# Demography and ecology of southern right whales *Eubalaena australis* wintering at sub-Antarctic Campbell Island, New Zealand

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## Abstract

Since the decimation of the southern right whale *Eubalaena australis* population in New Zealand by whaling, research on its recovery has focused on the wintering ground at the Auckland Islands, neglecting potentially important wintering habitat at Campbell Island. For the first time in 20 years we conducted an expedition to sub-Antarctic Campbell Island to document and describe *E. australis* occupying this wintering habitat. We used a variety of methods including photo-identification, genetic and stable isotope analyses of tissue samples, and visual surveys of abundance and distribution, to provide details on the demography, population connectivity and ecology of *E. australis* wintering at Campbell Island. Our primary findings include (1) a lack of calves observed at Campbell Island, (2) an age-class bias toward sub-adults encountered at Campbell Island, (3) nine photo-identification matches between individuals observed at Campbell Island and previously documented elsewhere in New Zealand, (4) no genetic differentiation between *E. australis* at Campbell Island and the broader New Zealand population, (5) increased abundance estimates of *E. australis* at Campbell Island over the last 20 years, and (6) indications that *E. australis* forage within the sub-Antarctic region based on stable isotope analyses. Our results confirm that the Auckland Islands are currently the only significant calving area for *E. australis* in New Zealand, and therefore previous abundance estimates based on demographic data from the Auckland Islands are applicable to the entire New Zealand population of *E. australis*. However, future periodic surveys to Campbell Island are recommended to monitor population recovery and expansion.

Keywords:

age-class, genetic analysis, population connectivity, stable isotope, sub-Antarctic, wintering ground, parentage analysis

## Introduction

It is estimated that prior to whaling there were 27,000 (95% CL 22,000, 38,000) southern right whales *Eubalaena australis* in New Zealand waters (Jackson et al. 2011). This large, long-lived species aggregates during winter in coastal waters to breed and calve and then migrates to offshore foraging grounds during summer months (Richards 2002). A key wintering ground was once mainland New Zealand (North and South Islands), where sheltered inshore waters were used for calving in winter (Dawbin 1986). However, between 1830 and 1970 up to 40,000 *E. australis* were killed in New Zealand waters (Carroll et al. 2014a) and the species was commercially extinct by 1851 (Jackson et al. 2011; Richards 2002).

Despite this intense whaling activity around mainland New Zealand, the sub-Antarctic Auckland Islands and Campbell Island (-52° 32' S, 169º 09' E; Fig. 1) served as a refuge for a portion of the population (Gaskin 1964; Richards 2002). Limited whaling occurred in these islands, including a fishery around Campbell Island that killed 63 *E. australis* between 1909 and 1913, including several cow/calf pairs (Gaskin 1964). Following global protection in 1935, domestic hunting of *E. australis* ceased. However, illegal Soviet whaling killed 256 whales near the Auckland Islands between 1963 and 1967 (Tormosov et al. 1998). The legacy of this exploitation was that no sightings of *E. australis* were reported around the mainland for approximately four decades and it was feared the New Zealand stock had been completely extirpated (Gaskin 1964). However, a small remnant group of *E. australis* continued to visit Campbell Island each winter, from which it is hypothesized the stock began a slow recovery (Richards 2002).

Research to monitor recovery over the last 20 years has focused on the more logistically accessible calving ground at the Auckland Islands (Carroll et al. 2013; Patenaude and Baker 2001; Rayment et al. 2012). Long-term genetic and photo-identification datasets exist for this population (Carroll et al. 2013; Carroll et al. 2011b; Rayment et al. 2015) and all demographic parameters estimated for the New Zealand stock are derived from the these data collected at the Auckland Islands, including a current population estimate of 2169 (95% CI: 1836-2563; Carroll et al. 2013). While these research efforts have been thorough, they do not consider potential *E. australis* over-wintering at Campbell Island.

Staff based at the New Zealand meteorological station on Campbell Island reported seeing small groups of *E. australis*, including mating groups and cow/calf pairs, in the region during winter months from 1942 up to 1983 (Bailey and Sorensen 1962). The most recent systematic surveys for *E. australis* at Campbell Island were conducted from 1995-1997 and documented the presence of *E. australis* throughout winter, but no cow-calf pairs were reported (Stewart and Todd 2001). The majority of sightings were recorded in Northwest Bay (Fig. 1, Stewart and Todd 2001), although it is unclear to what extent other potential habitats at Campbell Island were surveyed. Comparison of the 31 whales photo-identified around Campbell Island and 244 photo-identified around Auckland Islands between 1995-1998 produced one within-year and three between year matches (Patenaude and Baker 2001). Therefore, although there is interchange of *E. australis* between the sub-Antarctic Islands, the status of Campbell Island waters as a calving area remains equivocal, as is the current use of this historic wintering habitat by *E. australis*.

Female *E. australis* exhibit strong fidelity to their calving grounds (Best 1990; Payne 1986). Hence, a portion of the New Zealand population that winters at Campbell Island may be unsampled and unaccounted for in population estimates. Furthermore, maternally-directed fidelity to wintering grounds results in limited connectivity between New Zealand and Australian *E. australis* populations (Pirzl et al. 2009), leading to genetic differentiation based on maternally-inherited mitochondrial DNA markers (Carroll et al. 2011a). Assessing the degree of gene flow between Campbell Island, the Auckland Islands and mainland New Zealand in the context of fidelity to migratory destinations is important as such behavior can strongly impact local patterns of extinction and recolonization, thereby affecting large-scale population dynamics (Lande 1988; Storz 1999). Furthermore, Gaskin (1968) noted that the whales killed at Campbell Island in the early 1900s were not as large as those caught around the mainland, raising questions about the relative health or age-class of animals over-wintering at this location.

