

An evolutionarily distinct ringed seal in the Ilulissat Icefjord

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Abstract

The Earth's polar regions are low rates of inter- and intraspecific diversification. An extreme mammalian example is the Arctic ringed seal (*Pusa hispida hispida*), which is assumed to be panmictic across its circumpolar Arctic range. Yet, local Inuit communities in Greenland and Canada recognize several regional variants; a finding supported by scientific studies of body size variation. It is however unclear whether this phenotypic variation reflects plasticity, morphs or distinct ecotypes. Here, we combine genomic, biologging and survey data, to document the existence of a unique ringed seal ecotype in the Ilulissat Icefjord (locally 'Kangia'), Greenland; a UNESCO World Heritage site, which is home to the most productive marine-terminating glacier in the Arctic. Genomic analyses reveal a divergence of Kangia ringed seals from other Arctic ringed seals about 240 kya, followed by secondary contact since the Last Glacial Maximum. Despite ongoing gene flow, multiple genomic regions appear under strong selection in Kangia ringed seals, including candidate genes associated with pelage coloration, growth and osmoregulation, potentially explaining the Kangia seal's phenotypic and behavioural uniqueness. The description of 'hidden' diversity and adaptations in yet another Arctic species merits a reassessment of the evolutionary

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processes that have shaped Arctic diversity and the traditional view of this region as an evolutionary freezer. Our study highlights the value of indigenous knowledge in guiding science and calls for efforts to identify distinct populations or ecotypes to understand how these might respond differently to environmental change.

KEYWORDS

arctic, diversity, indigenous knowledge, local adaptation, marine mammal

1 | INTRODUCTION

As an attribute to their relatively young age and hostile environments, the polar regions are often characterized as evolutionary freezers with low levels of inter- and intraspecific diversity (Brochmann & Brysting, 2008; Hillebrand, 2004). However, this perception is challenged by recent observations from Arctic marine ecosystems that appear to hold larger levels of diversity than previously assumed (Miller et al., 2018; Rabosky et al., 2018). Indeed, cryptic levels of genetic diversity and differentiation have recently been reported across a range of Arctic marine taxa (Bringloe et al., 2020; Jacobsen et al., 2022; Laidre et al., 2022; Madsen et al., 2016; Mathiesen et al., 2017; Tempestini et al., 2020), highlighting the understudied nature of Arctic ecosystems. Identifying such inter- and intraspecific diversity and understanding its structure and drivers is important for assessing the adaptive potential and conservation needs of species and populations facing the extremely rapid rates of climate change currently underway in the Arctic.

The ringed seal is the most widely distributed Arctic marine mammal. It is the main prey for polar bears (*Ursus maritimus*), a key resource to Inuit communities, and plays a central role in high-Arctic marine ecosystems (Laidre et al., 2008). Throughout its Arctic range, the ringed seal exhibits limited population genetic structure (Davis et al., 2008; Lang et al., 2021; Martinez-Bakker et al., 2013) and individuals are known to undertake large-scale movements (Yurkowski et al., 2016), which have led to the species being described as a single panmictic population in the Arctic. However, Inuit hunters in Canada and Greenland recognize several types of ringed seals based on their body size, pelage patterns and their preferred habitats. The most numerous type is a relatively small seal that occupies pack ice in offshore areas, whereas a less numerous large type is found in the inner parts of fjords or other inshore areas with stable fast ice during winter (Figure 1a). Similarly, scientific studies have documented substantial variation in ringed seal body and skull size (Berta & Churchill, 2012; Finley et al., 1983; Kovacs et al., 2021), leading to speculations regarding the possible existence of multiple Arctic ringed seal ecotypes.

The Ilulissat Icefjord in West Greenland is home to the fastest moving marine-terminating glacier in the northern hemisphere called 'Sermeq Kujalleq' (or 'Jakobshavn Isbræ'). This area is listed as a UNESCO World Heritage site because of the dramatic and awe-inspiring natural phenomenon the glacier represents. The fjord is 800–1000 m deep, but it has a sill at about 245 m depth near the entrance,

where large icebergs strand and block the exit for sea ice, resulting in a dynamic environment with accumulation of glacial ice throughout the entire fjord system (Figure 1b). Ringed seals living in this fjord are morphologically different from other Arctic ringed seals with a pelage ranging from brownish to almost black with distinct white rings on their backs, which often extend up their necks and occasionally also cover their side and even their belly (Figure 1a, c–e; Figure S1). Local Inuit hunters refer to them as 'Kangiat' meaning 'those from Kangia' (i.e. the Ilulissat Icefjord's local name), and a recent study demonstrated that they are among the largest ringed seals in the Arctic (Kovacs et al., 2021).

To date, little scientific effort has been dedicated to document the putative genetic and ecological uniqueness of Kangia ringed seals. Thus, it is unclear whether their morphological distinctiveness is evidence of extreme morphological plasticity, size morphs or the existence of ecotypes (Kovacs et al., 2021). If multiple distinct and locally adapted ecotypes exist in ringed seals—or other Arctic species—these may respond differently to environmental change and human activities, provide some species-level resilience to climate warming and have different management and conservation needs. Here, we used an interdisciplinary approach—combining satellite tagging, population survey and population genomics—to assess the ecological and genetic uniqueness of the Kangia ringed seals.

2 | METHODS

2.1 | Satellite tagging

Tag deployments were carried out in nine consecutive field seasons during 2012–2020 in the inner part of the northern branch of the Kangia (Ilulissat Icefjord) system (Sikuijuitsoq; 69°21'N, 50°15'W, with tagging dates within the period 1 August to 16 September during 2012–2016 and 16 to 27 July during 2017–2020 (Table S1). A total of 31 Kangia ringed seals were caught in floating nylon monofilament nets set from the coast (Rosing-Asvid et al., 2020), of which 24 were tagged and provided data, one tagged but provided no data, and six were caught but not equipped with a tag. The tags, which measured 10.5 × 7 × 4 cm (545 g), were glued onto the seal's hair and provided positions via the ARGOS-satellite system (Boehme et al., 2009). All the 24 tagged seals were equipped with SMRU tags, of which 18 provided GPS positions and 6 only ARGOS positions. The tagging was conducted under the general permit of the

