



Genetic differentiation and population connectivity of humpback whales migrating through Aotearoa New Zealand waters

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ABSTRACT

Context. Historically, humpback whales migrating past Aotearoa New Zealand (NZ) were linked to western South Pacific wintering grounds and Antarctic feeding grounds. As populations have recovered, research has focused on contemporary connectivity patterns throughout the South Pacific. **Aims.** To determine the contemporary connectivity of winter breeding grounds for humpback whales on their northern and southern migrations past NZ, and those at the Kermadec Islands (Rangitāhua) migratory stopover. **Methods.** We generated DNA profiles (mitochondrial DNA (mtDNA) haplotypes, genetic sex and microsatellite genotypes) using skin samples collected from whales between 1998 and 2021. We used comparisons of DNA profiles and a mixed-stock analysis of mtDNA haplotypes to determine the most likely wintering grounds of genetically identified individuals. **Key results.** DNA profiles of 350 individual whales from NZ were compared to profiles from Oceania ($n > 2000$), Central and South America ($n = 452$) and East Australia ($n = 809$). This comparison revealed 35 genotype matches, mainly to New Caledonia and East Australia. The mixed-stock analysis showed that northbound whales ($n = 145$) had approximately equal assignment proportions to East Australia and New Caledonia whereas southbound whales ($n = 74$) showed a two-fold higher assignment to East Australia. In contrast, whales passing Rangitāhua ($n = 112$) assigned to New Caledonia and other Pacific wintering grounds but not to East Australia. **Conclusions.** Humpback whales passing mainland NZ on their north and southbound migrations are strongly associated with East Australia and New Caledonia wintering grounds. Those migrating south past Rangitāhua have a broader range of wintering ground destinations, including a connection to Central America.

Keywords: connectivity, genetics, humpback whale, migration, mixed stock assignment, mtDNA, New Zealand, Pacific Ocean.

Introduction

Commercial whaling throughout the 20th century caused the near total collapse of large whale populations in the Southern Hemisphere (Clapham and Baker 2018). Despite protection since the 1960s, there have been variable rates of recovery from very slow e.g. Antarctic blue whales (*Balaenoptera musculus musculus*) (Branch 2007) and southern right whales (*Eubalaena australis*) (e.g. Jackson *et al.* 2016) to rapid and fully recovered e.g. humpback whales (*Megaptera novaeangliae*) in the south-west Atlantic (Bortolotto *et al.* 2021). However, even among humpback whales that are capable of rapid rates of increase (Bejder *et al.* 2016; Pallin *et al.* 2018; Noad *et al.* 2019) there is variation in recovery rates. For example, the Oceania region has several populations using wintering grounds between New Caledonia and French Polynesia (Fig. 1) that show considerably slower rates of recovery (Constantine *et al.* 2012; Jackson *et al.* 2015) than the neighbouring East Australia population (Noad *et al.* 2019). Although the causes of the historically slow recovery of Oceania's whales are not fully understood, the huge illegal catches by the USSR south of

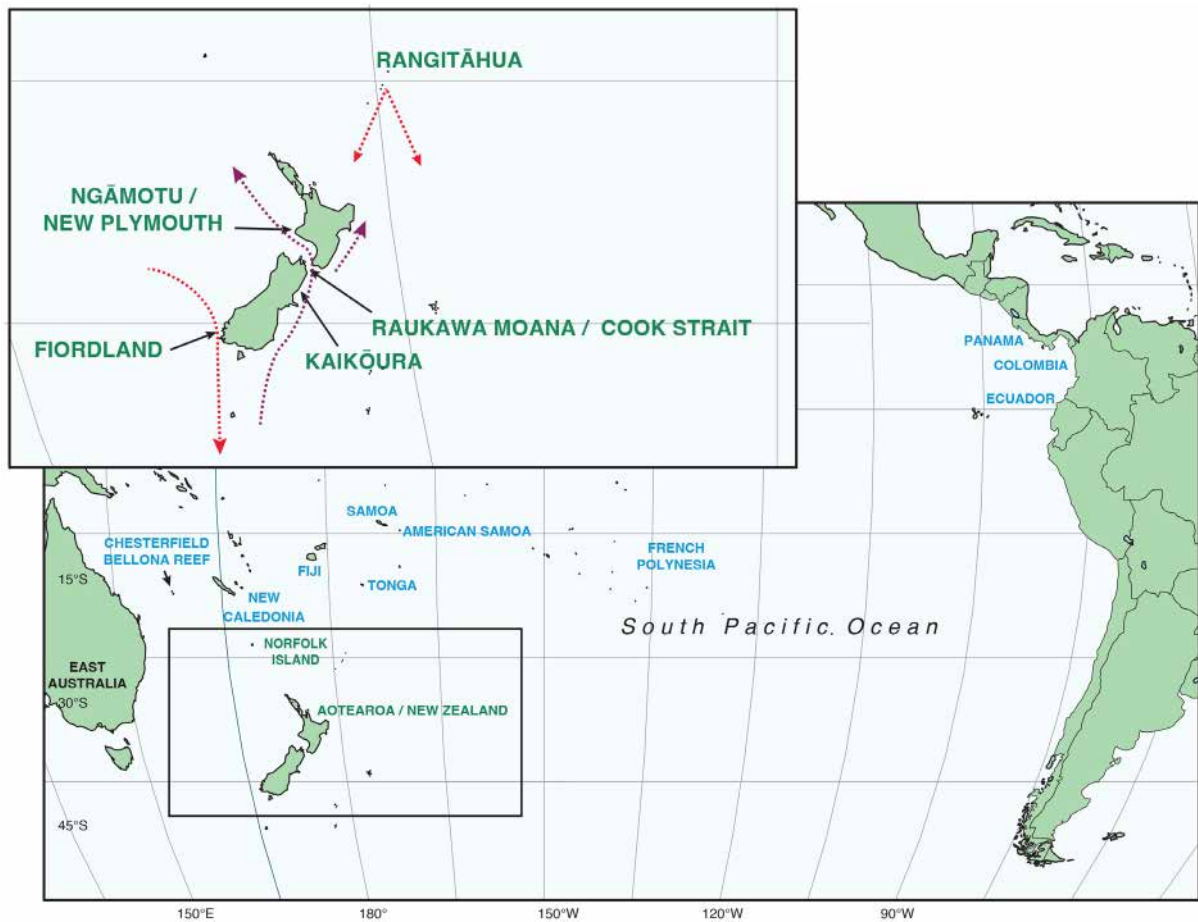


Fig. 1. Oceania humpback whale wintering ground connections (in blue) and migratory corridors (in green). The top left insert shows the locations of genetic sampling for the northbound (indicated by the purple dotted lines) and southbound (red dotted lines) migratory streams of humpback whales passing Aotearoa New Zealand.

Aotearoa New Zealand (NZ) in the late 1950s and early 1960s are likely a critical contributing factor (Clapham *et al.* 2009).

The endangered population of humpback whales in Oceania (Childerhouse *et al.* 2008) has a range of migratory destinations that span wintering grounds from New Caledonia (~160°E) to the French Polynesian archipelagos (~120°W). These are linked to a broad expanse of summer foraging grounds in the Southern Ocean from ~150°E to ~70°W (Constantine *et al.* 2014; Riekkola *et al.* 2018; Steel *et al.* 2018; Reisinger *et al.* 2021). There are also connections between East Australia, the western Oceania breeding grounds and NZ (e.g. Garrigue *et al.* 2011; Franklin *et al.* 2014; Andrews-Goff *et al.* 2018). Most of Oceania's humpback whales do not migrate past East Australia (Constantine *et al.* 2014), therefore NZ is the only large landmass on their migratory corridor in the western South Pacific Ocean. Indigenous knowledge of humpback whale use of Oceania and NZ waters pre-dates commercial whaling, as large numbers of whales frequented nearshore waters during winter, and/or were encountered by voyagers navigating among the Pacific Islands and further south to NZ. This includes the remote

Rangitāhua/Kermadec Island archipelago. In NZ, there are strong connections between Indigenous people – Māori – and whales, with well-established knowledge about whale song and their migration patterns reflecting the pre-whaling seasonal movements, historical abundance and eventual decline of whales (e.g. Grose *et al.* 2020).

