Climate change introduces threatened killer whale populations and conservation challenges to the Arctic

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Abstract

The Arctic is the fastest-warming region on the planet, and sea ice loss has opened new habitat for sub-Arctic species such as the killer whale (*Orcinus orca*). As apex predators, killer whales can cause significant ecosystem-scale changes, however, we know very little about killer whales in the Arctic. Setting conservation priorities for killer whales and their Arctic prey species requires knowledge of their evolutionary history and demography. We found that there are two highly genetically distinct, non-interbreeding populations of killer whales using the eastern Canadian Arctic—one population is newly identified as globally distinct. The effective sizes of both populations recently declined, and both are vulnerable to inbreeding and reduced adaptive potential. Furthermore, we present evidence that human-caused mortalities, particularly ongoing harvest, pose an ongoing threat to these populations. The certainty of substantial environmental change in the Arctic complicates conservation and management significantly. Killer whales bring top-down pressure to Arctic food webs, however, they also merit conservation concern. The opening of the Arctic to killer whales exemplifies the magnitude of complex decisions surrounding local peoples, wildlife conservation, and resource management as the effects of climate change are realized.

Keywords: marine mammal, genetic differentiation, effective population size, genomics

1. Background

The Arctic is warming four times faster than the global average[1], thus we expect to see the earliest and most significant effects of climate change in Arctic ecosystems. The increase in spatial extent and duration of the Arctic Ocean's ice-free season is of particular concern. All credible emission scenarios predict that Arctic summers will be ice-free by the mid-20th century[2]. This will cause substantial ecosystem disruption by threatening endemic Arctic species that rely on the seasonal features of Arctic environments and by forcing northern communities to adapt to new conditions[3,4]. For example, reduced sea ice coverage increases access to the region's resources, leading to human population growth and increasing pollution and shipping-related disturbances[5,6]. The loss of habitat for sea ice-dependent algae and phytoplankton results in negative bottom-up threats to unique sea ice ecosystems as these species underpin primary productivity at the base of the Arctic food web[3,7]. Finally, sea ice loss can result in considerable top-down pressure on Arctic food chains by providing access to predators not previously common in the region[8]. We must build our understanding of how climate change affects Arctic ecosystems to maintain what we can for people and wildlife and to hone our understanding of the complexities of ecosystem changes expected to become prevalent globally in the coming years.

Killer whales (*Orcinus orca*) are top predators with documented cascading effects on ecosystems[9–12]. The frequency of killer whale sightings in the eastern Canadian Arctic has increased considerably since the 1950s[13,14], so there is potential for them to induce substantial ecosystem-level change in this sensitive region[15]. Inuit knowledge indicates that small numbers of killer whales have long used the Arctic, but it is uncertain whether the increase in sightings is due to a growing population, more individuals from elsewhere using the Arctic, or both[15]. In any case, the growing presence of killer whales in the Arctic is likely climate-linked, as sea ice blocks access to the region for these animals[8]. With increasingly prolonged open-water seasons and growing numbers of killer whales in the region, the direct consumption of Arctic marine mammals is expected to rise[16–18]. In addition to directly affecting prey numbers, killer whales in the Arctic disrupt their prey's habitat use and behavior, which stands to reshape marine mammal distributions[19]. Conservation efforts require information on the origin of killer whales using the Arctic, their abundance, demographic trends, population structure, and threats to their persistence to understand the consequences of global change for Arctic ecosystems.

In this study, we used whole-genome data to explore the population structure and origins of Arctic killer whales and their contemporary effective population sizes. We also conducted a comprehensive survey of published killer whale mortalities in the western North Atlantic to explore possible anthropogenic causes of recent declines. By examining population genomics and threats in Arctic killer whales, we can better understand the consequences of climate warming for Arctic ecosystems and guide future conservation and management.

2. Methods

(a) Sample collection and sequencing

Killer whale samples were collected in the western North Atlantic (all samples and locations listed in table S1) through tissue biopsies from free-ranging killer whales (n = 20), tissue samples from harvested animals (n = 6), and teeth from fatally stranded killer whales (n = 3). We extracted DNA from skin tissue using a Qiagen DNeasy Blood and Tissue extraction kit, and DNA from tooth samples using a QIAamp DNA Investigator kit (Valencia, CA, USA). Sequencing libraries were built using sheared DNA extracts using NEBNext Ultra II DNA Library Prep Kit for Illumina (Ipswich, MA, USA) and sequenced on the Illumina HiSeq X platform (San Diego, CA, USA).

Sequencing read preparation and mapping were conducted following Foote et al.[20]. Briefly, we trimmed reads with Trimmomatic v0.35[21], then mapped the reads to a high-quality reference genome assembly (accession #GCA_000331955.1[22]) using BWA v0.7.12[23]. GATK v3.7.0[24] was used to create an interval file for suspect indels, combined with high-confidence single-nucleotide polymorphism (SNP) positions, and filtered to include only autosomal regions. We masked repeats and low-quality regions using BEDtools v2.27.1[25], then merged the aligned reads with Picard[26]. Finally, to identify genomic variants with the reference genome, we used Freebayes v1.2.0, which is a haplotype-based variant detector[27]. Variants were filtered with Vcftools v0.1.17[28] to remove indels, low quality sites (quality < 30), sites out of Hardy-Weinberg Equilibrium (p-value threshold < 0.005), and sites with missingness > 0.4. SNPs were further filtered for minor allele frequency < 0.05 and pruned for linkage disequilibrium (LD $r^2 > 0.8$) to create a dataset for population structure analyses. See supplemental materials for further details on sample collection, DNA extraction, and sequencing reads.