In addition, there is evidence for maternally-directed learning of summer feeding grounds in many baleen whales, including *E. australis* (Carroll et al. 2015; Valenzuela et al. 2009). Whales that share feeding ground preferences, inferred from stable isotope profiles, are more likely to share mtDNA haplotypes (Valenzuela et al. 2009) and have higher levels of relatedness based on bi-parentally inherited microsatellite markers (Carroll et al. 2015). However, there are limited data on the diet of *E. australis* in Australasian waters.  The best available information comes from the stomachs of animals killed by Soviet whalers between 1960 and 1971 documented by Tormosov et al. (1998). The stomach contents of whales taken south of 50° S primarily (99.4%) contained euphausiids (krill species; Tormosov et al. 1998). In contrast, stomach contents of whales killed north of 40° S consisted almost entirely (91.7%) of copepods (*Calanus* spp.), and whales caught in intermediate latitudes showed a more mixed diet dominated by copepods (71.4%), secondly euphausiids (24.3%), and small crustacea (4.3%). A habitat analysis of 19$^{th}$ century offshore whaling data during non-winter months in the New Zealand region between 30° and 52° S identified strong association patterns between *E. australis* distribution and temperature in the upper 200 m, and predicted high habitat suitability in close proximity to the sub-tropical front surrounding 45° S (Torres et al. 2013). Confirmation of *E. australis* foraging grounds in the New Zealand region is lacking, as is the description of the surviving genetic lineages that occur on such feeding grounds.

The New Zealand population of *E. australis* is recovering (Carroll et al. 2013; Carroll et al. 2014b), necessitating a full understanding of its population dynamics at all wintering areas to enable effective management. This study investigates *E. australis* use of Campbell Island during the austral winter (July) using a variety of methods including photo-identification, genetic and stable isotope analysis of tissue samples, and surveys of abundance and distribution. Our work aims to fill important knowledge gaps about *E. australis* wintering at Campbell Island including distribution patterns, demographic units, genetic composition, abundance, connectivity to Auckland Islands and mainland New Zealand populations, and summer trophic foraging patterns.

## Materials and methods

Overview An experienced marine mammal survey team sailed to Campbell Island from mainland New Zealand aboard the RV *Tiama* on 9 July 2014 and returned on 10 August 2014 (Fig. 1). Campbell Island has a rugged coastline indented with bays of varying sizes. The westward side is more exposed to prevailing wind and swells. While at Campbell Island four types of data were collected on *E. australis*: (1) vessel-based survey around the island to gather distribution data, (2) vessel-based survey data in Northwest Bay to generate abundance estimates, (3) vessel-based photo-identification and skin biopsy sample collection for mark-recapture abundance estimates, genetic and stable isotope analyses and population connectivity, and (4) land-based visual counts of *E. australis* present in Northwest Bay to replicate survey methods conducted in 1997 (Stewart and Todd 2001). The methods for each approach are described below.

*Vessel-based surveys* In order to assess habitat use and distribution patterns of *E. australis* around Campbell Island, vessel-based visual surveys were conducted aboard RV *Tiama* at 8 knots within 2 km of shore, entering most of the main bays and harbors (Fig. 1a). Based on the known near-shore distribution of *E. australis*, survey effort traced the coastline including sheltered bays and harbours. One observer scanned both sides of the vessel from behind the cockpit (eye-height above sea level = 2.5 m) using naked-eye and binoculars, with an estimated search distance for an *E. australis* of 3 km in all directions. Surveys were conducted in Beaufort sea state (BSS) of three or less. During these visual surveys, a closing mode (where the vessel leaves the trackline to approach spotted whales) was employed to record a GPS location and behavior data, obtain photo-identification data, and allow group size confirmation and age-class determination. Calves were defined as a whale less than half the length of an accompanying adult

(Carroll et al. 2011b; Rayment et al. 2012). No attempt was made to classify non-calves as juvenile or adult, due to the inability to positively differentiate between the two age classes.

Two replicate vessel-based visual surveys were also conducted in Northwest Bay aboard RV *Tiama* at 8 knots along a pre-determined survey route using a passing mode (where the vessel maintained the pre-determined track without approaching whales) to generate minimum abundance counts in the Bay. The survey route was designed to cover the area of highest whale density in Northwest Bay (Stewart and Todd 2001), and to not cross paths so that the chance of double counting was minimized. In this high density area, two observers were used, one scanning each side of the vessel, while a third person recorded details of the whale sightings. . No other data were collected during passing mode.

*Photo-id* Photographs of individual *E. australis* were taken from *Tiama* using digital SLR Nikon D90 cameras and 70-200mm lenses. Images obtained from sightings were included in the photo-ID analysis if they were in sharp focus and clearly showed the pattern of callosities on the whale's head, or other permanent distinguishing marks, such as dorsal blazes or "grey-morph" coloration (Carroll et al. 2014b; Payne et al. 1983; Schaeff et al. 1999). Comparison of images was facilitated by classification of each individual according to a suite of 17 distinguishing characteristics (e.g., nature of lip callosity, number of rostral islands: Pirzl et al. 2006). These data were stored in a custom-written database, "BigFish" (Pirzl et al. 2006), which could be queried each time a new image was compared to the existing catalogue. Images were compiled into two separate catalogues of left hand sides (LHS) and right hand sides (RHS), with each individual assigned a unique alphanumeric code. Where the LHS and RHS of the same individual could be established from the same sighting, they were linked in the separate catalogues by assigning the same code. It should be emphasized that if the LHS and RHS could not be linked in the same sighting, or if an individual had its LHS and RHS photographed in different sightings, the same individual could occur in each catalogue with different codes.

Abundance of *E. australis* at Campbell Island was estimated using photo-ID capture-recapture methods (e.g., Barlow et al. 2011). The study period was divided into two equal-length capture periods and the number of individuals encountered during each capture period was calculated. The abundance estimate (*Nm*) was derived using the Chapman modification of the two sample Lincoln-Petersen estimator (Chapman 1951) as follows:

$$Nm = \{(n_1 + 1)(n_2 + 1) / (m + 1)\} - 1 \qquad \text{(Eq. 1)}$$

where $n_1$ is the number of unique individuals photographed during the first capture period, $n_2$ is the number photographed during the second capture period, and $m$ is the number photographed during both capture periods. Log-normal 95% confidence intervals were calculated, as these better represent the uncertainty in abundance estimates (Buckland et al. 2001). Separate estimates were calculated using the LHS and RHS capture histories.

The Lincoln-Petersen estimator has the following assumptions (Pollock et al. 1990): (1) the population is closed to additions (births and immigrants) and deletions (deaths and emigrants) during the survey period, (2) all animals are equally likely to be captured, and (3) marks are not lost and are correctly identified. We can safely assume that the population was demographically closed and that identifying marks were not lost over the short study period (15 days). We attempted to minimize the risk of misidentification by using a suite of identifying characteristics and having at least two experienced researchers confirm photo-ID matches. Geographic closure (no immigration or emigration during the sampling period) was assessed by examining a discovery curve of individuals over the study period.