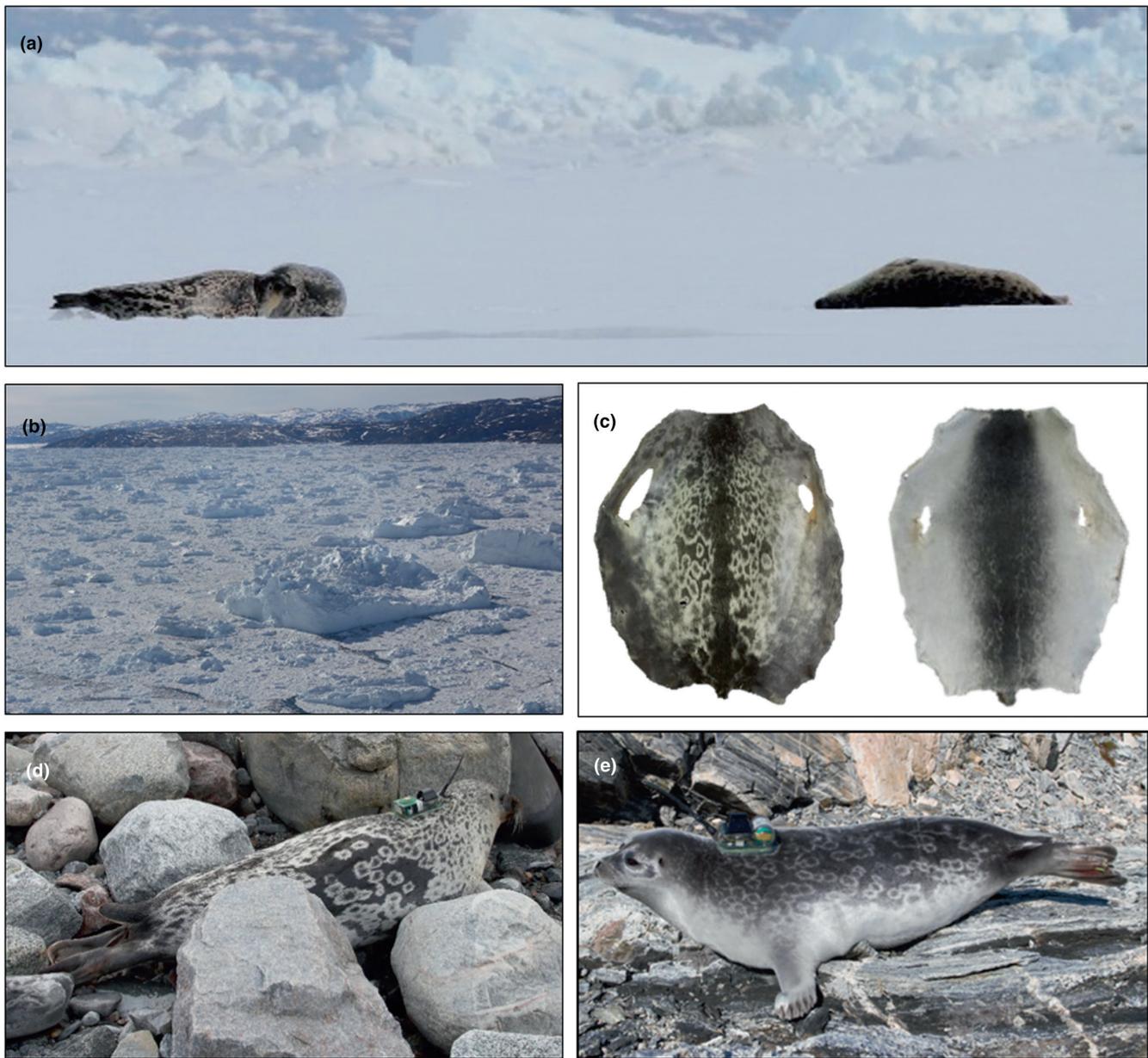


FIGURE 1 Unusual population of ringed seals in the Ilulissat Icefjord system, West Greenland. (a) Kangia ringed seals hauling out on sea ice. (b) The dynamic Ilulissat Icefjord system. (c) Pelage of Kangia (left) and typical Arctic ringed seals (right). (d) Kangia ringed seal instrumented with a satellite tag (image edited to remove person in background. Original image provided in (d)). (e) Typical Arctic ringed seal instrumented with a satellite tag (movement data not shown). All photographs by Greenland Institute of Natural Resources.

Greenland Institute of Natural Resources issued by the Greenland Government (Anonymous, 2010). Maps with tracks were generated using QGIS. The ARGOS data were not filtered but are presented both as best location quality (uncertainty < 250 m), as well as all data regardless of location quality, whereas GPS data were assumed to be associated with high accuracy and hence plotted without filtering.

2.2 | Population size survey

The abundance and distribution of ringed seals in the Ilulissat Icefjord system was assessed by aerial visual surveys following

established ringed seal survey protocols (Born et al., 1998). Briefly, we used a Partenavia Observer P68 airplane with large bubble windows, one observer on each side, and a cruising speed of 90 knots (167 km/h) at an altitude of 500 feet (152 m). The survey was carried out during the ringed seal moulting season over three consecutive days, of which the first day was a reconnaissance survey used to plan dedicated surveys on Days 2 and 3. Surveys were conducted across multiple strata at Beaufort Sea state < 2 and visual sightings were recorded using Sony ICD-SX712 Digital Flash Voice Recorders, the cruise track recorded via an external GPS, and declination angle to sightings was measured when animals were abeam using Suunto inclinometers. At each visual sighting, defined as animals at least three

body lengths (5 m) from other animals, we recorded angle of declination when a ringed seal (individual or group) was a beam, group size and whether the seal was seen hauled out on ice or in the water. Abundance estimates and densities were calculated using an effective strip half-width (ESW) distance sampling method that yielded absolute densities of seals at the surface, that is the number of animals/km² with the associated 95% confidence interval (CI) and coefficient of variation (Buckland et al., 2001). The data were analysed in DISTANCE 7.0 software package (Thomas et al., 2010) using a right truncation of 10% (441 m) leaving 207 sightings for analysis. Based on Akaike's Information Criterion (AIC), a half-normal detection function model with no adjustment terms was chosen (χ^2 goodness-of-fit, $p=0.063$), and a regression of mean group size against estimated detection probability indicated that mean group size did not increase with distance from the line. Distribution maps were created using ArcMAP version 10.5 (Redlands, CA: Environmental Systems Research Institute, Inc., 2020). Area and transect lengths were calculated using GIS software with WGS1984 as the geographic coordinate system and projected as Transverse Mercator UTM zone 24N. Additional information is available in the Appendix S1.