(b) Genomic analyses

First, we estimated kinship through R-package SNPRelate v1.30.1[29] and plink v1.9[30], and removed duplicates and one individual from each close kin pair in downstream analyses (removed individuals are marked in table S1). Next, to assess Arctic killer whale population structure, we used Principal Component Analysis (PCA) with R-package adegenet v2.1.7[31,32] and examined ancestral admixture through sparse non-negative matrix factorization (sNMF) in the R-package LEA v3.8.0[33]. We used R-package StAMPP v1.6.3[34] to calculate a fixation index (F_{ST}) to measure genetic differentiation between the two putative populations (High Arctic and Low Arctic). Following parameters used in Foote et al.[35], we examined runs of homozygosity (ROH) across individual genomes using plink v1.9[30] then measured the frequency of ROH across the genome.

To place the Arctic killer whales within a global context of killer whale populations, we compared individuals from the two Arctic populations to genomes sampled from 25 additional sites worldwide[20]. Associations among all samples were investigated using PCA, then plotted as a covariance matrix. ABBA BABA statistics (Patterson's D statistics) were used to test for introgression[36,37] among High and Low Arctic, and samples in the global dataset (X) at sites where X had a derived allele (i.e., an allele different to that in an ancestral outgroup).

Demographic history was assessed with several methods to examine historic and contemporary effective population sizes (N_e). Using SMC++ v1.15.2[38], we identified historic changes in N_e over time and estimated when the two killer whale populations diverged. Here, we used a mutation rate of 2.34 x 10^{-8} based on Dornburg et al.[39] and a generation time of 25.7 years for this species[40]. To estimate recent changes in N_e (within the last 150 generations), we used a linkage-based method in the program GONE[41] and followed parameters used in Kardos et al.[42]. Finally, we estimated contemporary effective population sizes for both populations separately through StrataG v2.5.1[43], using a SNP dataset that was further filtered and randomly down-sampled to 25,000 SNPs.

For further detail on genomic analyses methods, please refer to the supplemental materials.

(c) Survey of anthropogenic killer whale mortalities

To assemble a database of killer whale mortalities from anthropogenic causes in the western North Atlantic, we searched for records of these events bounded by 45°W longitude (south of Cape Farwell, Western Greenland) and 10°N latitude (to Trinidad and Tobago). Mortality types were divided into categories for commercial whaling, subsistence harvests, opportunistic harvests, fishing gear entanglement, and retaliatory. Some uncertainty in the number of records could be due to some sources pooling catch records by month, a likely underestimated number of commercial kills, potential under-reported struck and loss rates, and discrepancies between sources. We did not include mortality from natural causes.

3. Results and discussion

(a) Population structure and evolutionary origins of Arctic killer whales

We found clear, consistent evidence for two genetically distinct populations using the eastern Canadian Arctic. One population comprised individuals sampled in the eastern Canadian High Arctic and Newfoundland (hereafter referred to as the "High Arctic" population); the second included individuals sampled from the Canadian Low Arctic and Greenland (hereafter referred to as the "Low Arctic" population) (figure 1). Although the geographical range of these two populations overlaps temporally in the Arctic, they were highly genetically distinct (F_{ST} = 0.198; 0.198 to 0.200 95% CI). When comparing the Arctic whales with the global dataset, High Arctic killer whale genomes were distinct with this analysis as well, and Low Arctic whales were genetically similar to individuals sampled from the eastern North Atlantic (Greenland, Norway, and Iceland) (figure 2). These analyses suggest that there is very limited or no contemporary gene flow between the two groups. Notably, the High Arctic individuals were genetically distinct from all other sampled populations—they thus comprise a newly genetically identified population of killer whales. It is possible that the High Arctic population is the Arctic population Inuit communities have long seen in the region, but genetic confirmation of this would require older samples than are currently available.

The evolutionary origins of the High and Low Arctic killer whales suggest their co-occurrence in eastern Canadian Arctic waters is a secondary contact between an ancestral Atlantic population and a derived sub-Arctic population. Analyses of shared ancestry among the global sample of killer whales suggest that High Arctic killer whales are derived from an ancestral Atlantic population; they harbored an excess of derived alleles shared with killer whales sampled in Brazil and Newfoundland. In contrast, Low Arctic killer whales likely derived from a population that expanded into the eastern North Atlantic from Greenland, Iceland, and Norway (table S2; figure S1). We estimated the timing of divergence between the High and Low Arctic populations to have occurred near the end of the Last Glacial Maximum approximately 9–20 kya ago (figure S2). The lack of strong genetic similarity and shared ancestry with killer whales outside the Atlantic Ocean suggest that these two populations evolved within the Atlantic rather than via colonization from a different region.

We know relatively little about the ecology of the killer whales that use the Arctic[15]. However, ecological divergence and specialization underlie genetic differentiation between killer whale populations elsewhere. For example, killer whales in the northeastern Pacific Ocean and the Southern Ocean have recognizable ecotypes based on diet, social behavior, morphology, and genetics[44–49]. The level of differentiation between the High and Low Arctic killer whales is comparable to the difference between ecotypes from within the Antarctic and Pacific oceans[50]. However, it is much less clear whether North Atlantic populations can be ecologically categorized as discretely[51,52].

Fatty acid signatures from killer whales and their prey point to gradients in diet across the region—killer whales in the western North Atlantic, including Canadian waters, primarily consumed other whale species (e.g., [53]), and individuals from Greenland prey mainly on seals and fish such as herring (*Clupea harengus)* and mackerel (*Scomber scombrus*)[54]. Direct observations of killer whales feeding in the Canadian Arctic support these findings, with beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) observed as prey most often, followed by bowhead whales (*Balaena mysticetus*), ringed (*Pusa hispida*), harp (*Pagophilus groenlandicus*), bearded (*Erignathus barbatus*), and hooded (*Cystophora cristata*) seals[13,55]. In Greenland, Inuit hunters report seals as the main killer whale prey, followed by fish and minke whales and narwhals in the northernmost part of West Greenland[56–58]. Therefore, we have limited data to support ecological discreteness, but strong evidence for genetic differentiation in killer whale populations of the eastern Canadian Arctic.

