Journal of Heredity, 2023, **114**, 587–597
https://doi.org/10.1093/jhered/esad048
Advance access publication 14 August 2023
Original Article

American Genetic Association
OXFORD

Original Article

Diversity of mitochondrial DNA in 3 species of great whales before and after modern whaling

Angela L. Sremba[1,2,*], Anthony R. Martin[3], Peter Wilson[4], Ana Lúcia Cypriano-Souza[5,6], Danielle L. Buss[7,8], Tom Hart[9], Marcia H. Engel[6], Sandro L. Bonatto[5], Howard Rosenbaum[10,11], Tim Collins[11], Carlos Olavarría[12], Frederick I. Archer[13], Debbie Steel[2], Jennifer A. Jackson[7] and C. Scott Baker[2]

[1]Cooperative Institute for Marine Ecosystem and Resource Studies, Oregon State University, Newport, OR, United States,
[2]Marine Mammal Institute, Oregon State University, Newport, OR, United States,
[3]Centre for Remote Environments, University of Dundee, Dundee, United Kingdom,
[4]34 Captain's Place, Southampton, United Kingdom,
[5]Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, RS, Brazil,
[6]Projeto Baleia Jubarte/Instituto Baleia Jubarte Caravelas, Caravelas, BA, Brazil,
[7]British Antarctic Survey, Cambridge, United Kingdom,
[8]Department of Archaeology, University of Cambridge, Cambridge, United Kingdom,
[9]Department of Zoology, University of Oxford, Oxford, United Kingdom,
[10]Wildlife Conservation Society, Ocean Giants Program, Bronx, NY, United States,
[11]American Museum of Natural History, Sackler Institute, New York, NY, United States,
[12]Centro de Estudios Avanzados en Zonas Áridas (CEAZA), La Serena, Chile,
[13]Southwest Fisheries Science Center, La Jolla, CA, United States

[*]Corresponding author: Cooperative Institute for Marine Ecosystem and Resource Studies, Oregon State University, 2030 SE Marine Science Drive, Newport, OR, 97365, United States. Email: srembaa@oregonstate.edu

Corresponding Editor: Elizabeth Alter

Abstract

The 20th century commercial whaling industry severely reduced populations of great whales throughout the Southern Hemisphere. The effect of this exploitation on genetic diversity and population structure remains largely undescribed. Here, we compare pre- and post-whaling diversity of mitochondrial DNA (mtDNA) control region sequences for 3 great whales in the South Atlantic, such as the blue, humpback, and fin whale. Pre-whaling diversity is described from mtDNA extracted from bones collected near abandoned whaling stations, primarily from the South Atlantic island of South Georgia. These bones are known to represent the first stage of 20th century whaling and thus pre-whaling diversity of these populations. Post-whaling diversity is described from previously published studies reporting large-scale sampling of living whales in the Southern Hemisphere. Despite relatively high levels of surviving genetic diversity in the post-whaling populations, we found evidence of a probable loss of mtDNA lineages in all 3 species. This is evidenced by the detection of a large number of haplotypes found in the pre-whaling samples that are not present in the post-whaling samples. A rarefaction analysis further supports a loss of haplotypes in the South Atlantic humpback and Antarctic blue whale populations. The bones from former whaling stations in the South Atlantic represent a remarkable molecular archive for further investigation of the decline and ongoing recovery in the great whales of the Southern Hemisphere.

Key words: blue whale, fin whale, humpback whale, mtDNA diversity, pre-whaling

Introduction

Over 2 million whales were killed by commercial whalers in the Southern Hemisphere during the 20th century (Rocha et al. 2014). This included 345,775 Antarctic blue whales (*Balaenoptera musculus intermedia*) (Branch et al. 2008), 215,848 humpback whales (*Megaptera novaeangliae*), and an astounding 726,461 fin whales (*Balaenoptera physalus*) (Rocha et al. 2014). This "remorseless havoc" resulted in a demographic collapse in many great whale populations (Clapham et al. 1999). In the extreme case of the Antarctic blue whale, only 0.15% of the population is estimated to have survived (about 400 individuals; Branch 2008).

Most studies investigating the impact of whaling on genetic diversity have relied on interpretations or inference from the genetic diversity, or lack of diversity, of post-whaling populations. For this, sequences of the mitochondrial DNA (mtDNA) control region have been the most common marker of choice because of the ease of extraction, amplification, and sequencing from

Received January 15, 2023; Accepted August 11, 2023

© The Author(s) 2023. Published by Oxford University Press on behalf of The American Genetic Association. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

small amounts of tissue, and its maternal, haploid mechanism of inheritance. Due to the latter, mtDNA diversity (i.e. haplotype diversity) is lost more quickly than nuclear DNA diversity (i.e. heterozygosity), declining at approximately 1/Nef per generation, compared with 1/2Ne per generation for nuclear heterozygosity, where Nef is the effective number of females in a population and Ne is the effective number of males and females in a population (Allendorf 1986). Over the last several decades, the mtDNA diversity of contemporary populations has been characterized using samples from relatively large numbers of living whales (e.g. LeDuc et al. 2007; Olavarria et al. 2007; Rosenbaum et al. 2009; Sremba et al. 2012; Archer et al. 2013; Jackson et al. 2014). Several of these formerly exploited populations, such as right whales, have low mtDNA diversity, hypothesized to have resulted from exploitation (Baker et al. 1999; Malik et al. 2000). Other populations of great whales, however, have retained relatively high mtDNA diversity (Baker et al. 1993; Sremba et al. 2012) and some authors have questioned the impact of whaling on genetic diversity given the generation time of whales relative to the duration of the bottleneck (Amos 1996). However, given the longevity of these whales (e.g. over 100 yr for blue whales, https://genomics.senescence.info/species/) and the relatively recent exploitation bottleneck, it is possible that the loss of mtDNA diversity is ongoing as contemporary diversity measurement may include whales that survived the bottleneck but may not pass on their mtDNA haplotype (i.e. males), resulting in a future decline in extant mtDNA diversity (Sremba et al. 2012).

Several studies have attempted to compare estimates of pre-whaling genetic diversity to measures of post-whaling genetic diversity (Rosenbaum et al. 2000; Rastogi et al. 2004; Borge et al. 2007; Alter et al. 2012a, 2012b). While these studies have been limited by both the relatively small number of pre-whaling samples and the technical challenges of recovering degraded DNA, they have confirmed the potential for historical material to provide insight into the genetic diversity that existed prior to whaling.

In the South Atlantic, the vast number of bones scattered along the coast of South Georgia offer the opportunity to explore the impact of the 20th century commercial whaling industry on genetic diversity. The first commercial whaling industry in the Southern Hemisphere was established at Grytviken, South Georgia, in 1904 (Headland 1984). During the early years of whaling at South Georgia, floating factories were the predominant whaling stations on the island (Headland 1984). At these stations, moored in harbors, whales were processed and their carcasses were discarded after being flensed. Bones from carcasses washed up on shore and remain there today. After 1921, the whaling industry made full use of the carcass and bones, presumably ending contributions to this "molecular archive." Throughout the 61-yr commercial whaling industry at South Georgia, 175,250 whales were killed including 41,525 blue whales, 26,754 humpback whales, and 87,555 fin whales (Headland 1984).

Previously, Sremba et al. (2015) sequenced a fragment of the mtDNA control region from a collection of bones from South Georgia to confirm that species composition is most similar to the catch record from the early years of modern whaling (1905 to 1914). This reflected an initial concentration on the hunting of humpback whales followed by fin and blue whales. Here, we compare pre-whaling diversity of these mtDNA haplotypes from the bones of South Georgia with post-whaling diversity from large-scale studies of post-whaling populations of blue, humpback, and fin whales.