2.3 | Population genomics

The population genomic analyses were based on samples from 92 ringed seal tissue samples provided by local hunters or obtained from live-caught animals (Table S2). DNA was extracted using the Thermo Scientific KingFisher Cell and Tissue DNA Kit following the manufacturer's protocol. The animals were sequenced to an average depth of 5.5 \times of which 71 (12 from Canada, 59 from Greenland) were sequenced to average depth of 2.9 \times (minimum 0.13 \times , maximum 5.5 \times) on Illumina 4000 platform at the GeoGenetics Sequencing Core, Globe Institute, University of Copenhagen, and 21 (10 from Svalbard, 11 from Baltic) were sequenced to an average depth of 9.0 \times (minimum 5.2 \times , maximum 22.0 \times) on an Illumina NextSeq500 platform at DNA Sequencing and Genomics Laboratory, HiLIFE Institute of Biotechnology, University of Helsinki. The reference genome was based on a Baltic ringed seal sequenced to a depth of 27.5 \times using the 10 \times Genomics Chromium technology and assembled with Supernova v. 2.1.1 (Weisenfeld et al., 2017).

The haploid assembly consisted of 7702 contigs, totalling 2.356 Gbp, but only the longest 300 contigs (minimum length of 76.9 kbp) covering 98.61% of the total assembly length were used in our analyses. The genome was repeatmasked with RepeatMasker v. open-4.0.7 (Smit, 2004) and, for the complex part, a positive mask was created using *snppable* (Li, 2009). The WGS data were processed with *bwa-mem* (v. 0.7.15; Li, 2016), Genome Analysis Toolkit (GATK; v. 3.7; McKenna et al., 2010) and *samtools* (v. 1.9; Li et al., 2009). Inference of population structure in the form of PCA and admixture plots were generated with *PCAngsd* (v. 0.981; Meisner & Albrechtsen, 2018) after inferring genotype likelihoods with *ANGSD* (v. 0.921; Korneliussen et al., 2014). F_{ST} statistics were computed with *realSFS* (v. 0.921) from the *ANGSD* package with confidence

intervals estimated by dividing the contigs into 100 blocks and computing the standard deviation of the block estimates with R (R Core Team). Site frequency spectra (SFS) for demographic analyses were estimated with *ANGSD* based on a random selection of 100 million sites; for joint analyses, 100 replicates of each SFS were created using block-bootstrapping. One animal sampled in Kangia clustered with other Arctic populations in the PCA and had a non-Kangia ancestry in the admixture analysis and was hence considered a recent migrant. This individual was excluded from all population-specific analyses.

Measures of genetic diversity were derived from one- and two-dimensional SFS computed in windows as in Momigliano et al. (2021), and $\Delta\pi$ and the Δd_{xy} were calculated as per Fang et al. (2021). Briefly, $\Delta\pi$ is a centred measure of change in π across the genome, which controls for processes that govern diversity levels within genomes (e.g. background selection) taking advantage of the correlation of π across the genomes of closely related populations. Δd_{xy} is an analogous measure of relative divergence obtained as the residuals from a linear model with d_{xy} as the dependent variable and π of a putative source population as the predictor.

In the analysis of selection, genomic positions were lifted over to the dog genome (CanFam3.1.dna_sm.toplevel) using *CrossMap* (v. 0.2.4; Zhao et al., 2014) and a chain file was created with *LAST* (v.9.21; Frith et al., 2010) and UCSC Kent source utilities (downloaded in October 2019; Haeussler et al., 2019). Gene annotations for the high- F_{ST} regions were generated from aligned dog transcripts using a custom script. Allele frequencies of the SNPs within the high- F_{ST} regions were computed with *ANGSD*, and their consequences were annotated using the R package *VariantAnnotation* (v.1.24.5; Obenchain et al., 2014) and the dog gene models. The gene models and associated data were visualized using the R package *Gviz* (v.1.22.3; Hahne & Ivanek, 2016).

The demographic analyses first estimated past changes in effective population size using one-dimensional SFS (1d-SFS; Momigliano et al., 2021) and the multiepoche model implemented in the software *Stairway plot v2* (Liu & Fu, 2015). With the joint SFS (*jSFS*) for Kangia-Qaanaaq and Kangia-Iltoqqortoormiit, we used *moments* to optimize parameters and tested two nested divergence scenarios under isolation with migration (IM) and secondary contact (SC), including modifications to allow for heterogeneity of gene flow across the genome (IM_{2M} and SC_{2M}). To remove errors from low sequencing coverage and mismatching reads across paralogous copies, we masked singletons and SNPs with MAF of 0.5 in both populations. Parameter optimization was carried out following the approach originally developed for *dadi* by Portik et al. (2017) and modified by Momigliano et al. (2021) for *moments*. To account for linked data, we used the approach by Coffman et al. (2016) to carry out likelihood ratio tests (LRT) and estimated uncertainties around scaled parameters using block bootstraps and the Godambe information matrix (Coffman et al., 2016). Parameters were converted to time and size units using the polar bear mutation rate of 1.825728e⁻⁸ substitutions per site per generation (Liu et al., 2014), and uncertainty around parameters was estimated following the rules of propagation

of uncertainty (Ku, 1966). Additional information on the population genomics data analyses is available in the Appendix S1.

3 | RESULTS AND DISCUSSION

3.1 | Kangia ringed seals are distinct from other Arctic ringed seals

Data on the movement behaviour and site fidelity of the *Kangia* ringed seals were obtained from 24 animals (15 juveniles; 3 sub-adults; 6 adults) equipped with satellite-linked data loggers in the period 2012–2020 as part of a long-term study of the fjord system (Mernild et al., 2015) (Table S1). On average, 171 contact days per animal (range 28–270 days) were obtained, during which all sub-adults and adults, as well as 12 out of 15 juveniles, remained within the Ilulissat Icefjord system or at the mouth of the fjord (Figure 2a; Figure S2). Two juveniles made brief movements into the neighbouring Disko Bay area, but returned after 1.5 and 5 days, respectively, whereas one juvenile tagged 2 August 2013 left the Ilulissat Icefjord system on 7th August and had not returned when the tag stopped transmitting on 9th February 2014. This high level of site fidelity differs markedly from other ringed seal populations studied to date, in which juvenile animals often exhibited movements on the scale of thousands of kilometres across vast expanses of the Arctic (Hamilton et al., 2015; Yurkowski et al., 2016).