(b) Population demography and threats to Arctic killer whales

The most important quantities for understanding population biology, and for conservation and management decision-making, are the number of individuals in a population, the effective population size, and whether these values are trending up or down. The number of individuals in a population governs population ecology, and the effective population size shapes several evolutionary processes[59]. The effective population size is an estimate of the strength of genetic drift a population experiences. The smaller the effective population size, the faster a population loses genetic diversity. This is important because genetic diversity contributes to population mean fitness and the capacity to adapt to current and future environmental change[60]. Additionally, the efficiency of natural selection is inversely proportional to the strength of drift, meaning small populations will have difficulties adapting to environmental change. In practice, the effective population size will be much smaller than, and not well correlated with, the census population size due to variation in reproductive success and output across individuals and the population's demographic history. For conservation and management, it is important to note that population sizes increase much faster than genetic diversity due to the slow rate at which mutations accrue. Thus, growing and even relatively large populations can be at risk, evolutionarily speaking, if their effective size is low. Below we explore threats to Arctic killer whale populations related to trends in effective population size and the numbers of individuals in the populations.

The genetic diversity and demographic histories of the Canadian Arctic killer whale populations strongly suggest that they warrant conservation concern. We found the effective population sizes of the High and Low Arctic populations are 20 (N_e = 19.67; 19.65 to 19.69 95% CI) and 14 (N_e = 13.92; 13.89 to 13.94 95% CI), respectively. These very small effective population sizes mean that these populations will have difficulty adaptively responding to future environmental change. Recently, the United Nations Convention on Biodiversity adopted the Kunming-Montreal global biodiversity framework to guide biodiversity conservation interventions. This agreement prioritized two indicators of population genetic risk. First, the agreement considers effective population sizes < 500 to be at high genetic risk due to loss of adaptive capacity [headline indicator A.5 for Goal A and Target 4CBD, 2022[61]]. The effective sizes identified here are approximately 14x to 20x below United Nations guidelines for limiting genetic risk. While the relationships between effective population size and genetic risk are context-dependent, the low effective population sizes in the High and Low Arctic are concerning for their capacities to maintain genetic diversity and adaptive resilience. The second headline indicator for evolutionary risk is the loss of genetically distinct populations. The genetically distinct Arctic populations we identify merit conservation and management concern based on both criteria.

The two Arctic populations arrived at their similarly low effective population sizes differently and in ways that will affect conservation efforts and likely their outcomes. The populations drifted genetically following their initial divergence (figure S2) and the effective population sizes of both populations were stable for most of the last 4000 years (figure 3a). However, both populations have experienced notable recent declines (figure 3a). The High Arctic population decline was much more pronounced than in the Low Arctic population, which had a much smaller effective population size across those 4000 years. Although both populations' contemporary effective sizes are similar, the Low Arctic population is much more inbred than the High Arctic population, as shown by the greater proportion of runs of homozygosity (figure 3b). The difference in inbreeding between the High Arctic and Low Arctic is likely due to the recency and magnitude of the decline in effective population size in the High Arctic whales, as genetic drift and inbreeding accumulate for many generations after the initial population declines. Given the similar contemporary effective population sizes, we should expect ongoing inbreeding in the Low Arctic population with the levels of genetic diversity in both populations eventually converging.

The very low contemporary effective population sizes suggest that Arctic killer whales are vulnerable to inbreeding depression. Inbreeding depression causes reduced survival and reproduction in small populations due to increased homozygosity of partially recessive deleterious alleles. The well-documented negative effects of inbreeding in Southern Resident killer whales are instructive for the Arctic populations[42]. The Southern Resident and Low Arctic populations have very comparable recent demographic histories and patterns of runs of homozygosity, and all three populations have comparable contemporary effective population sizes (Southern Resident $N_e = 27$, Kardos et al.[42]; High Arctic $N_e = 20$; Low Arctic $N_e = 14$). Using long-term individual based monitoring data in the Southern Resident population, Kardos et al.[42] found convincing evidence that inbreeding depression limits population growth in Southern Resident killer whales, and predicted further population declines in the system due to inbreeding. Given historical and contemporary demographic similarities with the Low Arctic population, those findings bear on the current and future effects of inbreeding for the Arctic whales—inbreeding depression will likely limit population recovery. While both Arctic populations may be threatened by inbreeding, the smaller runs of homozygosity in the High Arctic population mean that conservation action focused on extrinsic threats and maintaining population size could mitigate the risk of inbreeding depression in this population.

Census population size estimates help put effective population sizes into context regarding human-caused mortalities. The number of killer whales in the northern Baffin Island region is estimated to be between 136 to 190 individuals, based on photographic capture recapture[18]. In our survey of published killer whale mortalities in the western North Atlantic (table S3, figure S5), we found that commercial whaling and subsistence harvest were the leading documented sources of mortality. The earliest whaling record in the region was from Nuuk, West Greenland, in 1756[56,62]. Harvest has continued since then, with Greenland introducing a bounty on killer whales from 1960-1975[56]. This harvest continues to this day with a distinct increase in southeast Greenland starting in 2009, following a climate-related ecosystem shift caused by the collapse of drifting sea ice during summer and a consequent increase in the number of killer whales in the area[58,63]. Of the 500 mortalities we document, all but two (fishing gear entanglement) were intentional kills. This literature survey is very likely an underestimate of human-caused mortality. Kills in Canadian waters are under-reported but second and third-hand accounts suggest they occur[64]. Killer whales are often difficult to retrieve as they readily sink after being killed due to having relatively little blubber, decreased buoyancy in cold waters[65], and because they are or were not killed for consumption—killer whales are sometimes seen as threats to people and valued wildlife[58]. These deaths often go unreported but could be substantial in number. For example, during three hunts in Greenland, interviewed hunters reported landing 4 whales with an additional 9 whales killed, unretrieved, and unreported in harvest data[58].