Methods

Data used for post-whaling population comparisons

As no description of post-whaling mtDNA diversity exists for the whales that have returned to South Georgia, we compare our estimates of pre-whaling diversity to sampled populations of blue, humpback, and fin whales elsewhere within the South Atlantic. The comparisons presented here were constrained by the availability of descriptions of diversity in these post-whaling populations. The impact of commercial whaling on the population abundance of the different populations used in the comparisons can be seen in Table 1. We also considered multiple geographic scales for our comparisons where data were available.

As blue whales killed at South Georgia are believed to have been Antarctic blue whales, rather than the less intensively exploited "pygmy" subspecies, *B. musculus brevicauda* (Rojas-Cerda et al. 2022),we compared the pre-whaling mtDNA diversity of blue whale bones to the post-whaling samples from Antarctic blue whales on the Southern Ocean feeding grounds (Table 1). No specific breeding areas have been identified for the Antarctic blue whale and no genetic samples are available from lower latitudes where breeding is assumed to occur. The only description of genetic diversity of the post-whaling population is from the Southern Ocean feeding grounds (Sremba et al. 2012). In our analysis, we consider an ocean-basin scale throughout the Southern Ocean and a regional comparison using Antarctic Feeding Areas I–VI (Donovan 1991) as designated by the International Whaling Commission (IWC). Weak but significant differentiation in mtDNA has been described across these Areas (Sremba et al. 2012; Attard et al. 2016), indicating some degree of population structure.

The humpback whales killed at South Georgia are thought to represent the breeding stock that winters along the coast of Brazil (Breeding Stock A, following IWC terminology). As humpback whales disappeared from South Georgia, until recently (Kennedy et al. 2020), there are no collections of post-whaling samples from these waters. Instead, we compared the humpback whale bones to post-whaling breeding and feeding populations of humpback whales in the South Atlantic, including the breeding population off the coast of Brazil (Zerbini et al. 2006; Engel et al. 2008; Engel and Martin 2009; Cypriano-Souza et al. 2010). As migratory destinations may be changing as the populations recover, we also compared the pre-whaling dataset from South Georgia to a breeding population off the coast of Gabon and to whales feeding off the West Antarctic Peninsula. These are 2 post-whaling populations in the South Atlantic that show migratory connections to other regions (Rosenbaum et al. 2014, Albertson et al. 2017).

As there is little known about the population structure and genetic diversity of fin whales, this comparison was limited to the largest description of post-whaling Southern Hemisphere population collected primarily in Antarctic Area III (0°–70°E) in the southeast Atlantic (Archer et al. 2013).

Validation of "pre-whaling" mtDNA haplotpes

The pre-whaling dataset is represented by blue, humpback, and fin whale bones collected from abandoned whaling stations on South Georgia (Sremba et al. 2015). These whale bones were collected in 2006/07 and identified to species by sequencing the mtDNA control region as described in detail

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

Table 1. Estimates of pre-whaling abundance, minimum population abundance, and population recovery for populations used in the post-whaling comparisons.

	Antarctic blue	95% CL	Brazil (BSA) Humpback	95% CL	Gabon (BSB1) Humpback	95% CL	Southern Hemisphere Fin
Year of pre-exploitation abundance	c. 1900		1830		c. 1900		NA
Pre-exploitation abundance	256,000	235,000 to 307,000	27,193	22,821 to 33,578	18,282	13,345 to 36,452	NA
Year of predicted minimum population abundance	1972		1958		1960		NA
Minimum population abundance	396	235 to 804	440	198 to 1,399	1,510	366 to 6,363	NA
Year of post-whaling abundance from surveys	1998		2012		NA		NA
Post-whaling abundance from surveys	2,280	1,160 to 4,500	20,389		NA		NA
Year of predicted recovery in abundance	NA		2030		2015		NA
References	Branch (2007, 2008)		Bortolotto et al. (2017) and Zerbini et al. (2019)		IWC (2016)		
Year of protection	1966		1963		1963		1986
Generation time (in years)	21.70		14.50		14.50		19.6

"Year of predicted recovery in abundance" refers to the predicted recovery to pre-exploitation abundance (i.e. carrying capacity), as estimated with a population dynamic model use by the IWC. Humpback whale abundance estimates are taken from Zerbini et al. (2019). Antarctic blue whale abundance estimates are from Branch (2008). Generation length estimates are from Taylor et al. (2007). NA indicates that data are not available.

by Sremba et al. (2015). For this initial analysis, species identification was based on relatively short sequences (174 to 194 bp). Here, the sequence lengths have been extended using original chromatograms, sequences and primers in Sremba et al. (2015) to better represent the haplotype diversity. The total sample of 224 bones described by Sremba et al. (2015) included blue whales (n = 18), humpback whales (n = 158), and fin whales (n = 48). The collection of blue whale bones from South Georgia was supplemented by 27 additional bones collected as follows: 7 samples from South Georgia in 2016 and 5 samples from Mikkelson Harbor and Port Lockroy in the West Antarctic Peninsula in 2016 (under permits at OSU), in addition to 2 samples collected from the South Orkney Islands in 2015 and 13 collected from King George Island in the South Shetland islands off the West Antarctic Peninsula in 2017 (under permits at the British Antarctic Survey). The total of 45 blue whale samples represents pre-whaling diversity believed to be from the same time period. A comparison of mtDNA haplotype frequencies supported combining of the datasets, referred to as the pre-whaling population of South Georgia and the Antarctic Peninsula for the remainder of this manuscript.

The additional blue whale samples collected under OSU permits were extracted, amplified, and sequenced using methods and primers described in Sremba et al. (2015). The additional blue whale samples collected under BAS permits were extracted using a modified Dabney et al. (2013) approach. The mtDNA control region was amplified using a Hotstart *Taq* polymerase (Takara *Taq*) with Tpro-whale (Dalebout et al. 2004) and Dlp 5 primers (Dalebout et al. 1998).

The chromatograms of mtDNA control region sequences from the pre-whaling populations were reviewed visually and edited using Sequencher v4 (Gene Codes Corporation). Following guidelines for data quality control (Morin et al. 2010), the quality of each sequence was assessed using Phred scores (Ewing et al. 1998) as analyzed by Sequencher v4. Sequences reporting more than 10% of base pairs with a Phred score of <20 were re-sequenced or excluded from the final dataset. For each species, the pre-whaling mtDNA control region haplotypes were trimmed to the longest consensus length possible, given the limitations of amplifying fragmented DNA often found in degraded historical samples. The mtDNA haplotypes found in the post-whaling samples were trimmed to the consensus sequence length of the pre-whaling sequences. A mtDNA haplotype described by only 1 sample was re-sequenced to verify its identity.

Validation of "post-whaling" mtDNA haplotypes

The post-whaling datasets of Antarctic blue, South Atlantic humpback, and Southern Ocean fin whale were compiled from published sources and internal databases at the Cetacean Conservation and Genomics Laboratory at Oregon State University (Table 2; Engel et al. 2008; Rosenbaum et al. 2009; Sremba et al. 2012; Archer et al. 2013; Cypriano-Souza et al. 2017; Steel et al. 2018). The geographical relationship of pre- and post-whaling samples of populations used in this study can be seen in Fig. 1.

