

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

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1 **Abstract**

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

21

22 **Keywords:**

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

25

26 **Introduction**

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

35

36 Despite this intense whaling activity around mainland New Zealand, the sub-Antarctic Auckland
37 Islands and Campbell Island (-52° 32' S, 169° 09' E; Fig. 1) served as a refuge for a portion of
38 the population (Gaskin 1964; Richards 2002). Limited whaling occurred in these islands,
39 including a fishery around Campbell Island that killed 63 *E. australis* between 1909 and 1913,
40 including several cow/calf pairs (Gaskin 1964). Following global protection in 1935, domestic
41 hunting of *E. australis* ceased. However, illegal Soviet whaling killed 256 whales near the
42 Auckland Islands between 1963 and 1967 (Tormosov et al. 1998). The legacy of this exploitation

43 was that no sightings of *E. australis* were reported around the mainland for approximately four
44 decades and it was feared the New Zealand stock had been completely extirpated (Gaskin 1964).
45 However, a small remnant group of *E. australis* continued to visit Campbell Island each winter,
46 from which it is hypothesized the stock began a slow recovery (Richards 2002).

47
48 Research to monitor recovery over the last 20 years has focused on the more logistically
49 accessible calving ground at the Auckland Islands (Carroll et al. 2013; Patenaude and Baker
50 2001; Rayment et al. 2012). Long-term genetic and photo-identification datasets exist for this
51 population (Carroll et al. 2013; Carroll et al. 2011b; Rayment et al. 2015) and all demographic
52 parameters estimated for the New Zealand stock are derived from the these data collected at the
53 Auckland Islands, including a current population estimate of 2169 (95% CI: 1836-2563; Carroll
54 et al. 2013). While these research efforts have been thorough, they do not consider potential *E.*
55 *australis* over-wintering at Campbell Island.

56
57 Staff based at the New Zealand meteorological station on Campbell Island reported seeing small
58 groups of *E. australis*, including mating groups and cow/calf pairs, in the region during winter
59 months from 1942 up to 1983 (Bailey and Sorensen 1962). The most recent systematic surveys
60 for *E. australis* at Campbell Island were conducted from 1995-1997 and documented the
61 presence of *E. australis* throughout winter, but no cow-calf pairs were reported (Stewart and
62 Todd 2001). The majority of sightings were recorded in Northwest Bay (Fig. 1, Stewart and
63 Todd 2001), although it is unclear to what extent other potential habitats at Campbell Island were
64 surveyed. Comparison of the 31 whales photo-identified around Campbell Island and 244 photo-
65 identified around Auckland Islands between 1995-1998 produced one within-year and three
66 between year matches (Patenaude and Baker 2001). Therefore, although there is interchange of
67 *E. australis* between the sub-Antarctic Islands, the status of Campbell Island waters as a calving
68 area remains equivocal, as is the current use of this historic wintering habitat by *E. australis*.

69
70 Female *E. australis* exhibit strong fidelity to their calving grounds (Best 1990; Payne 1986).
71 Hence, a portion of the New Zealand population that winters at Campbell Island may be
72 unsampled and unaccounted for in population estimates. Furthermore, maternally-directed
73 fidelity to wintering grounds results in limited connectivity between New Zealand and Australian
74 *E. australis* populations (Pirzl et al. 2009), leading to genetic differentiation based on maternally-
75 inherited mitochondrial DNA markers (Carroll et al. 2011a). Assessing the degree of gene flow
76 between Campbell Island, the Auckland Islands and mainland New Zealand in the context of
77 fidelity to migratory destinations is important as such behavior can strongly impact local patterns
78 of extinction and recolonization, thereby affecting large-scale population dynamics (Lande 1988;
79 Storz 1999). Furthermore, Gaskin (1968) noted that the whales killed at Campbell Island in the
80 early 1900s were not as large as those caught around the mainland, raising questions about the
81 relative health or age-class of animals over-wintering at this location.