Movement within a population is important to consider when looking into anthropogenic mortalities, since hunting pressure in one location may affect the population inhabiting multiple areas. Our genomic results suggest the High Arctic population range between Mittimatalik and Newfoundland and photographic recaptures support this. Two individual killer whales (DI02 and DI03) first identified near Disko Island, Greenland in 2011[66] were re-sighted near Mittimatalik, Nunavut in 2019 (ECA072 and ECA071, respectively)[67]. This evidence shows that killer whales are moving between eastern Canadian Arctic and west Greenland waters, indicating that killer whales in the High Arctic population are subject to harvest pressure in Greenland. It is likely that harvest has contributed to the recent population declines we document and is a threat to population recovery.

4. Conservation implications

The task of conservation given climate change presents a classic 'wicked problem' that will continue to play out globally. Accumulated greenhouse gas emissions and future emissions targets ensure that the planet's ecosystems will be highly altered regardless of future mitigations. With conservation of the present state in many regions ranging from impractical to impossible we are forced to conserve what we can and manage wildlife for an uncertain future. The case of killer whales in the Arctic exemplifies the magnitude of complex decisions related to people and wildlife conservationists and managers will face as the effects of climate change are realized throughout the planet. The current small, genetically homogeneous, and potentially ecologically distinct killer whale populations in the eastern Canadian Arctic are susceptible to inbreeding and harvest, as well as a high exposure to contaminants[68]. Conservation and management issues are made more complex by the lack of foundational knowledge in these systems, exemplified by the newly identified High Arctic population. At the same time, the increasing use of the Arctic and consumption of Arctic marine mammals by killer whales could also cause significant ecosystem-scale change concurrent with other threats through trophic cascades (e.g., [9–11,69]; although see [70,71]). Arctic marine mammals use sea ice to reduce the risk of killer whale predation. With the loss of ice cover, killer whale predation could lead to severe consequences for their prey populations. The marine mammals that the killer whales hunt while in northern waters are culturally and economically important to indigenous communities, so these species also merit conservation and management concern in light of killer whale populations moving into the Arctic. Effective conservation and management of killer whale populations and their ecosystems will require a holistic approach that considers their genetic background, and complex interactions among killer whale populations, changing prey interactions, and other human-induced threats in the context of ongoing climate change. This will require collaborations among scientists, policymakers, and stakeholders across national and international borders. Finally, it will require a commitment to address the root causes of threats to killer whale populations, including climate change and human activities such as past and current whaling.

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References

1. Rantanen M, Karpechko AY, Lipponen A, Nordling K, Hyvärinen O, Ruosteenoja K, Vihma T, Laaksonen A. 2022 The Arctic has warmed nearly four times faster than the globe since 1979. *Commun Earth Environ* **3**, 1–10. (doi:10.1038/s43247-022-00498-3)

2. Kim Y-H, Min S-K, Gillett NP, Notz D, Malinina E. 2023 Observationally-constrained projections of an ice-free Arctic even under a low emission scenario. *Nat Commun* **14**, 3139. (doi:10.1038/s41467-023-38511-8)

3. Post E *et al.* 2013 Ecological Consequences of Sea-Ice Decline. *Science* **341**, 519–524. (doi:10.1126/science.1235225)

4. Krupnik I, Aporta C, Gearheard S, Laidler GJ, Kielsen Holm L, editors. 2010 *SIKU: Knowing Our Ice: Documenting Inuit Sea Ice Knowledge and Use*. Dordrecht: Springer Netherlands. (doi:10.1007/978-90-481-8587-0)

5. Dawson J, Carter N, van Luijk N, Parker C, Weber M, Cook A, Grey K, Provencher J. 2020 Infusing Inuit and local knowledge into the Low Impact Shipping Corridors: An adaptation to increased shipping activity and climate change in Arctic Canada. *Environmental Science & Policy* **105**, 19–36. (doi:10.1016/j.envsci.2019.11.013)

6. Mudryk LR, Dawson J, Howell SEL, Derksen C, Zagon TA, Brady M. 2021 Impact of 1, 2 and 4 °C of global warming on ship navigation in the Canadian Arctic. *Nat. Clim. Chang.* **11**, 673–679. (doi:10.1038/s41558-021-01087-6)

7. Koch CW *et al.* 2023 Year-round utilization of sea ice-associated carbon in Arctic ecosystems. *Nat Commun* **14**, 1964. (doi:10.1038/s41467-023-37612-8)

8. Higdon JW, Ferguson SH. 2009 Loss of Arctic sea ice causing punctuated change in sightings of killer whales (*Orcinus orca*) over the past century. *Ecological Applications* **19**, 1365–1375. (doi:10.1890/07-1941.1)

9. Estes JA, Tinker MT, Williams TM, Doak DF. 1998 Killer Whale Predation on Sea Otters Linking Oceanic and Nearshore Ecosystems. *Science* **282**, 473–476. (doi:10.1126/science.282.5388.473)

10. Springer AM, Estes JA, van Vliet GB, Williams TM, Doak DF, Danner EM, Forney KA, Pfister B. 2003 Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences* **100**, 12223–12228. (doi:10.1073/pnas.1635156100)