*Biopsy sampling* During biopsy effort while in a closing survey mode, skin samples were collected using a lightweight biopsy dart fired from a modified veterinary capture rifle (Krützen et al. 2002) (New Zealand Department of Conservation permit HO-2990-03; University of Auckland Animal Ethics approval 000908). All darts were tethered to a fishing reel to pull the dart back after impact because the darts typically stick to *E. australis*. A skin sample was also opportunistically collected from *Tiama*'s anchor chain the morning after a whale was heard hitting the chain. Samples of sufficient size were divided for genetic and stable isotope analyses, and genetic samples were stored in 99% ethanol and stable isotope samples were frozen.

*Genetic analysis:* We constructed DNA profiles, comprising genetically identified sex, mtDNA haplotype (500 bp) and microsatellite genotype (up to 13 loci), for *E. australis* samples collected around Campbell Island. This was done following previously published methodology (Carroll et al. 2013; Carroll et al. 2011b) and is summarized in the Online Resource 1.

*Movement of individuals:* To investigate movement of individuals among wintering grounds, the Campbell Island photo-ID catalogue was compared with catalogues of *E. australis* images compiled from sightings around the Auckland Islands and the New Zealand mainland. The Auckland Islands catalogue consists of high quality images of *E. australis* gathered during systematic boat-based photo-ID surveys between 2006 and 2012 and contains 692 unique individuals (W. Rayment, unpublished data). The New Zealand mainland catalogue consists of images of 43 whales obtained during opportunistic encounters between 2003 and 2010 (Carroll et al. 2014b). The data associated with the Auckland Islands and mainland catalogues are stored in separate BigFish databases in order to facilitate multiple comparisons. The same protocols were followed as for matching the Campbell Island images described above and all photo-ID matches were confirmed by at least two experienced researchers.

In addition, we compared the DNA profiles of the whales sampled around Campbell Island to the 'DNA register' previously established from whales sampled around the Auckland Islands and mainland New Zealand. Specifically, we used the DNA profiles from 710 individually-identified adult SRW and 66 dependent calves captured at the Auckland Islands between 1995-2009 (Carroll et al. 2013) and 47 individually-identified *E. australis* sampled around mainland New Zealand between 2003 and 2010 (Carroll et al. 2011a; Carroll et al. 2014b). After reconciliation of replicates within these samples, the Campbell Island genotypes were compared with a total of 793 *E. australis* sampled around New Zealand between 1995 and 2010 (362 males, 431 females, and 8 whales of unknown sex due to PCR amplifications failure).

The comparison of DNA profiles was based on 13 loci, with associated mtDNA haplotypes and sex, and matching proceeded following previously described methodology (Carroll et al. 2013). Briefly, matching genotypes were identified using CERVUS v3.0 (Kalinowski et al. 2007). As a precaution against false exclusion due to allelic dropout and other genotyping errors, the initial comparison allowed for mismatches at up to three loci. To assess the observed versus the expected number of recaptures between the New Zealand and Campbell Island DNA profile catalogues, we undertook a simulation study in the programming language R (R Development Core Team 2013) (Online Resource 2).

*Tests of differentiation and matrilineal relatedness:* To investigate the movements and relationship of *E. australis* between different New Zealand regions using the genetic data, we conducted several analyses. Firstly, we compared the identity and level of genetic diversity of the mtDNA data, a proxy for maternal lineages, between the Auckland Islands and Campbell Island. We did this by calculating mtDNA haplotype and nucleotide diversity using program Arlequin v3.5 (Excoffier and Lischer 2010). In addition, we calculated the mean number of alleles, and observed and expected heterozygosities for the microsatellite data for both the Auckland Islands and Campbell Island samples, using GENEPOP v4.0 (Rousset 2008).

Secondly, we tested for genetic differentiation between the Auckland Islands and Campbell Island. For the mtDNA data, we used Arlequin v3.5 to calculate pairwise $F_{ST}$ values and tested significance in the same program using a permutation procedure (10,000 permutations, with significance set at $\alpha = 0.05$). Given the small sample size from Campbell Island, we also carried out comparisons using an exact test of differentiation (1,000,000 Markov chain steps; 10,000 dememorization steps, with significance set at alpha=0.05). For the microsatellite data, we estimated the pairwise $F_{ST}$ value using GENEPOP v4.0. We used the exact *G* test (Raymond and Rousset 1995) in the same program to test for significant differences in allele frequencies between wintering grounds.

Thirdly, we conducted a maternity analysis to identify the mothers of whales sampled around Campbell Island within the New Zealand genotype database. This was conducted because of a hypothesized bias towards sub-adults at Campbell Island. We used the strict exclusion (Ex) and maximum likelihood (ML) method implemented in program CERVUS. The Ex method means that mother and offspring must match at one allele per locus to be considered a parent-offspring pair. However, this does not account for genotyping error. The ML method of Kalinowski et al (2007) compares the likelihood of the two most likely mothers, accounting for a user-specified value of genotyping error. For each offspring, the difference between the likelihoods of the two most likely mothers produces a delta score. Simulations were conducted to estimate the critical delta value required to assign maternity with 80% and 95% confidence. Campbell Island samples were clustered by mtDNA haplotype and simulations and analysis were run on a per-haplotype basis. As mtDNA is maternally-inherited, mother and offspring must share the same mtDNA haplotype. Simulations require an assumption of the number of potential mothers in the population per haplotype, which was worked out using published haplotype frequencies (Carroll et al. 2011a) and an estimated total non-calf female population size of 1521 whales in 2014 (see Online Resources 2). Additionally, the proportion of these females that were genotyped (Table 1) is required. We ran the simulations under the assumption that the genotyping error rate was 1% (Carroll et al. 2013) and individuals were typed at a least nine of 13 loci.

