has focused on mitigating the effects of anthropogenic pressures, increasing the scientific basis and transparency of population monitoring and conservation, and on developing non-invasive research methods. We encourage continuous development and adoption of novel research and conservation tools as a central part of conservation efforts. For example, provisioning of artificial nests can be one of the remarkable conservation interventions in the future. Ongoing work in the ringed seal genome and photo-ID projects should provide powerful methods and genetic marker systems for both population- and individual-level monitoring, e.g., for inferring the structure of social networks and habitat use and breeding success of individuals. Molecular-genetic approaches could also be implemented for continuous evaluation of parasitism and health status within the population. Furthermore, research activities should increasingly involve citizen science-based approaches, in order to increase local acceptance of conservation measures and to improve the flow of information between the public, researchers, conservationists and policymakers.

The situation of the Saimaa ringed seal is unique, as nowhere else in the world do humans and an entire seal population live in such close proximity. Despite the endangered status of this endemic freshwater seal, we believe that as long as external anthropogenic threats can be mitigated, the subspecies still has a great potential for long-term survival. It should be emphasized that the Saimaa ringed seal is a charismatic umbrella species for the whole lake ecosystem, and that the diverse conservation measures focused on the subspecies aid also co-occurring species. In particular, the endemic and critically endangered Lake Saimaa populations of Atlantic salmon (*Salmo salar* m. *sebago*) and Arctic charr (*Salvelinus alpinus*) benefit from the enlarged fishing closures aimed at protecting the seals. We hope that the Saimaa ringed seal could eventually become a textbook example of how combining regulatory measures, intensive multidisciplinary research, innovative conservation actions, and engagement of local inhabitants can allow recovery and continued existence of wildlife in the midst of a considerable human population.

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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