82
83 In addition, there is evidence for maternally-directed learning of summer feeding grounds in
84 many baleen whales, including *E. australis* (Carroll et al. 2015; Valenzuela et al. 2009). Whales
85 that share feeding ground preferences, inferred from stable isotope profiles, are more likely to
86 share mtDNA haplotypes (Valenzuela et al. 2009) and have higher levels of relatedness based on
87 bi-parentally inherited microsatellite markers (Carroll et al. 2015). However, there are limited
88 data on the diet of *E. australis* in Australasian waters. The best available information comes

89 from the stomachs of animals killed by Soviet whalers between 1960 and 1971 documented by
90 Tormosov et al. (1998). The stomach contents of whales taken south of 50° S primarily (99.4%)
91 contained euphausiids (krill species; Tormosov et al. 1998). In contrast, stomach contents of
92 whales killed north of 40° S consisted almost entirely (91.7%) of copepods (*Calanus* spp.), and
93 whales caught in intermediate latitudes showed a more mixed diet dominated by copepods
94 (71.4%), secondly euphausiids (24.3%), and small crustacea (4.3%). A habitat analysis of 19th
95 century offshore whaling data during non-winter months in the New Zealand region between 30°
96 and 52° S identified strong association patterns between *E. australis* distribution and temperature
97 in the upper 200 m, and predicted high habitat suitability in close proximity to the sub-tropical
98 front surrounding 45° S (Torres et al. 2013). Confirmation of *E. australis* foraging grounds in the
99 New Zealand region is lacking, as is the description of the surviving genetic lineages that occur
100 on such feeding grounds.

101
102 The New Zealand population of *E. australis* is recovering (Carroll et al. 2013; Carroll et al.
103 2014b), necessitating a full understanding of its population dynamics at all wintering areas to
104 enable effective management. This study investigates *E. australis* use of Campbell Island during
105 the austral winter (July) using a variety of methods including photo-identification, genetic and
106 stable isotope analysis of tissue samples, and surveys of abundance and distribution. Our work
107 aims to fill important knowledge gaps about *E. australis* wintering at Campbell Island including
108 distribution patterns, demographic units, genetic composition, abundance, connectivity to
109 Auckland Islands and mainland New Zealand populations, and summer trophic foraging patterns.

110

111 **Materials and methods**

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

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

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

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

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

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

$$163 \quad Nm = \{(n_1 + 1)(n_2 + 1) / (m + 1)\} - 1 \quad (\text{Eq. 1})$$

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

169 The Lincoln-Petersen estimator has the following assumptions (Pollock et al. 1990): (1) the
170 population is closed to additions (births and immigrants) and deletions (deaths and emigrants)
171 during the survey period, (2) all animals are equally likely to be captured, and (3) marks are not
172 lost and are correctly identified. We can safely assume that the population was demographically

173 closed and that identifying marks were not lost over the short study period (15 days). We
174 attempted to minimize the risk of misidentification by using a suite of identifying characteristics
175 and having at least two experienced researchers confirm photo-ID matches. Geographic closure
176 (no immigration or emigration during the sampling period) was assessed by examining a
177 discovery curve of individuals over the study period.

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

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

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

201 In addition, we compared the DNA profiles of the whales sampled around Campbell Island to the
202 'DNA register' previously established from whales sampled around the Auckland Islands and
203 mainland New Zealand. Specifically, we used the DNA profiles from 710 individually-identified
204 adult SRW and 66 dependent calves captured at the Auckland Islands between 1995-2009
205 (Carroll et al. 2013) and 47 individually-identified *E. australis* sampled around mainland New
206 Zealand between 2003 and 2010 (Carroll et al. 2011a; Carroll et al. 2014b). After reconciliation
207 of replicates within these samples, the Campbell Island genotypes were compared with a total of
208 793 *E. australis* sampled around New Zealand between 1995 and 2010 (362 males, 431 females,
209 and 8 whales of unknown sex due to PCR amplifications failure).

210 The comparison of DNA profiles was based on 13 loci, with associated mtDNA haplotypes and
211 sex, and matching proceeded following previously described methodology (Carroll et al. 2013).
212 Briefly, matching genotypes were identified using CERVUS v3.0 (Kalinowski et al. 2007). As a

213 precaution against false exclusion due to allelic dropout and other genotyping errors, the initial
214 comparison allowed for mismatches at up to three loci. To assess the observed versus the
215 expected number of recaptures between the New Zealand and Campbell Island DNA profile
216 catalogues, we undertook a simulation study in the programming language R (R Development
217 Core Team 2013) (Online Resource 2).