*Stable isotope analysis* Eighteen *E. australis* skin biopsy samples were analyzed for carbon and nitrogen stable isotope values. Once in the lab, ethanol was evaporated from the biopsies under a stream of nitrogen gas prior to freeze drying. A sub-sample of skin (0.7-1.0 mg) was then weighed into tin boats for stable isotope analysis. Stable isotope analyses were carried out on a Delta$^{Plus}$ (Thermo-Fisher Scientific, Bremen, Germany) continuous flow, isotope ratio mass spectrometer linked to an NA 1500 elemental analyzer (Fisons Instruments, Rodano, Italy). For details of the analytical set-up refer to Morrison et al. (2014). C isotope data were corrected for lipid content following equations in Fry (2002). Repeated analyses of National Institute of Standards and Technology (NIST) and laboratory standards had a precision (1 s.d.) of better than 0.2 ‰ and 0.1 ‰ for $\delta^{15}N$ and $\delta^{13}C$ values, respectively. Duplicate analysis of skin samples gave a precision (1 s.d.) of better than 0.3 ‰ for $\delta^{15}N$ and 0.4 ‰ for $\delta^{13}C$.

*Land-based survey* Land-based visual counts were undertaken near the shore-side hut at Northwest Bay at approximately 9 m above sea level, where a clear view of the bay was achieved (Fig. 1b). Dedicated hourly counts over 10 to 15 min were undertaken on 2 and 3 August 2015, weather permitting (no rain, snow or fog; BSS < 4), replicating Stewart and Todd (2001) counts. One observer scanned with naked eye while another scanned with binoculars. During these counts, the number of groups and number of individuals within a group were recorded. Whales were considered part of a group when in close proximity (< ~15 m) to each other and engaged in similar behavior.

## Results

*Vessel-based survey*: Survey effort for *E. australis* around Campbell Island using closing mode was conducted on four days in July 2014 (Fig. 1a). Outside of Northwest Bay (15, 19, 27 July 2014), eight *E. australis* encounters were made of 17 individuals: one sighting outside Monument Harbour (two individuals), two sightings in Perseverance Harbour (five individuals), one sighting near East Cape (one individual), one sighting outside Northeast Harbour (five individuals), and three sightings along the northwest coast (four individuals). These whales were typically observed resting or travelling, and no social behavior was observed. During a closing mode visual survey in Northwest Bay with dedicated photo-ID effort on 16 July 2014, 14 *E. australis* encounters were recorded (over 50 individuals observed) and whales were often engaged in social behavior within surface active groups (SAGs; Kraus and Hatch 2001). The southwest side of Campbell Island from Monument Harbour to Northwest Bay was not surveyed due to poor bathymetric data and many pinnacles that made coastal navigation a safety risk.

Two visual surveys using passing mode were conducted along a 9.6 km survey line within Northwest Bay (Fig. 1b) to determine minimum abundance counts. On 22 July 2014, 30 *E. australis* were observed (3.1 whales per km) and on 27 July 2014, 28 *E. australis* were observed (2.9 whales per km). Dedicated biopsy sampling with complimentary photo-ID effort was conducted in Northwest Bay on 22 and 25 July 2014 (Fig. 1c).

No *E. australis* calves were observed on any of the vessel-based surveys.

*Photo-identification:* Images of sufficient quality for photo-ID analysis were obtained from 97 encounters. The LHS and RHS catalogues contained 55 and 46 whales respectively, of which 16 appeared in both catalogues. Only seven individuals were photographed on more than one day, and the discovery curve shows no sign of reaching an asymptote (Fig. 2), suggesting a high rate of turnover of whales in the study area.

The capture-recapture analyses of the two within-season samples resulted in abundance estimates of 278 (95% CI = 105-735) and 288 (95% CI = 124-670) using the RHS and LHS catalogues, respectively.

*Microsatellite genotyping and individual identification*: A total of 24 skin biopsy samples were collected from *E. australis* at Campbell Island and made available for genetic analysis. Of these, 23 passed the quality control measure of amplifying at nine or more microsatellite loci with an average of 12.8 of 13 loci per sample. Matching within the Campbell Islands dataset revealed that two whales had been sampled twice, so a total of 21 individually identified whales (10 females and 11 males) were captured. Both resamplings were of males first captured on 22 July 2015 and the recaptured on 25 July 2015[1]. Mitochondrial sequencing produced haplotype sequences for 19 of the 21 unique genotypes.

M*ovement of individuals:* Comparison with the other New Zealand catalogues revealed nine photo-ID matches with whales that had previously been seen at the Auckland Islands between 2009 and 2012, one of which had also been seen at the New Zealand mainland in 2007. None of these whales had ever been seen accompanied by a calf and all were of unknown sex.

Comparison of the 21 unique genotypes, assumed to represent individual whales sampled at Campbell Island, with the register of 793 DNA profiles from *E. australis* previously sampled around the Auckland Islands and mainland New Zealand, produced no matches. This was unexpected given the assumptions of random mixing in our simulation model. The mean number of expected matches under the assumptions was 5.4 (95% CI 1.5 – 9.3 matches) and >99% of simulations had one or more matches (see Online Resource 2, Fig. 1).

*Tests of differentiation and maternal relatedness:* Six of the twelve haplotypes previously documented in *E. australis* sampled at New Zealand wintering grounds were also found in *E. australis* sampled at the Campbell Island wintering ground (Fig. 3). Levels of mtDNA haplotype and nucleotide diversity were similar between the two wintering grounds, as were observed and expected heterozygosities (Table 2). The average number of alleles (k) was smaller for the Campbell Island samples, as expected from the small sample size (Table 2).

Comparison of the Campbell Island and New Zealand datasets showed weak but significant difference in mtDNA haplotypes (pairwise $F_{ST}$=0.04, exact test $p$=0.02) but no significant differences in microsatellite allele frequencies (pairwise $F_{ST}$=0.00, $p$=0.54, exact $G$ test result).

Of the 19 Campbell Island samples with mtDNA haplotypes and microsatellite genotypes available, Ex maternity analysis identified nine putative mothers and the ML method identified two at 80% confidence and five at the 95% confidence level. There was overlap between these methods, and putative mothers of ten whales sampled around Campbell Island were found in the

[1] Resamples matched at 13 loci and had probability of identities of 4.28E-23 and 2.67E-22.

broader New Zealand dataset (Table 1). One Campbell Island whale had two non-excluded mothers, however, only one of these was identified by ML as the mother with 95% confidence (Online Resource 3, Table 1).

Stable isotope analysis: Mean $\delta^{13}C$ for 18 skin biopsy samples was -19.82 (range: -21.24 to -18.85; 1 SD: 0.56), and mean $\delta^{15}N$ was 8.09 (range: 7.08 to 9.31; 1 SD = 0.65; Table 3; Fig. 4). No significant difference was detected between males and females for $\delta^{13}C$ ($t = 0.10$, $p = 0.92$) or $\delta^{15}N$ ($t = 0.72$, $p = 0.48$; Fig. 4). For reference, Antarctic $\delta^{13}C$ signatures are typically more depleted than -22 and tropical $\delta^{13}C$ values are more positive than -17 (Cherel et al. 2013).