The *Discovery* marking program conducted during the commercial whaling era linked southbound mainland NZ humpback whales to the migratory corridor of East Australia and northbound mainland NZ humpback whales to the migratory corridors of Norfolk Island and East Australia, and wintering grounds in Fiji (Dawbin 1959, 1964). These connections were largely lost with the decline in abundance and near collapse of East Australia and Oceania humpback whale populations resulting in an end to coastal commercial whaling in this area in the 1960s (Goodhand 1963; Chittleborough 1965; Clapham and Baker 2018). Today, humpback whales are slowly returning to Fijian waters but the historical population was possibly extirpated and the habitat is currently being colonised by whales from other breeding grounds (Gibbs *et al.* 2006; Miller *et al.* 2015).

Historically, Raukawa Moana/Cook Strait was a well-documented migration path for humpbacks on their northbound migration and the location for a land-based whaling station was active until the 1960s (Dawbin 1966). The south-west region of Te Waipounamu/the South Island (from Ōkahu/Jackson Bay, Te Rua-o-Te-Moko/northern Fiordland to Raratoka/Centre Island, Te Ara a Kiwa/Foveaux Strait) was identified as a migration path for southbound whales, with large aggregations of whales reported by sighting surveys during the whaling era (Dawbin 1956). Foraging behaviour and residency times of several days were also documented in this region, suggesting that this was a provisioning area for whales before they continued to their primary summer foraging areas in the Antarctic (Dawbin 1956).

Post-whaling knowledge of humpback whale movements around mainland NZ has largely relied on opportunistic sighting records collected since 1970, with most of the 157 sightings of the whales' northbound migration primarily reported from Kaikōura and Cook Strait (Gibbs and Childerhouse 2000) between 1970 and 1999. Until 2004, most of the data enabling the genetic or photographic identification of individual whales were collected opportunistically, with small sample sizes. This made the comprehensive assessment of the winter breeding and summer feeding ground connectivity of whales migrating past mainland NZ difficult (Constantine *et al.* 2007, 2012; Garrigue *et al.* 2011; Franklin *et al.* 2014). In 2004, systematic annual surveys were undertaken at an old whaling lookout site at the Kura Te Au/Tory Channel entrance to Cook Strait for 12 years. Here, photo-identification and small tissue biopsy samples were collected in the main 'hotspot' for humpback whale sightings during their northbound migration from May to August (Dawbin 1956; Gibbs *et al.* 2018) (Fig. 1). A preliminary study using only 30 genetic samples from NZ suggested that whales migrating northward through Cook Strait were most closely affiliated with humpbacks from the New Caledonia breeding grounds (Olavarría *et al.* 2006). Opportunistic sightings during the southbound migration from September to November, and recent satellite telemetry results show that some southbound East Australia whales migrate towards south-western NZ (Andrews-Goff *et al.* 2018). As a result, dedicated boat-based surveys for humpbacks in the Fiordland region started in 2017, with a focus on collecting genetic samples and individual fluke identification photographs.

In addition to the mainland sightings, in the mid-2000s Te Papa Atawhai/Department of Conservation (DOC) rangers based at Rangitāhua (part of the Kermadec archipelago) reported an increasing number of southbound humpback whales from September to mid-November but only occasional sightings of whales on their northbound migration from April to June. Rangitāhua is remote, ~1100 km north-east of mainland NZ (Fig. 1) and an area of well-documented historical whale presence (Grose *et al.* 2020). Land-based, single-day surveys between 2008 and 2014 revealed an increase in whale numbers with one 4-h survey period in 2010 estimating up to 153 whales (see Brown 2010 and Gibson 2014). Research

voyages to Rangitāhua revealed that whales stopped for ~5 days on their southbound migration from a 3600 km expanse of Oceania wintering grounds; in particular from New Caledonia (Garrigue *et al.* 2016; Clark *et al.* 2017; Riekkola *et al.* 2018; Owen *et al.* 2019). Whales subsequently continued their migration south-eastward to Antarctic feeding grounds, with very few whales passing close to mainland NZ (Riekkola *et al.* 2018).

Since the initial description of mitochondrial DNA (mtDNA) haplotypes from mainland NZ humpback whales (Olavarría *et al.* 2006), the continued collection of tissue samples from living and occasionally beachcast whales (Thompson *et al.* 2013) from their north and southbound migrations has greatly increased the number of genetic samples available. There has also been a concerted effort to standardise genetic markers for a 'DNA profile' to provide mtDNA haplotypes, and sex and microsatellite genotype (Constantine *et al.* 2012; Steel *et al.* 2018). This has enabled a comprehensive investigation using genetically identified individuals to investigate the whales' likely wintering ground connections. Previous research suggests that the population affiliation of humpback whales passing NZ on their southern migration may differ from that of northern migrating whales (Valsecchi *et al.* 2010; Riekkola *et al.* 2018). As recovering whale populations can also change habitat use and migration patterns (e.g. Clapham and Zerbini 2015; Weir and Stanworth 2020), we consider three separate migration streams; northbound mainland NZ, southbound mainland NZ and southbound Rangitāhua. We use DNA profile data to investigate individual-based connectivity across the Pacific and mtDNA data to assess migratory habitat level connectivity. The latter is due to the highly informative nature of this marker for population structure in species such as humpback whales that show maternally directed fidelity to migratory habitats (e.g. Kershaw *et al.* 2017). In so doing, we also re-examine genetic differentiation across East Australia, Oceania, and the South and Central America wintering grounds with a larger dataset, to further investigate population structure and connectivity in this slowly recovering population of humpback whales.

Methods

Sample collection

New Zealand migratory streams

In all research locations, when a pod of humpback whales was sighted, attempts were made to collect skin biopsy samples using a modified veterinary capture rifle (Krützen *et al.* 2002) or crossbow (e.g. Lambertsen 1987; Palsbøll *et al.* 1991) and collect photo-identification images of the underside of the whales' flukes (Katona *et al.* 1979). Skin samples used for genetic analysis were stored in 70–90% ethanol and any blubber present was sub-sectioned from the epidermis and

frozen at -20°C . Where possible, a biopsy sample and photo-identification image were collected from the same individual, providing two sources of individual identification. Samples from beachcast whales were collected by hand and stored as described above.

Data collection particular to the different locations is briefly outlined as follows.

Northbound mainland NZ sampling – Cook Strait. Dedicated surveys for humpback whales were conducted at Tory Channel, Cook Strait (Fig. 1) during the austral winters (i.e. July–August) of 2004–2012 (see Gibbs *et al.* 2018 for details). Land-based surveys were conducted by four or more dedicated observers from a site ($41^{\circ}12.45'\text{S}$, $174^{\circ}19.43'\text{E}$) 127 m above sea level. Surveys were conducted in favourable weather conditions, typically up to Beaufort 5. When possible, a boat-based research team collected samples and photo-identification, as guided by the land-based researchers.