11. Springer A, Estes J, van Vliet G, Williams T, Doak D, Danner E, Pfister B. 2008 Mammal-eating killer whales, industrial whaling, and the sequential megafaunal collapse in the North Pacific Ocean: A reply to critics of Springer et al. 2003. *Marine Mammal Science - MAR MAMMAL SCI* **24**, 414–442. (doi:10.1111/j.1748-7692.2008.00185.x)

12. Towner AV, Kock AA, Stopforth C, Hurwitz D, Elwen SH. 2023 Direct observation of killer whales preying on white sharks and evidence of a flight response. *Ecology* **104**, e3875. (doi:10.1002/ecy.3875)

13. Higdon JW, Hauser DDW, Ferguson SH. 2012 Killer whales (Orcinus orca) in the Canadian Arctic: Distribution, prey items, group sizes, and seasonality. *Marine Mammal Science* **28**, E93–E109. (doi:10.1111/j.1748-7692.2011.00489.x)

14. Higdon JW, Westdal KH, Ferguson SH. 2014 Distribution and abundance of killer whales (Orcinus orca) in Nunavut, Canada—an Inuit knowledge survey. *Journal of the Marine Biological Association of the United Kingdom* **94**, 1293–1304. (doi:10.1017/S0025315413000921)

15. Lefort KJ, Matthews CJD, Higdon JW, Petersen SD, Westdal KH, Garroway CJ, Ferguson SH. 2020 A review of Canadian Arctic killer whale (*Orcinus orca*) ecology. *Can. J. Zool.* **98**, 245–253. (doi:10.1139/cjz-2019-0207)

16. Shelden KEW, Rugh DJ, Mahoney BarbaraA, Dahlheim ME. 2003 Killer Whale Predation on Belugas in Cook Inlet, Alaska: Implications for a Depleted Population. *Marine Mammal Science* **19**, 529–544. (doi:10.1111/j.1748-7692.2003.tb01319.x)

17. Ferguson SH, Higdon JW, Chmelnitsky EG. 2010 The Rise of Killer Whales as a Major Arctic Predator. In *A Little Less Arctic: Top Predators in the World's Largest Northern Inland Sea, Hudson Bay* (eds SH Ferguson, LL Loseto, ML Mallory), pp. 117–136. Dordrecht: Springer Netherlands. (doi:10.1007/978-90-481-9121-5_6)

18. Lefort KJ, Garroway CJ, Ferguson SH. 2020 Killer whale abundance and predicted narwhal consumption in the Canadian Arctic. *Global Change Biology* **26**, 4276–4283. (doi:10.1111/gcb.15152)

19. Breed GA, Matthews CJD, Marcoux M, Higdon JW, LeBlanc B, Petersen SD, Orr J, Reinhart NR, Ferguson SH. 2017 Sustained disruption of narwhal habitat use and behavior in the presence of Arctic killer whales. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 2628–2633. (doi:10.1073/pnas.1611707114)

20. Foote AD *et al.* 2019 Killer whale genomes reveal a complex history of recurrent admixture and vicariance. *Mol Ecol* , mec.15099. (doi:10.1111/mec.15099)

21. Bolger AM, Lohse M, Usadel B. 2014 Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* **30**, 2114–2120. (doi:10.1093/bioinformatics/btu170)

22. Foote AD *et al.* 2015 Convergent evolution of the genomes of marine mammals. *Nat Genet* **47**, 272–275. (doi:10.1038/ng.3198)

23. Li H, Durbin R. 2009 Fast and accurate short read alignment with Burrows–Wheeler transform. *Bioinformatics* **25**, 1754–1760. (doi:10.1093/bioinformatics/btp324)

24. McKenna A *et al.* 2010 The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome Res* **20**, 1297–1303. (doi:10.1101/gr.107524.110)

25. Quinlan AR, Hall IM. 2010 BEDTools: a flexible suite of utilities for comparing genomic features. *Bioinformatics* **26**, 841–842. (doi:10.1093/bioinformatics/btq033)

26. Broad Institute. 2019 Picard Toolkit. *GitHub Repository*. See https://broadinstitute.github.io/picard/ (accessed on 15 August 2023).

27. Garrison E, Marth G. 2012 Haplotype-based variant detection from short-read sequencing. (doi:10.48550/arXiv.1207.3907)

28. Danecek P *et al.* 2011 The variant call format and VCFtools. *Bioinformatics* **27**, 2156–2158. (doi:10.1093/bioinformatics/btr330)

29. Zheng X, Levine D, Shen J, Gogarten SM, Laurie C, Weir BS. 2012 A high-performance computing toolset for relatedness and principal component analysis of SNP data. *Bioinformatics* **28**, 3326–3328. (doi:10.1093/bioinformatics/bts606)

30. Purcell S *et al.* 2007 PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am J Hum Genet* **81**, 559–575. (doi:10.1086/519795)

31. Jombart T. 2008 adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* **24**, 1403–1405. (doi:10.1093/bioinformatics/btn129)

32. Jombart T, Ahmed I. 2011 adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics* **27**, 3070–3071. (doi:10.1093/bioinformatics/btr521)

33. Frichot E, François O. 2015 LEA: An R package for landscape and ecological association studies. *Methods in Ecology and Evolution* **6**, 925–929. (doi:10.1111/2041-210X.12382)

34. Pembleton LW, Cogan NOI, Forster JW. 2013 StAMPP: an R package for calculation of genetic differentiation and structure of mixed-ploidy level populations. *Mol Ecol Resour* **13**, 946–952. (doi:10.1111/1755-0998.12129)

35. Foote AD *et al.* 2021 Runs of homozygosity in killer whale genomes provide a global record of demographic histories. *Molecular Ecology* **30**, 6162–6177. (doi:10.1111/mec.16137)

36. Durand EY, Patterson N, Reich D, Slatkin M. 2011 Testing for Ancient Admixture between Closely Related Populations. *Molecular Biology and Evolution* **28**, 2239–2252. (doi:10.1093/molbev/msr048)

