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A piece of the puzzle: analyses of recent strandings and historical records reveal new genetic and ecological insights on New Zealand sperm whales

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ABSTRACT: Cetacean strandings provide important opportunities to extend current knowledge on species or populations, particularly for species that are notoriously difficult to study, such as sperm whales *Physeter macrocephalus* (parāoa). Between 25 May and 9 June 2018, 13 male sperm whales stranded in Taranaki, New Zealand (NZ), with an additional male stranding 1 mo later in Clifford Bay, Marlborough. We profiled these 14 males for mitochondrial DNA (mtDNA) and carbon and nitrogen stable isotopes to examine their similarity to sperm whales from other geographic areas. Analyses of mtDNA revealed 7 haplotypes, including 1 not previously described ('New'), and an additional haplotype ('M') new to NZ that had been previously reported in sperm whales of the Pacific region. Analysis of rare haplotypes found in NZ males suggested genetic links within NZ and the Southwest Pacific. Differences in stable isotope ratios indicated that, despite the close temporal proximity of these stranding events, individuals originated from at least 2 separate groups, with the whale stranded in Clifford Bay identified as being a regular visitor to Kaikōura, South Island. The analysis of stranding records in NZ dating back to 1873 indicated an increase in recorded single strandings since 1970, and a peak in single strandings in the austral summer months, but no seasonality for mass strandings. Sex predicted latitudinal location for single strandings, with 95.1% of female strandings occurring north of 42° S, fitting the general global distribution of female sperm whales limited to lower latitudes. This study provides the first temporal and spatial assessment of sperm whale strandings in NZ and highlights the need for future research on movements and genetic exchange between NZ sperm whales and sperm whales in the wider Pacific region.

KEY WORDS: *Physeter macrocephalus* · Stable isotopes · $\delta^{15}N$ · $\delta^{13}C$ · Genetics · Haplotype diversity · mtDNA

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Māori abstract

TUHINGA WHAKARĀPOPOTO: E mihi ana mātou ki a Tangaroa (ā, e ai ki ētahi iwi a Te Tai Tokerau, ki a Tāne-Mahuta anō hoki) rāua ko Hinemoana, te kāinga o te parāoa. Ka mihi hoki mātou ki ngā whānau, ngā hapū, me ngā iwi e tiaki i tēnei taonga. Hoki atu ki te parāoa, nāna i whakapapa pounamu te moana hei ara mō te rangahau nei. I tua atu ki te hiranga o te pae parāoa (*Physeter macrocephalus*) ki ngā Māori (he kai, he mea whakairo hoki nā te kaiwhakairo), he mea hira ki te ao pūtaiao i te mea he āheinga tēnei ki te whakahōhonu tō tātou mātauranga kararehe o te moana. He kōtuku rerenga tahi te mahi rangahau parāoa. Mai i te 25 o Mei ki te 9 o Hune 2018, tekau mā toru ngā parāoa taurawhi e pae ana i ngā uta o Taranaki. Āpiti atu ki tērā, kōtahi te parāoa taurawhi e pāea i te Hūrae 2018 kei Te Tauihu-o-te-waka (Clifford Bay). Mā te mtDNA (he momo ira e tukua iho ngā māmā anake) me te kanoirite pūmau (te waro me te hauota) ka whakaahuatia ngā parāoa taurawhi. Ka whakaahua, ka kite ngā ritenga ki ngā tini parāoa nō ngā wāhi kē. E whitu ngā momo mtDNA e hua ana mai i te tātaritanga nei. Inarā, ko tētahi o ngā momo mtDNA he momo hou ('New'), ko tētahi atu he momo kāore anō i kitea kei Aotearoa engari i kitea kei Te Moana-nui-a-Kiwa whānui ('M'). E ai ki ngā momo mtDNA mokorea, he kaha ake te whanaungatanga o ngā parāoa taurawhi o Aotearoa ki ngā parāoa uwha nō Aotearoa, nō te māuru-mā-tonga o Te Moana-nui-a-Kiwa hoki. Ko ngā rerekētanga o ngā ōwehenga kanoirite pūmau e whakahahaki he rerekē te kāhui parāoa kei Taranaki ki te parāoa kei Clifford Bay, ahakoa he tata te wā e pae ana ngā parāoa nei i uta. Riterite tonu te parāoa i pāea kei Clifford Bay ki te toro ki Kaikōura. Ko ngā hua o te tātaritanga o ngā pūkete pāea kei Aotearoa (mai rā ano i te tau 1873), e tini piki ai ngā nama o te parāoa kōtahi e pae ana i uta mai rā anō i te tau 1970. I te raumati, ka tūtuki te tihi o ngā pae parāoa kōtahi. Heoi anō, he ōrite te nama o ngā pae parāoa e maha, puta noa i te tau. Ko te ira o te parāoa e aweawe te wahi e pāea. Arā, koni atu i te 95.1% o ngā parāoa uwha kōtahi e pae i ngā uta ki te tokerau o te ahopae 42°S. Orua tonu tēnei ki te mōhiohio ka noho ngā parāoa uwha ki ngā wai mahana, kei ngā ahopae o raro. Ahakoa kua kī te kete o Te Ao Māori i te mātauranga o ngā parāoa me ngā kāhui parāoa, ko tēnei te wā tuatahi e whakatere, e whakamānu te waka rangahau ki te rapu mātauranga parāoa mo te ao pūtaiao e pā ana ki ngā wahi me ngā wā i pae ai ngā parāoa ki Aotearoa. Kāore anō te kete mātauranga kia kī. He tino hira ngā hua o tēnei rangahau, engari he nui ngā pātai e toe ana. Me kohi tonu te mātauranga mō ngā haerenga o te parāoa, me te whakawhiti ira o ngā parāoa o Aotearoa me ngā parāoa o Te Moana-nui-a-Kiwa whānui. Whaowhia te kete.

1. INTRODUCTION

Deep-diving cetaceans are among the most challenging marine vertebrates to study, due their typically offshore distributions and extended time spent underwater. However, strandings of deep-diving species occur relatively frequently, providing opportunities to collect valuable information (Mesnick et al. 2011, Chiquet et al. 2013). Sperm whales *Physeter macrocephalus* are highly mobile top predators found in deep waters around the globe. Sperm whales have large home ranges and a complex social structure, making this species particularly challenging to study. Females live in partly matrilineal family units of ~10 females and their young (Whitehead 2003), while maturing males leave their natal group between 4 and 21 yr of age to form bachelor groups of varying size with other males of similar age (Best 1979). Males increase their range poleward with advancing age, with bachelor groups decreasing in size until fully mature males live largely solitarily (Whitehead 2018). Female-dominated social groups inhabit warmer waters at lower latitudes (up to ~40–50° north and south of the equator), while males generally reside in cooler waters at higher latitudes, except when pursuing breeding opportunities (Autenrieth et al. 2018, Schnitzler et al. 2018, Whitehead 2018). Although they are a highly mobile species, genetic information (e.g. maternally inherited mitochondrial DNA, mtDNA) has revealed that sperm whales, in particular female-dominated social groups, can display restricted geographical ranges in at least some ocean basins, such as the Indian Ocean (Alexander et al. 2016). In contrast, males disperse from their natal groups, and bachelor groups have long been thought to be comprised exclusively of non-related individuals. However, recent genetic evidence suggests that related males may be found within at least some bachelor groups (Girardet et al. 2022).

Sperm whales are classified as 'Vulnerable' in the International Union for the Conservation of Nature (IUCN) Red List, but are listed as 'data deficient' under the New Zealand Threat Classification System (Baker et al. 2019), since no abundance estimates exist. To date, most information on New Zealand sperm whales has been derived from field research conducted off Kaikōura, South Island, where a tourism industry is centred around transient and seasonally resident males (Jaquet et al. 2000b, Sagnol et al. 2014). Stable isotope analyses of sloughed skin of this population revealed differences in foraging patterns among individual males and seasons, indicating some level of individual foraging specialisation in a shared habitat (Guerra et al. 2020b). Beyond Kaikōura, very little is known about New Zealand sperm whales, their population structure, and their connection to other populations.