Southbound mainland NZ sampling – Fiordland. Dedicated non-systematic boat-based surveys were conducted in 2017, 2018, 2020 and 2021 on the 22 m DOC liveaboard vessel *Southern Winds* from Taitetimu/Caswell Sound ($40^{\circ}00'\text{S}$, $167^{\circ}08'\text{E}$) in the north to Rakituma/Preservation Inlet ($46^{\circ}05'\text{S}$, $166^{\circ}37'\text{E}$) in the south including the coastal and inner fiord regions (see Corne 2023). Two to four observers conducted 90° scans along the transect line in weather conditions up to Beaufort 5 and up to 12 km offshore.

Southbound Rangitāhua sampling. Dedicated non-systematic boat-based surveys were conducted in the austral spring 2015, 2016 and 2017 from different live-aboard vessels or, more frequently, from ~4 to 6 m small-boats deployed from the main vessel (see Clark *et al.* 2017 and Riekkola *et al.* 2018 for details). Data were collected throughout the archipelago with a focus on Rangitāhua ($29^{\circ}16'\text{S}$, $177^{\circ}56'\text{W}$), an area with the highest number of whales. Surveys were conducted in Beaufort 3 or less and typically within 2 km of land.

Beachcast and opportunistic whale samples. In addition to biopsy samples of living whales, tissue collected from beachcast whales by DOC rangers from 1998 to 2012 were included (Thompson *et al.* 2013). Samples were preserved in 70% ethanol on location and sent to the University of Auckland/Waipapa Taumata Rau for curation in the NZ Cetacean Tissue Archive (NZCeTA) where they are stored at -20°C . Samples in this collection were split into northbound or southbound based on sampling date; samples collected between 1 September and 30 November over the 14 year time period were assigned to southbound, samples collected between 1 April and 31 July were assigned to northbound, and samples outside these date ranges were considered unknown and were not used in further analysis.

Hereafter, we refer to three migratory streams: (1) NZ-northbound (NZnth) comprises whales primarily sampled in Cook Strait and the beachcast samples collected during the northward migration period; (2) NZ-southbound (NZsth) comprises whales primarily sampled in Fiordland and the beachcast samples collected during the southward migration period; and (3) Rangitāhua comprises only samples from southbound whales, as there were no beachcast specimens from this area.

Wintering grounds

To enable comparison of the NZ migratory streams with wintering grounds, we compiled previously published datasets (see later section) and generated new reference data. Specifically, to increase the sample size of available DNA profiles, members of the South Pacific Whale Research Consortium (SPWRC) collected further biopsy or sloughed skin samples from the wintering grounds of American Samoa (2010–2019) and French Polynesia (2008–2012). Biopsy or sloughed skin samples were also collected off the Pacific coast of Colombia (2015–2018 by Fundación Macuáticos and Universidad de los Andes), the coast of Ecuador (2006–2010 by Fernando Felix, Pontificia Universidad Católica del Ecuador) and the Pacific coast of Panama (2016–2019 by Panacetacea Organization).

DNA extraction and profiling

Total genomic DNA was extracted from skin biopsy samples either using standard proteinase K digestion and phenol/chloroform methods (Sambrook *et al.* 1989), as modified for small samples by Baker *et al.* (1994), or the Puregene DNA isolation kit (Gentra).

DNA profiles for each sampled whale included mtDNA control region haplotypes (470 bp), sex markers, and up to 15 microsatellite loci. Molecular identification of sex and sequencing of the mtDNA control region (470 bp) followed methods previously described by Olavarría *et al.* (2007). Microsatellite genotyping at up to 15 microsatellite loci (EV1, EV14, EV21, EV37, EV94, EV96 and EV104 (Valsecchi and Amos 1996); GATA28 and GATA417 (Palsbøll *et al.* 1997); RW31, RW410 and RW48 (Waldick *et al.* 1999); GT23, GT211 and GT575 (Bérubé *et al.* 2000)) followed methods previously described by Constantine *et al.* (2012). Amplicons from 4 to 5 loci were co-loaded for capillary electrophoresis with an ABI 3730 or an ABI 3130. Alleles were sized with Genemapper v4.0 (Applied Biosystems) and all automated calling was confirmed by visual inspection (Bonin *et al.* 2004). To ensure that alleles were binned consistently between runs, replicate samples (3–10) from individuals of known genotypes were included in each run to act as 'allelic ladders', following best practice (e.g. Bonin *et al.* 2004). As a precaution against poor DNA quality, only samples that amplified at a minimum of 11 microsatellite loci were retained for further analyses (QC11 dataset).

Data management, analyses of microsatellite allele frequency and analysis of probability of identity for each

microsatellite locus and mtDNA were conducted using the program GenAlEx (Peakall and Smouse 2006). A binomial exact test was used to test sex bias within each of the NZ migratory streams.

Inclusion of previously published DNA profiles

Existing DNA profiles were available for individuals from the wintering grounds associated with International Whaling Commission breeding stocks spanning from West Australia to the Pacific Coast of South America (IWC 2016). Most of these profiles consist of the same loci and were generated by the methods described in the previous section as part of a long-term collaboration by members of the SPWRC and will be referred to here as the 'SPWRC dataset'. These wintering ground individual profiles are as follows: $n = 78$ from the Great Barrier Reef, Queensland, Australia and $n = 1402$ from New Caledonia (see Garrigue *et al.* 2020); $n = 346$ from Tonga, $n = 88$ from Samoa and American Samoa, $n = 207$ from French Polynesia and $n = 111$ from the Pacific Coast of Colombia (Steel *et al.* 2018).

Previously published DNA profiles were also available for the West and East Australia wintering grounds (Anderson *et al.* 2003; Schmitt *et al.* 2014a). These were both generated by different research groups but had previously been standardised with the SPWRC dataset through an exchange of calibrated samples (Anderson *et al.* 2003; Morin *et al.* 2010; Schmitt *et al.* 2014a, 2014b). The 204 individual DNA profiles available for West Australian whales were generated from samples collected off Exmouth and consisted of up to 10 microsatellite loci, all of which overlapped with the SPWRC dataset (Schmitt *et al.* 2014a). The 734 DNA profiles available for East Australia were generated from samples collected off the northern coast of New South Wales and the southern coast of Queensland, and consisted of up to 13 microsatellite loci, 12 of which overlapped with the SPWRC dataset but only 8 overlapped with the West Australian dataset (Anderson *et al.* 2010).

Duplicate removal, recapture identification and genetic diversity

The program CERVUS v3.0 was used to compare QC11 DNA profiles between- and within-years (Kalinowski *et al.* 2007). Within-year matches provide an indication of residency times between sampling events and locations, and between-year matches give an indication of migratory fidelity to NZ. For the final DNA register, only one copy of the DNA profile per region for each individual whale was retained and assigned a unique genetic-identification.

Confidence in matches was given by the average probability of identity (PID: Paetkau and Strobeck 1994), calculated in GenAlEx (Peakall and Smouse 2006). As a precaution against false exclusion due to allelic dropout and other genotyping errors (Waits and Leberg 2000; Waits *et al.* 2001), the initial comparison allowed for mismatches at up to three loci. The electropherograms of the mismatching loci were

subsequently reviewed and either corrected based on this visual inspection or the loci were repeated. A minimum overlap of eight loci was required to identify duplicate samples of an individual due to some incomplete genotypes. Where a pair-wise comparison did not meet this minimum overlap, the missing loci for the limiting genotype were repeated or the sample was removed from the dataset. Arlequin v3.5.2.2 (Excoffier and Lischer 2010) was used to estimate haplotype and nucleotide diversity of the mtDNA haplotypes and estimate diversity of microsatellite loci.

Connectivity and differentiation with wintering grounds

Both individual-based and population-level approaches were used to investigate connectivity of NZ with wintering grounds in Australia, Oceania and the east Pacific Ocean (Panama, Colombia and Ecuador). At an individual level, the DNA register (i.e. the collection of DNA profiles of unique individual humpback whales sampled on NZ migratory streams), was compared with the DNA registers of humpback whales sampled in the wintering grounds of East Australia, Oceania and the east Pacific to assess the movement of individuals between these regions.