37. Green RE *et al.* 2010 A Draft Sequence of the Neandertal Genome. *Science* **328**, 710–722. (doi:10.1126/science.1188021)

38. Terhorst J, Kamm JA, Song YS. 2017 Robust and scalable inference of population history from hundreds of unphased whole genomes. *Nat Genet* **49**, 303–309. (doi:10.1038/ng.3748)

39. Dornburg A, Brandley MC, McGowen MR, Near TJ. 2012 Relaxed Clocks and Inferences of Heterogeneous Patterns of Nucleotide Substitution and Divergence Time Estimates across Whales and Dolphins (Mammalia: Cetacea). *Molecular Biology and Evolution* **29**, 721–736. (doi:10.1093/molbev/msr228)

40. Taylor B, Chivers S, Larese J, Perrin W. 2007 Generation length and percent mature estimates for IUCN assessments of cetaceans. *NOAA, NMFS, Southwest Fisheries Science Center Administrative Report LJ-07-01*

41. Santiago E, Novo I, Pardiñas AF, Saura M, Wang J, Caballero A. 2020 Recent Demographic History Inferred by High-Resolution Analysis of Linkage Disequilibrium. *Molecular Biology and Evolution* **37**, 3642–3653. (doi:10.1093/molbev/msaa169)

42. Kardos M *et al.* 2023 Inbreeding depression explains killer whale population dynamics. *Nat Ecol Evol* (doi:10.1038/s41559-023-01995-0)

43. Archer FI, Adams PE, Schneiders BB. 2017 stratag: An r package for manipulating, summarizing and analysing population genetic data. *Molecular Ecology Resources* **17**, 5–11. (doi:10.1111/1755-0998.12559)

44. Baird RW, Stacey PJ. 1988 Variation in saddle patch pigmentation in populations of killer whales (Orcinus orca) from British Columbia, Alaska, and Washington State. *Can. J. Zool.* **66**, 2582–2585. (doi:10.1139/z88-380)

45. Barrett-lennard LG, Ford JKB, Heise KA. 1996 The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour* **51**, 553–565. (doi:10.1006/anbe.1996.0059)

46. Ford JK, Ellis GM, Barrett-Lennard LG, Morton AB, Palm RS, Balcomb III KC. 1998 Dietary specialization in two sympatric populations of killer whales (Orcinus orca) in coastal British Columbia and adjacent waters. *Can. J. Zool.* **76**, 1456–1471. (doi:10.1139/z98-089)

47. Barrett-Lennard LG, Ellis GM. 2001 Population Structure and Genetic Variability in Northeastern Pacific Killer Whales: Towards an Assessment of Population Viability. *Canadian Science Advisory Secretariat*

48. Pitman RL, Ensor P. 2003 Three forms of killer whales (Orcinus orca) in Antarctic waters. *J. Cetacean Res. Manage.* **5**, 131–139. (doi:10.47536/jcrm.v5i2.813)

49. Pitman RL, Durban JW, Greenfelder M, Guinet C, Jorgensen M, Olson PA, Plana J, Tixier P, Towers JR. 2011 Observations of a distinctive morphotype of killer whale (Orcinus orca), type D, from subantarctic waters. *Polar Biol* **34**, 303–306. (doi:10.1007/s00300-010-0871-3)

50. Foote AD *et al.* 2016 Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nat Commun* **7**, 11693. (doi:10.1038/ncomms11693)

51. Foote AD, Newton J, Piertney SB, Willerslev E, Gilbert MTP. 2009 Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology* **18**, 5207–5217. (doi:10.1111/j.1365-294X.2009.04407.x)

52. Foote AD. 2023 Are “Type 2” killer whales long in the tooth? A critical reflection on the discrete categorization of Northeast Atlantic killer whales. *Marine Mammal Science* **39**, 345–350. (doi:10.1111/mms.12964)

53. Whitehead H, Glass C. 1985 Orcas (Killer Whales) Attack Humpback Whales. *Journal of Mammalogy* **66**, 183–185. (doi:10.2307/1380982)

54. Remili A *et al.* 2023 Quantitative fatty acid signature analysis reveals a high level of dietary specialization in killer whales across the North Atlantic. *Journal of Animal Ecology* , 1365-2656.13920. (doi:10.1111/1365-2656.13920)

55. Ferguson SH, Higdon JW, Westdal KH. 2012 Prey items and predation behavior of killer whales (Orcinus orca) in Nunavut, Canada based on Inuit hunter interviews. *Aquatic Biosystems* **8**, 3. (doi:10.1186/2046-9063-8-3)

56. Heide-Jørgensen MP. 1988 Occurrence and hunting of killer whales in Greenland. *Rit Fiskideildar* **11**, 115–135.

57. Foote AD, Newton J, Ávila-Arcos MC, Kampmann M-L, Samaniego JA, Post K, Rosing-Asvid A, Sinding M-HS, Gilbert MTP. 2013 Tracking niche variation over millennial timescales in sympatric killer whale lineages. *Proc. R. Soc. B.* **280**, 20131481. (doi:10.1098/rspb.2013.1481)

58. NAMMCO-North Atlantic Marine Mammal Comission. 2022 Report of the 28th meeting of the NAMMCO Scientific Committee. 24 – 28 January 2022 (online).