The post-whaling diversity of Antarctic blue whales is represented by published sequences of 183 samples collected from the contemporary population in the Southern Ocean (Sremba et al. 2012). The post-whaling diversity of humpback whales is represented by published mtDNA sequences from 158 samples collected from individuals in a breeding population off the coast of Brazil (BSA) (Engel et al. 2008; Rosenbaum et al. 2009; Cypriano-Souza et al. 2017), 466 individuals from a breeding population off the coast of Gabon (BSB1, Rosenbaum et al. 2009), and 64 individuals from a feeding population from the Antarctic Peninsula (AP, Steel et al. 2018). The post-whaling diversity of fin whales is

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

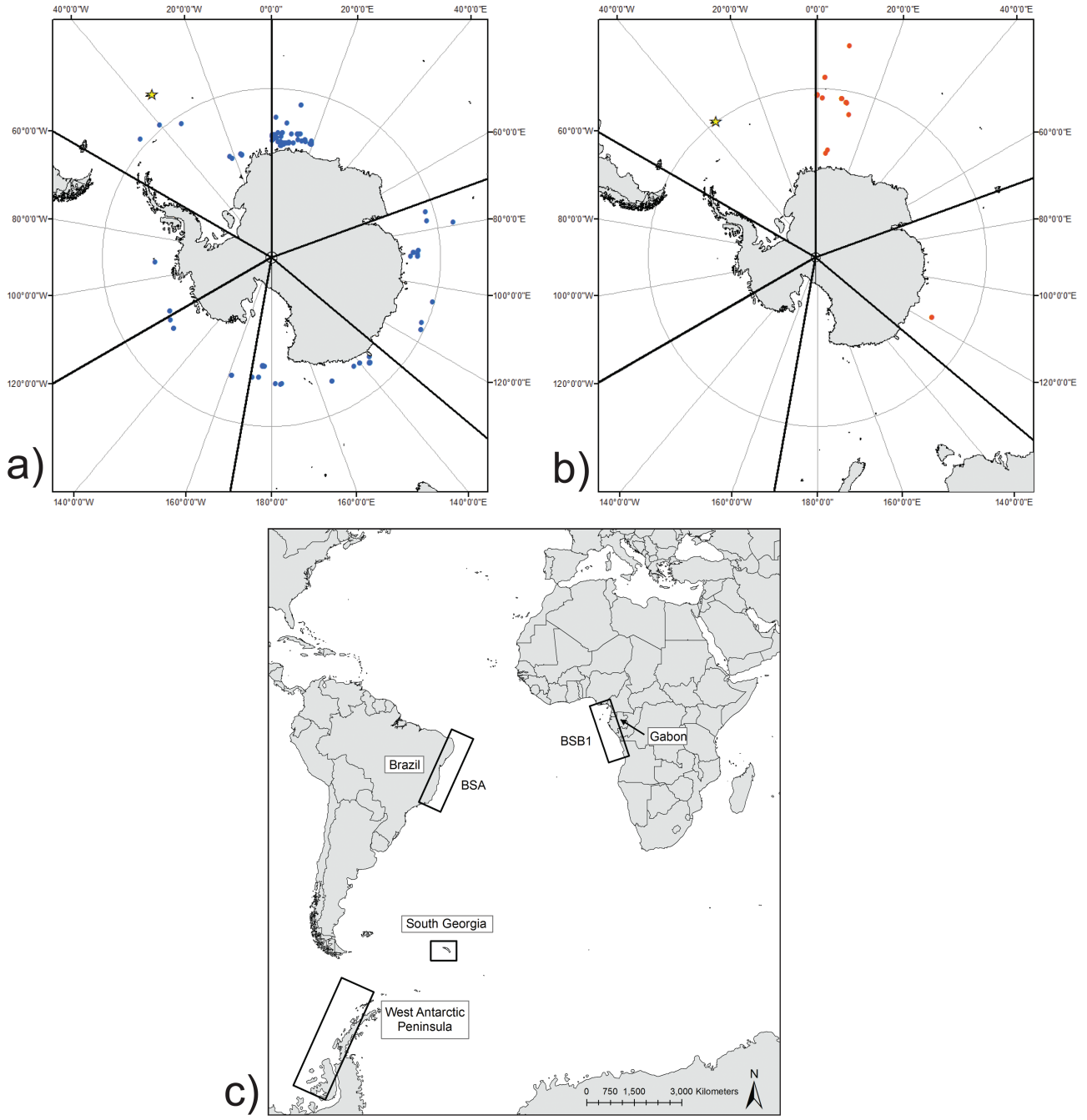

Fig. 1. Locations of post-whaling samples of a) blue whales, b) fin whales, and c) humpback whales in relation to pre-whaling population of South Georgia (denoted by star in a and b). Regional populations of blue and fin whales as recognized by the IWC management Areas I–VI marked in darker lines (Area I 120°W to 60°W, Area II 60°W to 0°, Area III 0° to 70°E, Area IV 70°E to 130°E, Area V 130°E to 170°W, and Area VI 170°W to 120°W).

represented by published sequences of mtDNA collected from this species primarily in Area III (0°–70°E) of the Southern Ocean (Archer et al. 2013).

Test of loss or change in mtDNA diversity

We first tested for a change in haplotype or nucleotide diversity in the post-whaling populations or, where available, regional populations in the South Atlantic. Haplotype and nucleotide diversities were calculated for each population in Arlequin v3.5 (Excoffier et al. 2005). To assess a loss of mtDNA diversity over time, we tested for a reduced haplotype or nucleotide diversity in the post-whaling population using a permutation procedure in R (genetic_diversity_diffs v1.0.3; R Core Team 2015; Wickham 2015; Alexander 2017).

We also examined the loss of "rare" haplotypes by comparing pre-whaling haplotypes to haplotypes found in the post-whaling population. Shared and unshared haplotypes were identified through a comparison of the identity of the mtDNA haplotypes described in the pre- and post-whaling populations on a global and regional scale. Haplotypes in the pre-whaling South Georgia populations, which were not found in the post-whaling samples, were submitted for a BLAST search of the worldwide collection of peer-reviewed post-whaling sequences on GenBank.

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

Table 2. Estimates of mtDNA diversity in the pre- and post-whaling Antarctic blue, South Atlantic humpback, and Southern Ocean fin whale populations.

Species	Population	*n*	bp	Haplotypes	cnbp	Haplotypes	Haplotype diversity	Nucleotide diversity
Antarctic blue whale	South Georgia and Antarctic Peninsula	45	–	–	343	39	0.994 ± 0.0060	2.33 ± 0.0123%
	Southern Ocean[a]	183	410	52	343	52	0.969 ± 0.0038	1.67 ± 0.0089%
South Atlantic humpback whale	South Georgia	158	–	–	278	64	0.963 ± 0.0079	3.19 ± 0.016%
	Brazil[b,c,d]	158	464	54	278	51	0.971 ± 0.0044	3.24 ± 0.0166%
	Gabon[c]	466	486	100	278	87	0.971 ± 0.0027	3.25 ± 0.0166%
	Antarctic Peninsula[e]	64	470	22	278	21	0.926 ± 0.0170	2.99 ± 0.016%
Southern Hemisphere fin whale	South Georgia	49	–	–	288	34	0.984 ± 0.0072	1.50 ± 0.0084%
	Southern Hemisphere[f]	46	412	41	288	38	0.991 ± 0.0066	1.68 ± 0.0093%

Reference populations, mtDNA control sequence length (bp) and original haplotypes described are indicated in addition to consensus sequence length used in this study (cnbp) and number of haplotypes at the consensus length for each population. Haplotype and nucleotide diversities for pre- and post-whaling population based on the consensus sequence length are listed for each population.
[a]Sremba et al. (2012).
[b]Engel et al. (2008).
[c]Rosenbaum et al. (2009).
[d]Cypriano et al. (2017).
[e]Olavarria et al. (2007) Steel et al. (2018) and internal CCGL databases.
[f]Archer et al. (2013).