The abundance of *Kangia* seals was estimated by aerial surveys recording animals hauling out on sea ice during the moulting season in late May 2018 along 400 km transect lines, with an effective strip width of 295 m covering large parts of the entire fjord area of 670 km² (Figure 2b; Figure S3). A total of 225 visual sightings of 890 hauled-out ringed seals were made, comprised of single animals (48%), groups of 2–10 individuals (44%) and groups of 11–35 individuals (8%). Ringed seals were sighted throughout the entire Ilulissat Icefjord system at an average density of 1.3 hauled-out animals per km², but the main aggregations occurred in the mid-section of the main fjord, where densities were remarkably high for this species (3.5 hauled-out animals per km²). These numbers extrapolate to a total of 1641 hauled-out animals ($cv=0.23$; 95% CI 1030–2616) or a total population of approximately 3000, using a factor-2 conversion to account for animals submerged during the survey as suggested by Stirling and Øritsland (1995).

The genetic relationships between *Kangia* and other Arctic ringed seals in Greenland, Canada and Svalbard (Norway), as well as the Baltic Sea subspecies as a reference, were determined by sequencing 92 nuclear genomes (Figure 3a). As expected, a principal component analysis (PCA) of genetic variation and admixture analysis separated the Baltic Sea subspecies from Arctic ringed seals, but showed only minor genetic differentiation within most of the Arctic, agreeing with a generally panmictic Arctic population structure (Figure 3b; Figure S4). Unexpectedly, but agreeing with the morphological distinctiveness of *Kangia* ringed seals, the PCA

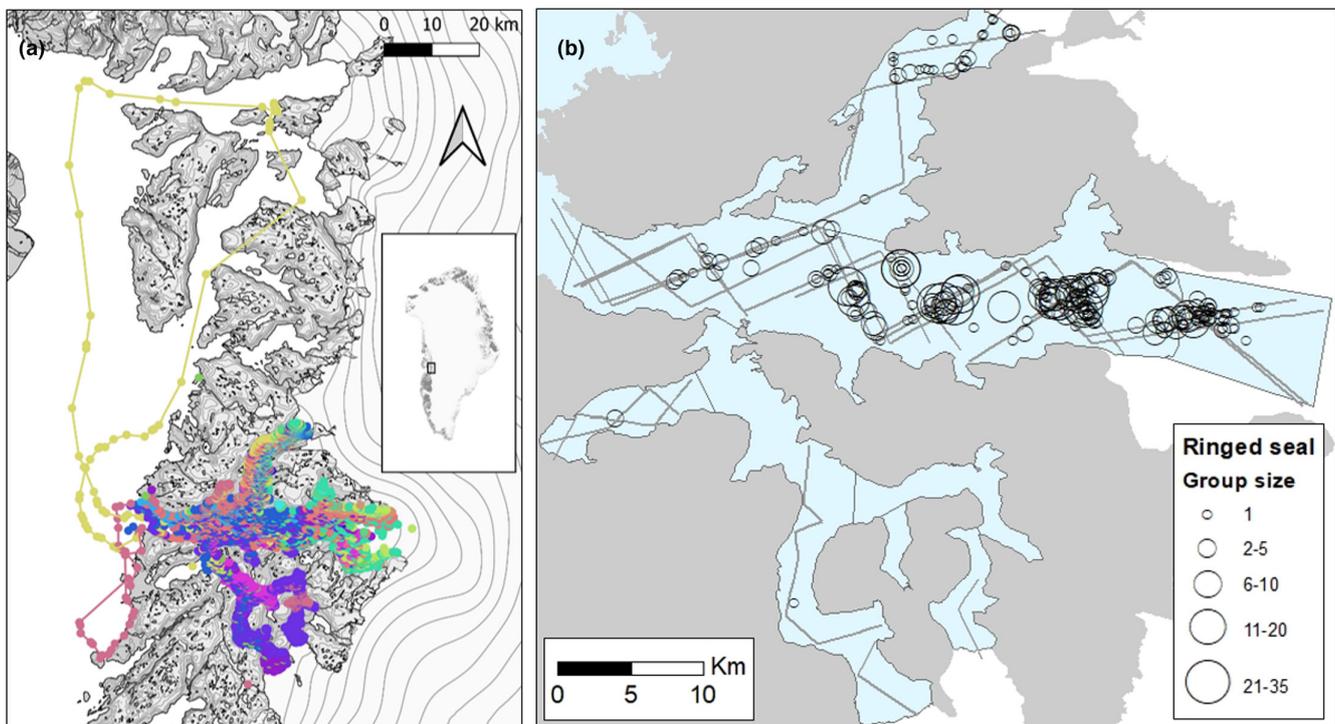


FIGURE 2 *Kangia* seal movement and survey data. (a) Satellite tracks based on 21,136 positions for 18 *Kangia* ringed seals equipped with GPS tags, including three seals that left the fjord temporarily and returned. Positions for the six animals equipped with ARGOS tags are provided in Figure S2. (b) Distribution and abundance of *Kangia* seals determined by aerial survey. Additional information on survey strata and transects is provided in Figure S3.