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

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

235 Thirdly, we conducted a maternity analysis to identify the mothers of whales sampled around
236 Campbell Island within the New Zealand genotype database. This was conducted because of a
237 hypothesized bias towards sub-adults at Campbell Island. We used the strict exclusion (Ex) and
238 maximum likelihood (ML) method implemented in program CERVUS. The Ex method means
239 that mother and offspring must match at one allele per locus to be considered a parent-offspring
240 pair. However, this does not account for genotyping error. The ML method of Kalinowski et al
241 (2007) compares the likelihood of the two most likely mothers, accounting for a user-specified
242 value of genotyping error. For each offspring, the difference between the likelihoods of the two
243 most likely mothers produces a delta score. Simulations were conducted to estimate the critical
244 delta value required to assign maternity with 80% and 95% confidence. Campbell Island samples
245 were clustered by mtDNA haplotype and simulations and analysis were run on a per-haplotype
246 basis. As mtDNA is maternally-inherited, mother and offspring must share the same mtDNA
247 haplotype. Simulations require an assumption of the number of potential mothers in the
248 population per haplotype, which was worked out using published haplotype frequencies (Carroll
249 et al. 2011a) and an estimated total non-calf female population size of 1521 whales in 2014 (see
250 Online Resources 2). Additionally, the proportion of these females that were genotyped (Table 1)
251 is required. We ran the simulations under the assumption that the genotyping error rate was 1%
252 (Carroll et al. 2013) and individuals were typed at a least nine of 13 loci.

253 Stable isotope analysis Eighteen *E. australis* skin biopsy samples were analyzed for carbon and
254 nitrogen stable isotope values. Once in the lab, ethanol was evaporated from the biopsies under a
255 stream of nitrogen gas prior to freeze drying. A sub-sample of skin (0.7-1.0 mg) was then
256 weighed into tin boats for stable isotope analysis. Stable isotope analyses were carried out on a
257 Delta^{Plus} (Thermo-Fisher Scientific, Bremen, Germany) continuous flow, isotope ratio mass
258 spectrometer linked to an NA 1500 elemental analyzer (Fisons Instruments, Rodano, Italy). For
259 details of the analytical set-up refer to Morrison et al. (2014). C isotope data were corrected for
260 lipid content following equations in Fry (2002). Repeated analyses of National Institute of
261 Standards and Technology (NIST) and laboratory standards had a precision (1 s.d.) of better than
262 0.2 ‰ and 0.1 ‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, respectively. Duplicate analysis of skin samples gave
263 a precision (1 s.d.) of better than 0.3 ‰ for $\delta^{15}\text{N}$ and 0.4 ‰ for $\delta^{13}\text{C}$.

264 Land-based survey Land-based visual counts were undertaken near the shore-side hut at
265 Northwest Bay at approximately 9 m above sea level, where a clear view of the bay was
266 achieved (Fig. 1b). Dedicated hourly counts over 10 to 15 min were undertaken on 2 and 3
267 August 2015, weather permitting (no rain, snow or fog; BSS < 4), replicating Stewart and Todd
268 (2001) counts. One observer scanned with naked eye while another scanned with binoculars.
269 During these counts, the number of groups and number of individuals within a group were
270 recorded. Whales were considered part of a group when in close proximity (< ~15 m) to each
271 other and engaged in similar behavior.

272 **Results**

273 Vessel-based survey: Survey effort for *E. australis* around Campbell Island using closing mode
274 was conducted on four days in July 2014 (Fig. 1a). Outside of Northwest Bay (15, 19, 27 July
275 2014), eight *E. australis* encounters were made of 17 individuals: one sighting outside
276 Monument Harbour (two individuals), two sightings in Perseverance Harbour (five individuals),
277 one sighting near East Cape (one individual), one sighting outside Northeast Harbour (five
278 individuals), and three sightings along the northwest coast (four individuals). These whales were
279 typically observed resting or travelling, and no social behavior was observed. During a closing
280 mode visual survey in Northwest Bay with dedicated photo-ID effort on 16 July 2014, 14 *E.*
281 *australis* encounters were recorded (over 50 individuals observed) and whales were often
282 engaged in social behavior within surface active groups (SAGs; Kraus and Hatch 2001). The
283 southwest side of Campbell Island from Monument Harbour to Northwest Bay was not surveyed
284 due to poor bathymetric data and many pinnacles that made coastal navigation a safety risk.

285 Two visual surveys using passing mode were conducted along a 9.6 km survey line within
286 Northwest Bay (Fig. 1b) to determine minimum abundance counts. On 22 July 2014, 30 *E.*
287 *australis* were observed (3.1 whales per km) and on 27 July 2014, 28 *E. australis* were observed
288 (2.9 whales per km). Dedicated biopsy sampling with complimentary photo-ID effort was
289 conducted in Northwest Bay on 22 and 25 July 2014 (Fig. 1c).

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

291 Photo-identification: Images of sufficient quality for photo-ID analysis were obtained from 97
292 encounters. The LHS and RHS catalogues contained 55 and 46 whales respectively, of which 16

293 appeared in both catalogues. Only seven individuals were photographed on more than one day,
294 and the discovery curve shows no sign of reaching an asymptote (Fig. 2), suggesting a high rate
295 of turnover of whales in the study area.