To test the extent of potential haplotype loss, a rarefaction approach was used to estimate whether the number of haplotypes identified in the pre-whaling population was greater than the post-whaling population, taking into account differences in sample size. Rarefaction analyses were implemented in the R package *Sprex* (Archer 2016). For this, we calculated the expected number of haplotypes for both the pre- and post-whaling samples using the haplotype frequency distributions, where the larger sample size was rarefied to match the smaller sample size. We calculated an unconditional variance for both the pre- and post-whaling samples from the haplotype frequency distribution, with the Chao1 estimator used to calculate the number of unsampled haplotypes (Chao 1984; Colwell et al. 2012). A lack of overlap of 95% confidence intervals was interpreted as a significant difference at $P < 0.05$ (Colwell et al. 2012). The difference in the number of haplotypes was interpreted as the potential loss of lineages as a result of the exploitation bottleneck (Allendorf 1986).

Finally, we tested for a significant differentiation in haplotype and nucleotide diversities between the pre-whaling bone samples and those from the post-whaling samples of regional populations using conventional pairwise F_{ST} and ϕ_{ST} analyses performed in Arlequin v.3.5 (Excoffier et al. 2005).

Results

Blue whale pre-whaling diversity

The mtDNA diversity of the pre-whaling samples of blue whales from South Georgia was described from 18 bones collected in 2006/07 as reported in Sremba et al. (2015) and an additional 27 bone samples collected from other regions of the Antarctic. For the Sremba et al. (2015) samples, the extension of sequences to a length of 343 bp did not further resolve any of the 16 described haplotypes. The additional 27 bone samples added a further 23 haplotypes with a final dataset of 45 pre-whaling blue whales represented by 39 haplotypes at 343 bp. A comparison of the South Georgia and Antarctic mtDNA haplotype frequencies showed they were not significantly different ($P = 0.20$), supporting combining the 2 pre-whaling sampling locations for downstream analysis. These pre-whaling samples were characterized by a high haplotype and nucleotide diversity ($h = 0.994$, $\pi = 2.33\%$, Table 2).

Blue whale post-whaling diversity

At the 343 bp consensus sequence, the sample of 183 post-whaling Antarctic blue whales in the global Southern Ocean population resolved to the same 52 haplotypes described previously (Sremba et al. 2012), i.e. the shorter length available for the bones did not collapse any of the haplotypes resolved previously from the 410 bp sequences available from the post-whaling samples. The post-whaling Antarctic blue whale samples were also characterized by a relatively high haplotype diversity, but a lower nucleotide diversity ($h = 0.969$, $\pi = 1.67\%$, Table 2).

Loss of mtDNA diversity or identity in the blue whale?

Despite the relatively high diversity of the post-whaling samples, the permutation procedure showed a significant loss of both haplotype and nucleotide diversities in the post-whaling population (10,000 simulations, $P < 0.05$), compared with the pre-whaling samples from South Georgia and the Antarctic Peninsula. A comparison of mtDNA haplotype identity between the pre- and post-whaling samples of Antarctic blue whales also suggested a loss in the number of these lineages. Only 11 haplotypes were shared between pre- and post-whaling samples (Table 3), i.e. 28 pre-whaling haplotypes were not found in the post-whaling samples of the Antarctic. A BLAST search of GenBank identified a match to 1 additional haplotype, first described in the eastern South Pacific and since found in the North Pacific (Hap q, LeDuc et al. 2007). After accounting for this match, there were 27 haplotypes found only in the pre-whaling samples (GenBank search July 2023).

This potential loss of haplotype identity in the post-whaling samples was quantified by the rarefaction analysis. Here, the pre-whaling estimate of haplotypes (39 ± 1.52)

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

Table 3. The number of individuals (*n*), sequence length (bp), number of haplotypes (*H*) described in the pre-whaling South Georgia and post-whaling Antarctic blue, South Atlantic humpback, and Southern Ocean fin whale populations.

Species	Population	*n*	bp	*H*	*H* shared	F_{ST}
Antarctic blue whale	South Georgia and Antarctic Peninsula	45	343	39	–	–
	Southern Ocean	183	343	52	11	0.0107 *P* = 0.003
South Atlantic humpback whale	South Georgia	158	278	64	–	–
	Brazil	158	278	51	22	0.012 *P* < 0.005
	Gabon	466	278	87	27	0.007 *P* < 0.005
	Antarctic Peninsula	64	278	21	4	0.043 *P* < 0.005
Southern Hemisphere fin whale	South Georgia	49	288	34	–	–
	Southern Ocean	46	288	38	13	<0.001 *P* = 0.385

Pre-whaling populations are highlighted in gray. The number of haplotypes shared (*H* shared) between the pre-whaling population of South Georgia and each post-whaling population and genetic differentiation as measured by F_{ST} is listed.

was significantly greater than the estimate from the circumpolar post-whaling samples (26.77 ± 0.63). The difference in haplotype estimates was even greater when pre-whaling samples were compared only to post-whaling samples from Areas II and III in the South Atlantic (*n* = 110, hap = 38). Here, the rarefied estimate of post-whaling samples was 24.05 (±0.69), suggesting a 40% loss in the number of surviving maternal lineages.

Finally, the pre-whaling samples showed significant differentiation in haplotype frequencies (F_{ST} = 0.011, *P* = 0.003; ϕ_{ST} = 0.019, *P* = 0.006) in comparison to the circumpolar post-whaling samples (Table 3). This effect was also evident in pairwise comparisons of the pre-whaling samples from the IWC management Areas, showing significant differentiation in haplotype frequency with Areas II, III, IV, V, and VI (*P* < 0.05, Fig. 1, Table 4).

Humpback whale pre-whaling diversity

The pre-whaling population of humpback whales from South Georgia was represented by 158 bone samples. From a consensus sequence length of 278 bp of the mtDNA control region, a total of 64 haplotypes were resolved. Like the pre-whaling samples of blue whales, this sample showed high haplotype and nucleotide diversities (*h* = 0.963, π = 3.19%, Table 2).

Humpback whale post-whaling diversity

The post-whaling populations of humpback whales in the South Atlantic were represented by a large number of samples and haplotypes at a consensus length of 278 bp, with a total of 688 individuals and 109 resolved haplotypes. There was also a large number of haplotypes identified in each of the regional samples (Table 3). The wintering grounds populations of Brazil and Gabon presented the highest haplotype and nucleotide diversities (*h* = 0.971, π = 3.24%; *h* = 0.971, π = 3.25%, respectively) (Table 2). The Antarctic Peninsula feeding ground population (associated with breeding grounds in Colombia and Ecuador) was characterized by a lower haplotype and nucleotide diversity Atlantic (*h* = 0.926, π = 2.99%) in comparison to the post-whaling breeding populations in the South.

Loss of mtDNA diversity or identity in the humpback whale?