Land-based survey: The land-based visual survey counts were undertaken on eight occasions and the number of *E. australis* ranged between 33 and 59, with a mean of 44 (Table 4). No *E. australis* calves were observed.

## Discussion

Our study suggests that Campbell Island is not currently an important calving area for *E. australis* in New Zealand. No sightings of calves were made either from vessel-based or shore-based surveys, despite all likely calving habitat being surveyed at least once. We are confident that calves would have been sighted if present, since *E. australis* calves are easy to recognize in the field and the surveys were timed to coincide with known peak abundance of *E. australis* at other calving habitats in New Zealand (Carroll et al. 2014b; Patenaude and Baker 2001). This result confirms that the Auckland Islands are currently the primary known calving area in New Zealand (see Patenaude and Baker 2001; Rayment et al. 2012) and that demographic estimates from there (e.g., Carroll et al. 2013) are likely representative of the whole New Zealand population, until the population re-establishes other calving areas. The lack of calves at Campbell Island during this survey in 2014 relative to historic observations from the whaling era and previous surveys may be due to (1) a reduction in suitable calving habitat at Campbell Island (e.g., sheltered waters; Rayment et al. 2015) due to shifts in prevailing currents and winds, or increased use by non-calving whales that disturbs calving females, (2) loss of maternal lineage of this calving ground due to whaling, (3) use of Campbell Island by mother/calf pairs outside our sampling period (e.g., other seasons or other cohort years), or (4) a combination of these and other factors.

However, a relatively large number of *E. australis* were observed at Campbell Island, indicating that this is an important wintering habitat for some portion of the New Zealand population. Although calves were not observed at Campbell Island, it may serve as a gathering location for sub-adult *E. australis*, possibly for social interactions. This hypothesized population bias toward sub-adults is supported by a number of findings: (1) no mature females (individuals observed prior to 2009, or individuals observed previously with a calf) were identified at Campbell Island through photo-id analysis; (2) the lack of genetic matches between samples collected at Campbell Island and other *E. australis* wintering areas may be related to the fact that 80% of DNA profiles in the database are of whales that are age > six years, and hence not considered sub-adults; (3) the Campbell Island samples were more genetically similar to a sub-group of juveniles sampled from the Auckland Islands, rather than a sub-group of samples from older whales. Specifically, we found no genetic differentiation between the Campbell Island dataset and a sample of 66 calves sampled around the Auckland Islands from 2006-2009 (mtDNA

$F_{ST}$=0.00, Online Resource 3). In contrast, there was a significant difference between the mtDNA haplotype frequencies of the Campbell Island dataset and the whales sampled around the Auckland Islands between 1995-1998, which represents an older generation of whales ($F_{ST}$=0.05, *p*=0.02, Online Resource 3); (4) if the Campbell Island samples are representative of juveniles from the broader New Zealand population, parents of Campbell Island juveniles should be identifiable within the New Zealand DNA register. Indeed, maternity analyses found putative mothers for ten of 19 tested Campbell Island samples within the New Zealand genetic database. Taken together, these findings suggest that there may be a generational bias towards sub-adult *E. australis* at Campbell Island. Wintering grounds for *E. australis* in other regions have also noted areas used by distinct age-classes. For example, Best (2000) described areas of the South African coast as 'mating' and 'nursery' areas. Interestingly, historical accounts suggest *E. australis* caught around Campbell Island were smaller than those killed around mainland New Zealand (Gaskin 1968), perhaps due to a predominance of juveniles in the region.

Adult *E. australis* were also present at Campbell Island during our survey period because one individual was photographically matched with a sighting made at the New Zealand mainland in 2007, making it more than 7 years old. Furthermore, nine photo-id matches were made between *E. australis* observed at Campbell Island and the Auckland Islands between 2009 and 2012. Further confirmation of connectivity between these two wintering areas is based on the absence of genetic differentiation between individuals sampled at Campbell Island and at the Auckland Islands. This is consistent with previous research in the 1990s that also found matches between Auckland and Campbell Islands (Patenaude et al. 2001).

Although similarity of the photo-ID capture-recapture abundance estimates from the LHS (288) and RHS (278) catalogues lends weight to the reliability of these values, these estimates should be interpreted with caution. Firstly, the low level of survey effort, coupled with high turnover rates of whales in the study area, resulted in very few recaptures. Low capture probabilities exacerbate the negative bias likely to be present due to the heterogeneity of capture probability common to many capture-recapture studies (e.g., Hammond 1990; Lukacs 2013). Furthermore, the discovery curve and low recapture rates suggest immigration and emigration during the study period, likely violating the assumption of geographic closure. Violation of this assumption leads to an overestimate of abundance in the study area (Kendall 1999; Seber 1982). However, assuming that immigration and emigration are random, a closed-capture model can still yield unbiased estimates of the super-population (i.e. all individuals that used the study area during the study period), albeit with poor precision (Kendall 1999). While acknowledging the likely violations of the capture-recapture assumptions, our results suggest that the number of *E. australis* using the nearshore Campbell Island habitat during the survey period was probably between 100 and 700. In comparison, the latest photo-ID derived estimate of annual abundance from the Auckland Islands suggests that 359 whales (95% CI: 298 – 436), including 68 calves, used the calving habitat during a 3-week period in July/August 2011 (Rayment, unpublished data).

Distribution surveys demonstrated that although *E. australis* were encountered at various coastal locations around the island, animals were concentrated in Northwest Bay where SAGs were frequently encountered, whereas *E. australis* encountered at other places around the island were travelling and not engaged in social activity. Dedicated vessel-based survey results within

Northwest Bay indicated a relatively high *E. australis* density of three whales observed per km surveyed. Additionally, land-based surveys determined a mean of 44 animals in Northwest Bay. In comparison to the maximum number of whales counted per day in Northwest Bay in June-Sep 1983 (*n*=30 from 56 survey days), July 1995 (*n*=24 from 24 survey days), and Jun-Aug 1997 (*n*=28 from 54 survey days) as reported by Stewart and Todd (2001), our results indicate that the number of *E. australis* using Northwest Bay has increased over the last 20 years by about 4% a year, which is similar to estimated annual increase for the New Zealand population (5-7%; Carroll et al 2013. Yet, sampling in multiple years is necessary to determine the true population trend at Campbell Island.