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

299 *Microsatellite genotyping and individual identification:* A total of 24 skin biopsy samples were
300 collected from *E. australis* at Campbell Island and made available for genetic analysis. Of these,
301 23 passed the quality control measure of amplifying at nine or more microsatellite loci with an
302 average of 12.8 of 13 loci per sample. Matching within the Campbell Islands dataset revealed
303 that two whales had been sampled twice, so a total of 21 individually identified whales (10
304 females and 11 males) were captured. Both resamplings were of males first captured on 22 July
305 2015 and the recaptured on 25 July 2015¹. Mitochondrial sequencing produced haplotype
306 sequences for 19 of the 21 unique genotypes.

307 *Movement of individuals:* Comparison with the other New Zealand catalogues revealed nine
308 photo-ID matches with whales that had previously been seen at the Auckland Islands between
309 2009 and 2012, one of which had also been seen at the New Zealand mainland in 2007. None of
310 these whales had ever been seen accompanied by a calf and all were of unknown sex.

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

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

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

326 Of the 19 Campbell Island samples with mtDNA haplotypes and microsatellite genotypes
327 available, Ex maternity analysis identified nine putative mothers and the ML method identified
328 two at 80% confidence and five at the 95% confidence level. There was overlap between these
329 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.

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

333 Stable isotope analysis: Mean $\delta^{13}\text{C}$ for 18 skin biopsy samples was -19.82 (range: -21.24 to -
334 18.85; 1 SD: 0.56), and mean $\delta^{15}\text{N}$ was 8.09 (range: 7.08 to 9.31; 1 SD = 0.65; Table 3; Fig. 4).
335 No significant difference was detected between males and females for $\delta^{13}\text{C}$ ($t = 0.10$, $p = 0.92$) or
336 $\delta^{15}\text{N}$ ($t = 0.72$, $p = 0.48$; Fig. 4). For reference, Antarctic $\delta^{13}\text{C}$ signatures are typically more
337 depleted than -22 and tropical $\delta^{13}\text{C}$ values are more positive than -17 (Cherel et al. 2013).

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

341 Discussion

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

359
360 However, a relatively large number of *E. australis* were observed at Campbell Island, indicating
361 that this is an important wintering habitat for some portion of the New Zealand population.
362 Although calves were not observed at Campbell Island, it may serve as a gathering location for
363 sub-adult *E. australis*, possibly for social interactions. This hypothesized population bias toward
364 sub-adults is supported by a number of findings: (1) no mature females (individuals observed
365 prior to 2009, or individuals observed previously with a calf) were identified at Campbell Island
366 through photo-id analysis; (2) the lack of genetic matches between samples collected at
367 Campbell Island and other *E. australis* wintering areas may be related to the fact that 80% of
368 DNA profiles in the database are of whales that are age > six years, and hence not considered
369 sub-adults; (3) the Campbell Island samples were more genetically similar to a sub-group of
370 juveniles sampled from the Auckland Islands, rather than a sub-group of samples from older
371 whales. Specifically, we found no genetic differentiation between the Campbell Island dataset
372 and a sample of 66 calves sampled around the Auckland Islands from 2006-2009 (mtDNA

373 $F_{ST}=0.00$, Online Resource 3). In contrast, there was a significant difference between the mtDNA
374 haplotype frequencies of the Campbell Island dataset and the whales sampled around the
375 Auckland Islands between 1995-1998, which represents an older generation of whales ($F_{ST}=0.05$,
376 $p=0.02$, Online Resource 3); (4) if the Campbell Island samples are representative of juveniles
377 from the broader New Zealand population, parents of Campbell Island juveniles should be
378 identifiable within the New Zealand DNA register. Indeed, maternity analyses found putative
379 mothers for ten of 19 tested Campbell Island samples within the New Zealand genetic database.
380 Taken together, these findings suggest that there may be a generational bias towards sub-adult *E.*
381 *australis* at Campbell Island. Wintering grounds for *E. australis* in other regions have also noted
382 areas used by distinct age-classes. For example, Best (2000) described areas of the South African
383 coast as 'mating' and 'nursery' areas. Interestingly, historical accounts suggest *E. australis* caught
384 around Campbell Island were smaller than those killed around mainland New Zealand (Gaskin
385 1968), perhaps due to a predominance of juveniles in the region.