59. Waples RS. 2022 What Is *N* e, Anyway? *Journal of Heredity* **113**, 371–379. (doi:10.1093/jhered/esac023)

60. Kardos M, Armstrong EE, Fitzpatrick SW, Hauser S, Hedrick PW, Miller JM, Tallmon DA, Funk WC. 2021 The crucial role of genome-wide genetic variation in conservation. *Proceedings of the National Academy of Sciences* **118**, e2104642118. (doi:10.1073/pnas.2104642118)

61. Hoban S *et al.* 2020 Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. *Biological Conservation* **248**, 108654. (doi:10.1016/j.biocon.2020.108654)

62. Winge H. 1902 Grønlands pattedyr [Mammals of Greenland]. *Medd om Grønl* **21**.

63. Heide-Jørgensen MP *et al.* 2023 A regime shift in the Southeast Greenland marine ecosystem. *Global Change Biology* **29**, 668–685. (doi:10.1111/gcb.16494)

64. Higdon JW. 2007 Status of knowledge on killer whales (Orcinus orca) in the Canadian Arctic. *Canadian Science Advisory Secretariat*

65. Moore MJ, Mitchell GH, Rowles TK, Early G. 2020 Dead Cetacean? Beach, Bloat, Float, Sink. *Frontiers in Marine Science* **7**.

66. Nielsen J. 2011 Photo-ID of Killer Whales in Greenland Waters (Orcinus orca). *Deep Sea Creatures of the North Atlantic*. See https://www.descna.com/en/knowledge-base/photo-id-catalogue-killer-whale-orcinus-orca.

67. Kucheravy CE, Lefort KL, Matthews CJD, Petersen SD, Higdon JW, Ferguson SH. 2023 Killer whale photographic-identification catalogue for the Tallurutiup Imanga National Marine Conservation Area and Cumberland Sound, 2009-2020. *Canadian Technical Report of Fisheries and Aquatic Sciences 3564*: v + 58 p.

68. Desforges J-P *et al.* 2018 Predicting global killer whale population collapse from PCB pollution. *Science* **361**, 1373–1376. (doi:10.1126/science.aat1953)

69. Ripple WJ *et al.* 2014 Status and Ecological Effects of the World's Largest Carnivores. *Science* **343**, 1241484. (doi:10.1126/science.1241484)

70. Mizroch SA, Rice DW. 2006 Have North Pacific killer whales switched prey species in response to depletion of the great whale populations? *Marine Ecology Progress Series* **310**, 235–246. (doi:10.3354/meps310235)

71. Wade PR *et al.* 2007 Killer Whales and Marine Mammal Trends in the North Pacific—a Re-Examination of Evidence for Sequential Megafauna Collapse and the Prey-Switching Hypothesis. *Marine Mammal Science* **23**, 766–802. (doi:10.1111/j.1748-7692.2006.00093.x)

Figures

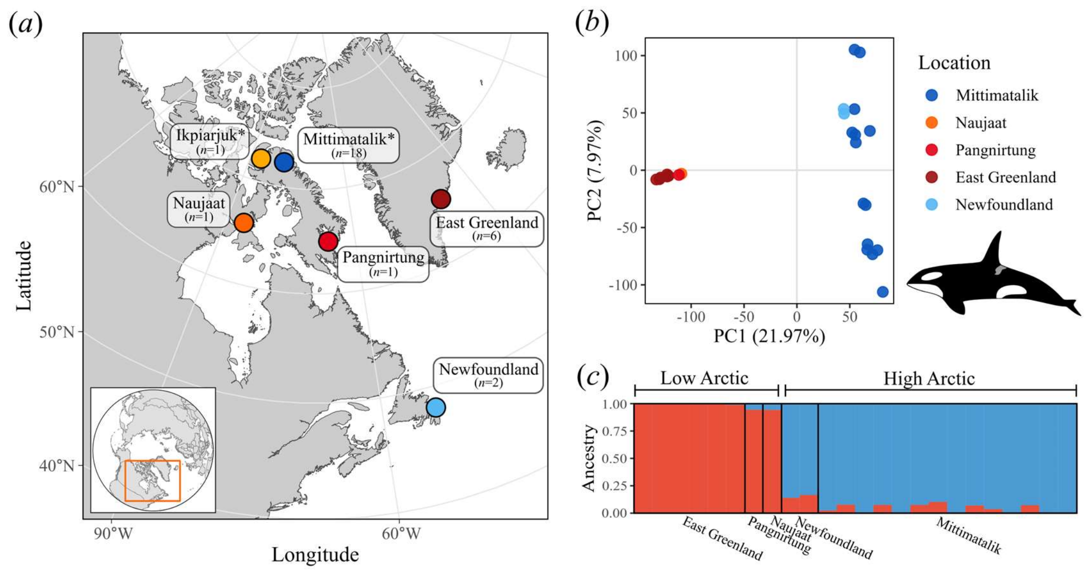

Figure 1. Two sympatric killer whale populations in the eastern Canadian Arctic. (*a*) Sampling locations with respective sample sizes in parentheses (*n* = 29). Locations with an asterisk (*) include individuals from close kin or duplicate pairs that were excluded in population structure analyses. (*b*) PCA containing high proportion of variance and (*c*) admixture results support evidence of two genetic populations.