There was no measurable loss of haplotype or nucleotide diversity in the post-whaling wintering populations of Brazil and Gabon, in comparison to the pre-whaling South Georgia population (10,000 simulations; Brazil haplotype diversity *P* = 0.171, nucleotide diversity *P* = 0.678; Gabon haplotype diversity *P* = 0.121, nucleotide diversity *P* = 0.497, Table 2 lists the haplotype and nucleotide diversities being compared). The post-whaling feeding population in the Antarctic Peninsula was characterized by a significantly lower haplotype diversity than South Georgia (*P* < 0.001) but not nucleotide diversity (*P* = 0.164, Table 2 lists the haplotype and nucleotide diversities being compared).

In a comparison of haplotype identity of the pre-whaling South Georgia population to the post-whaling breeding populations, 22 haplotypes were shared with Brazil, 27 were shared with Gabon, and 4 were shared with the post-whaling feeding population of the West Antarctic Peninsula (Table 3). A total of 33 of the 64 haplotypes described at South Georgia were not found in either Brazil or Gabon or the Antarctic Peninsula (Table 3). A BLAST search of all worldwide records of mtDNA control region sequences from humpback whales on GenBank failed to find an identical match for 25 of the haplotypes from South Georgia (GenBank search July 2023). Two additional matches were found with unpublished internal data in the CCGL, resulting in 23 mtDNA control region haplotypes from South Georgia that did not match any previously defined haplotype.

A loss of rare mtDNA lineages was also suggested by the rarefaction analysis. Brazil was estimated to have a significantly lower number of haplotypes in the post-whaling population in comparison to South Georgia (Brazil, 51 ±

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

Table 4. Regional comparison of mtDNA diversity in the Antarctic blue whale.

	I	II	III	IV	V	VI	SG+
	***n* = 4**	***n* = 10**	***n* = 100**	***n* = 20**	***n* = 39**	***n* = 11**	***n* = 45**
I		0.0214	0.0789	0.0000	0.0347	0.0118	0.0000
		0.3546	*0.0916*	*0.6275*	*0.2419*	*0.4032*	*0.8163*
II	0.0525		0.0000	0.0402	0.0013	0.0252	0.0000
	0.1710		*0.5561*	*0.1241*	*0.4035*	*0.2865*	*0.6397*
	0.1703						
III	0.0224	**0.0326**		**0.0489**	0.0024	**0.0436**	**0.0296**
	0.2029	***0.0337***		***0.0060***	*0.3084*	***0.0487***	***0.0022***
	0.0137	0.0750					
IV	0.0355	0.0534	**0.0274**		**0.0420**	0.0569	0.0034
	0.2623	*0.0263*	***0.0069***		***0.0278***	*0.0626*	*0.3369*
	0.2281	0.0513	**0.0106**				
V	0.0136	**0.0519**	**0.0236**	**0.0213**		0.0079	**0.0221**
	0.3123	***0.0109***	***0.0003***	***0.0459***		*0.3050*	***0.0208***
	0.1337	**0.0100**	***P* < 0.001**	**0.0405**			
VI	0.0318	**0.0816**	**0.0582**	0.0386	0.0128		0.0249
	0.2839	***0.0115***	***0.0024***	*0.0560*	*0.2113*		*0.1210*
	0.1897	**0.0129**	***P* < 0.001**	0.1571	0.2094		
SG+	0.0000	**0.0284**	**0.0159**	**0.0213**	**0.0237**	**0.0426**	
	0.7177	***0.0076***	***0.0007***	***0.0040***	***P < 0.0001***	***0.0001***	
	0.7514	0.6668	***P* < 0.001**	0.2336	**0.0004**	0.0639	

IWC management Areas I–VI are compared with the pre-whaling population of South Georgia and the Antarctic Peninsula (SG+). Sample sizes are listed below each Area. F_{ST} is listed below the diagonal and ϕ_{ST} is listed above; permutation *P*-value listed below test statistic in italics. Exact test *P*-value is listed below permutation *P*-value and significant differentiation between populations is denoted in bold. Area I sample size is too low to be considered for the statistical analysis but is included for completeness.

0.51; South Georgia 64 ± 0.83). The post-whaling population of Gabon also presented a significantly lower estimate of haplotypes (Gabon 57.33 ± 0.71). However, when post-whaling samples from the South Atlantic were combined (i.e. Brazil and Gabon), the rarefied estimate of haplotypes (75.63 ± 0.73) was greater than that for South Georgia.

The pre-whaling South Georgia haplotypes were significantly different from each of the post-whaling populations off Brazil, Gabon, and the Antarctic Peninsula (F_{ST} see Tables 3 and 5). However, when the molecular distance between the haplotypes was taken into account, the pre-whaling samples were not different to the post-whaling samples from populations off either Brazil or Gabon, but were significantly different from the Antarctic Peninsula (ϕ_{ST} = 0.050, P < 0.005, Table 5).

Fin whale pre-whaling diversity

The mtDNA diversity of the pre-whaling samples of fin whales was represented by DNA from 49 whale bone samples. The 288 bp consensus sequence length resolved 34 mtDNA control region haplotypes compared with the 20 reported in Sremba et al. (2015). The pre-whaling South Georgia fin whale population was characterized by a haplotype diversity even higher than that of blue or humpback whales (h = 0.984, π = 1.50%, Table 2).

Fin whale post-whaling diversity

The post-whaling population was represented by 46 individual fin whales sampled from primarily Area III in the Southern Ocean (0°–70°E). A total of 38 haplotypes were identified among the post-whaling sequences at 288 bp, collapsing 3 haplotypes described at 412 bp by Archer et al. (2013). The post-whaling fin whale population was also characterized by a high haplotype diversity (h = 0.991, π = 1.68%, Table 2).

Loss of mtDNA diversity or identity in the fin whale?

The pre-whaling South Georgia fin whale population and post-whaling fin whale population did not differ in haplotype or nucleotide diversity (10,000 simulations, P = 0.148 and 0.233, respectively). A total of 13 haplotypes were shared between the 2 populations (Table 3), resulting in 21 haplotypes unique to South Georgia. Three additional haplotype matches to haplotypes described in the eastern South Pacific (Pérez-Alvarez et al. 2021; Kraft et al. 2023) were found in a GenBank search (July 2023), this resulted in 18 South Georgia haplotypes not found in any previously described population. The Southern Hemisphere post-whaling population presented a larger number of haplotypes (38 ± –1.46) than the pre-whaling population of South Georgia (32.57 ± 1.17). The pre-whaling South Georgia fin whale population and post-whaling fin whale population were not significantly different in a comparison of mtDNA haplotype frequencies between the populations (F_{ST} = 0.001, P = 0.385; ϕ_{ST} = 0.000, P = 0.462) (Table 3).

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

Table 5. Genetic differentiation of pre-whaling samples from humpback whales taken in South Georgia (SG) and post-whaling samples from populations in the South Atlantic (Brazil, Gabon) and the Antarctic Peninsula.

	South Georgia	Brazil	Gabon	Antarctic Peninsula
	n **= 158**	***n*** **= 158**	***n*** **= 466**	***n*** **= 64**
South Georgia	–	0.004	0.001	**0.050**
		P = 0.110	*P* = 0.200	***P*** **< 0.005**
Brazil	**0.012**	–	0.007	**0.063**
	P **< 0.005**		*P* = 0.017	***P*** **< 0.005**
Gabon	**0.007**	**0.007**	–	**0.049**
	P **< 0.005**	***P*** **< 0.005**		***P*** **< 0.005**
Antarctic Peninsula	**0.043**	**0.046**	**0.043**	–
	P **< 0.005**	***P*** **< 0.005**	***P*** **< 0.005**	

F_{ST} is listed below the diagonal and ϕ_{ST} is listed above with levels of *P* significance shown beneath value. Significant differentiation between populations is listed in bold.