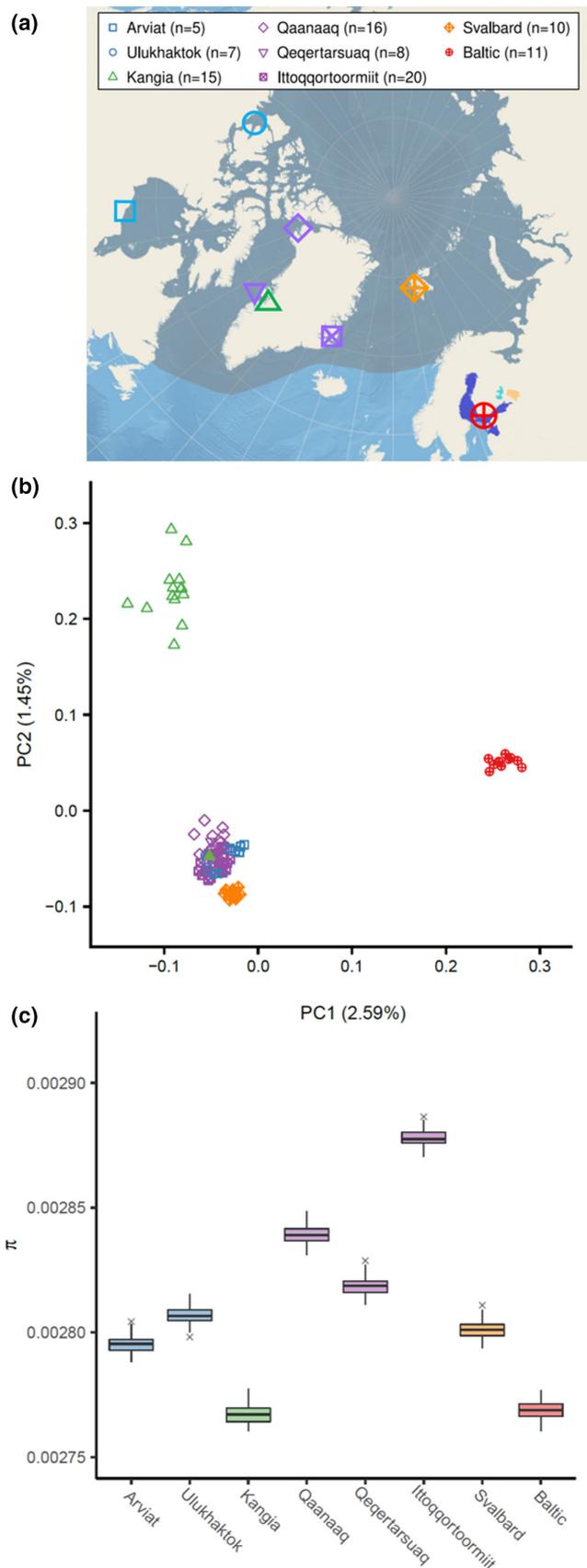


FIGURE 3 Kangia ringed seals are genetically distinct from other Arctic ringed seals. (a) The ringed seal's circumpolar range and the sampling sites used for genomic analyses. Map modified from <http://www.nammco.no/ringed-seal/>. (b) PCA plot based on 92 nuclear genomes showing the genetic distinctiveness of Kangia ringed seals (green open triangles, with the Kangia animal clustering with other Arctic localities highlighted in solid green). (c) Genetic diversity (π) for each of the sampled ringed seal localities.

localities, although we note that a single animal sampled in Kangia clusters with other Arctic ringed seals and hence appears to be an immigrant (Figures S5 and S6). Similarly, the genome-wide estimates of pairwise genetic distances between Arctic populations were greatest in pairwise comparisons to Kangia ($F_{ST}=0.0305-0.0408$; mean $F_{ST}=0.0343$) and they were significantly lower ($F_{ST}=0.0163-0.0267$; mean $F_{ST}=0.0226$) among other Arctic populations (Table S3). The Kangia ringed seals' level of genetic diversity was similar to that of the isolated Baltic ringed seal, but lower than other Arctic ringed seals (Figure 3c; Table S4). That is, despite a modest sample size and genomic coverage, all our analyses point to the genetic uniqueness of Kangia seals. This observation is striking in that the Ilulissat Icefjord system opens into Disko Bay and neighbouring Baffin Bay and Davis Strait, allowing free movement in and out of the fjord system. Thus, in contrast to earlier studies on Arctic ringed seals (Davis et al., 2008; Martinez-Bakker et al., 2013; Yurkowski et al., 2016), the tracking, survey and genetic data from Kangia ringed seals demonstrate that these have remarkable levels of site fidelity, high population density and genetic differentiation. Finally, while the patterns are not as clear as for Kangia, we note that the PCA and F_{ST} estimates among Arctic localities indicate the existence of additional substructure in the Arctic, for example Svalbard and the Canadian Arctic. Confirming this requires additional sampling and increased genomic coverage.

3.2 | Evidence of selection for pelage pattern, body size and glacial habitat

To examine putative local genomic adaptations relating to the Kangia ringed seal's glacial habitat and observed phenotypic characteristics, we performed a genome-wide F_{ST} outlier analysis between Kangia ringed seals and a combined set of other Greenlandic and Canadian ringed seals. For the high- F_{ST} regions, we computed differences in nucleotide diversity $\Delta\pi$, genetic divergence Δd_{xy} (Fang et al., 2021) and allele frequency (ΔAF s) between the two population sets and—given the lack of well-annotated pinniped genomes—studied them in the context of gene annotations lifted from the Ensembl dog data (Cunningham et al., 2019). We detected multiple signs of genetic differentiation, potentially resulting from adaptive selection, with strong and remarkable signatures on dog chromosomes 7, 18 and 24 (Figure 4a). In chromosomes 7 and 18, the diversity patterns show high Δd_{xy} but no significant deviation in $\Delta\pi$ (Figure 4b,c,e,f), consistent with the genetic characteristics of Kangia ringed seals arising through selection on standing genetic variation (Barrett &

suggested that Kangia ringed seals are separated from all other sampled Arctic ringed seal populations. This was also evident when the PCA and admixture analyses were restricted to Arctic

