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Preliminary Genomic And Isotopic Insights From Whaling Era Southern Right Whale Bone From Mainland Aotearoa New Zealand

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Note: Figure 2 was corrected in May 2023

PRELIMINARY GENOMIC AND ISOTOPIC INSIGHTS FROM WHALING ERA SOUTHERN RIGHT WHALE BONE FROM MAINLAND AOTEAROA NEW ZEALAND

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ABSTRACT

Southern right whales (*Eubalaena australis*) experienced a dramatic demographic decline due to whaling. Previous global simulations suggest this has decreased mitochondrial DNA (mtDNA) richness by between 32% and 75%. In Aotearoa New Zealand, a single stock assessment suggested a decline from 30,000 prior to whaling to as few as 40 whales in 1920. Despite the population rebounding to approximately 2000 whales in 2009, this decline lasted for approximately five generations, with possible population level consequences for genetic diversity. Here we undertake an analysis of bone samples from historical whaling sites, assumed to represent the mainland New Zealand whaling era population. Combining mtDNA sequencing and stable isotope analyses, we present preliminary analyses comparing these historical samples to the contemporary population. Of 18 whale bone samples analysed, 13 yielded Sanger sequencing data of the mtDNA control region, confirming the presence of 11 southern right whales and two humpback whales. Of the 11 southern right whale sequences, 10 were of high quality and enabled population diversity statistics to be calculated. These 10 sequences included nine haplotypes (217 bp), only one of which has been observed to date in the contemporary New Zealand population (n=692 whales). Despite a relatively small sample size, the haplotype and nucleotide diversity of the historical population was substantially greater than that of the contemporary population. In addition, we extracted bone collagen and generated stable isotope data ($\delta^{13}C$ and $\delta^{15}N$) for four southern right whale samples and one humpback whale. These samples fell to one end of the distribution of contemporary samples but indicated a potential shift in foraging patterns that will only be elucidated through the analysis of additional historical samples. Overall, these preliminary results provide a first glimpse of the genetic diversity once present among past southern right whale populations in New Zealand, and highlight the potential to understand changes in foraging patterns over time through the analysis of data from both historical and contemporary samples.

INTRODUCTION

Southern right whales (SRW, *Eubalaena australis*) underwent a prolonged, circumpolar demographic bottleneck due to whaling in the 19th and 20th centuries (Jackson *et al.* 2008). Based on simulation studies, this decline in abundance resulted in a reduction in mtDNA richness of between 32% and 75% worldwide (Jackson *et al.* 2008). However, understanding the decline in abundance and concomitant loss of genetic diversity is best done on a population level, given the stock structure of this species driven by site fidelity and a migratory culture (Carroll *et al.* 2019).

Here we focus on the New Zealand population of SRW - tohorā nō Aotearoa (Figure 1). Historically, the population numbered around 30,000 SRW but declined to as few as 40 individuals by 1920 (Jackson *et al.* 2016). Despite the setback of illegal Soviet whaling, the population has recovered and abundance was estimated at around 2,000 individuals in 2009, with an annual growth rate of 7% (CI 5-9%) from 1995-2009 (Carroll *et al.* 2013).

The New Zealand SRW population currently makes use of multiple areas during the austral winter: their primary nursery ground is around the Auckland Islands (Maungahuka), but Campbell Island and increasingly mainland (North and South Island) waters are also key wintering habitats. The known foraging grounds of this population are more wide ranging, extending from east of New Zealand to south of Australia (Figure 1). Genetic population structure studies indicate that whales found in these areas currently form a single interbreeding population, with photo-ID and genotype resightings indicating within- and between-year movement across regions (Carroll *et al.* 2014).