Discussion

High levels of historical and contemporary mtDNA diversity

The pre-whaling populations of blue, humpback, and fin whales, represented by the bone samples from South Georgia and the Antarctic Peninsula, were characterized by a high diversity of mtDNA haplotypes. Despite a history of intense exploitation, the post-whaling populations of blue whales, South Atlantic humpback whales, and Southern Ocean fin whales were also characterized by relatively high diversity of haplotypes. This relatively high genetic diversity in post-whaling populations of exploited whales has been noted previously, and attributed to the longevity of these species and the short duration of exploitation. The loss of haplotype diversity during a population bottleneck is dependent on the duration of the bottleneck, in relation to the generation time of the species, and the population size at the time of the bottleneck (Nei et al. 1975; Allendorf and Luikart 2013). Modern whaling of humpback, blue, and fin whales in the Southern Hemisphere was concentrated in the first half of the 20th century and was mostly over by the 1960s (Rocha et al. 2014). The Antarctic blue whale, the longest lived species of the 3 included in this study (Taylor et al. 2007), was protected in 1966. Compared with the long-generation spans of great whales (Taylor et al. 2007; Jackson et al. 2015), this period of exploitation was of relatively short duration. The population size at the exploitation bottleneck may also have been larger than previously assumed. Historical reconstructions of minimum abundance at the time of the bottleneck suggest that several hundred individuals may have survived commercial whaling (Table 1).

A loss of haplotype identity

A more sensitive measure of a genetic bottleneck is a loss of rare haplotypes, rather than haplotype diversity, which is influenced by both the frequencies, as well as the identity of haplotypes (Allendorf 1986). Here, we detected mtDNA haplotypes, or maternal lineages, in the pre-whaling samples that were not identified in the post-whaling populations of the Antarctic blue, South Atlantic humpback, and Southern Ocean fin whale, nor in a search of GenBank representing worldwide populations. The rarefaction analyses indicated a loss of mtDNA lineages and identified a larger number of haplotypes in the pre-whaling samples from South Georgia in comparison to post-whaling samples of blue whales in the Southern Ocean and post-whaling wintering populations of humpback whales in the South Atlantic. Evidence was more equivocal for a loss of haplotypes in the post-whaling samples of fin whales, which may be due to a limited sample sizes and high diversity in both time periods.

A loss of local subpopulations?

In the absence of post-whaling samples from the surviving South Georgia populations, a significant difference may be due to random genetic drift (diversity lost at a quicker rate due to exploitation), loss of overall diversity due to exploitation or due to change in population structure as a result of a local extirpation of a population unit (Clapham et al. 2008). The loss of diversity in the post-whaling samples of blue and humpback whales could be explained by a loss of individual haplotypes, as populations of all 3 species population abundance declined due to hunting throughout the Southern Hemisphere. Alternatively, but not exclusively, the differentiation of pre-whaling samples from South Georgia and those from post-whaling populations could be due to a loss of local fidelity to a historically important feeding area or subpopulation.

The number of whales sighted around South Georgia remained low for several decades after whaling (Moore et al. 1999; Richardson et al. 2012), suggesting that local subpopulations were extirpated by the intensive commercial whaling industry. A loss of cultural memory or maternal fidelity to the South Georgia feeding area could have contributed to the slow of return of these whales to South Georgia, even as their numbers have increased elsewhere (Clapham et al. 2008). This pattern now seems to be changing and the most recent surveys of South Georgian waters report a rapid increase in the number of blue and humpback whales (Calderan et al. 2020).

The importance of maternal fidelity in structuring the recovery of whale populations is further suggested by the strong differentiation of the pre-whaling samples of humpback whales from South Georgia, with those from the post-whaling samples of the feeding grounds of the Western Antarctic Peninsula. While occasional movements between these areas have been reported with photo-ID (Marcondes et al. 2021), our study and previous genetic evidence indicate that there is very limited migratory exchange between the

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

Western Antarctic Peninsula and the South Atlantic population of humpback whales (Engel et al. 2008; Cypriano-Souza et al. 2017), despite the proximity of these feeding areas.

Fin whale diversity and haplotype identity

Evidence for a loss in diversity or identity of fin whales was the most equivocal of the 3 species. Despite the intensity of hunting of this species, the mtDNA diversity of the pre-whaling samples from South Georgia did not differ from the post-whaling samples of fin whales representing Area III in the Southern Ocean. However, only 13 of the 34 pre-whaling haplotypes were shared with the post-whaling population, with 53% of the pre-whaling haplotypes found to be exclusive to South Georgia. Little is known about the post-whaling Southern Hemisphere fin whale population distribution and population structure. A recent genetic study did not find evidence of Southern Hemisphere-wide structuring within fin whales (Pérez-Alvarez et al. 2021), suggesting that Area III samples may be representative of the broader contemporary population. However, further sampling of this species in the Southern Hemisphere is needed to evaluate the potential for local or circumpolar loss of lineages.

Conclusion

Given that migratory destinations are influenced by early maternal experience in baleen whales, a local extirpation may have led to a cultural loss of known feeding areas and migratory routes within the wider distribution of each species (Clapham et al. 2008). The slow return of great whales in the large numbers that were once present suggests a loss of local memory of South Georgia as an important feeding ground or subpopulations from South Georgia. Such a loss is also consistent with the analyses of pre- and post-whaling mtDNA diversity presented here, especially for the humpback and blue whales. However, South Georgia remains a productive habitat and sightings of some species are increasing (Calderan et al. 2020; Jackson et al. 2020). This provides the opportunity to document the natural reestablishment of these former feeding grounds, similar to what has been documented for the southern right whale around New Zealand (Carroll et al. 2011). It is important to continue sampling these populations to monitor recovery and to determine whether the recovering populations are a remnant of the pre-whaling South Georgia populations or representative of a rediscovery and recolonization of this productive feeding habitat.

Acknowledgments

Bone samples were collected by Oregon State University under permit 2016-008 from the Government of South Georgia and the South Sandwich Islands, and permit 2016-006 under the Antarctic Conservation Act. Support for collecting samples came from the National Geographic/Lindblad Expeditions Conservation Fund. ALS and CSB would like thank R. Pitman for assistance with bone collection.

Funding

Funding for this research was provided by a grant from the International Whaling Commission, Southern Ocean Research Partnership [to ALS, CSB, and JAJ], and a Mamie Markham Research award [to ALS]. Bones from South Georgia were collected by the British Antarctic Survey specimens from South Georgia were collected under permits Regulated Activity Permit 2016-009 issued by the Government of South Georgia and the South Sandwich Islands. Laboratory analyses of samples collected by the British Antarctic Survey were funded by an NERC-Cambridge ESS Doctoral Training Partnership from the Natural Environment Research Council (NE/L002507/1 to DLB). Projeto Baleia Jubarte was sponsored by Petróleo Brasileiro S.A. (PETROBRAS).

Conflict of interest statement. None declared.

Data availability

The primary data underlying these analyses have been deposited in Dryad: doi:10.5061/dryad.mkkwh715j.

References

Albertson GR, Friedlaender AS, Steel DJ, Aguayo-Lobo A, Bonatto SL, Caballero S, Constantine R, Cypriano-Souza AL, Engel MH, Garrigue C, et al. Temporal stability and mixed-stock analyses of humpback whales (*Megaptera novaeangliae*) in the nearshore waters of the Western Antarctic Peninsula. *Polar Biol*. 2017:41:323–340.