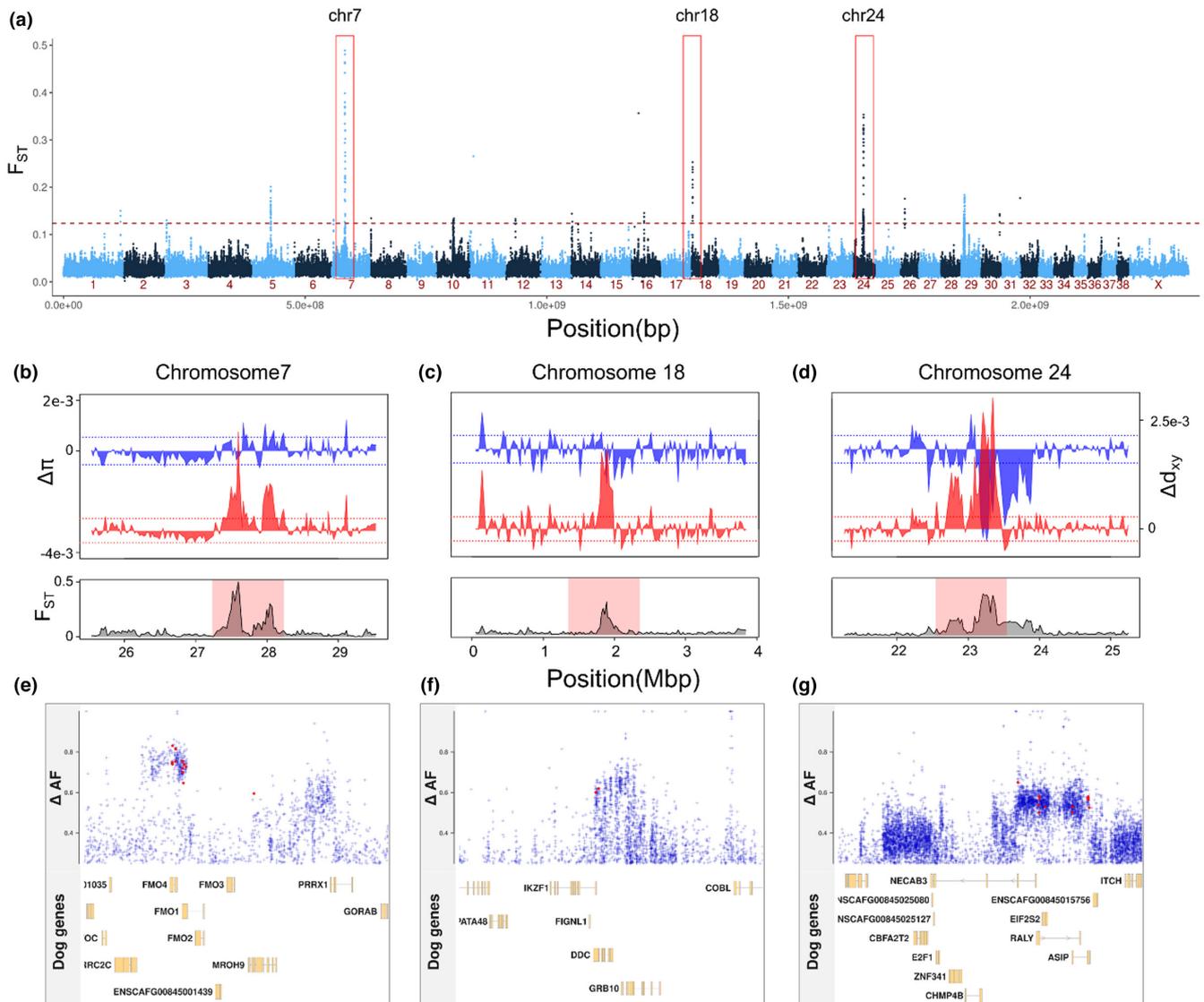


FIGURE 4 Genomics of local adaptation in *Kangia* ringed seals. (a) F_{ST} outlier analysis of chromosomal regions under selection with the three strongest outliers in chromosomes 7, 18 and 24 highlighted. (b–d) $\Delta\pi$ (blue), Δd_{xy} (red) and F_{ST} (grey) estimates for 25 kbp windows across the regions on chromosomes 7, 18 and 24 showing signs of selection. Elevated Δd_{xy} and F_{ST} without change in $\Delta\pi$ in (b, c) indicates selection on old haplotypes, whereas strong decrease in $\Delta\pi$ in (d) is consistent with a recent sweep. Pink rectangles denote the regions shown in the bottom panel. (e–g) Allele frequency differences (ΔAF) in the context of all gene annotations that could successfully be lifted from the Ensembl dog data for the regions on chromosomes 7, 18 and 24 showing signs of selection. Blue marks represent individual variants and those inferred to cause nonsynonymous changes in a coding gene are highlighted in red.

Schluter, 2008). In chromosome 24, however, the region under selection is highly diverged (increased Δd_{xy}) and shows a strong decrease in nucleotide diversity ($\Delta\pi$; Figure 4d,g) consistent with a recent selective sweep.

The identified regions hold multiple gene annotations lifted from the dog genome, including RALY and IKZF1 (immune function), DDC and NECAB3 (neurotransmission), EIF2S2 (protein synthesis), FIGNL1 (DNA repair) and MROH9 (development of reproductive organs; Figure 4e–g). However, while there is also a risk of cherry picking, we find three genes of particular interest in relation to the *Kangia* phenotype: the FMO (Flavin-containing monooxygenase) genes 1–4, the Grb10 (Growth factor receptor-bound protein 10) gene and the ASIP (agouti) gene, respectively.

The FMO genes are xenobiotic detoxification catalysts with a wide functional repertoire (Krueger & Williams, 2005; Ziegler, 2002). In euryhaline fish migrating between freshwater and marine environments, FMO genes play a fundamental role in osmoregulation and acclimatization (Lavado et al., 2013; Rodriguez-Fuentes et al., 2008; Schlenk et al., 1996). The ability to occupy a range of environmental salinities is well known in ringed seals and other aquatic mammals (Ortiz, 2001); however, FMO genes have not previously been suggested as candidates for osmoregulation in mammals. While speculative, we hypothesize that selection on FMO genes in *Kangia* seals may have occurred during an extended period of isolation in a glacial freshwater environment in side branches of the Ilulissat Icefjord, when the advancing Sermeq Kujalleq glacier blocked access to the sea (see below).

In mice (*Mus musculus*), downregulation of the *Grb10* gene increases fetal overgrowth, resulting in adult mice with increased muscle mass and reduced adiposity (Charalambous et al., 2003; Smith et al., 2007). Intriguingly, *Grb10* is imprinted in a tissue-specific manner and the paternal allele has been associated with the regulation of social behaviours, whereas the maternal allele regulates growth (Dent et al., 2020; Garfield et al., 2011; Rienecker et al., 2020). Although we cannot validate a direct genotype–phenotype link, these findings are in line with the larger body size of Kangia ringed seals (Kovacs et al., 2021) and their more aggressive behaviour (A. Rosing-Asvid, personal observation) compared with other Arctic ringed seals. The large body size may be an adaptation to the observed deep-diving behaviour of Kangia seals (A. Rosing-Asvid, unpublished data), which allows them to exploit a wider prey base, but it could also play a role in reproductive territory defence, given the unusually high population density of Kangia ringed seals in the Ilulissat Icefjord system.

Finally, the ASIP (agouti) gene is known to play a prominent role in pelage pigmentation and seasonal polyphenisms across a broad range of mammals (Bannasch et al., 2021; Jones et al., 2018; Pfeifer et al., 2018; Silvers & Russell, 1955). To our knowledge, this is the first time ASIP is implicated in pinniped pelage coloration, yet it fits well with the very distinct ringed patterns of the Kangia seal's pelage compared with other ringed seals. This phenotypic trait could be under positive selection as a sexual trait or to provide better camouflage when foraging (Barrett & Hoekstra, 2011; Gould & Lewontin, 1979). A slight difference in pelage colour arising neutrally during a period of isolation could have helped individual animals to distinguish between local Kangia seals and other Arctic ringed seals, resulting in a selective sweep around the ASIP in chromosome 24, around the most recent period of secondary contact or earlier.