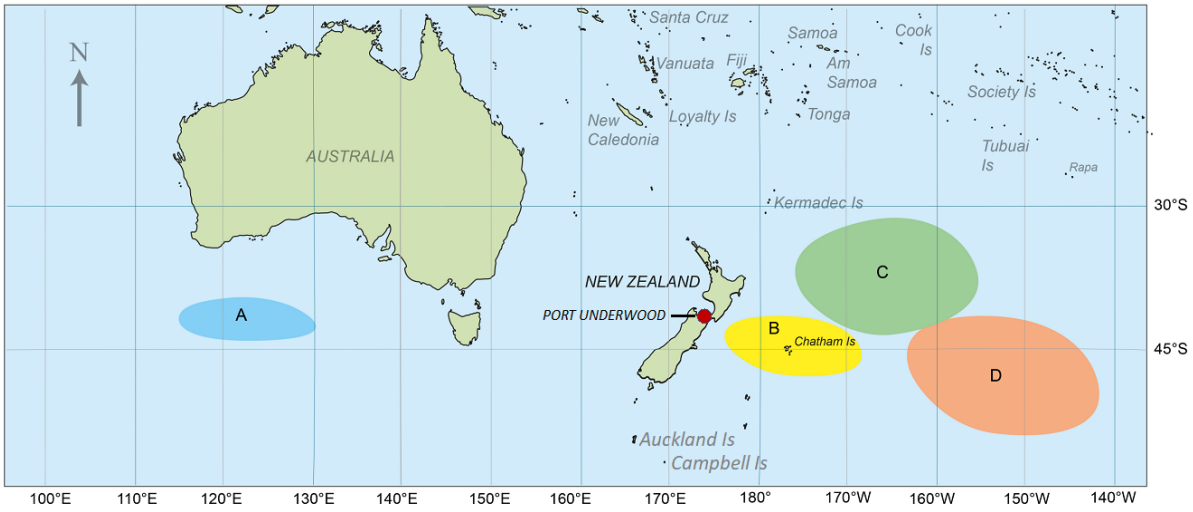

Figure 1: Map of the Indo-Pacific region with contemporary (A) and historical (B-D) areas known to be used as foraging grounds by New Zealand SRW, based on satellite tracking studies (A) or whaling catch data (B-D). Also shown are Port Underwood (bone sampling site) as well as the New Zealand mainland, Auckland Islands and Campbell Island (nursery/wintering grounds).

One question that has remained unanswered is whether New Zealand was home to multiple stocks of SRW prior to and during the whaling era (1827 to 1935). Historical records suggest there could have been two distinct coastal whaling grounds in New Zealand: one around the mainland and one around the sub-Antarctic islands. Catch series data for mainland waters recorded an abundance of mothers and calves, indicating that SRW used bays and inlets primarily as calving grounds during the austral winter (Dawbin 1986; Sherrin 1886). In the sub-Antarctics, SRW arrived as early as February, and it is unclear whether this region was historically a feeding or breeding ground (Richards 2002). Additionally, it is unclear whether foraging strategies used by the historical population are extant. For example, SRW were killed in large numbers north and east of New Zealand by 'Yankee' whalers from the USA (Smith *et al.* 2012) but there are few contemporary sightings of this species in the area. The admittedly few satellite tracked SRW from the contemporary population have headed west rather than east (Mackay *et al.* 2020; Riekkola *et al.* 2021).

Here we undertake an analysis of SRW bone samples from historical New Zealand whaling sites, assumed to represent the mainland New Zealand whaling era population. Combining mtDNA sequencing and stable isotope data, we present preliminary analyses comparing these historical samples to the contemporary SRW population.

METHODS AND MATERIALS

Bone sampling and provenance

Bone samples were collected from the farms of Mr and Mrs Guard and Mr Alan Perano at Port Underwood, South Island, New Zealand (Figure 1). Both families once established whaling stations in the area, and have collections of bone that are known or presumed to date back to the whaling era (circa 1827 to 1964; SRW whaling until 1935).

Two types of bone sample were collected at Port Underwood. The first were small fragments (bone 'chunks') that were chipped off, or had fallen off, larger bone sections. The second were drilled sub-samples (bone 'powder') from larger pieces of bone. For the latter, the bones were initially sanded, then drilled, and sterilised aluminium foil was used to collect the bone powder. All samples were stored in clean, sealed plastic bags after collection.

DNA extraction and mtDNA sequencing

DNA was extracted following a protocol developed for ancient bone, with silica spin column purification (Rohland *et al.* 2018). All steps were carried out in a dedicated ancient DNA clean room (the Palaeomolecular

Anthropology Laboratory at the University of Auckland), which is spatially separate from post-PCR laboratories. To minimise surface contaminants, bone sub-samples were initially soaked in 0.5% bleach for 10 mins then washed three times in Type I water prior to extraction.

Amplification of the mtDNA control region was conducted using 25 μL nested PCRs, with primers M13Dlp1.5 and Dlp5 (Dalebout *et al.* 1998), followed by M13Dlp1.5 and Dlp4 (Dalebout *et al.* 2004). Sanger sequencing was performed by the Auckland Genomics Centre at The University of Auckland.