For comparison with this individual-based approach, population level tests of genetic differentiation were conducted. Specifically, Arlequin v3.5.2.2 was used to estimate differentiation in mtDNA haplotypes (F_{ST} and Φ_{ST} ; Wright 1949; Weir and Cockerham 1984) between the NZ migratory streams and the wintering grounds. First the level of differentiation between wintering grounds was assessed and non-significant wintering grounds collapsed to regions. The NZ migratory streams were compared to these wintering regions. The significance of these differences was tested with a permutation procedure in Arlequin using 10,000 random permutations. To allow comparison to previously published analyses, Φ_{ST} was calculated by the same method as Olavarria *et al.* (2007), using unadjusted pair-wise differences. Φ_{ST} was also calculated after conducting model tests in MEGA v11.0.13 (Tamura *et al.* 2021) to determine the optimal substitution model. Genepop v4.7.5 (Rousset 2008) was used to estimate differentiation of the eight shared microsatellite loci between the three NZ migratory streams and the wintering regions.

Mixed-stock analysis

To assess the proportion of whales from different wintering grounds migrating past NZ, a mixed-stock analysis was conducted using mtDNA and the Rannala and Mountain model as implemented in SPAM v3.7 (Debevec *et al.* 2000). For this analysis, each of our three NZ migratory streams – NZnth, NZsth and Rangitāhua – were considered 'mixed stocks' and the wintering grounds were considered the 'source stocks'. The standard error of the apportionment was derived in SPAM v3.7 using 10,000 bootstrap re-samplings. Simulations conducted by Schmitt *et al.* (2014a) on a very similar dataset showed mtDNA data alone were slightly more accurate at

reapportioning a 'pure stock' than when combined with microsatellite data, although the combined data showed slightly more precise estimates. Given the reduced number of microsatellite loci available for this analysis (eight overlapping loci among datasets compared to 10 loci used in Schmitt *et al.* (2014a)) and likely improved results from mtDNA-based analyses, we chose to use the latter.

Results

Sample collection, quality control and individual identification

New Zealand migratory streams

Between 1998 and 2021, 306 skin samples were collected from humpback whales along mainland NZ: 190 from Cook Strait (northbound, NZnth), 94 from Fiordland (southbound, NZsth) and 22 from beachcast samples or opportunistic biopsy samples held in the NZCeTA. The number of samples per year ranged between 1 (1998 and 2003) and 47 (2012; Table 1). Eighteen of the NZCeTA samples were allocated to either northbound ($n = 12$) or southbound ($n = 6$) migration

Table 1. Number of skin samples collected from humpback whale migratory streams in Aotearoa New Zealand (NZ).

Year	NZnth		NZsth		Unknown	Rangitāhua
	Survey	NZCeTA	Survey	NZCeTA		
1998	0	0	0	0	1	0
2003	0	0	0	1	0	0
2004	12	1	0	1	1	0
2005	11	1	0	0	0	0
2006	10	1	0	0	0	0
2007	10	1	0	0	0	0
2008	16	0	0	0	0	0
2009	20	1	0	2	1	0
2010	24	0	0	0	0	0
2011	40	2	0	1	0	0
2012	47	5	0	1	1	0
2015 ^A	0	0	0	0	0	84
2016	0	0	0	0	0	34
2017	0	0	6	0	0	21
2018	0	0	32	0	0	0
2020	0	0	22	0	0	0
2021	0	0	34	0	0	0
Total	190	12	94	6	4	136

NZnth comprises dedicated surveys in Cook Strait (Survey), NZsth dedicated surveys in Fiordland (Survey) and in Rangitāhua, and from beachcast whales or opportunistic biopsies that have been placed in a migratory stream or unknown based on available sampling date information (NZCeTA).

^AResults from this year previously published in Riekkola *et al.* (2018).

based on the date of sampling and added to the NZnth and NZsth datasets respectively. The four remaining samples were removed from further analyses.

In addition to the 84 samples from 72 individuals collected from Rangitāhua in 2015 (Riekkola *et al.* 2018), a further 55 samples were collected in 2016 ($n = 34$) and 2017 ($n = 21$). When combined with the 302 samples collected around mainland NZ this gave a total dataset of 438 samples of which 415 (95%) successfully passed the quality control criteria of genotyping at a minimum of 11 loci.

After reconciling matches of DNA profiles between- and within-years, these 415 DNA profiles were found to represent 350 individual whales: 346 whales sampled one or more times within the same year and four sampled at least once in two or more years. Twelve of the individuals were beachcast at the time of sampling and were therefore unavailable for recapture in subsequent years. Three of the between-year recaptures were males sampled during the Cook Strait surveys (northbound): one whale was seen in 2004, 2005 and 2007, another in 2010 and 2011, and the third whale was seen in 2011 and 2012. The remaining between-year match was a female first sampled in Rangitāhua in 2015 and again in 2017. All matches were supported by an average of 13.4 matching microsatellite loci (range = 10–15). For a minimum of 10 loci the probability of a match by chance (PID) ranged from 1.0×10^{-8} to 4.1×10^{-14} depending on the variability of the loci in a given match. Based on this PID we are confident that the markers used were able to differentiate individuals in a population of a few thousand whales (Constantine *et al.* 2012).

After duplicates were removed there were 157 individuals in the NZnth migratory stream, 77 individuals in the NZsth migratory stream and 116 in the Rangitāhua migratory stream. There was a significant male bias in the sex ratio of sampled whales in the NZnth stream ($P < 0.0001$), consistent with findings from the East Australia migratory corridor (Brown *et al.* 1995) and wintering grounds in Oceania (Constantine *et al.* 2012). However, there was no significant sex bias in either of the southbound migratory streams (NZsth, $P = 0.3618$; Rangitāhua, $P = 0.1137$).

Wintering grounds

A further 824 samples were collected from the wintering grounds of American Samoa ($n = 138$), French Polynesia ($n = 272$), and the Pacific coasts of Panama ($n = 200$), Colombia ($n = 158$) and Ecuador ($n = 56$). Thirty-five of these samples failed to amplify for a minimum of 11 loci and were removed from the dataset, while the remaining 789 samples amplified for an average of 14.5 loci. The DNA profiles generated from samples collected from American Samoa, French Polynesia and Colombia were merged with the previously published dataset (Steel *et al.* 2018) and within-region duplicates were removed from all datasets. This resulted in a total of 214 individuals identified in American Samoa, 353 in

French Polynesia, 163 in Panama, 247 in Colombia and 49 in Ecuador (Table 2).

DNA profiles of the 78 individuals identified from samples collected on the Great Barrier Reef, Australia (Garrigue *et al.* 2020) were compared to the profiles of the 734 individuals from northern New South Wales and southern Queensland, Australia (Anderson *et al.* 2010) and three duplicates were identified. These duplicates were removed to form the 'Combined East Australia' DNA register (Table 2).

Individual connectivity of New Zealand migratory streams

Comparison of the NZnth, NZsth and Rangitāhua DNA registers showed no recaptures between these three migratory streams. However, there were 35 recaptures between NZ whales and wintering grounds. Comparison of the NZnth migratory stream and the wintering grounds of Australia, Oceania and the eastern Pacific revealed 23 recaptures

(Table S1), most (72%, $n = 18$) of which were with New Caledonia. Twelve (67%) of these 18 recaptures were males and six (33%) were females, reflective of the male sampling bias on both the wintering ground and for the northbound whales, where our data were predominantly from whales migrating through Cook Strait. There was one within-year recapture; a male was sampled in Cook Strait in 2012 and subsequently in the New Caledonian wintering ground in the same year, while the other 22 recaptures were in different years. The remaining five recaptures of the NZnth migratory stream were whales on the East Australia wintering ground, comprising three males and two females (Table S1).