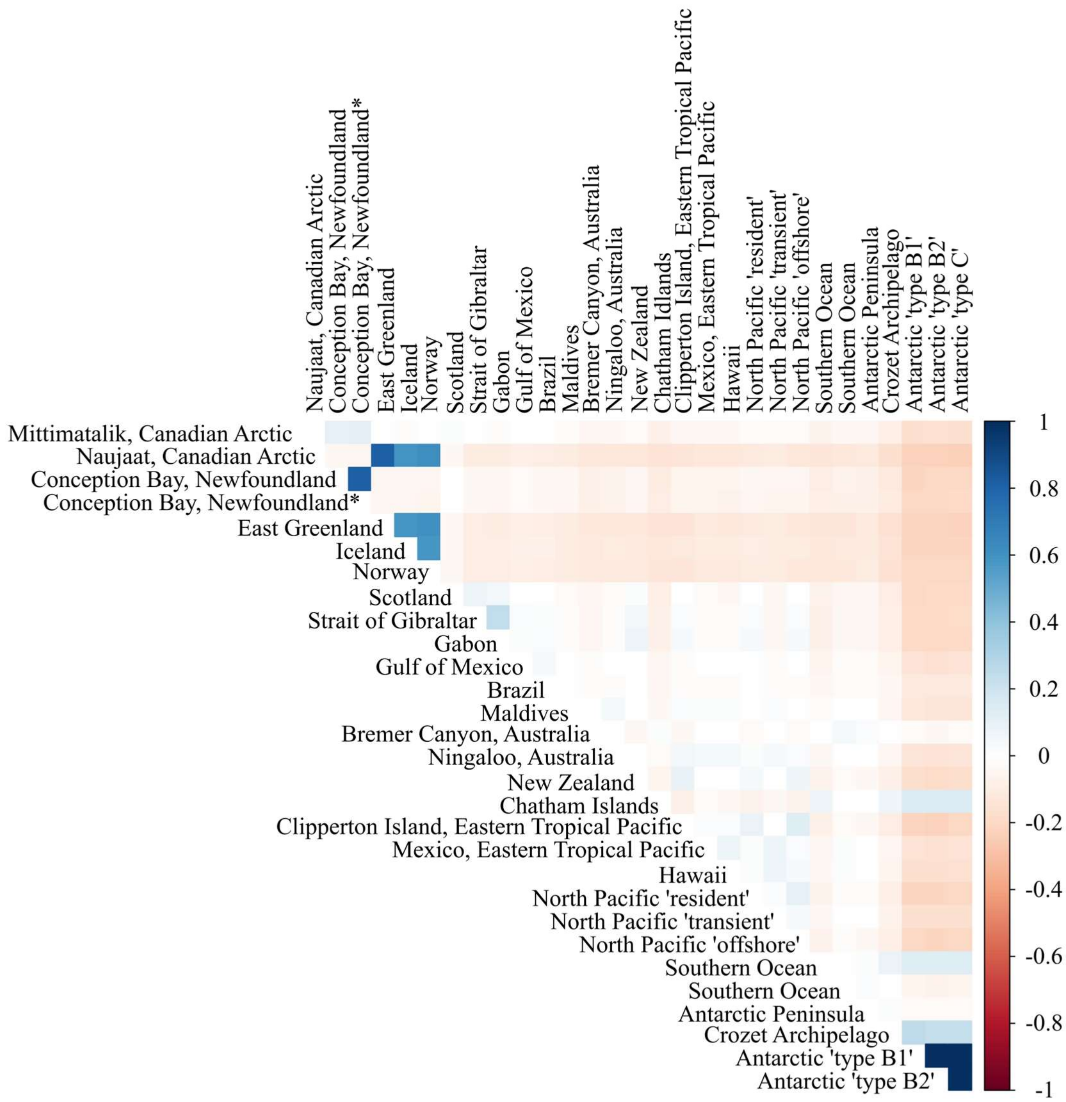

Figure 2. Arctic killer whales positively covaried with whales sampled in Newfoundland and eastern North Atlantic. Covariance matrix from a PCA among global killer whales with two samples from this study and samples from a previously published global dataset in Foote et al. (2019). "Mittimatalik, Canadian Arctic" represents the High Arctic population; and "Naujaat, Canadian Arctic" represents the Low Arctic population.

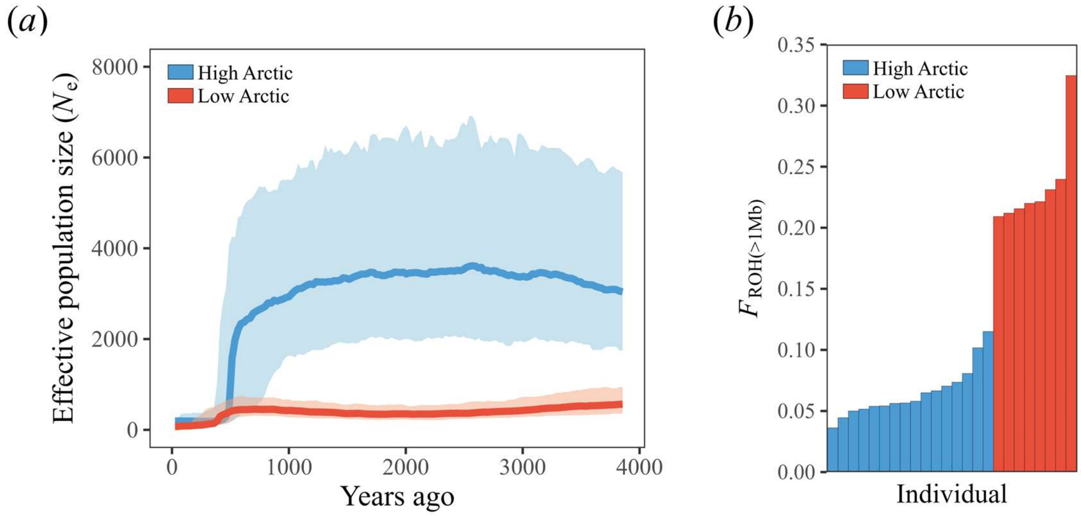

Figure 3. Recent population declines and levels of inbreeding. (*b*) Arctic killer whale effective population sizes across over the past 150 generations (generation time of 25.7 years[40]) (see figure S3 for the model without minor allele frequency filter). Bolded lines represent the median estimates and shaded regions are 95% confidence intervals. (*b*) Proportions of runs of homozygosity (ROH) using a minimum ROH length of 1 Mb for each killer whale individual from the eastern Canadian Arctic (see figure S4 with a minimum ROH length of 1.5 Mb).