Forward and reverse sequences were assembled to generate consensus sequences for each sample. These were aligned to existing mtDNA haplotypes for contemporary SRW and all sequences were trimmed to the same length (217 bp) in Geneious Prime (v2021.0.3; Kearse *et al.* 2012). Using POPART (v1.7; Leigh & Bryant 2015), haplotype frequencies and sequences for the historical and contemporary population (Carroll *et al.* 2019) were used to generate a median joining network (Bandelt *et al.* 1999). Additionally, DnaSP (v6.12.03; Rozas *et al.* 2017) was used to estimate haplotype (h) and nucleotide diversity (π), and to estimate genetic differentiation statistics between the historical and contemporary samples.

Collagen extraction and stable isotope analysis

Bone samples were prepared for decalcification using a modified version of the protocol described by Tuross (2012). Sub-samples of bone 'chunks' (~1g) were cleaned in Type 1 water and sonicated to remove all sand (~6 washes of 5 mins). The samples were then gently decalcified in EDTA over a period of 2 weeks at room temperature until no colour change was visible and no effervescence persisted. For bone 'powder', samples were not rinsed (no sand was present) and were decalcified in EDTA for 48 hours. All samples were washed 14 times in Type 1 water to remove the EDTA before solubilization. The resultant pseudomorphs were solubilized in pH 3 water at 70ºC for 48 hrs. The collagen solution was separated from the remaining insoluble residue then frozen and lyophilized. Of the seven samples, five yielded good quality collagen for analysis. All five of these samples met the standard quality criteria for bone collagen (C:N ratio, Nitrogen % w/w, and Carbon % w/w) established by Van Klinken (1999).

For comparison of data from historical (bone) and contemporary (skin) samples, bone collagen δ13C and δ15N were transformed from collagen to diet, then diet to skin using diet-tissue discrimination factors for fin whales published by Borrell *et al.* (2012). Ideally, a species-specific diet-tissue correction could be applied, but a review of the literature yielded no published SRW diet-tissue discrimination factors. While Sabadel et al. (2020) investigated the Suess effect in NZ from 1955 to the present, no specific correction could be found for NZ during the whaling period. Instead, a generic carbon correction of 0.80 was applied to account for the impact of the Suess effect on carbon isotope values from historic (late 1800s) to modern samples (Eide *et al*. 2017; Francey *et al*. 1999; Sonnerup *et al*. 1999).

RESULTS AND DISCUSSION

DNA extraction and mtDNA sequencing success

A total of 18 bone samples were collected from the Guard and Perano family farms (Table 1). DNA extraction, PCR and mtDNA sequencing were successful for 13 samples, leading to the identification of 11 samples as SRW and two as humpback whale bone. For one SRW sample, sequence quality was low (48.9% HQ) therefore this sequence was excluded from further analyses.

The two historical humpback whale sequences both matched contemporary haplotypes, one (SP40) found among individuals in the South Pacific and one (EA004) in East Australia (Olavarria *et al.* 2007; Anderson 2013).

Historical mtDNA genetic diversity

High quality mtDNA sequencing data were obtained for a total of 10 historical SRW samples (Table 1). Nine unique mtDNA haplotypes were present, with only two samples (S012 and S013) exhibiting the same haplotype. Of these nine haplotypes, two have been observed previously among contemporary southern right whales: one (BakHapE) in the New Zealand, Australian and South African wintering grounds, and the other (ValHapEE) in the contemporary Argentinean population. The other seven haplotypes (HistNZA-G) have never before been observed in New Zealand or any other wintering ground among contemporary populations.

Around 10% of the estimated global population of SRWs (1300 individuals) have had their mtDNA haplotype characterised, so it is likely that many haplotypes remain unsampled on a global scale (Carroll *et al.* 2019). However, of the New Zealand population, a larger proportion have been sampled and sequenced (>40% as of 2009: Carroll *et al.* 2013) and most whales (~70%) have one of two haplotypes: BakHapA and BakHapB, neither of which were found in this historical sample. The mtDNA haplotype network of contemporary and historical New Zealand samples is shown in Figure 2.