There were two recaptures between the NZsth migratory stream and the wintering grounds of East Australia and Oceania. One was a male first sampled in East Australia in 2001 and subsequently in Fiordland in 2020. The other was a female first sampled opportunistically by DOC off Ngāmotu/New Plymouth (Fig. 1), west coast NZ in 2009 and subsequently again in New Caledonia in 2011 (Table S1).

Table 2. Collection years, number of samples that passed the quality control criteria (QC) of amplifying for a minimum of 11 loci (QC11), and number of individuals (# Ind. represented by a unique genotype) for humpback whales sampled on wintering grounds and the migratory streams of New Zealand.

Region	Abbreviation	Years	QC11	# Ind.	# M	# F	# U	# mtDNA
Australia wintering grounds								
West Australia ^A	WA	2007	—	204				185
Great Barrier Reef ^B		2011–2017	92	78	52	26	—	77
East Australia ^C		1996–2004	—	734	403	311	20	316
Combined East Australia	CEA			809	454	335		392
Oceania wintering grounds								
New Caledonia ^B	NC	1995–2017	1919	1402	827	549	26	1363
Tonga ^D	Tg	1991–2005	483	346	224	112	10	337
American Samoa/Samoa ^{D,E}	AS/Sa	2001–2019	232	214	155	58	1	206
French Polynesia ^{D,E}	FP	1997–2012	562	353	190	154	9	343
FP/AS/Sa		1997–2019	794	546	329	207	10	528
East Pacific wintering grounds								
Colombia ^{D,E}	Co	1991–1999, 2015–2018	293	247	152	64	31	222
Ecuador ^F	Ec	2006–2010	52	49	33	7	9	46
Panama ^E	Pa	2016–2019	200	163	106	57	—	159
Co/Ec/Pa		1991–1999, 2006–2019	545	452	287	125	40	420
Migratory streams								
New Zealand – northbound ^E		2004–2012	180	157	108	42	7	145
New Zealand – southbound ^E		2003–2021	100	77	38	34	5	74
Rangitāhua – southbound ^{E,F}		2015–2017	135	116	51	65	—	112

The number of males (#M), females (#F) and unknown sex (#U), and number with a mtDNA control region haplotype are also given.

^ASchmitt *et al.* (2014a).

^BGarrigue *et al.* (2020).

^CAnderson *et al.* (2010).

^DSteel *et al.* (2018).

^EIndicates additional samples analysed as part of this study.

^FRiekkola *et al.* (2018).

In addition to the four recaptures reported in Riekkola *et al.* (2018), a further five recaptures were identified between individuals sampled at Rangitāhua and the wintering grounds of Oceania. Four recaptures were from New Caledonia, bringing the total number of recaptures between these two regions to five (three males and two females). The remaining recapture was between a male first sampled in Tonga in 2002 and subsequently again at Rangitāhua in 2016. This brings the total number of recaptures between Rangitāhua and Tonga to three (one male and two females). The remaining recapture to Oceania was a male first sampled in American Samoa in 2009 and subsequently sampled in Rangitāhua in 2015 (reported in Riekkola *et al.* (2018)). Finally, one recapture was identified between Rangitāhua and the breeding ground of Panama in the east Pacific. This was a male first sampled in Rangitāhua in 2017 and subsequently again in Panama in 2018.

Between-region DNA profile recaptures matched at an average of 12.29 microsatellite loci, genetically identified sex and mtDNA control region haplotype. The probability of identity as calculated in Cervus ranged between 1.26×10^{-7} and 8.3×10^{-22} for the individual matches (Table S1).

Population level comparisons of migratory habitats

Wintering ground identity and mtDNA differentiation

The previously unpublished DNA profiles included here represent a substantial increase in the DNA register from the wintering grounds of French Polynesia, American Samoa and Colombia (Olavarria *et al.* 2007; Albertson *et al.* 2018). They also allow for new comparisons of these regions with Panama and Ecuador. With these additional samples and locations, an initial test of mtDNA differentiation was conducted between all wintering ground sampling locations to assess the level of genetic structure across the South Pacific. This showed no differentiation between the wintering grounds of Colombia, Ecuador and Panama, and confirmed the lack of differentiation between the wintering grounds of American Samoa/Samoa and French Polynesia first reported from a smaller dataset in Albertson *et al.* (2018) (Table S2). Given these results, these five wintering grounds were collapsed into two wintering regions, Colombia/Ecuador/Panama, hereafter Co/Ec/Pa, and French Polynesia/American Samoa/Samoa, hereafter FP/AS/Sa, and within region duplicates were removed (Table 2). Pairwise tests of mtDNA differentiation between the wintering grounds, and measures of haplotype and nucleotide diversity were repeated after the revision of these two regions (Table 3). The microsatellite-based genetic differentiation and diversity results were broadly similar to the mtDNA-based analyses but were less informative (Tables S3–S5), therefore we focus on the mtDNA results in the remainder of this paper.

Across all wintering grounds, a total of 117 mtDNA control region haplotypes were described from 3181 individuals. Patterns of regional haplotype and nucleotide diversity were similar to those reported in Olavarria *et al.* (2007) and Albertson *et al.* (2018), with New Caledonia having the

Table 3. Pairwise test of differentiation for mtDNA control region sequences of individual humpback whales sampled on wintering grounds of the east Indian Ocean and the South Pacific: WA (West Australia), CEA (Combined East Australia includes the Great Barrier Reef and other sites along the coast), NC (New Caledonia), Tg (Tonga), FP/AS/Sa (French Polynesia/American Samoa/Samoa) and Co/Ec/Pa (Colombia/Ecuador/Panama).

	<i>n</i>	WA	CEA	NC	Tg	FP/AS/Sa	Co/Ec/Pa
WA	185	–	0.0165	0.0143	0.0160	0.0303	0.0576
CEA	392	0.0336	–	0.0054	0.0145	0.0317	0.0567
NC	1363	0.0202	0.0043 0.0025	–	0.0067	0.0250	0.0512
Tg	337	0.0216	0.0054 0.0097	0.0013 0.0956	–	0.0132	0.0535
FP/AS/Sa	528	0.0585	0.0173	0.0202	0.0189	–	0.0681
Co/Ec/Pa	420	0.0536	0.0330	0.0328	0.0360	0.0435	–

Haplotype frequency, F_{ST} , differentiation shown above the diagonal, nucleotide, Φ_{ST} , differentiation shown below the diagonal. All P -values were <0.0001 except for the three shown in *italics*.

highest values for both measures ($h = 0.9735$ and $\pi = 2.08\%$), the east Pacific wintering ground of Co/Ec/Pa having the lowest haplotype diversity ($h = 0.9044$) and FP/As/Sa having the lowest nucleotide diversity ($\pi = 1.80\%$) (Table S6).