Sperm whales regularly live-strand or beach-cast along the New Zealand coastline, with New Zealand being 1 of 3 areas where mass stranding events of sperm whales frequently occur, with the other areas being the North Sea (Jauniaux et al. 1998, Pierce et al. 2007, Vanselow et al. 2009, IJsseldijk et al. 2018) and southern Australian waters (Evans et al. 2004, Sundaram et al. 2006). Marine mammal strandings offer valuable information on populations and species, including population dynamics, ecology, life history and morphology, toxicology, histology, and genetic relationships (Chiquet et al. 2013, Betty et al. 2019, Peters et al. 2020, Lischka et al. 2021, Stockin et al. 2021, Reeves et al. 2022). These data can indicate health status of individuals and populations (IJsseldijk et al. 2018), even if only tissue samples such as skin can be collected and archived long-term (Mazzariol et al. 2011).

Strandings occurring on New Zealand's mainland and offshore islands are recorded in the New Zealand Whale Strandings Database (NZWSDB) administered by the New Zealand Department of Conservation. While this resource has been used historically to gain a better understanding of whale strandings in New Zealand (Brabyn 1991, Brabyn & McLean 1992, Betty et al. 2020), the NZWSDB has yet to be extensively examined to specifically assess trends for sperm whales. Recent international studies have focussed on causation of sperm whale stranding events including geographical and biological factors and anthropogenic impacts (Unger et al. 2016, IJsseldijk et al. 2018, Mazzariol et al. 2018, Schnitzler et al. 2018). However, within New Zealand, only 3 sperm whale mass stranding events (dated 1987, 1994, 1997) out of 24 have undergone a forensic post mortem examination (NZWSDB), limiting inferences about causality to observed gross pathology. For example, blunt force trauma injuries (which may be indicative of vessel strike) are noted during external examinations, but it is difficult to determine if such injuries occurred ante versus post mortem, without any appropriate histopathological sampling.

This study represents the first temporal and spatial assessment of historical and contemporary stranding data of sperm whales in New Zealand. We also opportunistically used the stranding of 14 males between May and July in 2018 in New Zealand (13 mass stranded in Taranaki, and an additional individual stranded at Clifford Bay, northern South Island) to further examine potential connections to other populations through mtDNA and stable isotope analysis. The Taranaki event represents the largest sperm whale stranding in New Zealand since 2000, and the second largest recorded male sperm whale mass stranding in the country's history. The marked sexual segregation in distribution of sperm whales and the dispersal of males from their natal social groups leads to intriguing questions about how sperm whale bachelor groups form, and what the ultimate origins of individuals in these groups are. Our objectives were to (1) use mtDNA haplotypes to investigate potential geographic origins of New Zealand stranded males relative to other sperm whale populations, (2) assess carbon and nitrogen isotope values of the stranded individuals to gain insights into their foraging ecology and region, and (3) analyse contemporary and historical sperm whale stranding records in New Zealand to identify spatial and temporal trends in stranding events.

2. MATERIALS AND METHODS

2.1. Sampling and photo-identification of individuals stranded in 2018

We obtained skin and/or blubber samples from the 13 individuals that mass stranded in the Kaupokonui area of the South Taranaki Bight, south-west of Taranaki, North Island, and from the single animal stranded at Marfells Beach, Clifford Bay, South Island, in 2018 (Fig. 1; Table S1 in Supplement 1; both Supplements available at www.int-res.com/articles/suppl/m690p201_supp/). Tissues were stored at −20°C until processing.

We checked whether any of the stranded whales were individuals previously sighted at Kaikōura, a foraging ground where male sperm whales are re-

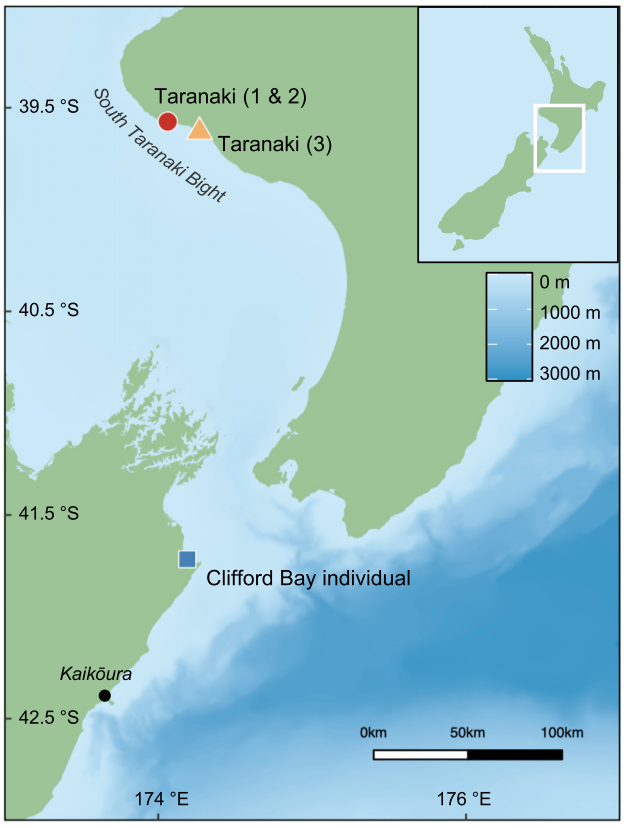

Fig. 1. Locations of sperm whales *Physeter macrocephalus* stranded in 2018. Subgroups are denoted by colour and labelled as location (subgroup). Bathymetry is depicted with darker shades of blue representing deeper waters (reprinted from NIWA under a Creative Commons BY licence, with permission from NIWA original copyright; CANZ 2008). Inset: location of pictured area in relation to New Zealand

ported routinely (Jaquet et al. 2000b). To identify potential matches between these individuals and the 256 unique individuals in the male sperm whale photo-ID catalogue of Kaikōura (Childerhouse et al. 1995), photographs of the flukes were manually matched by a single, experienced observer (M. Guerra). These comparisons were based on the natural marks (e.g. nicks and notches) along the trailing edge of the flukes.

2.2. Genetic sexing

We extracted DNA from the skin (and blubber in the case of 1 sample where the skin was not attached) using Qiagen DNeasy Blood and Tissue Kits following the manufacturer's protocol. Molecular sexing was undertaken by targeting the SRY and ZFX gene loci (Rosel 2003). We carried out PCR in 25 µl volumes using the MyTaq™ DNA Polymerase Kit (Bioline) including: 0.3 µM of the primers PMSRYF (Richard et al. 1994), ZFX0582F and ZFX0923R (Bérubé & Palsbøll 1996); 0.6 µM of the primer TtSRYR (Rosel 2003); and 50–75 ng of template DNA. Thermocycling followed the protocol described by Rosel (2003) and entailed an initial denaturation at 92°C for 30 s, followed by 35 cycles of 94°C for 30 s, 41°C for 45 s and 72°C for 45 s. We ran the PCR products plus a negative control on a 2.8% agarose gel at 80 V for 1 h, to observe the separation of amplicons indicating male (2 bands) or female (1 band).

2.3. Analyses of mtDNA

We amplified and sequenced the first 399 bp of the hypervariable region of the mtDNA control region using the primer Pmac D, designed specifically for sperm whales, and the generic cetacean primer TRO (Mesnick et al. 2011). PCR was carried out using the MyTaq DNA polymerase kit and entailed an initial denaturation at 90°C for 2 min, followed by 35 cycles of 94°C for 10 s, 48°C for 10 s and 72°C for 10 s, with a final extension at 72°C for 5 min as per the protocol of Mesnick et al. (2011). These amplicons were purified using the ExoSap reagents and protocol (Thermo Fisher Scientific) and forward and reverse Sanger sequenced by Macrogen Korea. Sequence chromatogram examination (by eye) and quality control were carried out in Geneious 9.0.5 (Biomatters Development Team). We trimmed primer sequences and poor-quality reads from the beginning and end of each sequence. We aligned the forward and reverse sequences, checked for consistency (ignoring any nucleotides with a Base Call Quality <20 according to Geneious), and created a consensus sequence for each individual.

To compare the mtDNA haplotypes found among New Zealand males with diversity elsewhere, we aligned our sequences with haplotypes from Alexander et al. (2016), Girardet et al. (2022) and Day et al. (2021) using the Geneious 9.0.5 algorithm. Haplotypes unique over a 624 bp consensus region (ignoring missing data at the beginning/end of sequences), corresponding to the start of GenBank sequences MT939514–MT939515 from Day et al. (2021) and the end of KU719571 from Alexander et al. (2016), were exported in nexus format (see Supplement 2 Alignment_including_IO_network.nex) and used to construct a haplotype network using the median-joining method (Bandelt et al. 1999) in PopArt (Leigh & Bryant 2015). Despite the shorter length of the sequences from our study (399 bp), the position

of variable sites allowed us to assign our sequences to 1 of the 47 unique haplotypes included in this alignment. To broadly investigate potential geographic links between New Zealand male strandings and other locations, we visualised haplotypes based on whether they were previously found in New Zealand, the Indian Ocean, the Pacific Ocean, SW Australia or SE Australia. SW and SE Australia were visualised separately from the oceanic data due to Australia's position straddling the Indian and Pacific Oceans and its proximity to New Zealand.