386
387 Adult *E. australis* were also present at Campbell Island during our survey period because one
388 individual was photographically matched with a sighting made at the New Zealand mainland in
389 2007, making it more than 7 years old. Furthermore, nine photo-id matches were made between
390 *E. australis* observed at Campbell Island and the Auckland Islands between 2009 and 2012.
391 Further confirmation of connectivity between these two wintering areas is based on the absence
392 of genetic differentiation between individuals sampled at Campbell Island and at the Auckland
393 Islands. This is consistent with previous research in the 1990s that also found matches between
394 Auckland and Campbell Islands (Patenaude et al. 2001).

395
396 Although similarity of the photo-ID capture-recapture abundance estimates from the LHS (288)
397 and RHS (278) catalogues lends weight to the reliability of these values, these estimates should
398 be interpreted with caution. Firstly, the low level of survey effort, coupled with high turnover
399 rates of whales in the study area, resulted in very few recaptures. Low capture probabilities
400 exacerbate the negative bias likely to be present due to the heterogeneity of capture probability
401 common to many capture-recapture studies (e.g., Hammond 1990; Lukacs 2013). Furthermore,
402 the discovery curve and low recapture rates suggest immigration and emigration during the study
403 period, likely violating the assumption of geographic closure. Violation of this assumption leads
404 to an overestimate of abundance in the study area (Kendall 1999; Seber 1982). However,
405 assuming that immigration and emigration are random, a closed-capture model can still yield
406 unbiased estimates of the super-population (i.e. all individuals that used the study area during the
407 study period), albeit with poor precision (Kendall 1999). While acknowledging the likely
408 violations of the capture-recapture assumptions, our results suggest that the number of *E.*
409 *australis* using the nearshore Campbell Island habitat during the survey period was probably
410 between 100 and 700. In comparison, the latest photo-ID derived estimate of annual abundance
411 from the Auckland Islands suggests that 359 whales (95% CI: 298 – 436), including 68 calves,
412 used the calving habitat during a 3-week period in July/August 2011 (Rayment, unpublished
413 data).

414
415 Distribution surveys demonstrated that although *E. australis* were encountered at various coastal
416 locations around the island, animals were concentrated in Northwest Bay where SAGs were
417 frequently encountered, whereas *E. australis* encountered at other places around the island were
418 travelling and not engaged in social activity. Dedicated vessel-based survey results within

419 Northwest Bay indicated a relatively high *E. australis* density of three whales observed per km
420 surveyed. Additionally, land-based surveys determined a mean of 44 animals in Northwest Bay.
421 In comparison to the maximum number of whales counted per day in Northwest Bay in June-Sep
422 1983 ($n=30$ from 56 survey days), July 1995 ($n=24$ from 24 survey days), and Jun-Aug 1997
423 ($n=28$ from 54 survey days) as reported by Stewart and Todd (2001), our results indicate that the
424 number of *E. australis* using Northwest Bay has increased over the last 20 years by about 4% a
425 year, which is similar to estimated annual increase for the New Zealand population (5-7%;
426 Carroll et al 2013. Yet, sampling in multiple years is necessary to determine the true population
427 trend at Campbell Island.

428
429 Stable isotope results indicate foraging within the sub-Antarctic region based on $\delta^{13}\text{C}$ values that
430 are depleted relative to sub-tropical water masses, and enriched relative to the polar zone, based
431 on tracking-isotope studies of seabirds (Cherel et al. 2013; Jaeger et al. 2010). Foraging within
432 sub-Antarctic waters is supported by Torres et al. (2013) that predicted *E. australis* foraging
433 habitat in the New Zealand region to occur in the sub-Antarctic. Variation in $\delta^{15}\text{N}$ across all *E.*
434 *australis* sampled was 2.2 ‰, which could reflect variation in diet among individuals or variation
435 in prey isotope values (i.e., the same prey species in different regions may have different isotope
436 values). This variation could be driven by temporal or spatial variations in the foraging patterns.
437 Despite this apparent inter-individual variation, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for this sampled *E.*
438 *australis* population at Campbell Island is less varied than values reported for *E. australis*
439 breeding in Argentina (Valenzuela et al. 2009), although the Argentinean study utilized a much
440 larger dataset ($n=131$).