The haplotype differentiation of mtDNA was highly significant between the six designated wintering regions ($P < 0.0001$) (Table 3). Tests of nucleotide differentiation were also significant ($P < 0.0001$) for most pairwise comparisons, the exception being tests between East Australia, New Caledonia and Tonga. Within these, East Australia was significantly different to both New Caledonia ($P = 0.0025$) and Tonga ($P = 0.0097$), however Tonga and New Caledonia were not differentiated ($P = 0.0956$). This is different from results reported in Olavarria *et al.* (2007) where New Caledonia and Tonga were weakly differentiated at the nucleotide level ($P = 0.045$).

mtDNA differentiation between New Zealand migratory streams

Sequences of the mtDNA control region were available for 145 of the NZnth individuals, 74 of the NZsth individuals and 112 of the individuals at Rangitāhua (Table 2). A total of 69 mtDNA haplotypes was described from all three migratory streams. Both haplotype and nucleotide diversity were highest in Rangitāhua ($h = 0.9706$ and $\pi = 2.2\%$ respectively, Table 4). For the NZnth and NZsth whales, haplotype diversity and nucleotide diversity were very similar ($h = 0.9696$, $\pi = 2.16\%$, and $h = 0.9711$, $\pi = 2.13\%$, respectively, Table 4). Pairwise tests of mtDNA haplotype differentiation between the three regions showed that Rangitāhua was significantly different from both NZnth and NZsth ($F_{ST} = 0.0087$, $P \leq 0.0001$ and $F_{ST} = 0.0104$, $P = 0.0003$, respectively) but NZnth and NZsth were not significantly different from each other ($F_{ST} = 0.0015$, $P = 0.2492$). At the nucleotide level none of the three migratory

Table 4. mtDNA control region diversity of the three New Zealand (NZ) migratory streams; Rangitāhua – southbound, NZ northbound (NZnth) and NZ southbound (NZsth).

Migratory stream	n	k	Variable sites	h	π (%)
Rangitāhua	112	44	52	0.9706 ± 0.0049	2.2 ± 1.12
NZnth	145	41	51	0.9696 ± 0.0040	2.16 ± 1.10
NZsth	74	39	49	0.9711 ± 0.0075	2.13 ± 1.09

The total number of mtDNA haplotypes (*k*), number of variable sites, haplotype diversity (*h*) and nucleotide diversity (*π*) are given for each migratory stream.

streams were significantly different from each other, with Φ_{ST} values ranging from 0.0016 ($P = 0.2995$) between NZsth and Rangitāhua, to 0.0075 between NZnth and both NZsth ($P = 0.0946$) and Rangitāhua ($P = 0.0536$).

mtDNA differentiation between New Zealand migratory streams and wintering grounds

A total of 140 haplotypes including seven previously undescribed haplotypes (GenBank PX148109 to PX148115; Table S7) was identified in the entire dataset, with one haplotype present in the Rangitāhua stream not found in any of the wintering grounds EC007 (Riekkola *et al.* 2018). Pairwise tests of mtDNA haplotype differentiation showed that the three NZ migratory streams were significantly different from the six wintering grounds except for NZsth and the wintering ground of East Australia ($F_{ST} = 0.0002$, $P = 0.4077$; Table 5a). However, the differentiation between NZnth and East Australia was only weakly significant ($P = 0.0404$), suggesting a connection between both north and southbound migratory streams passing mainland NZ and the wintering ground of East Australia. For the Rangitāhua migratory stream, population pairwise tests agree with those reported in Riekkola *et al.* (2018), with all comparisons showing significant differentiation.

Most pairwise tests of nucleotide differentiation were also significantly different but weaker than for pairwise tests of haplotype frequency differences (Table 5a, b). The Rangitāhua stream is not differentiated from either the wintering grounds of New Caledonia ($P = 0.1358$) or Tonga ($P = 0.1468$). The NZsth whales were not differentiated from New Caledonia ($P = 0.4338$), Tonga ($P = 0.3240$) or East Australia ($P = 0.8305$). The NZnth stream is differentiated from all six wintering grounds but the level of differentiation is weak for the New Caledonia comparison ($P = 0.0458$).

Mixed-stock apportionment

Given the significant regional differentiation in mtDNA haplotypes, a mixed-stock analysis was considered appropriate for describing the apportionment of the three NZ migratory streams to the six wintering grounds. Results from these analyses suggest different but overlapping composition of wintering grounds for humpbacks migrating past NZ (Table S8,

Table 5. Pairwise tests of (a) haplotype frequencies and (b) nucleotide differentiation for mtDNA of individual humpback whales sampled on the three New Zealand (NZ) migratory streams (Rangitāhua – southbound, NZ northbound (NZnth) and NZ southbound (NZsth), with wintering grounds of the east Indian Ocean and the South Pacific (*P*-values given in parentheses).

Wintering ground	N	Rangitāhua (n = 112)	NZnth (n = 145)	NZsth (n = 54)
(a) Haplotype frequency differentiation				
WA	185	0.0172 (<0.0001)	0.0149 (<0.0001)	0.0140 (0.0001)
CEA	392	0.0114 (<0.0001)	0.0023 (0.0404)	0.0002 (0.4077)
NC	1363	0.0030 (0.0105)	0.0037 (0.0007)	0.0041 (0.0143)
Tg	337	0.0039 (0.0161)	0.0116 (<0.0001)	0.0148 (<0.0001)
FP/AS/Sa	528	0.0195 (<0.0001)	0.0260 (<0.0001)	0.0307 (<0.0001)
Co/Ec/Pa	420	0.0538 (<0.0001)	0.0553 (<0.0001)	0.0551 (<0.0001)
(b) Nucleotide differentiation				
WA	185	0.0245 (0.0004)	0.0254 (0.0002)	0.0285 (0.0013)
CEA	392	0.0095 (0.0135)	0.0119 (0.0033)	0.0000 (0.8305)
NC	1363	0.0024 (0.1358)	0.0040 (0.0458)	0.0000 (0.4338)
Tg	337	0.0030 (0.1468)	0.0095 (0.0117)	0.0008 (0.3240)
FP/AS/Sa	528	0.0222 (0.0005)	0.0360 (<0.0001)	0.0195 (0.0048)
Co/Ec/Pa	420	0.0352 (<0.0001)	0.0443 (<0.0001)	0.0308 (0.0006)

Locations are WA, West Australia; CEA, Combined East Australia includes the Great Barrier Reef and other sites along the east coast; NC, New Caledonia; Tg, Tonga; FP/AS/Sa, French Polynesia/American Samoa/Samoa; Co/Ec/Pa, Colombia/Ecuador/Panama.

Fig. 2). The apportionment of the Rangitāhua stream is consistent with results reported in Riekkola *et al.* (2018), with ~50% of the population apportioned to the wintering ground of New Caledonia, ~31% to Tonga and the remaining ~18% to FP/AS/Sa. Most of the NZnth stream apportioned to East Australia (53.9%, s.e. = 10.18%) and New Caledonia (45.9%, s.e. = 10.18%) with smaller apportionment to Tonga (1.5%) and FP/AS/Sa (0.9%), with the latter two wintering grounds having standard errors that overlapped with zero. The NZsth stream also showed the greatest apportionment to East Australia (60.8%, s.e. = 12.08%) with lower but still significant apportionment to New Caledonia (20.8%, s.e. = 11.79%) and West Australia (18.4%, s.e. = 6.25%).