Haplotype frequency information collated from Alexander et al. (2016), Day et al. (2021), Girardet et al. (2022) (and references therein) was used: (1) to visualise haplotype frequency differences between the 2018 Taranaki male strandings and other regions within the Indian and Pacific Oceans (using haplotype_data.txt provided in Supplement 2 as input) and (2) to calculate Weir & Cockerham's (1984) F_{ST} and Fisher's exact tests of differentiation between these regions, using R 4.05 (R Core Team 2022) and the R package 'hierfstat' v 0.5-9 (Goudet 2005). See Supplement 2 for code (Plotting_haplotypes.R) and details of R packages used to create visualisations (Text S1 in Supplement 1). We carried out similar broad-scale comparisons using haplotype frequency as those investigated for the haplotype network. In addition, we used the regional areas within the Indian Ocean, Pacific Ocean and Australia defined by previous publications (Alexander et al. 2016, Day et al. 2021, Girardet et al. 2022) to investigate geographic affinities at a finer scale.

2.4. Stable isotope analysis

We used the stable isotope ratios of carbon (^{13}C:^{12}C, referred to as $\delta^{13}C$) and nitrogen (^{15}N:^{14}N, referred to as $\delta^{15}N$) of 13 skin samples (12 from the Taranaki stranding plus the whale stranded in Clifford Bay) as proxies for habitat and trophic position, respectively. Using a stainless-steel scalpel, we cut approximately 10 mg of each sample in very fine slices and then oven dried them for 24–48 h.

To avoid reporting biased $\delta^{13}C$ values caused by ^{13}C-depleted lipids present in cetacean skin (DeNiro & Epstein 1978, Hebert & Keenleyside 1995, Lesage et al. 2010, Ryan et al. 2012, Giménez et al. 2017), we lipid-extracted all samples (following methods reported by Peters et al. 2020). As lipid extraction can affect $\delta^{15}N$ values in unpredictable and non-linear ways which are not possible to correct for, we used the non-lipid extracted $\delta^{15}N$ values for all samples.

We sealed 0.5–1.0 mg of dried homogenised sample into tin capsules which we analysed using a DELTA V Plus continuous flow isotope ratio mass spectrometer linked to a Flash 2000 elemental analyser with a MAS 200 R autosampler (Thermo Fisher Scientific). Details of analytical set up can be found in Peters et al. (2020). Repeat analysis of National Institute of Standards and Technology (NIST) standards produced data accurate to within better than 0.15‰ for both $\delta^{15}N$ and $\delta^{13}C$, and a precision of better than 0.22‰ for $\delta^{15}N$ and 0.24‰ for $\delta^{13}C$.

Isotopic ratios were calculated as:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N, and R_{sample} and $R_{standard}$ are the ^{13}C:^{12}C and ^{15}N:^{14}N ratios in the sample standard, respectively (see the extended methods in Text S1 for more details on the analytical protocol).

We calculated mean ± 1 SD for $\delta^{15}N$ and $\delta^{13}C$ values across all 13 samples. As the trophic position and foraging grounds of individuals can differ with age, we assessed the correlation between both $\delta^{15}N$ and $\delta^{13}C$ values and total body length (as a proxy for age) using the Spearman correlation test.

2.5. Demographic and spatial analysis of sperm whale records

The NZWSDB comprises over 3500 cetacean stranding events, systematically recorded since the 1970s by the Department of Conservation (Berkenbusch et al. 2013), with some historical records dating back to the 1800s. We extracted all stranding records including sperm whales, and cross checked these to remove any duplicates and any individuals that had been refloated and thus could potentially have stranded again and be double counted. We also removed all records for which species identification could not be confidently confirmed either by photograph or body morphometric diagnostic measurements (e.g. dorsal fin height, mouth gape, snout to blow hole), resulting in 278 vetted records involving 594 individuals. A 'single stranding' was defined as involving only 1 individual or a mother–calf pair, a 'mass stranding' was defined as 2 or more independent individuals (i.e. not a mother–calf pair), as per Betty et al. (2020). Strandings are usually defined as individuals that are found alive or freshly dead (Stockin et al. 2009), which indicates that they had originally washed ashore alive. However, many records in the historical database have been recorded

post mortem with no way of determining whether the animal stranded alive or died at sea. Therefore, in this study, we refer to 'strandings' but also include beachcast individuals (i.e. individuals which, to our knowledge, could have already been dead when washed ashore). Events including single sperm whales comprise a mixture of live strandings and beachcast individuals (or parts thereof) as well as reports of animals found floating dead at sea. Individuals involved in mass stranding events generally wash ashore while still alive and usually die as a consequence of being stranded (Cordes 1982). Historical records were further reviewed based on their temporal and spatial proximity to determine potential associations between events. Events within 30 d of occurrence and a distance of <200 km were categorised as 'potentially associated'. Since 'potentially associated' single stranding events could not confidently be assigned to either mass or single stranding events, we excluded them from further analyses. Based on the temporal and spatial separation between events, and on our findings (size of individuals and isotopic differences, see Section 3), we considered the 2018 male strandings as 2 independent events for further analysis: 1 mass stranding comprising 13 individuals in Taranaki, and a single stranding of a male sperm whale at Clifford Bay.

We determined age class within the stranding records as adult or juvenile, based on recorded morphometric measurements of total body length (m). Female and male sexual maturity is estimated to be 8.8–10.7 m (median 9.75 m) and 9.4–15.7 m (median 12.55 m), respectively, in the northern hemisphere (Clarke 1956, Nishiwaki et al. 1958, Rice et al. 1986), and 8.2–8.8 m (median 8.5 m) and 10.1 m, respectively, in the southern hemisphere (Best 1968, Clarke et al. 2013). As these values are based on very few studies, we used the average of the medians of both hemispheres for each sex (9.1 m for females, 11.3 m for males) as our threshold estimates of maturity. For sex determination of historical records, we used previously published genetic sex-determination (Alexander et al. 2016) and external anatomical features where available. Given the evidence for the formation of social bonds within groups of either sex (Christal & Whitehead 2001, Kobayashi et al. 2020), it is likely that stranded groups had social bonds between individuals. However, because we cannot confirm that the individuals involved in mass strandings recorded by the NZWSDB were members of a cohesive social group, here we refer to mass strandings consisting of males as 'male-dominated groups' as opposed to 'bachelor groups' and to those consisting of females or a mix of females and males as 'female-dominated groups'.

For descriptive purposes, we categorised the location of each stranding event as follows: East Coast, West Coast, South Coast, or Offshore Islands, including Rakiura/Stewart Island, Rangitāhua/Kermadec Islands, and Rēkohu/Chatham Islands. East and West Coast were delineated by Cape Reinga and Lake Ferry (North Island), and Marlborough Sound (South Island). South Coast was defined as the southern coastline of the South Island from Papatowai to Coal Island.

Due to the different nature of single strandings and mass strandings (see Section 4), we analysed these independently. When analysing the stranding records, we investigated the following (details below): temporal trends in frequency of strandings (i.e. over time), seasonal trends in frequency of strandings, differences in seasonal occurrence of stranding events in regard to group type or sex, latitudinal stranding location in regard to sex and season, differences in group size for male- and female-dominated groups and differences in presumed age class for single strandings.

We investigated temporal trends in stranding events by testing for a correlation between each decade and the number of events per decade, using the Spearman correlation test. We assessed differences in stranding frequency between seasons irrespective of group type or sex using a chi-squared test. To compare seasonality between group type and sex, we used Fisher's exact test (for group type of mass strandings) and a chi-squared test (for sex of single strandings).