Stable isotope results indicate foraging within the sub-Antarctic region based on $\delta^{13}C$ values that are depleted relative to sub-tropical water masses, and enriched relative to the polar zone, based on tracking-isotope studies of seabirds (Cherel et al. 2013; Jaeger et al. 2010). Foraging within sub-Antarctic waters is supported by Torres et al. (2013) that predicted *E. australis* foraging habitat in the New Zealand region to occur in the sub-Antarctic. Variation in $\delta^{15}N$ across all *E. australis* sampled was 2.2 ‰, which could reflect variation in diet among individuals or variation in prey isotope values (i.e., the same prey species in different regions may have different isotope values). This variation could be driven by temporal or spatial variations in the foraging patterns. Despite this apparent inter-individual variation, the $\delta^{13}C$ and $\delta^{15}N$ values for this sampled *E. australis* population at Campbell Island is less varied than values reported for *E. australis* breeding in Argentina (Valenzuela et al. 2009), although the Argentinean study utilized a much larger dataset (*n*=131).

Our efforts to describe the *E. australis* population segment that winters at Campbell Island fills many remaining knowledge gaps about the demography and ecology of the New Zealand *E. australis* population. Although Campbell Island does not appear to be a calving area, it represents a significant wintering habitat for sub-adult and adult *E. australis*, especially in Northwest Bay. We have also generated further evidence of foraging in the sub-Antarctic region south of the sub-tropical front by *E. australis* that are breeding in New Zealand. Additionally, we have demonstrated connectivity between all three *E. australis* wintering grounds (Campbell Island, Auckland Islands, and mainland New Zealand) directly with individuals sighted at each location, and indirectly, through genetic and maternity analyses, which reinforces previous evidence for one New Zealand population of *E. australis* (Carroll et al. 2011a; Carroll et al. 2014b). Based on these findings, we recommend that previous demographic studies of *E. australis* at the Auckland Islands are suitably representative of the whole New Zealand population, yet periodic surveys (i.e., every 5 years) of other wintering grounds, particularly Campbell Island, is warranted to continually monitor population growth and range expansion, as has been seen at other *E. australis* wintering grounds (Groch et al. 2005; Harcourt et al. 2012; Rowntree et al. 2001).

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Tables

Table 1: Summary of maternity analysis inputs and results. Campbell Island southern right whale *Eubalaena australis* samples were grouped by mtDNA haplotype (Haplotype) and maternity analysis was done using females from the New Zealand genotype databases that shared the same haplotype. Table shows, per haplotype, the female population size ($N_{POP}$), the number of females sampled ($N_{MAT}$), *E. australis* sample size at Campbell Island ($N_{CI}$), the number of assignments made with 95% or 80% confidence using the maximum likelihood (ML) and strict exclusion (Ex) methods (see methods).

| Haplotype | $N_{POP}$ | $N_{MAT}$ | $N_{CI}$ | 95% | 80% | Ex | Total |
|---|---|---|---|---|---|---|---|
| BakHapA | 560 | 143 | 6 | 1 | 1 | 4 | 4 |
| BakHapB+ | 505 | 106 | 5 | 1 | 0 | 2 | 2 |
| BakHapB' | 171 | 44 | 1 | 0 | 0 | 0 | 0 |
| BakHapC | 130 | 36 | 3 | 2 | 0 | 2 | 2 |
| BakHapD | 179 | 45 | 1 | 0 | 0 | 0 | 0 |
| PatHap04 | 39 | 11 | 3 | 1 | 1 | 1 | 2 |
| | | Total | 19 | 5 | 2 | 9 | 10 |

Table 2: Genetic diversity of the Campbell Island and overall New Zealand southern right whale *Eubalaena australis* wintering grounds. Microsatellite data is based on 13 loci and shows the sample size (2N), mean number of alleles per locus (k), and observed ($H_{OBS}$) and expected ($H_{EXP}$) heterozygosities. The mtDNA data are based on sequencing 500 bp of the mitochondrial control region and shows the sample size (N), number of unique haplotype observed in the sample (NHAP) and the haplotype ($h$±SD) and nucleotide (π±SD) diversities.

| | microsatellites | | | | mtDNA | | | |
|---|---|---|---|---|---|---|---|---|
| | 2N | k | $H_{OBS}$ | $H_{EXP}$ | N | $N_{HAP}$ | $h$±SD | π±SD (%) |
| Campbell Island | 42 | 8.3 | 0.82 | 0.77 | 19 | 6 | 0.82±0.05 | 1.32±0.72 |
| New Zealand | 1420 | 11.77 | 0.81 | 0.78 | 692 | 12 | 0.76±0.01 | 1.40±0.01 |

Table 3. Stable isotope analysis results of skin biopsy samples collected from southern right whales *Eubalaena australis* at Campbell Island.

| | | $\delta^{15}N$ (‰) | | $\delta^{13}C$ (‰) | |
|---|---|---|---|---|---|
| | *n* | Mean ± 1 SD | Range | Mean ± 1 SD | Range |
| Males | 10 | 8.0 ± 0.8 | 7.1 to 9.3 | -20.0 ± 0.6 | -21.2 to -19.3 |
| Females | 8 | 8.1 ± 0.6 | 7.1 to 8.7 | -19.6 ± 0.5 | -20.2 to -18.9 |
| All | 18 | 8.0 ± 0.7 | 7.1 to 9.3 | -19.8 ± 0.6 | -21.2 to -18.9 |

Table 4. Land-based visual counts of southern right whales *Eubalaena australis* in Northwest Bay, Campbell Island.

| Date | Time | Effort (min) | N group | N individuals |
|---|---|---|---|---|
| 02/08/15 | 15:00 | 10 | 18 | 40 |
| 02/08/15 | 16:00 | 10 | 16 | 33 |
| 03/08/15 | 09:00 | 10 | 20 | 39 |
| 03/08/15 | 10:00 | 15 | 21 | 41 |
| 03/08/15 | 11:00 | 15 | 15 | 35 |
| 03/08/15 | 12:00 | 13 | 17 | 48 |
| 03/08/15 | 13:00 | 15 | 29 | 59 |
| 03/08/15 | 15:00 | 13 | 26 | 58 |