Alexander A. *genetic_diversity_diffs v1.0.3*. 2017 [accessed 2021 Apr]. https://github.com/laninsky/genetic_diversity_diffs

Allendorf FW. Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biol*. 1986;5:181–190.

Allendorf FW, Luikart G. *Conservation and the genetics of populations*. Malden (MA): Blackwell Publications; 2013.

Alter ES, Newsome SD, Palumbi SR. Pre-whaling genetic diversity and population ecology in eastern Pacific gray whales: insights from ancient DNA and stable isotopes. *PLoS One*. 2012a:7:e35039.

Alter ES, Rosenbaum HC, Postma LD, Whitridge P, Gaines C, Weber D, Egan MG, Lindsay M, Amato G, Dueck L, et al. Gene flow on ice: the role of sea ice and whaling in shaping Holarctic genetic diversity and population differentiation in bowhead whales (*Balaena mysticetus*). *Ecol Evol*. 2012b:2:2895–2911.

Amos B. Levels of genetic variability in cetacean populations have probably changed little as a result of human activities. *Report of the International Whaling Commission* 46. 1996. p. 657–658.

Archer FI. *sprex: species richness and extrapolation v. 1.4.2*. 2016 [accessed 2021 Apr]. https://github.com/EricArcher/sprex

Archer FI, Morin PA, Hancock-Hanser BL, Robertson KM, Leslie MS, Bérubé M, Panigada S, Taylor BL. Mitogenomic phylogenetics of fin whales (*Balaenoptera physalus*): genetic evidence for revision of subspecies. *PLoS One*. 2013;8:e63396.

Attard CR, Beheregara LB, Möller LM. Towards population-level conservation in the critically endangered Antarctic blue whale: the number and distribution of their populations. *Sci Rep*. 2016;6:22291.

Baker CS, Patenaude NJ, Bannister JL, Robins J, Kato H. Distribution and diversity of mtDNA lineages among southern right whales (*Eubalaena australis*) from Australia and New Zealand. *Mar Biol*. 1999;134:1–7.

Baker CS, Perry A, Bannister JL, Weinrich MT, Abernethy RB, Calambokidis J, Lien J, Lambertsen RH, Urban Ramirez J, Vasquez O, et al. Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proc Natl Acad Sci U S A*. 1993;90:8239–8243.

Borge T, Bachmann L, Bjørnstad G, Wiig O. Genetic variation in Holocene bowhead whales from Svalbard. *Mol Ecol*. 2007;16:2223–2235.

Bortolotto GA, Danilewicz D, Hammond PS, Thomas L, Zerbini AN. Whale distribution in a breeding area: spatial models of habitat use and abundance of western South Atlantic humpback whales. *Mar Ecol Prog Ser*. 2017;585:213–227.

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

Branch TA. Abundance of Antarctic blue whales south of 60°S from three complete circumpolar sets of surveys. *J Cetacean Res Manag*. 2007;9:87–96.

Branch TA. Current status of Antarctic blue whales based on Bayesian modeling. *Report (SC/60/SH7) to the Scientific Committee of the International Whaling Commission, available on request from the Secretariat International Whaling Commission, The Red House, 135 Station Road, Impington, Cambridge, Cambridgeshire CB24 9NP, UK*. 2008

Branch TA, Allison C, Mikhalev YA, Tormosov D, Brownell JRL. Historical catch series for Antarctic and pygmy blue whales. *Report (SC/60/SH9) to the Scientific Committee of the International Whaling Commission*. 2008.

Calderan SV, Black A, Branch TA, Collins MA, Kelly N, Leaper R, Lurcock S, Miller BS, Moore M, Olson PA, et al. South Georgia blue whales five decades after the end of whaling. *Endanger Species Res*. 2020;43:359–373.

Carroll E, Patenaude N, Alexander A, Steel D, Harcourt R, Childerhouse S, Smith S, Bannister J, Constantine R, Baker C. Population structure and individual movement of southern right whales around New Zealand and Australia. *Mar Ecol Prog Ser*. 2011;432:257–268.

Chao A. Nonparametric estimation of the number of classes in a population. *Scand J Stat*. 1984;11:265–270.

Clapham PJ, Young S, Brownell BRL Jr. Baleen whales: conservation issues and the status of the most endangered populations. *Mammal Rev*. 1999;29:35–60.

Clapham PJ, Aguilar A, Hatch LT. Determining spatial and temporal scales for management: lessons from whaling. *Mar Mammal Sci*. 2008;24:183–201.

Colwell RK, Chao A, Gotelli NJ, Lin S-Y, Mao CX, Chazdon RL, Longino JT. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J Plant Ecol*. 2012;5:3–21.

Cypriano-Souza AL, Engel MH, Caballero S, Olavarría C, Flórez-González L, Capella J, Steel D, Sremba A, Aguayo A, Thiele D, et al. Genetic differentiation between humpback whales (*Megaptera novaeangliae*) from Atlantic and Pacific breeding grounds of South America. *Mar Mammal Sci*. 2017;33:457–479.

Cypriano-Souza AL, Fernandex GP, Lima-Rosa CAV, Engel MH, Bonatto SL. Microsatellite genetic characterization of the humpback whale (*Megaptera novaeangliae*) breeding ground off Brazil (Breed Stock A). *J Hered*. 2010;101:189–200.

Dabney J, Knapp M, Glocke I, Gansauge M-T, Weihmann A, Nickel B, Valdiosera C, García N, Pääbo S, Arsuaga J-L. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc Natl Acad Sci U S A*. 2013;110:15758–15763.

Dalebout ML, Baker CS, Mead JG, Cockcroft VG, Yamada TK. A comprehensive and validated molecular taxonomy of beaked whales, family Ziphiidae. *J Hered*. 2004;95:459–473.

Dalebout ML, Van Hleden A, Van Waerebeek K, Baker CS. Molecular genetic identification of southern hemisphere beaked whales (Cetacea: Ziphiidae). *Mol Ecol*. 1998;7:687–694.

Donovan GP. A review of IWC stock boundaries. *Report of the International Whaling Commission (Special Issue 13)*. 1991. p. 39–68.

Engel MH, Fagundes NJR, Rosenbaum HC, Leslie MS, Ott PH, Schmitt R, Secchi E, Rosa LD, Bonatto SL. Mitochondrial DNA diversity of the Southwestern Atlantic humpback whale (*Megaptera novaeangliae*) breeding area off Brazil, and the potential connections to Antarctic feeding areas. *Conserv Genet*. 2008;9:1253–1262.

Engel MH, Martin AR. Feeding grounds of the western South Atlantic humpback whale population. *Mar Mammal Sci*. 2009;25:964–969.

Ewing B, Hillier L, Wedl MC, Green P. Base-calling of automated sequencer traces using *Phred*. I. Accuracy assessment. *Genome Res*. 1998;8:175–185.

Excoffier L, Laval G, Schneider S. Arlequin ver 3.0: an integrated software package for population genetics data analysis. *Evol Bioinform Online*. 2005;1:47–50.

Headland R. *The Island of South Georgia*. New York: Cambridge University Press; 1984.

IWC. Annex H: report of the Sub-Committee on Other Southern Hemisphere Stocks (SH). *J Cetacean Manag*. 2016;17:250–282.

Jackson JA, Kennedy A, Moore M, Andriolo A, Bamford CCG, Calderan S, Cheeseman T, Gittins G, Groch K, Kelly N, et al. Have whales returned to a historical hotspot of industrial whaling? The pattern of southern right whale *Eubalaena australis* recovery at South Georgia. *Endanger Species Res*. 2020;43:323–339.