To test if sex (male or female for single strandings) and group type (female- or male-dominated for mass strandings) or season predicts latitudinal stranding location, we analysed strandings with known type/sex, season and location (mass strandings n = 19, single strandings n = 139) using generalised linear models (McCullagh & Nelder 1989). The continuous response variable was latitude, and the categorical predictor variables were group type (female- versus male-dominated, for mass strandings), sex (for single strandings), and season (categorical variable with 4 levels corresponding to austral seasons: spring = September–November, summer = December–February, autumn = March–May, and winter = June–August). We used an inverse-Gaussian error structure with an inverse-square function. For each mass and single stranding, we built 5 models using all possible combinations of factors including their interactions, plus the null model, and compared models

according to Akaike's information criterion corrected for small sample size (AICc) (Burnham et al. 2011).

We tested for differences in presumed age classes for single strandings of male and female sperm whales using Fisher's exact test. To gain a better understanding of male and female sperm whale group size in New Zealand, we compared group size for mass strandings between female-dominated and male-dominated groups using a 2-sample randomisation test with 10 000 permutations at an α value of 0.05. This test compares the difference of the mean group size between female-dominated and male-dominated groups with the difference obtained by randomly allocating the group sizes among the 2 group types (Manly 1997).

All analyses were completed in R (version 4.1.0, R Core Team 2022).

3. RESULTS

3.1. Demographics and mtDNA haplotypes of 2018 stranded individuals

Between 25 May and 7 July 2018, a total of 13 male sperm whales stranded in South Taranaki, North Island, as well as 1 male at Clifford Bay, South Island (Fig. 1). Based on their total body lengths (Table S1), all 14 individuals were categorised as mature males. No matches were found between the 13 individuals stranded at Taranaki and the Kaikōura photo-identification catalogue (University of Otago Marine Mammal Research Group unpubl. data). The individual whale stranded at Clifford Bay was identified by local whale-watching tour operators from Kaikōura as 'HL50' (locally known as 'Kaha') based on its tail fluke. While there were no photographs showing the entire fluke, partial photographs of the fluke later confirmed the match to HL50 from the Kaikōura catalogue. This whale was first sighted at the Kaikōura Canyon in 2005, and was regularly sighted in 2017–2018 (University of Otago Marine Mammal Research Group unpubl. data).

We identified 7 mtDNA haplotypes among the 14 whales, including 1 haplotype ('New') that had not been previously described, including among novel haplotypes recently described by Day et al. (2021) and Girardet et al. (2022) (Fig. 2). This haplotype is 1 bp different from haplotype 'A', the most common global sperm whale mtDNA haplotype (Fig. 2). Five of the 7 haplotypes, i.e. all apart from the 'New' haplotype and haplotype 'M', had previously been described in New Zealand. Haplotype 'M' was previously described as being widespread but at low frequency in locations within the Pacific Ocean (Alexander et al. 2016). There was no obvious relationship of mtDNA haplotype and stranding subgroup (Table S1). The new haplotype described in this study has been deposited in GenBank (accession no. MZ666108), with the other haplotypes represented by the previously published sequences ('A': KU719571–74, 'B': KU719575–77, 'C': KU719578–80,

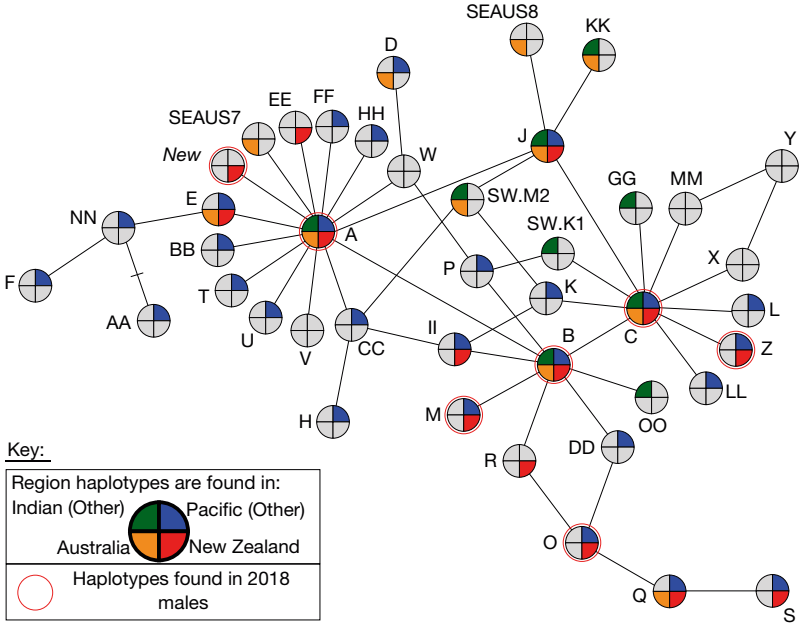

Fig. 2. Mitochondrial DNA haplotype network based on all globally available genetic data for sperm whales. Haplotypes are represented by circles alongside their identifying letter, and joined by a line to other haplotypes that are 1 nucleotide substitution different, or with a line and cross hatch when 2 substitutions differ. If haplotypes are not found in a region, or cannot be confidently assigned to a region based on published metadata, the appropriate segment is greyed out. Haplotypes found in the 2018 New Zealand strandings are outlined with a red circle; M was previously unknown from New Zealand, and 'New' is a previously undiscovered haplotype. Due to missing data, not all haplotypes displayed, including the following haplotypes previously found only in the Pacific (excluding New Zealand): I (represented by haplotype 'A' in haplotype network), JJ (represented by 'C'), and G (represented by 'E'); a haplotype ('N') widespread throughout the Indian and Pacific Oceans, Australia, and New Zealand (represented by 'B'); and a haplotype ('SEAUS1') restricted to Australia (represented by 'A')

'M': KU719591, 'O': KU719595 and 'Z': KU719606). All metadata for the samples from the 14 whales (including associated haplotypes) have been uploaded to the Genomics Observatories Metadatabase (GEOME; Deck et al. 2017, Riginos et al. 2020), available at GUID https://n2t.net/ark:/21547/Dyo2.

3.2. Genetic comparisons with other regions

Based on an examination of all mtDNA haplotype data available for sperm whales within the Indian and Pacific Oceans, including the individuals haplotyped in this study, we found that New Zealand males showed greater differentiation from regions of the Indian Ocean and SW Australia, than from SE Australia, New Zealand females, or Pacific Ocean populations (Fig. 3). The 2018 strandings (n = 14) and total New Zealand male sample (n = 34) show the lowest differentiation with the New Zealand female (n = 15) and Other Pacific Ocean samples (n = 967), and increasing differentiation to SE Australia (n = 72), Other Indian Ocean (n = 184), and SW Australia (n = 60). The greater differentiation between New Zealand males and populations within the Indian Ocean was also supported at a finer regional scale (Fig. S1 in Supplement 1).

As several sperm whale haplotypes have globally high frequencies (i.e. 'A', 'B', 'C', 'J', 'E' and 'N' are each present in >2% of sperm whales across both the Indian and Pacific Oceans; Fig. S2), we further examined rare haplotypes for more targeted information on the genetic relationships among populations following Rendell et al. (2012). Of the Indian and Pacific Ocean populations included in our comparison, only populations in the Pacific Ocean and Tasmania share rare haplotypes (<2% frequency in Indian and Pacific Oceans) that are present in New Zealand male strandings ('M', 'O', 'Q', 'R', 'S' and 'Z'; Fig. 4). Furthermore, outside of New Zealand, only the 'Southwest Pacific' region had an appreciable frequency of individuals (16.3%) that share these haplotypes (compared to 20% within New Zealand female samples). The 'Southwest Pacific' region was defined by Alexander et al. (2016) based on the broad geographic aggregation used in the previous studies of Whitehead et al. (1998) and Rendell et al. (2012), spanning roughly from east of Gisborne (38° 39′ 45″ S, 178° 1′ 4″ E) to ~150° W in longitude, and from Gisborne to the equator in latitude.