Discussion

Historically, the coastal waters of NZ were part of important migratory pathways for exploited baleen whales including blue whales (Branch *et al.* 2007), southern right whales (Dawbin 1986; Carroll *et al.* 2015), and humpback whales (Dawbin 1959). For some species the migratory connections and routes appear to be lost or limited likely due to intensive historical whaling (Clapham *et al.* 2009) as seen in southern right whales that have yet to recolonise formerly important

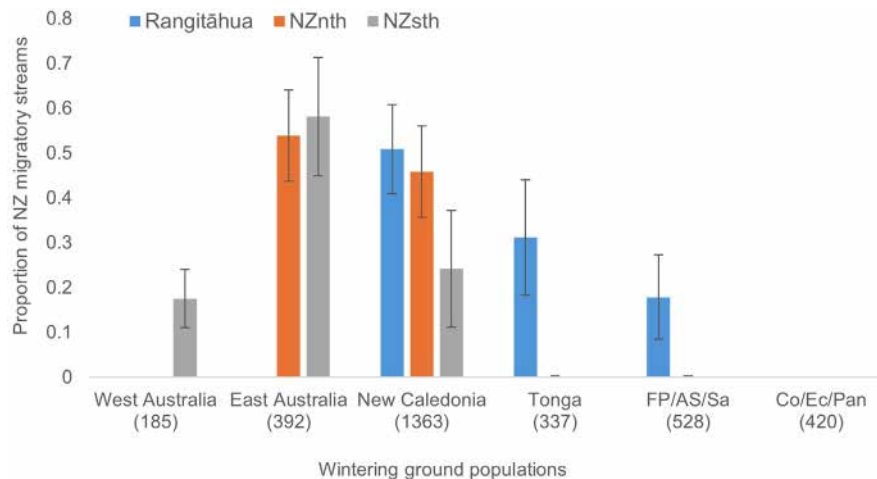


Fig. 2. Mixed-stock estimates of the three New Zealand (NZ) migratory streams, using mtDNA haplotypes and six wintering regions as source stocks; West Australia, East Australia, New Caledonia, Tonga, French Polynesia/American Samoa/Samoa (FP/AS/Sa) and Colombia/Ecuador/Panama (Co/Ec/Pan); sample size is under the region name. Blue bars represent proportion of each wintering ground estimated for the southbound Rangitāhua stream; orange bars represent proportion estimated for the northbound mainland NZ (NZnth) stream and grey bars represent proportion estimated for the southbound mainland (NZsth) stream. Error bars represent standard errors as derived in SPAM v3.7 using 10,000 bootstrap resamplings See Table S7 for details.

mainland NZ and offshore Rēkohu/Chatham Islands, and the Louisville Ridge regions (Richards 2002; Carroll *et al.* 2014; Cranswick *et al.* 2022). Antarctic blue whales have yet to recover in abundance but are acoustically detected in NZ waters mainly via their distinctive ‘Z-calls’, suggesting seasonal migration patterns (Warren *et al.* 2021). Humpback whales primarily use NZ waters as migratory pathways and short stopover locations rather than important feeding or wintering habitat (Dawbin 1959; Gibbs *et al.* 2018). Annual surveys of northbound humpback whales in the Cook Strait showed a small but significant increase in numbers over a 12-year survey period, suggesting slow recovery of this migratory population 50 years after an end to whaling (Gibbs *et al.* 2018). Migratory corridors or stopovers such as Cook Strait, Rangitāhua and Fiordland can serve as important geographic reference points for provisioning, socialising or resting to ensure successful onward migration. Feeding is well documented in East Australia waters (e.g. Owen *et al.* 2015; Pirotta *et al.* 2021), a region with strong connectivity to the Fiordland stream of whales in south-west NZ. Satellite tracking revealed humpback whales foraging in upwellings off the coast of Fiordland (Andrews-Goff *et al.* 2018), and some foraging behaviours (<10% of encounters) are observed in the nearshore fiord waters (Corne 2023). When whales from different breeding grounds interact at migratory sites, that contact can have effects that go beyond the individuals involved to influence the populations, such as the development of song (Garland *et al.* 2015; Owen *et al.* 2019). This is well known to the Indigenous people (Māori of the tribe Ngāti Kuri) that are kaitiaki

(guardians) of Rangitāhua (see Grose *et al.* 2020)) who, as ocean voyagers, have extensive knowledge of whales. Recent research on song (Owen *et al.* 2019) highlights the continued importance of remote habitats for whale aggregations as the whales recover throughout Oceania wintering grounds.

Humpback whale migratory streams through New Zealand waters

Whilst we have robust findings, of notable importance is that the three core sampling areas are geographically limited given the wide distribution of humpback whales in NZ waters. The genetic diversity and number of humpback sightings will increase with the recovery of this species. Future research may well find different patterns of genetic connectivity on the whales’ migration routes reflective of ongoing population growth. Individual movement and sharing of genetic diversity indicated connectivity between all three NZ migratory streams of humpback whales and the wintering grounds of New Caledonia. Unsurprisingly, there was a lack of connectivity to the east Pacific wintering grounds with one exception of a male humpback migrating south past Rangitāhua in September 2017 and subsequently sampled in Panama in September 2018. Perhaps further connections will be revealed through genetic or photo-identification matches in future work. With the relatively large sample size across the migratory streams in NZ waters, we found different patterns of association between each migratory stream and wintering grounds in the central Pacific and Australia.

Northbound migratory stream

Whales migrating north showed similar assignment proportions to both New Caledonia and East Australia in the mixed-stock analysis, although most of the individual recaptures were to New Caledonia, likely due to the larger and contemporaneous sample from this wintering ground available for comparison (Chero *et al.* 2020). Over the past 20 years, low levels of connectivity between whales migrating north to East Australia and New Caledonia have been reported via photo-identification, genetic and song analyses (e.g. Garrigue *et al.* 2000, 2011, 2020; Constantine *et al.* 2012; Franklin *et al.* 2014; Warren *et al.* 2020). During the *Discovery* marking program of the modern whaling era, most recaptures of NZ northbound whales were to East Australia followed by Fiji and Norfolk Island (Dawbin 1964). *Discovery* marks were deployed in New Caledonia, but the low number of deployments ($n = 32$) limited the chance of recapture and there was no whaling in that region, i.e. no chance for recapture of marks deployed elsewhere (Dawbin 1964). There are no contemporary samples from Fiji or Norfolk Island with which to assess current connectivity.

Southbound migratory stream

Whales migrating south had the strongest population level connectivity to East Australia, with one direct recapture, no significant genetic differentiation and the highest assignment values to this wintering ground. The mixed-stock analysis and one direct recapture also indicate a connection to the New Caledonia breeding ground. These findings are consistent with other methods, including satellite tracks from whales tagged in East Australia and New Caledonia including a female with a calf from New Caledonia that passed offshore of Fiordland (Garrigue *et al.* 2015; Andrews-Goff *et al.* 2018; Reisinger *et al.* 2021). The same tagged female was encountered in 2018 in the Ross Sea region, the feeding grounds to which she was tracked in 2012 (R. Constantine and C. Garrigue, unpubl. data). Historically, most records of humpback whales passing nearshore Fiordland were from their southern migration with very few records during the whales' northern migration (Dawbin 1956). The recent dedicated DOC surveys have revealed that most sightings of humpback whales occur during the late austral winter to spring but interestingly recent acoustic monitoring recorded whales throughout most of the year (Corne 2023). This may reflect the fully recovered East Australia population (Bejder *et al.* 2016; Noad *et al.* 2019), and overlapping north and south migration periods due to the different timing of demographic cohorts (e.g. Dawbin 1966; Franklin *et al.* 2011; Seyboth *et al.* 2023). Our mixed-stock analysis also suggested a connection between NZstH and West Australia that could reflect the occasional movement of whales between the west and east coasts of Australia (Noad *et al.* 2000; Andrews-Goff *et al.* 2018). Alternatively, this result could be due to the small sample sizes from each of these Australian populations relative to their current abundance; abundance in 2015 was estimated to be 24,545 for East Australia

(Noad *et al.* 2019) and 20,337 for West Australia (IWC 2016; Seyboth *et al.* 2023).