Levels of nucleotide diversity observed among the 10 historical bone samples analysed were substantially higher than among 692 contemporary individuals sampled in New Zealand waters (see Table 2). This suggests a significant loss of genetic diversity, and a loss of mtDNA lineages, among SRW since the whaling era. In terms of genetic differentiation, sequences from historical and contemporary samples differed by an average of 7.9 nucleotides ($k = 7.87$ sites; $Dxy = 0.036 \pm 0.008$ substitutions per site). 11 sites were polymorphic among historical samples only, four sites were polymorphic among contemporary samples only, and eight sites were polymorphic among both historical and contemporary samples. No fixed differences were present, consistent with idea that the contemporary population is not distinct from, but is lower in diversity than, the historical population.

Table 1: Summary of bone samples studied using mtDNA sequencing and stable isotope analyses.

Sample	**Type**	**DNA sequencing (Y/N)**	**Species ID**	**mtDNA haplotype**	**Collagen (Y/N)**	**Stable isotope (Y/N)**
EBL001	Powder	Y*	SRW	N/A	N/A	N/A
EBL003	Chunk	Y	SRW	HistNZA	Y	Y
EBL004	Powder	Y	SRW	HistNZB	Y	Y
EBL005	Powder	Y	Humpback	SP40	Y	Y
EBL008	Chunk	Y	SRW	VHEE	N/A	N/A
EBL010	Chunk	N	N/A	N/A	Y	Y
EBL012	Powder	Y	SRW	BHE	N/A	N/A
EBL013	Powder	Y	SRW	BHE	N/A	N/A
EBL015	Powder	Y	SRW	HistNZC	N/A	N/A
EBL016	Powder	Y	SRW	HistNZD	N/A	N/A
EBL017	Powder	N	N/A	N/A	N/A	N/A
EBL019	Powder	N	N/A	N/A	N/A	N/A
EBL020	Powder	N	N/A	N/A	N/A	N/A
EBL021	Powder	Y	Humpback	EA004	N/A	N/A
EBL022	Chunk	Y	SRW	HistNZE	N	N
EBL023	Chunk	Y	SRW	HistNZF	N	N
EBL024	Chunk	Y	SRW	HistNZG	Y	Y
EBL025	Chunk	N	N/A	N/A	N/A	N/A

*Low quality sequence excluded from haplotype network and genetic diversity analyses.

Table 2: Summary of mtDNA diversity statistics for historical (bone) and contemporary (skin) New Zealand southern right whale samples. Contemporary samples were collected on New Zealand wintering/nursery grounds.

	N	n_{hap}	length (bp)	*S* (bp)	*h* ± SD	π ± SD (%)	Source
Historic	10	9	217	19	0.98 ± 0.05	2.78 ± 0.43	This report
Contemporary	692	11	217	12	0.69 ± 0.01	1.91 ± 0.05	Carroll *et al.* (2019)

N = sample size; n_{hap} = number of haplotypes; *S* = number of segregating (polymorphic) sites; *h* = haplotype diversity; π = nucleotide diversity for the mtDNA control region.