3.3. Carbon and nitrogen stable isotope analysis

Isotopic values of the whales stranded at Taranaki ranged from −17.6 to −16.5‰ in $\delta^{13}C$, with a mean of −17.2 ± 0.3‰, and from 14.0 to 15.2‰ in $\delta^{15}N$, with a mean of 14.5 ± 0.3‰ (Fig. 5A, n = 12). Mean $\delta^{13}C$ values of the 12 analysed individuals overlapped with those reported in sperm whales off Kaikōura Canyon (South Island, New Zealand) during the austral winter (Kaikōura: −17.1 ± 0.4‰), but $\delta^{15}N$ values were lower (Kaikōura: 15.6 ± 0.7‰) (Fig. 5) (Guerra et al. 2020b). The male stranded at Clifford Bay (i.e. HL50 in the Kaikōura catalogue) had the highest

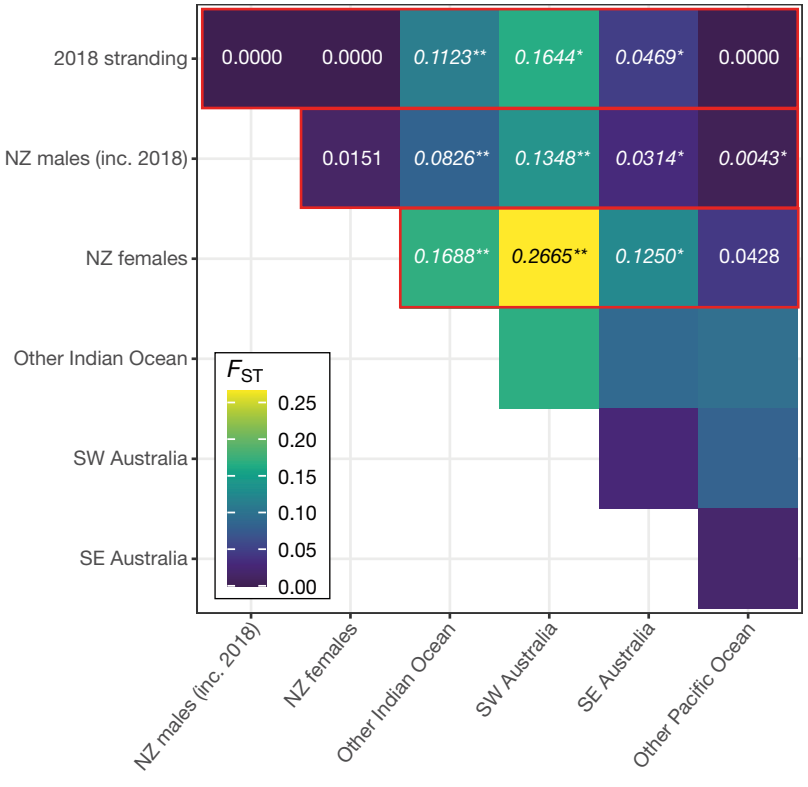

Fig. 3. Pairwise F_{ST} between New Zealand samples and broad groupings of regional populations ordered from east to west (see Fig. S1 for finer regional scales). Specific F_{ST} values in comparison to New Zealand samples are given. Significant differentiation between strata was tested using a Fisher's exact test, with *italics* denoting significance (*p < 0.05; **p < 0.001). In some cases, sample size corrections (Weir & Cockerham 1984) resulted in an F_{ST} of 0, while Fisher's exact test still detected significant differentiation in allele frequencies

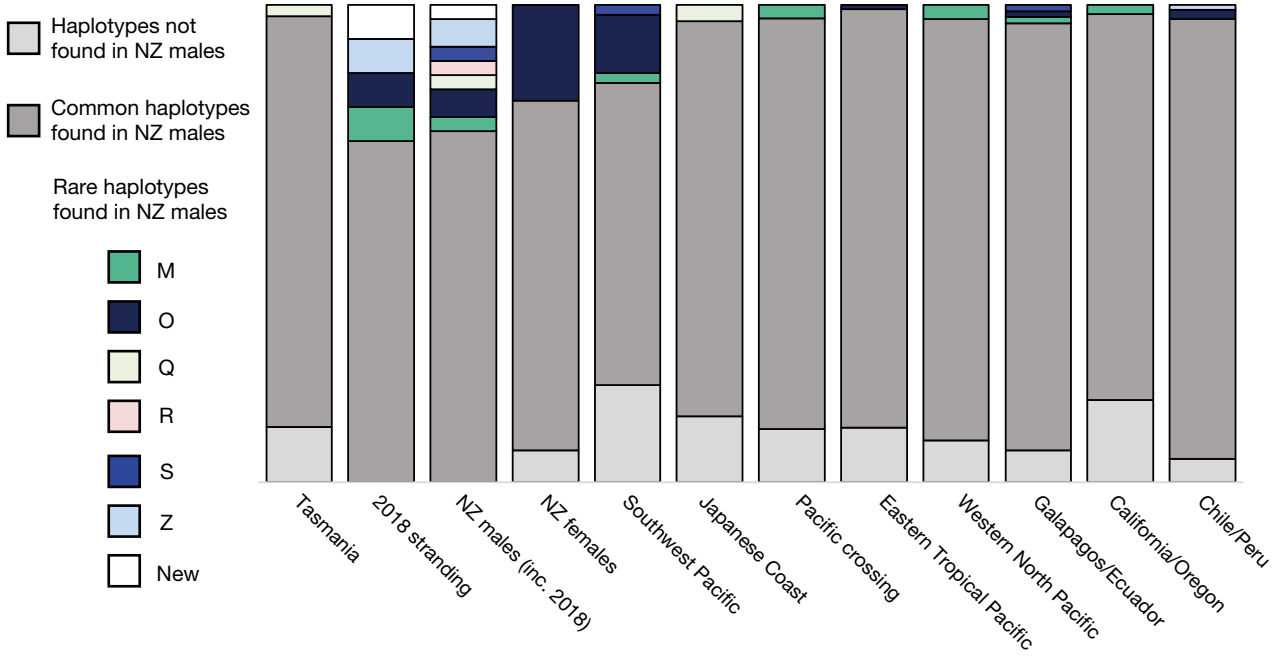

Fig. 4. Composition of haplotypes in regions that share rare haplotypes found in New Zealand male sperm whales ('M', 'O', 'Q', 'R', 'S', 'Z', 'New'), showing a greater percentage of shared rare haplotypes with New Zealand females and the 'Southwest Pacific'. Haplotype distributions and locations for all sampling localities shown in Fig. S2

$\delta^{13}C$ (–16.5‰) and $\delta^{15}N$ value (16.3‰) of all the 13 analysed individuals, overlapping with the values for sperm whales off Kaikōura in both $\delta^{13}C$ and $\delta^{15}N$ (Fig. 5A). The stable isotope values of this individual were almost identical to those previously measured in skin samples collected from the same individual, while still alive, at Kaikōura (most recent values from 2017: $\delta^{15}N$ = 16.3; $\delta^{13}C$ = –16.6; Guerra et al. 2020a). Body length was not significantly correlated with $\delta^{13}C$ (Spearman's rank, r = 0.31, p = 0.30) or $\delta^{15}N$ values (Spearman's rank, r = 0.51, p = 0.07, Fig. 5B,C).

3.4. Spatial and demographic analysis

Since 1873, a total of 596 sperm whales stranded in 280 separate events have been recorded in New Zealand (NZWSDB), comprising 24 mass strandings (13 male-dominated groups, 6 female-dominated groups, 5 groups of unknown type) and 235 single strandings (100 males, 41 females, 94 individuals of unknown sex; Fig. 6). Additionally, we identified 21 single stranding events which we deemed to have potentially been associated in groups of 2 or 3, thus representing a total of 10 potential mass stranding events (Fig. S3). These events were excluded from further analyses. Recorded numbers of both mass strandings and single strandings per decade increased throughout the study period, particularly since the second half of the 20th century (Fig. 7).

For mass strandings, the null model (containing no explanatory variables) was the best supported model, suggesting that sex and season do not predict latitudinal stranding location. Mass strandings were relatively evenly distributed across seasons (χ^2 = 0.85355, df = 3, p = 0.8366), albeit with a small sample size (spring = 33.3%, n = 8; summer = 16.7%, n = 4; autumn = 29.2%, n = 7; winter = 20.8%, n = 5), (Fig. 7; Table S2). No male-dominated mass strandings were recorded in summer; however, 3 of the 4 mass strandings recorded in summer were of unknown type, precluding further conclusions. The difference in season between female- and male-dominated groups was not significant (Fisher's exact test: p = 0.4298). In terms of group size, sperm whale mass strandings contained between 2 and 72 individuals (mean = 14.2 ± 18.1) across all 24 events. Stranded female-dominated groups (mean = 36.0 ± 23.7, range 2–72) were significantly larger than stranded male-dominated groups (mean = 7.8 ± 8.3, range 2–31) (randomisation test p < 0.0001; Table S2).