Rangitāhua migratory stream

Our additional samples confirmed previous reports highlighting the connections between the Rangitāhua migratory habitat and central Pacific wintering grounds (Riekkola *et al.* 2018). In comparison, there is only a single photo-identification connection between Rangitāhua and East Australia (Ngāti Kuri, unpubl. data) and no population level genetic data suggesting a strong connection to East Australia. To pass Rangitāhua, whales from Australia need to migrate eastwards either directly to Rangitāhua or via another Oceania wintering ground, rather than their more typical southern coastal route. Notably, with the connectivity between the growing populations in East Australia and New Caledonia (Orgeret *et al.* 2014; Garrigue *et al.* 2015; Noad *et al.* 2019; Chero *et al.* 2020), and more whales sighted in the former whaling area in the Chesterfield-Bellona Reef complex in the Coral Sea (Oremus and Garrigue 2014; Derville *et al.* 2020; Garrigue *et al.* 2020) in time there may be more whales from this region migrating past Rangitāhua, possibly including more northbound whales. Rangitāhua is the NZ migratory stream with connections to the most wintering grounds, with increasing numbers of whales from several different wintering grounds stopping for periods of up to 5 days to rest and socialise before they continue southeast to a 4500 km expanse of the Southern Ocean for feeding (Riekkola *et al.* 2018; Riekkola *et al.* 2019). Derville *et al.* (2019) predict that more southern regions, such as Rangitāhua, may become wintering grounds as increasing ocean temperatures make tropical Oceania waters unsuitable for humpbacks.

Fidelity to a migratory stream?

The low recapture of individuals across years within each of the three NZ migratory streams indicates either limited fidelity to a migratory route by individual humpback whales or suggests that large numbers of whales are passing through these migratory corridors, reducing the likelihood of between-year recaptures. For northbound whales, a recent acoustic study estimated 240 to 360 whales migrating north past Te Pātaka-o-Rākaihautū/Banks Peninsula which creates a pinch point, south of Kaikōura (Childerhouse *et al.* 2022). Based on acoustic recordings of humpback whale song offshore from Kaikōura, in the Cook Strait and in the South Taranaki Bight but very few recordings off Wairarapa (southeast North Island), most of the estimated 240 to 360 whales migrating along the Kaikōura coast are considered to move through the Cook Strait and into the Tasman Sea (Warren *et al.* 2020). This suggests that, currently, the low recapture rate in the Cook Strait surveys may be due to low fidelity of humpback whales to this migratory stream rather than many whales passing through this corridor. Alternatively, even though the estimated peak of migration was targeted with each annual Cook Strait

field season, interannual variability in migratory timing, particularly by different demographic cohorts of humpback whales (Dawbin 1966) possibly resulted in heterogeneity of sampling and a reduction in the likelihood of recaptures.

There is currently no estimate for the number of whales that join the southbound migratory stream passing Fiordland. Given the strong connection of this stream to the large East Australia population and the limited sampling as shown in our study, no conclusions about fidelity to this migratory route can be made. Similarly, increasing numbers of whales are passing Rangitāhua (Brown 2010; Gibson 2014; Riekkola *et al.* 2018) but there are no estimates of abundance for this remote island. There are photo-identification resights (e.g. Clark *et al.* 2017; Ngāti Kuri, unpubl. data) but with sporadic sampling and an increasing number of whales, we currently do not have sufficient genetic samples to observe the recaptures required to determine migratory fidelity.

Future migratory paths and connections

Given that the estimates of the wintering grounds are in the tens of thousands for both East and West Australia (see summary in Seyboth *et al.* (2023)), and thousands for Oceania (e.g. Constantine *et al.* 2012; Orgeret *et al.* 2014; Chero *et al.* 2020), recaptures with wintering grounds are likely influenced by the large numbers of whales in these regions. With the increased abundance of humpbacks throughout the Southern Hemisphere, and the vast expanse of Oceania winter breeding ground and Antarctic feeding grounds (Reisinger *et al.* 2021), connections with more remote locations, such as Central and South America and the West Antarctic Peninsula are more likely (e.g. Robbins *et al.* 2011; Stevick *et al.* 2013; Acevedo *et al.* 2022). Photo-identification has regularly been used to identify humpback whales in NZ waters since the 1990s (e.g. Constantine *et al.* 2007), and the increased use of automated platforms such as Happywhale (Cheeseman *et al.* 2022) and Flukebook (Blount *et al.* 2022) have increased the accessibility to images throughout the world, including citizen/community science. Many of the NZ humpback whale images have been uploaded into Happywhale and a preliminary assessment has revealed connections between whales migrating past NZ to East Australia, Norfolk Island, New Caledonia, Tonga and Panama, some of which we have also identified with DNA profiles (Cooper 2021).

The samples from dead, beachcast whales were valuable in supplementing dedicated biopsy survey samples and had the same patterns of connectivity. We recommend that these continue to be collected and curated in the National Archive (NZCeTA) as, over time, these samples may reveal other migratory streams e.g. north-east North Island that used to be a southbound migration route or whales from different populations. The presence of humpbacks almost year-round off Fiordland is interesting and worthy of further investigation (Corne 2023). The south-west coast of NZ was first identified as a provisioning area for humpback whales on southbound

migration during the whaling era (Dawbin 1956). More recently, area-restricted search behaviour identified by state-space modelling of satellite tagged whales (Andrews-Goff *et al.* 2018) and visual observation of foraging behaviour, most likely on zooplankton, and defecation of humpback whales (Corne 2023) indicate that the Fiordland region of the south-west coast continues to be a provisioning area. While the future environment in this region is uncertain due to climate change, modelling suggests that primary production will either increase or stay the same as primary productivity decreases in areas to the north (Chiswell and Sutton 2020). Under either scenario the Fiordland region will continue to be an important provisioning area for migrating humpback whales. As such, risks of interaction with anthropogenic activities such as tourism, fishing and aquaculture should be assessed and monitored.

One of the limitations of our study is sample size and determining how many whales are passing through NZ waters that are almost certainly growing each year, in line with population recovery rates (e.g. Gibson 2014; Gibbs *et al.* 2018). Quantifying the number of whales passing our three key study sites, and identifying increased sightings in other locations e.g. Kaikōura, Banks Peninsula (Childerhouse *et al.* 2022) will enable us to determine whether this issue is one of sample size, timing of sampling, fidelity to migration pathways or all three. With the collapse of some subpopulations due to whaling (e.g. Fiji, Gibbs *et al.* 2006; Miller *et al.* 2015), the whales using migratory paths through NZ waters may have been extirpated. This work reinforces previous studies showing that humpback whales can rediscover previously used migratory habitat (e.g. Clapham *et al.* 2008; Jackson *et al.* 2024), and in this case, have retained strong historical connections to the west Pacific region, including East Australia (Dawbin 1956, 1966). We suggest prioritising sampling in Fiji to understand contemporary connections of humpback whales to NZ and Oceania wintering grounds.

Conclusion

Despite more than 60 years since the collapse of humpback whale populations throughout Oceania (IWC 2015), our comprehensive genetic analysis of these three key migratory streams show that humpback whales retain the cultural memory and use of their pre-whaling migration routes. Using expanded DNA registers of whales from East Australia, Oceania and east Pacific wintering grounds, we revealed strong connections to the west Pacific region. Overall, the mainland NZ north and southbound migratory streams show strong individual and population level connections to East Australia and New Caledonia, with New Caledonia being the dominant migratory connection to Rangitāhua. Southbound whales passing Rangitāhua had connections to the widest range of wintering grounds supporting findings by Riekkola *et al.* (2018), reflecting the importance of this historic stopover

(Grose *et al.* 2020) as Oceania's humpback whales recover from near extinction.

Supplementary material

Supplementary material is available online.

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Data availability. The mtDNA haplotype GenBank codes and references to previously published research are provided in Table S7. To manage the data sovereignty of mana whenua – Māori (the Indigenous people of Aotearoa New Zealand) under Te Tiriti o Waitangi, use of the Aotearoa/New Zealand data that support this study will require permission upon reasonable request to the corresponding author (Rochelle Constantine r.constantine@auckland.ac.nz).

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