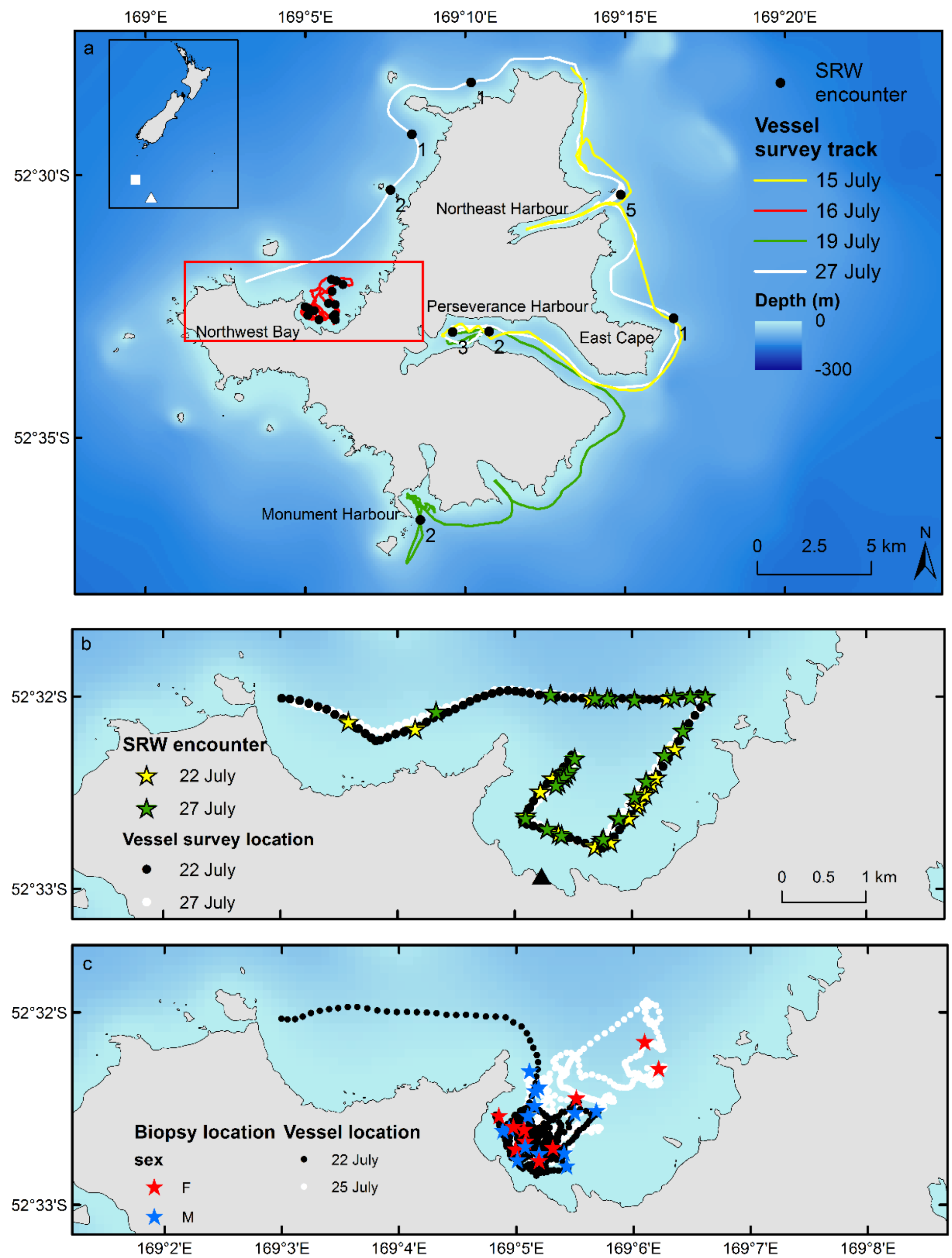


**Fig. 1** Survey effort and encounters of southern right whales *Eubalaena australis* (SRW) at Campbell Island (52° 32' S, 169º 09' E) during July 2014. (a) Daily tracks of vessel-based survey effort in closing mode and locations of *E. australis* encounters, with group size denoted for sightings outside Northwest Bay. Inset map shows location of Campbell Island (white triangle) and the Auckland Islands (white square) in the New Zealand sub-Antarctic. Red box indicates extent of (b) and (c). (b) Vessel-based survey effort in passing mode of Northwest Bay and *E. australis* encounter locations. Black triangle denotes location of hut used for land-based survey effort. (c) Skin biopsy sampling locations, color-coded by sex as determined by genetic analysis, and vessel survey track.