For single strandings (numbers summarised in Table S3), the best supported model retained sex as an explanatory variable for predicting latitude, ex-

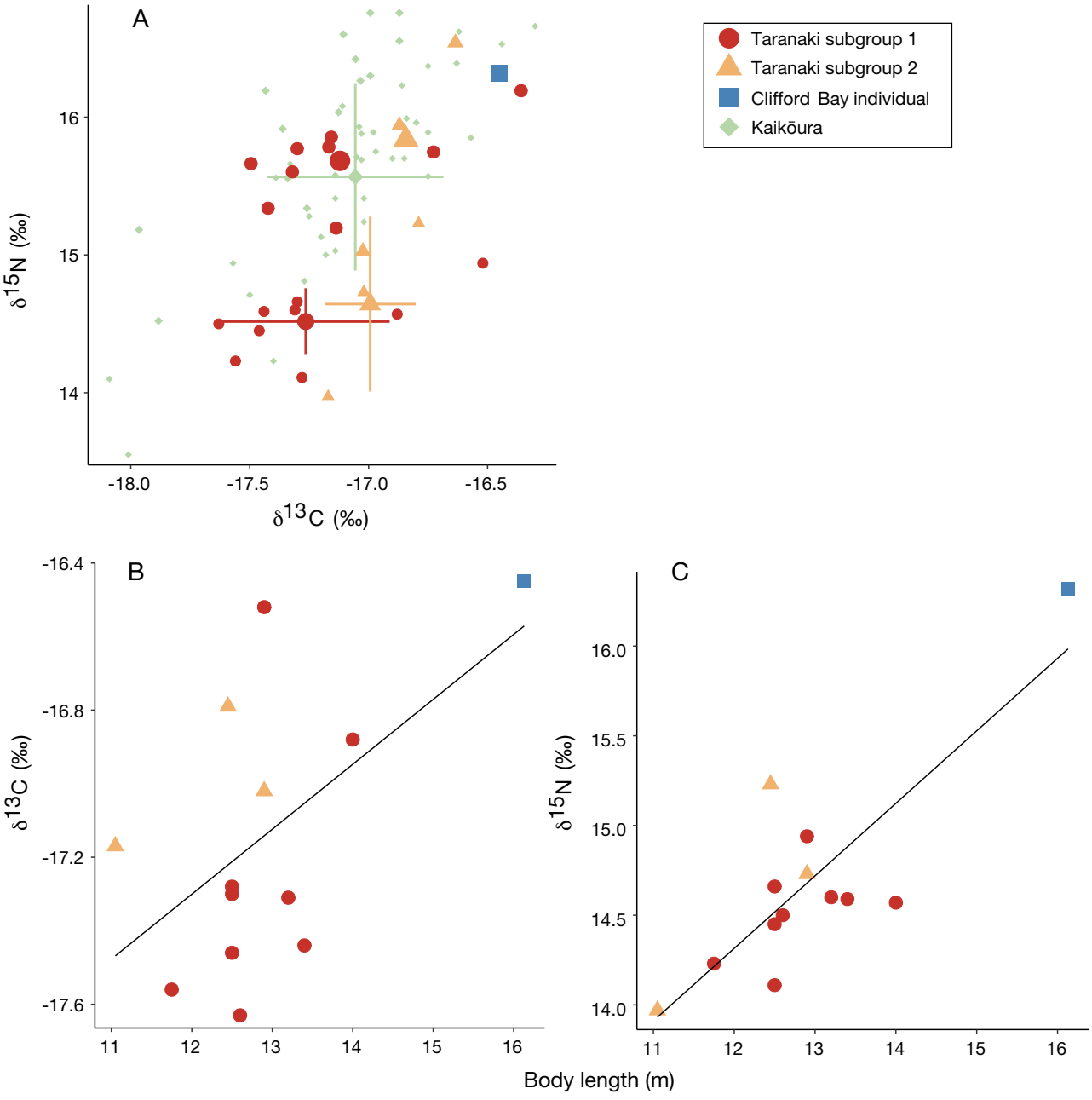

Fig. 5. (A) $\delta^{13}C$ and $\delta^{15}N$ values of sperm whales *Physeter macrocephalus* stranded in 2018 in New Zealand, as well as data of male sperm whales observed in Kaikōura during winter by Guerra et al. (2020b). Also shown are relationships between body length and (B) $\delta^{13}C$ and (C) $\delta^{15}N$. In panel A, large symbols show means, bars represent SD. Red dots and orange triangles indicate the subgroups of the Taranaki mass stranding, the blue square shows the single individual stranded at Clifford Bay, and green diamonds represent isotopic data from Guerra et al. (2020b)

plaining 12.04% of deviance (Table S4). Single strandings were not distributed evenly across seasons (χ^2 = 10.433, df = 3, p = 0.01522), showing a peak in the summer months (spring = 28.1%, n = 66; summer = 35.7%, n = 84; autumn = 17.9%, n = 42; winter = 17.7%, n = 42, but no difference regarding sex (χ^2 = 2.0369, df = 3, p = 0.5648, Fig. 7; Table S3).

Only 5.5% (2 out of 38) of female single strandings with known body length were classified as juvenile, compared to 14% (12 out of 85) of male single strandings, but this difference was not statistically significant (Fisher's exact test: p = 0.3483).

The number of strandings per decade was significantly correlated with decade for single strandings,

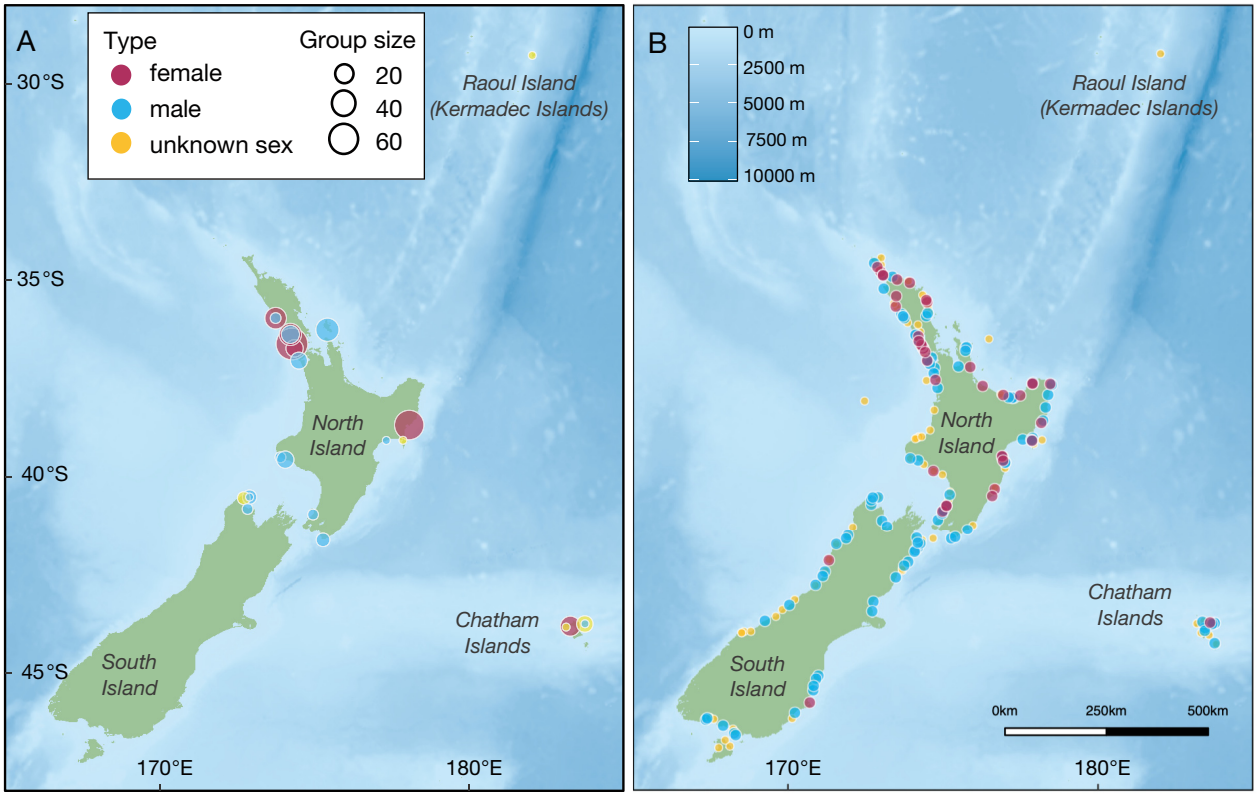

Fig. 6. Locations of sperm whale *Physeter macrocephalus* (A) mass and (B) single strandings recorded in New Zealand between 1873 and 2021 (blue = male-dominated groups/male individuals, red = female-dominated groups/female individuals, yellow = unknown sex composition/individual). For mass strandings, circle size indicates the group size

with an increase in frequency of single strandings over time (Spearman's rank, r = 0.830, p < 0.001), but not for mass strandings (Spearman's rank, r = 0.225, p = 0.440).