441 Our efforts to describe the *E. australis* population segment that winters at Campbell Island fills
442 many remaining knowledge gaps about the demography and ecology of the New Zealand *E.*
443 *australis* population. Although Campbell Island does not appear to be a calving area, it
444 represents a significant wintering habitat for sub-adult and adult *E. australis*, especially in
445 Northwest Bay. We have also generated further evidence of foraging in the sub-Antarctic region
446 south of the sub-tropical front by *E. australis* that are breeding in New Zealand. Additionally, we
447 have demonstrated connectivity between all three *E. australis* wintering grounds (Campbell
448 Island, Auckland Islands, and mainland New Zealand) directly with individuals sighted at each
449 location, and indirectly, through genetic and maternity analyses, which reinforces previous
450 evidence for one New Zealand population of *E. australis* (Carroll et al. 2011a; Carroll et al.
451 2014b). Based on these findings, we recommend that previous demographic studies of *E.*
452 *australis* at the Auckland Islands are suitably representative of the whole New Zealand
453 population, yet periodic surveys (i.e., every 5 years) of other wintering grounds, particularly
454 Campbell Island, is warranted to continually monitor population growth and range expansion, as
455 has been seen at other *E. australis* wintering grounds (Groch et al. 2005; Harcourt et al. 2012;
456 Rowntree et al. 2001).

457

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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 (N_{HAP}) and the haplotype ($h \pm SD$) and nucleotide ($\pi \pm SD$) diversities.

	microsatellites				mtDNA			
	2N	k	H_{OBS}	H_{EXP}	N	N_{HAP}	$h \pm SD$	$\pi \pm SD$ (%)
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.