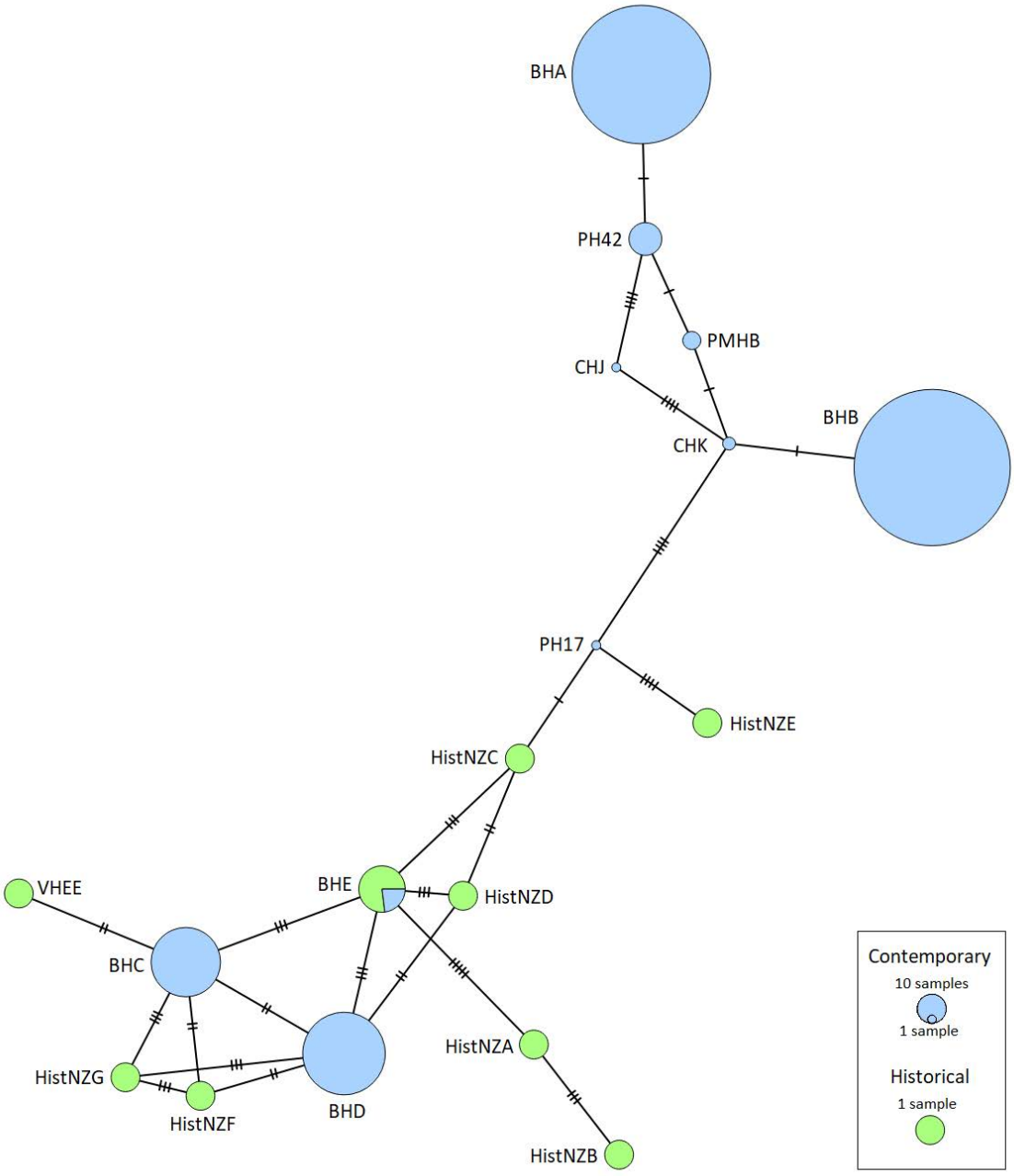

Figure 2: mtDNA haplotype network (based on 217 bp of control region) including the relative frequencies of each haplotype within contemporary (n=692) and historical (n=10) New Zealand SRWs.

Isotopic results and foraging patterns

Collagen extraction was carried out for seven bone samples and successful in five of these (four SRW and one humpback whale). Corrected δ13C and δ15N values for bone collagen in these five samples (Table 3) were within the range of contemporary data based on skin samples (Figure 3; Newsome, Dunshea & Carroll unpublished data). This suggests that (a) the corrections applied are appropriate and (b) the longer time averaged for the bone compared to the skin is averaging some of the variation present in the skin samples.

Whilst encompassed by the variation among contemporary samples, the historical humpback whale collagen was more depleted in 13C than 99% of contemporary New Zealand SRWs (Figure 3). More negative δ13C values, averaged over many years in bone, may indicate more time spent foraging away from coasts and in colder waters (St John Glew *et al.* 2020). In contrast, the four historical SRW samples were on average more enriched in 13C, and marginally more enriched in 15N, than contemporary SRW samples. In both cases, larger sample sizes are needed to determine the significance of these results.

These results highlight the potential of further analyses to characterise variation in carbon and nitrogen isotope values among historical SRW populations, and to reveal whether foraging traditions among SRW have changed over time.