3.3 | Pre-LGM divergence and local adaptation in the face of gene flow

We studied the evolutionary origin of the unique phenotypic and genomic characteristics of Kangia ringed seals with demographic analyses. Using stairway plot v2 (Liu & Fu, 2015), we first assessed the historical changes in effective population size (N_e) for the Kangia, as well as two reference populations for which we had a large sample size Qaanaaq and Ittoqqortoormiit, finding that the two latter experienced a profound increase in N_e approximately 100kya resulting in their current N_e being substantially larger than Kangia (Figure 5a). Next, we estimated the joint demographic history of Kangia-Qaanaaq and Kangia-Ittoqqortoormiit using *moments* (Jouganous et al., 2017). Since the site frequency spectra (SFS) strongly suggested ongoing migration, we tested two realistic demographic scenarios: isolation with continuous migration (IM) and isolation followed by a secondary contact (SC; Sousa & Hey, 2013). To accommodate the presence of islands of differentiation detected in the selection analysis, we included modifications of the models allowing

for heterogeneous migration rates across the genome (IM_{2M} and SC_{2M}; Momigliano et al., 2021; Tine et al., 2014). Variations of the models that also allowed for multiple changes in N_e resulted in parameter runaway behaviour, an indication of overparameterization.

The likelihood ratio tests identified SC_{2M} as the best model in both two-population analyses (Figure 5b–g; Figure S7; Tables S5 and S6). This model strongly supports a long period of strict isolation and suggests Kangia ringed seals split from other ringed seal populations roughly 240–220 kya (238.4–230.7 kya for Kangia-Qaanaaq), coinciding with the Marine Isotope Stage (MIS) 7 interglacial period, and regained secondary contact (T_{SC}) at around the time of the Last Glacial Maximum (LGM; 24.9–28.6 kya for Kangia-Qaanaaq; 24.4–32.1 kya for Kangia-Ittoqqortoormiit). Kangia ringed seals have substantially smaller effective population size ($N_e = 1.7$ – 15.2 k) than both Qaanaaq ($N_e = 81.4$ – 87.4 k) and Ittoqqortoormiit ringed seals ($N_e = 91.9$ – 97.6 k). In other words, the best supported demographic models suggest a divergence time possibly predating the penultimate and last glacial periods, with Kangia seals surviving as a small population in periods of isolation through at least one and possibly several glacial–interglacial cycles until the most recent secondary contact around the LGM.

We can only speculate about the likely underlying drivers of divergence and long-term isolation of Kangia ringed seals. They may have arisen in a manner similar to that proposed for the relict Baltic, Saimaa, Ladoga and Okhotsk ringed seal subspecies, as well as the Caspian and Baikal seals (*Pusa caspica* and *Pusa sibirica*, respectively; Palo et al., 2001; Palo & Väinola, 2006). Specifically, alternating climatic periods of glacial advance, isostatic rebound and sea-level changes could have resulted in the initial isolation of Kangia ringed seals from other Arctic ringed seals inside the Ilulissat Icefjord system, in calving bays in front of the Sermeq Kujalleq glacier, or elsewhere. Interestingly, in the 1850s, a group of ringed seals were observed in a small side branch of the fjord blocked by the Sermeq Kujalleq glacier (Rink, 1857). The Sermeq Kujalleq glacier appears to have persisted throughout the LGM and likely also during the preceding Eemian interglacial (MIS 5) and Saale glacial period (MIS 6; Cofaigh, C, et al., 2013; Hofmann et al., 2018) and hence could have supported a small ringed seal population for millennia. Indeed, unlike other pinnipeds, ringed seals are capable of overwintering in the High Arctic, utilizing ice crevices in front of marine-terminating glaciers or making breathing holes in the fast ice (Hamilton et al., 2016), which likely allowed them to remain in the Arctic during glacials.

Given the Kangia seal's marked phenotypic uniqueness, a surprising result of the demographic analyses is that Kangia ringed seals experience significant ongoing gene flow with slightly higher emigration (Effective number of migrants, $N_{em} = \approx 10$) than immigration ($N_{em} = \approx 5$ – 7) to neighbouring populations (Figure S6). We suggest that the phenotypic differences are maintained by the presence of localized genomic barriers to gene flow linked to local adaptation. This is supported by our observation of a small fraction (1%) of the genome having very low rates of gene flow ($N_{em} = \approx 1$), corresponding to 10% of the rates estimated for the rest of the genome (Table S6), with migration rates expected to be much smaller for just