4. DISCUSSION

We here present the first spatio-temporal examination of stranding records of New Zealand sperm whales. Comparisons of mtDNA haplotypes with those from other regions provide new insights into the connectivity of New Zealand sperm whales to neighbouring and distant populations, while analyses of stable isotope ratios of skin samples from 2 stranding events in 2018 shed light on the foraging ecology of New Zealand sperm whales.

4.1. Genetic insights from the 2018 strandings

Analyses of genetic differentiation suggested stronger genetic links between New Zealand males and Pacific Ocean and south-eastern Australian populations, in comparison to south-western Australia and Indian Ocean populations. As expected because of the less dispersive behaviour of female sperm whales, higher differentiation was seen between females and other population strata, than for the New Zealand males. Although the majority of New Zealand male individuals had globally common haplotypes (>2% frequency in the Indian and Pacific Oceans), analysis of the rare haplotypes possessed by the other New Zealand males (M′, 'O', 'Q', 'R', 'S', and 'Z') suggested the potential for greater genetic connectivity between New Zealand males and New Zealand females, as well as between New Zealand males and the Southwest Pacific Ocean. However, these rare haplotypes were also found elsewhere in the Pacific Ocean, demonstrating the limitation of solely using mtDNA to infer genetic origin.

4.2. Stable isotope insights from the 2018 strandings

Stable isotope analyses are widely used to investigate foraging ecology of mammals (Herman et al. 2005, Cherel et al. 2007, Mendes et al. 2007, Crawford

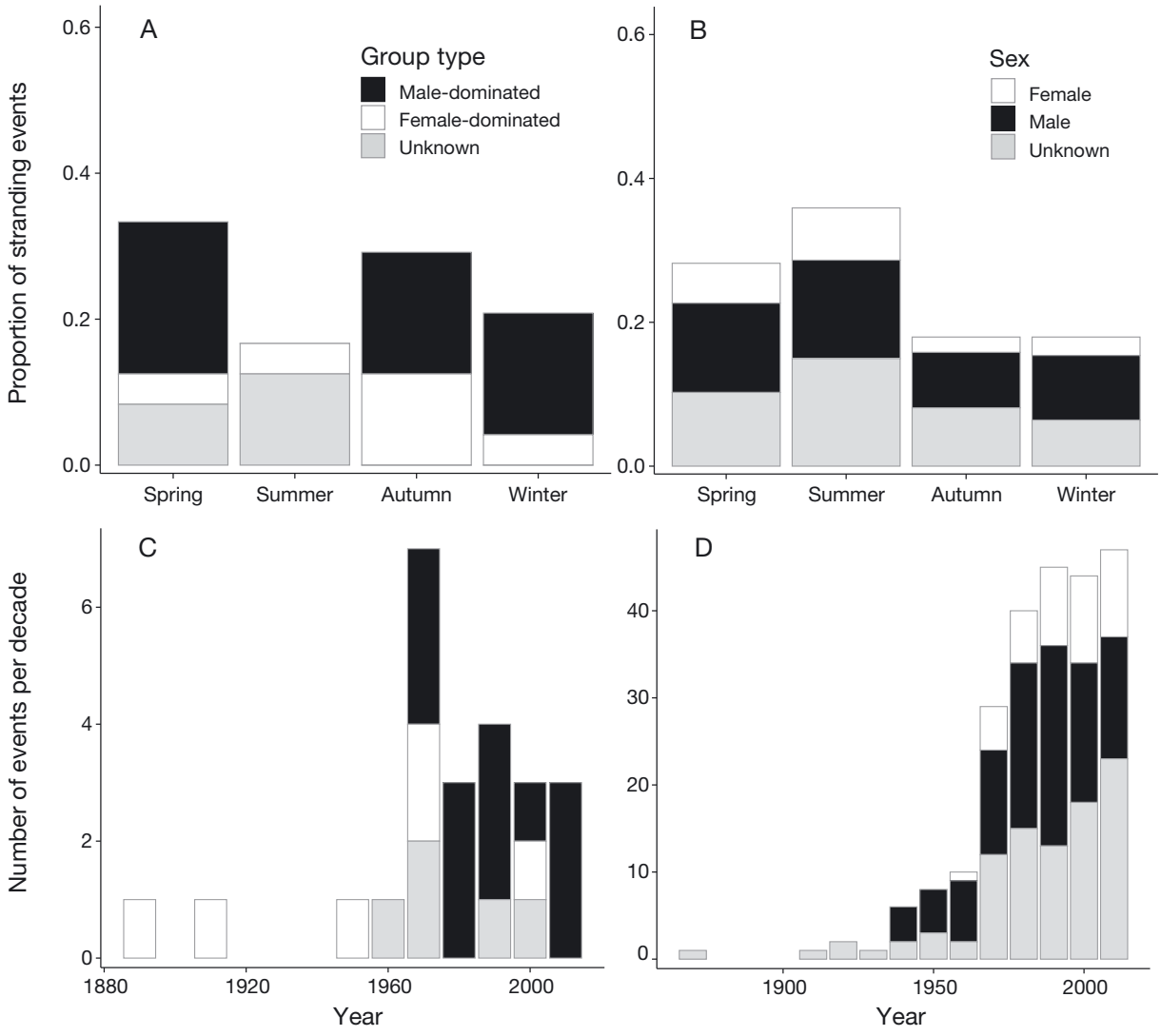

Fig. 7. (A,B) Seasonality and (C,D) timeline of sperm whale *Physeter macrocephalus* events (A,C = mass strandings, B,D = single strandings) recorded in New Zealand between 1873 and 2021. Group type and sex are denoted by colour. For mass strandings, proportion refers to the total number of events, not the number of individuals included. For C and D, bars represent the sum of events per decade. Seasons are austral seasons (spring = September–November, summer = December–February, autumn = March–May, and winter = June–August)

et al. 2008, Newsome et al. 2010, Newton 2010, Peters et al. 2020), with carbon isotopic values ($\delta^{13}C$) providing information on likely carbon sources relating to feeding habitat (Rubenstein & Hobson 2004), and nitrogen isotopic values ($\delta^{15}N$) indicating trophic level of the organism (Minagawa & Wada 1984, Post 2002). Due to the spatial variation in baseline isotope ratios of autotrophic sources, both $\delta^{13}C$ and $\delta^{15}N$ values of marine predators are also influenced by latitude and oceanographic processes within the foraging region (Cherel & Hobson 2007, Díaz-Gamboa et al. 2018).

The similarity in mean $\delta^{13}C$ values of the individuals stranded in Taranaki compared to those of sperm whales off Kaikōura (Guerra et al. 2020b) suggests a similar source of organic carbon supporting their food webs (e.g. phytoplankton). However, the lower $\delta^{15}N$ values suggest that the whales from the stranding may have foraged on lower-level trophic prey than those analysed by Guerra et al. (2020b). Alternatively, the Taranaki stranded whales may be reflecting a food web from a more pelagic or offshore environment, due to these food chains typically being shorter, resulting in lower $\delta^{15}N$ at high trophic levels (Iken et al. 2005). This is particularly likely given that sperm whales foraging over the Kaikōura Canyon were sampled in a relatively nearshore environment. Lastly, the observed differences are unlikely to be driven by differences in age/size classes,

due to the partial overlap in body length between the Taranaki individuals (11.1–16.1 m) and the whales from Kaikōura (12.9–15.9 m), and because we did not find a significant correlation between body length and $\delta^{15}N$ values, consistent with previous findings for male sperm whales off Kaikōura (Guerra et al. 2020b). However, even though not statistically significant, our results show a trend to increasing $\delta^{15}N$ values with increasing body length. It is possible that a larger sample size could yield a statistically significant positive correlation.