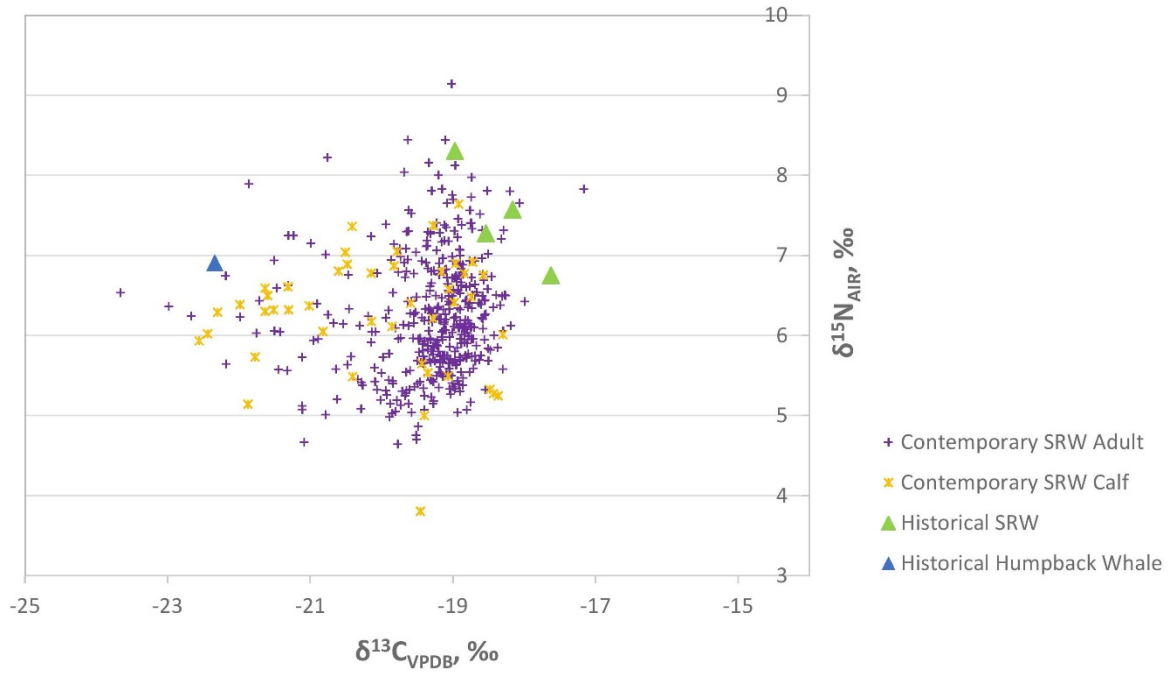

Figure 3: $\delta^{13}C$ and $\delta^{15}N$ for historical whale bone and contemporary skin samples. Contemporary data: Newsome, Dunshea, Carroll (unpublished).

Table 3: $\delta^{13}C$ and $\delta^{15}N$ and corrections applied for historical whale bone samples.

Sample Name	Species	$\delta^{15}N_{AIR}$ (‰)	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{AIR}$ (‰ adjusted to diet)	$\delta^{13}C_{VPDB}$ (‰ adjusted to diet)	$\delta^{15}N_{AIR}$ (‰ adjusted to skin)	$\delta^{13}C_{VPDB}$ (‰ adjusted to skin)	$\delta^{13}C_{VPDB}$ (‰ + Suess)
EBL003	SRW	6.49	-15.91	4.46	-19.02	7.28	-17.74	-18.54
EBL004	SRW	5.96	-14.99	3.93	-18.10	6.75	-16.82	-17.62
EBL005	Humpback	6.12	-19.71	4.09	-22.82	6.91	-21.54	-22.34
EBL010	SRW	6.78	-15.53	4.75	-18.64	7.57	-17.36	-18.16
EBL024	SRW	7.51	-16.34	5.48	-19.45	8.30	-18.17	-18.97

Conclusion and future directions

The 100-200 yr old whale bones found at two Port Underwood sites yielded DNA sufficient for species identification and mtDNA analyses. Preliminary analyses confirm that the predominant species found here was southern right whale. Only one of nine haplotypes observed among these whaling era samples has been previously identified in in the contemporary New Zealand population. Interestingly, the haplotypes most common in the contemporary population were absent from the historical sample (Figure 2). Furthermore, despite a relatively low sample size, levels of nucleotide diversity were greater among the historical (n=10) than contemporary (n=692) samples. This supports earlier simulations (Jackson *et al.* 2008), which suggest a reduction in mtDNA richness linked to a major population bottleneck during the whaling era.

Our results also highlight the potential of isotopic studies for identifying behavioural changes in foraging patterns between contemporary and historical populations. Following on from these successful pilot results, we aim to expand our analyses to genomic markers, additional isotope analyses, and a broader geographic scope, with the inclusion of samples from around the Indo-Pacific. Simulation analyses, based on this larger dataset, will be informative about the scale of loss of genetic and cultural diversity in SRW.

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