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

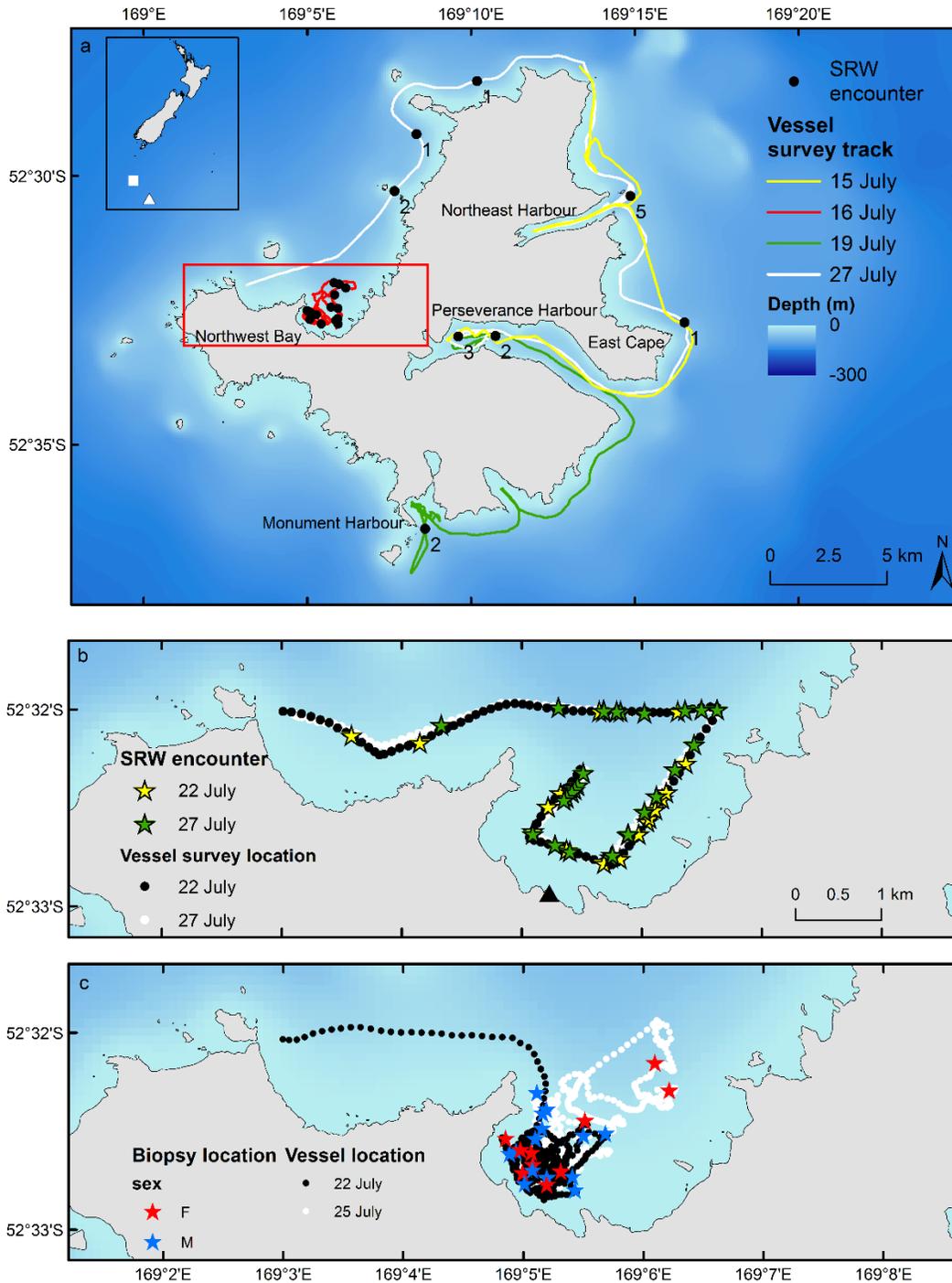


Fig. 1 Survey effort and encounters of southern right whales *Eubalaena australis* (SRW) at Campbell Island ($52^{\circ} 32' S$, $169^{\circ} 09' E$) during July 2014. (a) Daily tracks of vessel-based survey effort in closing mode and locations of *E. australis* encounters, with group size denoted for 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.

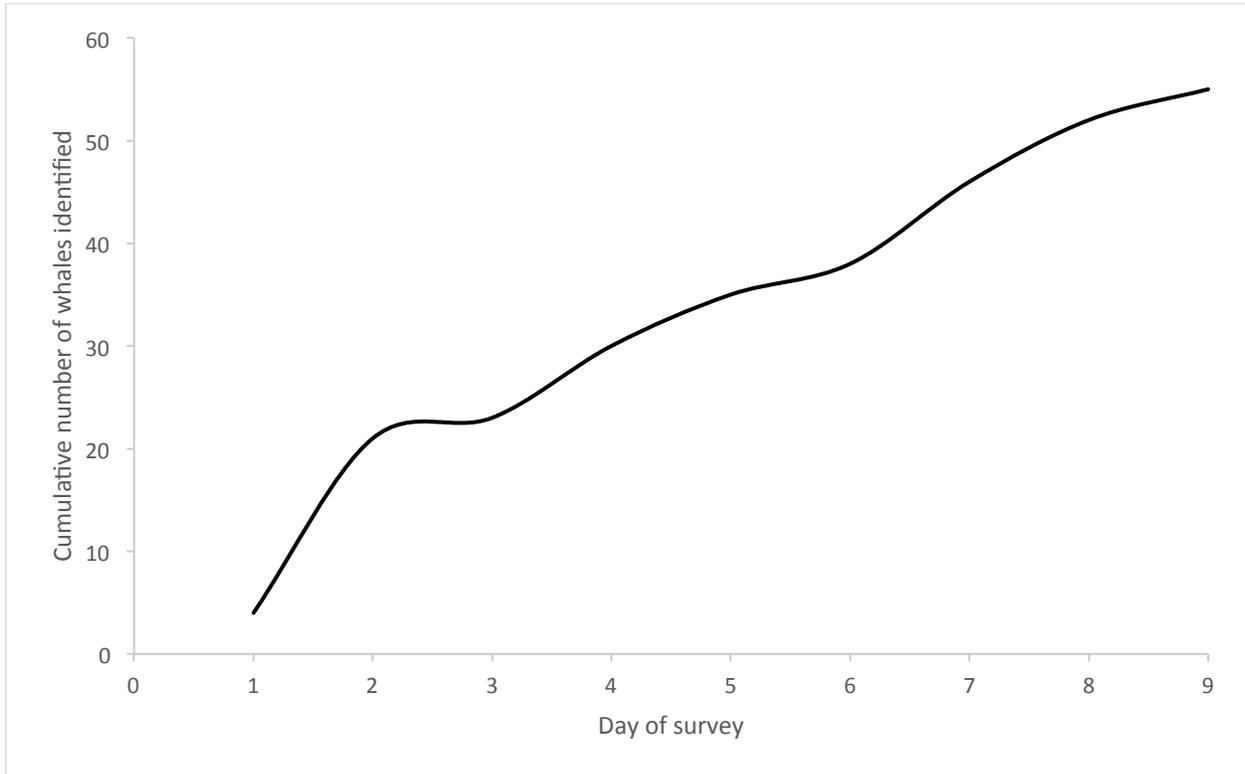


Fig. 2 Discovery curve of unique left hand sides of photo-identified southern right whales *Eubalaena australis* at Campbell Island during photo-ID surveys in July 2014