Jackson J, Ross-Gillespie R, Butterworth D, Findlay K, Holloway S, Robbins J, Rosenbaum H, Weinrich M, Baker CS, Zerbini A. Southern Hemisphere Humpback Whale Comprehensive Assessment. *A synthesis and summary: 2005–2015. Report (SC/66a/SH3) to the Scientific Committee of the International Whaling Commission*. 2015.

Jackson JA, Steel DJ, Beerli P, Congdon BC, Olavarría C, Leslie MS, Pomilla C, Rosenbaum H, Baker CS. Global diversity and oceanic divergence of humpback whales (*Megaptera novaeangliae*). *Proc R Soc B Biol Sci*. 2014;281:20133222.

Kennedy A, Carroll E, Baker CS, Bassoi M, Buss D, Collins MA, Calderan S, Ensor P, Fielding S, Leaper R, et al. Whales return to the epicentre of whaling? Preliminary results from the 2020 cetacean survey at South Georgia (Islas Georgias del Sur). *Report SC/68B/CMP/22 to the Scientific Committee of the International Whaling Commission*. 2020.

Kraft S, Rodríguez F, Olavarría C, Poulin E, Pérez-Álvarez MJ. Genetic analysis as a tool to improve the monitoring of stranded cetaceans in Chile. *Biology (Basel)*. 2023;12:748.

LeDuc RG, Dizon MG, Pastene LA, Kato H, Nishiwaki S, LeDuc CA, Brownell RL Jr. Patterns of genetic variation in Southern Hemisphere blue whales and the use of assignment test to detect mixing on the feeding grounds. *J Cetacean Res Manag*. 2007;9:73–80.

Malik S, Brown MW, Kraus SD, White BN. Analysis of mitochondrial DNA diversity within and between North and South Atlantic right whales. *Mar Mammal Sci*. 2000;16:545–558.

Marcondes MCC, Cheeseman T, Jackson JA, Friedlaender AS, Pallin L, Olio M, Wedekin LL, Daura-Jorge FG, Cardoso J, Santos JDF, et al. The Southern Ocean Exchange: porous boundaries between humpback whale breeding populations in southern polar waters. *Sci Rep*. 2021;11:23618.

Moore MJ, Berrow SD, Jensen BA, Carr P, Sears R, Rowntree VJ, Payne R, Hamilton PK. Relative abundance of large whales around South Georgia (1979–1998). *Mar Mammal Sci*. 1999;15:1287–1302.

Morin PA, Martien KK, Archer FI, Cipriano F, Steel D, Jackson J, Taylor B. Applied conservation genetics and the need for quality control and reporting of genetic data used in fisheries and wildlife management. *J Hered*. 2010;101:1–10.

Nei M, Maruyama T, Chakrabort R. The bottleneck effect and genetic variability in populations. *Evolution*. 1975:29:1–10.

Olavarria C, Baker CS, Garrigue C, Poole M, Hauser N, Caballero S, Florez-Gonzalez L, Brasseur M, Bannsiter J, Capella J, et al. Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Mar Ecol Prog Ser*. 2007;330:257–268.

Pérez-Alvarez M, Kraft S, Segovia NI, Olavarría C, Nigenda-Morales S, Urbán J, Viloria-Gómora RL, Archer F, Moraga R, Sepúlveda M, et al. Contrasting phylogeographic patterns among Northern and Southern Hemisphere fin whale populations with new data from the Southern Pacific. *Front Mar Sci*. 2021;8:774.

R Core Team. *R: a language and environment for statistical computing*. Vienna (Austria): R Foundation for Statistical Computing; 2015 [accessed 2021 Apr]. https://www.r-project.org/

Rastogi T, Brown MW, McLeod BA, Frasier TR, Grenier R, Cumbaa SL, Nadaraja J, White BN. Genetic analysis of 16th-century whale bones prompts a revision of the impact of Basque whaling on right

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024

and bowhead whales in the western North Atlantic. *Can J Zool*. 2004;82:1647–1654.

Richardson J, Wood A, Neil A, Nowacek D, Moore M. Changes in distribution, relative abundance, and species composition of large whales around South Georgia from opportunistic sightings: 1992 to 2011. *Endanger Species Res*. 2012;19:149–156.

Rocha RC, Clapham PJ, Ivashchenko YV. Emptying the oceans: a summary of industrial whaling catches in the 20th century. *Mar Fish Rev*. 2014;76:37–48.

Rojas-Cerda C, Buchan SJ, Branch TA, Malige F, Patris J, Hucke-Gaete R, Staniland I. Presence of Southeast Pacific blue whales (Balaenoptera musculus) off South Georgia in the South Atlantic Ocean. *Mar Mammal Sci*. 2022;38:1425–1441. https://doi.org/10.1111/mms.12946.

Rosenbaum HC, Egan MG, Clapham PJ, Brownell RL Jr, Malik S, Brown MW, White BN, Walsh P, Desalle R. Utility of North Atlantic right whale museum specimens for assessing changes in genetic diversity. *Conserv Biol*. 2000;14:1837–1842.

Rosenbaum HC, Maxwell SM, Kershaw F, Mate B. Long-range movement of humpback whales and their overlap with anthropogenic activity in the South Atlantic Ocean. *Conserv Biol*. 2014;28:604–615.

Rosenbaum HC, Pomilla C, Mendez M, Leslie MS, Best PB, Minton G, Ersts PJ, Collins T, Engel MH, Bonatto SL, et al. Population structure of humpback whales from their breeding grounds in the South Atlantic and Indian Ocean. *PLoS One*. 2009;4:1–11.

Sremba AL, Hancock-Hanser B, Branch TA, LeDuc RG, Bake CS. Circumpolar diversity and geographic differentiation of mtDNA in the critically endangered Antarctic blue whale (*Balaenoptera musculus intermedia*). *PLoS One*. 2012;7:e32579.

Sremba A, Martin AR, Baker CS. Species identification and likely catch time period of whale bones from South Georgia. *Mar Mammal Sci*. 2015;31:122–132.

Steel D, Anderson M, Garrigue C, Olavarría C, Caballero S, Childerhouse S, Clapham P, Constantine R, Dawson S, Donoghue M, et al. Migratory interchange of humpback whales (*Megaptera novaeangliae*) among breeding grounds of Oceania and connections to Antarctic feeding areas based on genotype matching. *Polar Biol*. 2018;41:653–662.

Taylor BL, Marinez M, Gerrodette T, Barlow J, Hrovat YN. Lessons from monitoring trends in abundance of marine mammals. *Mar Mammal Sci*. 2007;23:157–175.

Wickham HR. stringr: simple, consistent wrappers for common string operations. *R package version 1.0.0*. 2015 [accessed 2021 Apr]. https://CRAN.R-project.org/package=stringr

Zerbini AN, Adams G, Best J, Clapham PJ, Jackson JA, Punt AE. Assessing the recovery of an Antarctic predator from historical exploitation. *R Soc Open Sci*. 2019;6:190368.

Zerbini A, Ward E, Engel MH, Andriolo A, Kinas PG. A Bayesian assessment of the conservation status of humpback whales (*Megaptera novaeangliae*) in the Western Atlantic Ocean (Breeding Stock A). *Report SC/58/SH2 to the Scientific Committee of the International Whaling Commission*. 2006.

Downloaded from https://academic.oup.com/jhered/article/114/6/587/7242223 by NOAA Central Library user on 16 January 2024