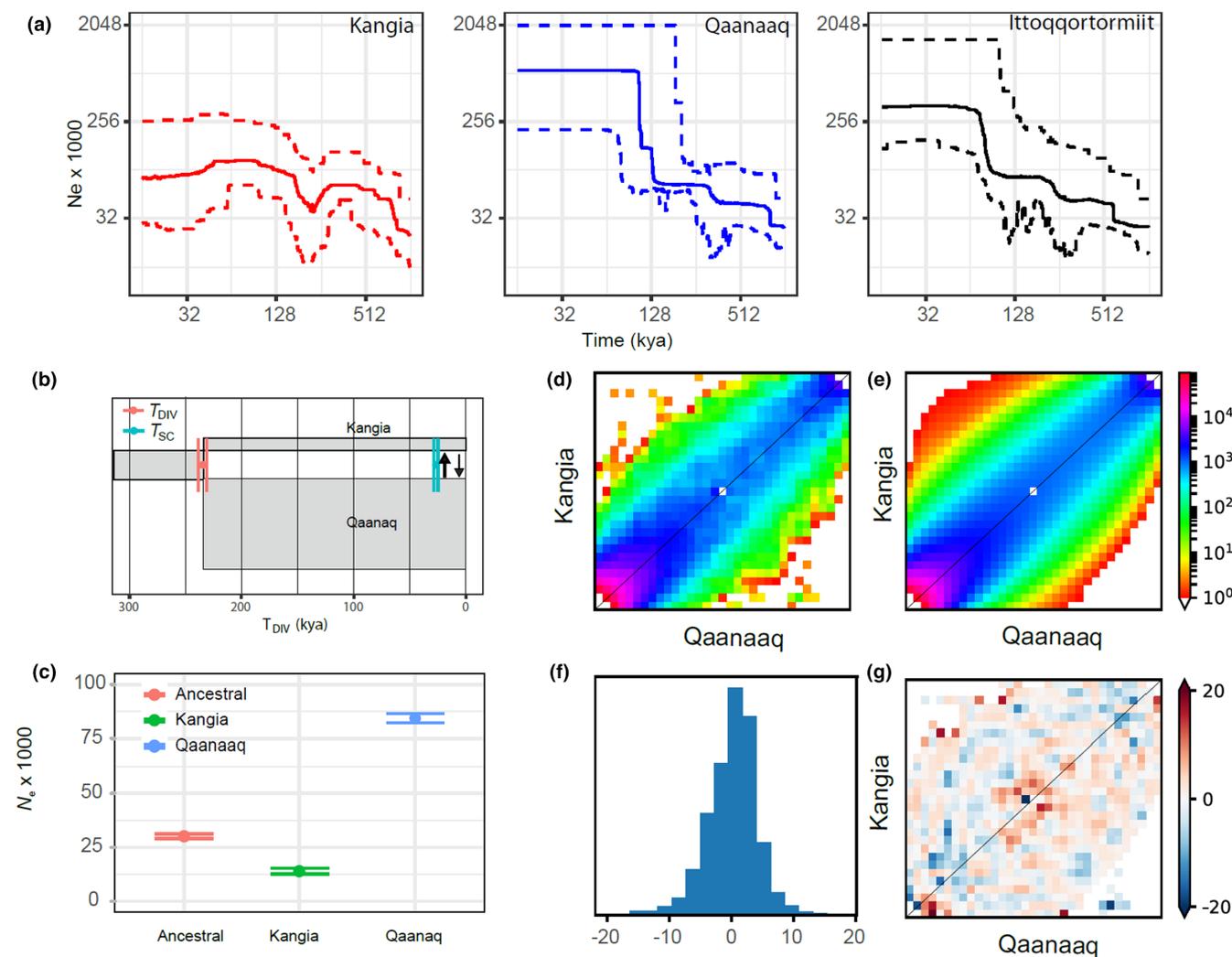


FIGURE 5 Demographic history of Kangia ringed seals. (a) Past changes in Ne in three populations reconstructed using stairway plot. Solid lines represent the median and dashed lines the 95% CI (b) Graphical representation of the best divergence model of seals from Kangia and Qaanaaq (SC_{2M} , with heterogeneous migration rates). Error bars represent confidence intervals for the divergence time (T_{DIV}) and the time where secondary contact (T_{SC}) was initiated. (c) Estimates of ancestral Ne and recent Ne from the best two population models. (d) Observed two-dimensional SFS with the scale reflecting the number of SNPs in each bin. (e) SFS fitted from the best two-population model. (f, g) Distribution of residuals between the observed SFS and the modelled SFS, showing a normal distribution of residuals and random distribution of residuals across the SFS, respectively.

the selected loci (not including linked loci). That is, while the local adaptations of Kangia ringed seals likely arose in allopatry during a 200kya period of isolation, the current levels of gene flow suggest that these adaptations are maintained in the form of old haplotype blocks resisting secondary introgression; an observation also supported by increased Δd_{xy} (Figure 4b–d; Cruickshank & Hahn, 2014). Genetic incompatibility cannot be excluded, but we predict it plays a minor role given the relatively recent divergence time of the populations. In addition to molecular mechanisms, the maintenance of genetic differentiation in Kangia seals from other nearby populations could result from their larger body size, aggressiveness and territoriality, high population density, unique breeding habitat and foraging behaviour, effectively excluding intruding ringed seals. Competitive exclusion from glacial habitats based on age class has been observed in Svalbard ringed seals (Hamilton et al., 2016).

4 | CONCLUSION

The discovery of a distinct ringed seal ecotype in the Ilulissat Icefjord adds to a growing list of Arctic marine species with newly detected genetic and/or phenotypic diversity (Bringloe et al., 2020; Jacobsen et al., 2022; Laidre et al., 2022; Madsen et al., 2016; Mathiesen et al., 2017; Tempestini et al., 2020). The Arctic environment is highly dynamic, with marine systems characterized by long- and short-term fluctuations in glacial extent and run-off, marine-freshwater clines, sea-level changes and isostatic rebound. These processes might facilitate both regional and local speciation, perhaps down to the scale of individual fjord systems or larger marine-terminating glacier fronts. Thus, while our study is the first to demonstrate the existence of a distinct Kangia ringed seal ecotype in the Ilulissat Icefjord, similar intraspecific diversity

and differentiation may exist elsewhere in both ringed seals and other Arctic marine species. Across the Arctic, marine-terminating glaciers, deep fjord systems and polynyas sustain high biological productivity and provide important foraging and resting habitats for marine organisms (Heide-Jørgensen et al., 2016; Lydersen et al., 2014; Meire et al., 2017). These areas may have constituted important high-latitude refugia and even micro-evolutionary speciation factories through glacial and interglacial periods, potentially supporting uniquely adapted populations of otherwise wide-spread and seemingly panmictic Arctic marine organisms. Some local populations may not easily respond to climate change by simply tracking their habitat northward, whereas others may harbour the adaptive potential providing species-level resistance to current climate warming. Our findings highlight the need for dedicated scientific efforts and thorough sampling to record and understand regional and local drivers of intraspecific diversity in the Arctic to provide information for nature management.

AUTHOR CONTRIBUTIONS

ARA and MTO were involved in conceptualization; ARA, RGH, RD, SHF, DH, FFR, KMK, CL, JJ, PA and MTO were involved in funding acquisition; ARA was involved in satellite tagging and data analysis; ARA and RGH were involved in population survey; ARA, MV, RD, SHF, JJ, FFR, KMK, CL, PA and MTO were involved in genetic sample collection; CHSO, MV and MTO were involved in molecular lab work; AL and PM were involved in population genetic data analysis; ARA, AL, PM and MTO were involved in the first draft of the manuscript; ARA, AL, PM, RGH and MTO were involved in the first draft of methods. All authors contributed to and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Whole-genome sequencing data have been submitted to the European Nucleotide Archive under projects PRJEB56329 (Greenland and Canada) and PRJEB56317 (Svalbard and Baltic) and the Baltic ringed seal reference genome under project PRJEB56521.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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