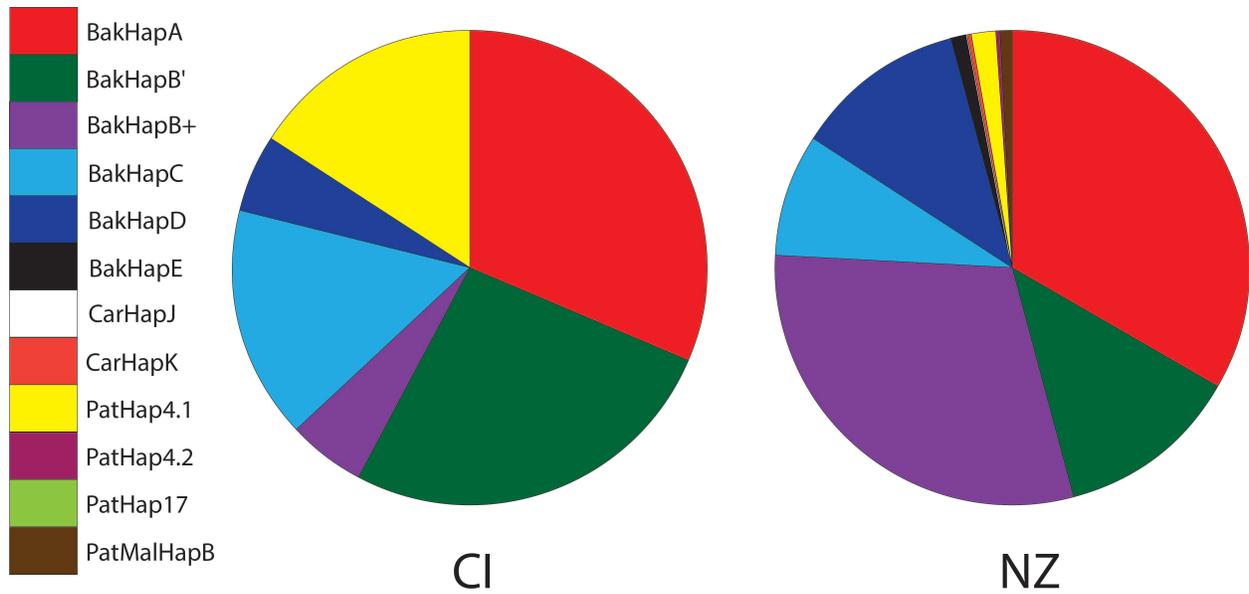


Fig. 3 Pie charts of haplotype frequencies for Campbell Island (left, $n=19$) and the New Zealand (right, $n=692$) southern right whale *Eubalaena australis* wintering grounds. Haplotypes are defined sequencing 500 bp of the mitochondrial control region

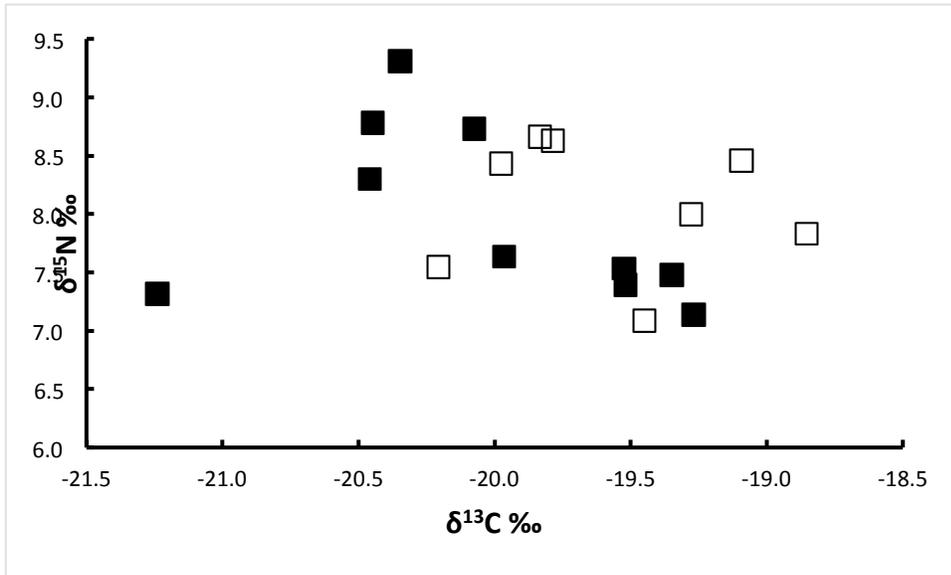


Fig. 4 Carbon and nitrogen isotope bi-plot from tissues samples of southern right whales *Eubalaena australis* sampled at Campbell Island, New Zealand. Males as solid squares, females as open squares.