The lack of photo-identification matches between the whales stranded at Taranaki and the Kaikōura photo-identification catalogue suggests that these whales were not regular visitors to Kaikōura. A lack of matches does not preclude some connectivity between the areas, however, as it is possible that whales from the stranding had visited Kaikōura but only occasionally, briefly, or further offshore. The single male that stranded at Clifford Bay separately from the other 3 subgroups (31–43 d later) had the highest $\delta^{13}C$ and $\delta^{15}N$ values, suggesting that this animal differed from the others in prey and/or feeding region. Instead, the isotope values of the single male were similar to those of other Kaikōura whales, and to values of the same whale previously measured at Kaikōura. This similarity is consistent with this individual foraging at Kaikōura, as indicated by the identification of this whale as an individual regularly sighted off that area. The distance between the Kaikōura Canyon and the stranding location of this whale was just over 100 km, a relatively small distance for the movements of a male sperm whale. Based on the association of the male stranded at Clifford Bay to Kaikōura, the difference in stable isotope values between this whale and the stranded Taranaki males, and the temporal separation between the 2 stranding events, we suggest it is unlikely that the single male was part of the larger group that stranded at Taranaki. With a total body length of 16.13 m, the Clifford Bay individual was the largest of all 14 stranded animals. Given that older males are often solitary outside the breeding season, this further suggests that this individual was not part of the mass stranding.

4.3. Spatial and temporal trends in sperm whale strandings in New Zealand

Our analysis of sperm whale strandings in New Zealand highlights a knowledge gap, as most New Zealand based research on sperm whales has focussed on males off the Kaikōura Canyon (Jaquet et al. 2000b, Sagnol et al. 2014, Guerra et al. 2020b, Somerford et al. 2022). However, sperm whales strand over much of the nation's coastline, and a notable proportion of those around the North Island are female (as we showed here, 32% of recorded mass strandings with known type were female-dominated, and 29% of single strandings with known sex were females). Our analysis also contributes to filling that knowledge gap by providing information on the distribution of single females as well as female-dominated social groups around New Zealand. We found sex to predict the latitudinal location of single strandings, which is reflected in only 2 records of known sex single strandings south of 42° S latitude being female (Fig. 6). Both were beachcast individuals, which means they could have been transported further south by oceanic drift (Santos et al. 2018). While the lack of female records in the south could be an artefact of the number of strandings with unknown sex in the database (28 single strandings of unknown sex were reported south of 42° S), our results are consistent with existing knowledge of females typically inhabiting warmer waters north of 42°S latitude for feeding and raising young (Schnitzler et al. 2018, Whitehead 2018).

We did not find sex to be a predictor for the latitudinal locations of mass strandings, despite only 1 recorded female mass stranding south of 42° S latitude, on the Chatham Islands. However, the ΔAICc for the second-best model that includes mass stranding type (female-dominated or male-dominated) was only 1.57, suggesting some support for stranding type being an important factor. While a much smaller sample size and narrower latitudinal distribution for mass strandings versus single strandings could contribute to this outcome, it is also important to note the difference in causality between mass and single strandings. While in many cases the reasons for cetacean strandings are still a mystery, it is generally understood that in most cases single stranding events are related to specific conditions or situations of the individual, such as disease, injury, accidents such as ship strike, or loss of the mother/social group (for calves) (Cordes 1982). Mass strandings, conversely, often consist of relatively healthy individuals and in many cases are assumed to be caused by a multitude of factors, including unusual environmental or oceanographic conditions. For example, locations with a specific topographical or bathymetric layout can cause cetaceans to get easily trapped, such as Farewell Spit, a notorious mass stranding hot spot for multiple cetacean species on the northernmost point of New Zealand's South Island (Brabyn & McLean 1992, Betty et al. 2020), and Cape Cod in USA (Moore et al. 2018,

Pulkkinen et al. 2020). Anthropogenic activities such as naval sonar and seismic surveys are also believed to promote the occurrence of mass strandings (Fernández et al. 2005, Southall et al. 2013). We found a notable absence of mass strandings (but not of single strandings) around the South Island (with the exception of Farewell Spit). While this could be due to the geography of the South Island's coastline not promoting mass strandings, it could also reflect that both female- and male-dominated social groups may be less common in this region, compared to the more solitary older males, which would be in line with previous knowledge of this species' social organisation and spatial distribution.

We found evidence for seasonality in single strandings, with more events in the austral summer months (December–February; Fig. S4). Similarly, mass strandings of long-finned pilot whales *Globicephala melas edwardii* in New Zealand occur more frequently in late austral spring and summer (October–February) (Betty et al. 2020). Like sperm whales, pilot whales are also deep-diving teutophagous species, meaning it is possible that the skew in stranding events towards the warmer months represents seasonal shifts in abundance and distribution of prey (Beasley et al. 2019). This is supported by previous studies on distribution and stable isotope analyses of Kaikōura whales indicating seasonal fluctuations in diet (Jaquet et al. 2000a, Guerra et al. 2020b).

In contrast, mass strandings of sperm whales in New Zealand seem to occur with no obvious seasonal pattern. Furthermore, season did not predict the latitudinal location of mass or single strandings. This indicates that sperm whales are present in New Zealand waters year-round, confirming what is known about males off Kaikōura (Somerford et al. 2022). There was no record of a male-dominated mass stranding in summer; however, 3 of the 4 mass strandings recorded in summer were of unknown sex, thus making it hard to draw conclusions.

Single strandings of sperm whales have been recorded increasingly over time in New Zealand, as well as on its offshore islands (Rangitāhua/Kermadec and Rēkohu/Chatham Islands) since recordings began in 1895 (mass strandings) and 1873 (single strandings) (Fig. 7). While a similar general trend is visible for mass strandings, we did not find a significant correlation between the number of events and the decade, likely due to a peak in observed mass stranding events in the 1970s. As the North and South Islands of New Zealand have a greater human population than the offshore islands, there is an observer bias towards mainland strandings. Observer biases also likely explain the increase in observations of mass and single strandings in the second half of the last century (Fig. 6b; Fig. S4). Sperm whales were heavily targeted by whalers and are long-lived, slow-breeding animals. While there may have been some population growth in recent decades since the cessation of commercial whaling, it is unlikely that populations have recovered to a level that would be evident in reported stranding events (Whitehead 2002). Therefore, the increase in reported events is most likely influenced by greater reporting effort due to an increase in human population and the advancement of detection technology such as drones. Additionally, the end of commercial whaling in New Zealand in 1956 and a shift in human perspective towards whales (Mazzoldi et al. 2019) has raised public awareness of strandings and their likelihood to report them.

4.4. Future directions

By combining the insights from mtDNA and stable isotope analysis of male sperm whales stranded in 2018, and of the general patterns of sperm whale stranding in New Zealand, this study has increased our current understanding of spatial and demographic trends of strandings, the foraging ecology and the genetic connectivity at local and global scales for New Zealand sperm whales. It provides a crucial baseline from which we can further refine our knowledge of sperm whales in New Zealand waters, but it also highlights the paucity of comprehensive post mortem examinations of stranded sperm whales in New Zealand. In addition, although mtDNA is a powerful tool for looking at geographic affinities of matrilines, genome-wide markers (e.g. Fuentes-Pardo & Ruzzante 2017) would provide greater insight into the relatedness of New Zealand sperm whales to other populations. A challenge of such an approach is sampling 'reference populations' in the Southwest Pacific Ocean to further refine the geographic origin of New Zealand sperm whales. While previous studies have focussed on analysing available tissue samples, there is potential for non-destructive DNA extraction from cultural artefacts made from whale teeth or bones, such as scrimshaw (Pichler et al. 2001). Such methods could possibly also be applied to taonga (artefacts such as pendants) made of whale bone in a collaborative partnership with Māori (the Indigenous people of New Zealand). This could offer further insight into changes in genetic connectivity among New Zealand sperm whales over time and increase our understanding of the species in a New

Zealand context. Likewise, collagen from bone could be analysed for bulk and compound-specific stable isotopes to better identify baseline $\delta^{15}N$ changes in the foraging areas. Furthermore, intersexual differences in foraging ecology have been shown for sperm whales in the Mediterranean (Pirotta et al. 2020), but to date, no isotopic information is available on female sperm whales in New Zealand waters. Given that sperm whales are apex predators, it is important to understand their role within the ecosystem. Gaining a better understanding of their ecology in New Zealand will aid in predicting their resilience to environmental change.

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