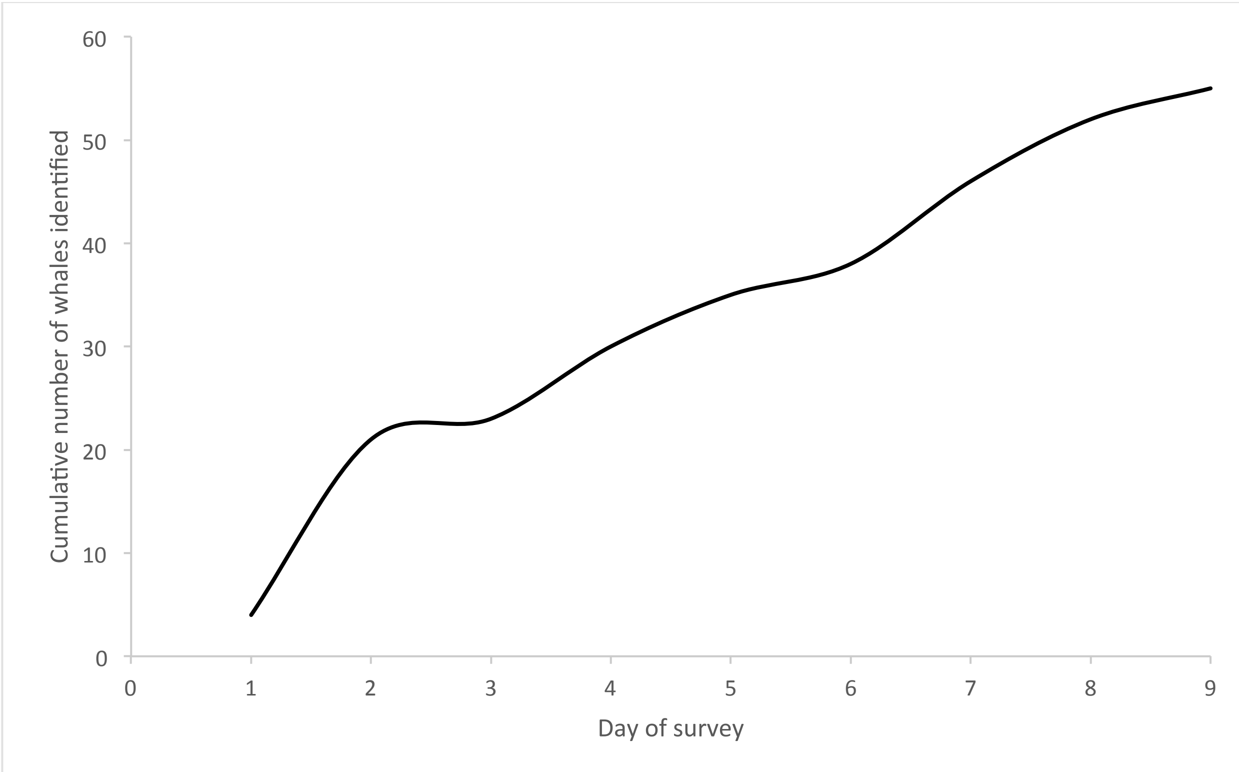


**Fig. 2** Discovery curve of unique left hand sides of photo-identified southern right whales *Eubalaena australis* at Campbell Island during photo-ID surveys in July 2014

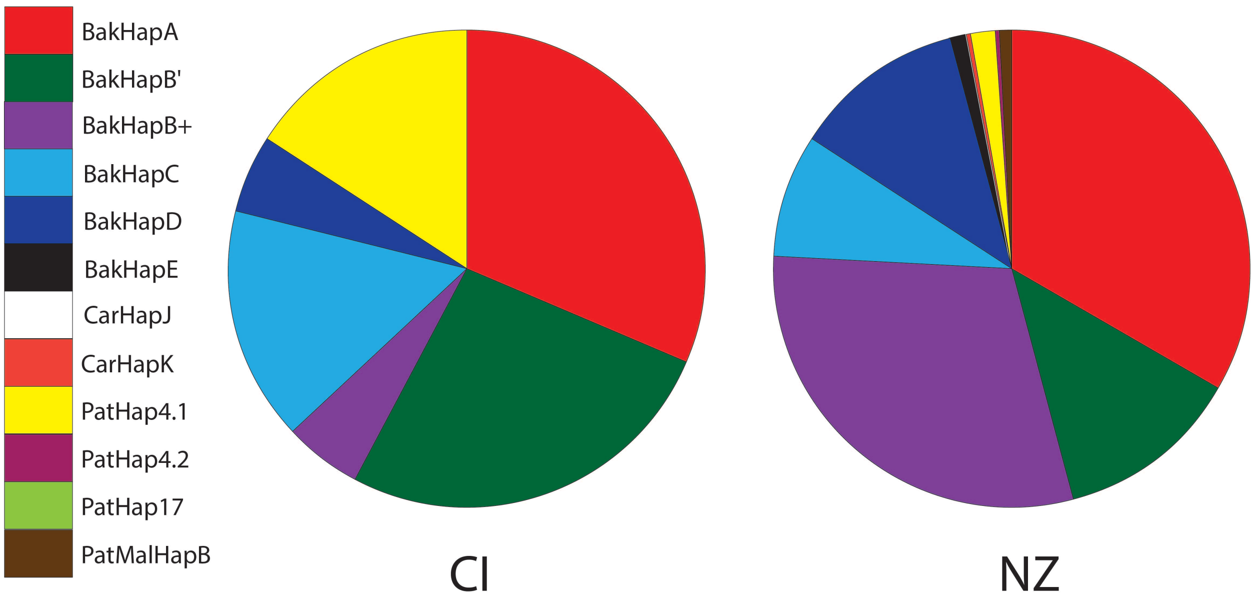


**Fig. 3** Pie charts of haplotype frequencies for Campbell Island (left, *n*=19) and the New Zealand (right, *n*=692) southern right whale *Eubalaena australis* wintering grounds. Haplotypes are defined sequencing 500 bp of the mitochondrial control region

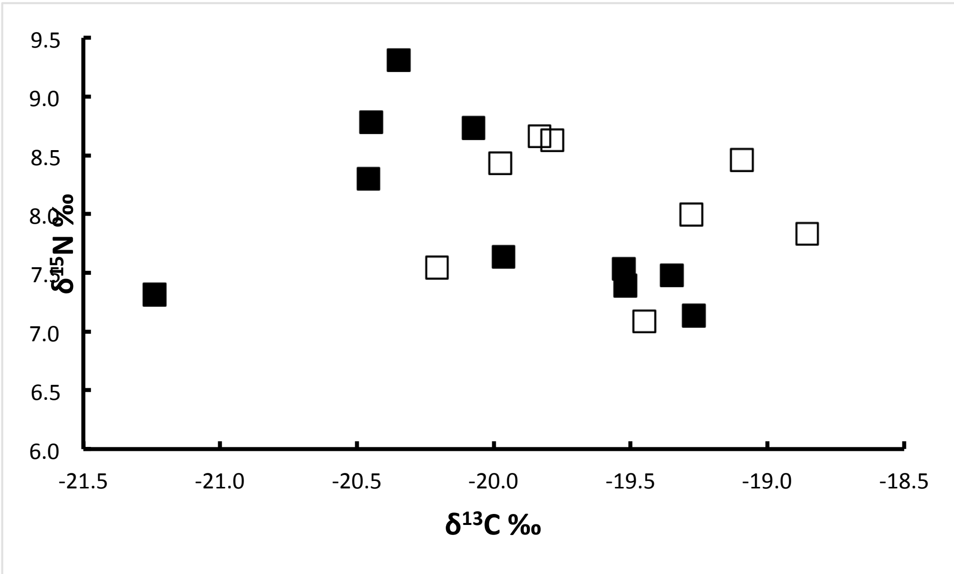


**Fig. 4** Carbon and nitrogen isotope bi-plot from tissues samples of southern right whales *Eubalaena australis* sampled at Campbell Island, New Zealand. Males as solid squares, females as open squares.