Stable isotopes (δ^{15}N, δ^{13}C, δ^{34}S) in skin reveal diverse food sources used by southern right whales *Eubalaena australis*

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ABSTRACT: Skin samples collected from living southern right whales (SRWs) off Península Valdés, Argentina, show a wide range of stable isotope values (δ^{15}N, δ^{13}C, δ^{34}S). These were compared to the isotopic signatures of euphausiids and copepods from different areas across the southwestern South Atlantic and the Atlantic sector of the Southern Ocean. Our results suggest that that this population of SRWs uses at least 3 distinct food sources. Each food source may represent a single feeding ground or a combination of feeding grounds with different prey species distributions. Individual whales pursue foraging strategies that vary substantially in the amounts of time they spend in different feeding grounds along their migratory paths. The 3 grounds that appear to contribute most to the diets of Península Valdés SRWs correspond to areas previously documented in the log books of whaling ships: the Patagonian Shelf, South Georgia and the waters of the Polar Front. It is possible that additional feeding areas are also currently being used in the South Atlantic. Age and sex classes differ isotopically, but these differences could be caused by biomechanical or physiological characteristics rather than by age- and sex-specific specialization in different feeding areas.

KEY WORDS: Distribution · Feeding grounds · Migration · Population · Baleen whales · Southern Ocean · Patagonia

INTRODUCTION

Southern right whales *Eubalaena australis* (SRWs) consume large quantities of zooplankton (Reilly et al. 2004), and their reproductive output responds to fluctuations in krill abundance linked to El Niño-Southern Oscillation (ENSO) (Leaper et al. 2006). Ocean warming is transforming the Southern Ocean ecosystem and thereby affecting all trophic levels from phytoplankton to large predators (McClintock et al. 2008). A regional warming of 1°C could lead to a 95% reduction in the abundance of Antarctic krill *Euphausia superba* over the next 100 yr across the southwestern South Atlantic (Murphy et al. 2007). Large whales may face extreme difficulty adjusting to such changes, which will be profound on the scale of an individual's lifetime (at least 65 yr on average for right whales; Hamilton et al. 1998). Furthermore, SRWs have an inherently low reproductive rate, with females typically bearing their first calf between 7 and 8 yr of age and then giving birth every 3 yr (Payne 1986, Brandão et al. 2011). In cases like this,

ecological flexibility at the individual level could strongly affect the survival of a species that finds its environment changing rapidly.

SRW matrilines show persistent attachments to particular feeding grounds, as demonstrated by stable isotopic and genetic analyses of skin samples collected at Península Valdés, Argentina (Valenzuela et al. 2009). This site fidelity appears to be strong enough that it could forestall the whales' discovery and utilization of alternative feeding grounds for several to many generations. Our limited knowledge of SRW foraging behaviour still derives largely from the records of whaling ships in the 1800s and 1900s (International Whaling Commission, IWC 2001), supplemented by recent opportunistic observations of feeding behaviour near shore (Hamner et al. 1988, Moore et al. 1999), line transect surveys of the Southern Ocean in summer (Reilly et al. 2004) and satellite tagging of individual whales (Best & Mate 2007, Mate et al. 2011, Zerbini et al. 2015, 2016). To improve our abilities to predict the whales' possible responses to short-term events such as ENSO, and to long-term changes in their ocean ecosystem, we will need to improve our understanding of their current habitat use and foraging ecology.

SRW foraging distribution and diet

SRWs migrate seasonally between calving grounds and feeding grounds. During the winter–spring calving season (June through December), they congregate along the coastal waters of Argentina, Brazil, South Africa, Australia and New Zealand, where they have been studied intensively (IWC 2012). During the summer–fall feeding season, they travel to remote offshore feeding locations that are mostly unknown. Six historic feeding grounds in the South Atlantic have been documented from catch locations of 19th and 20th century whalers (Fig. 1) (IWC 2001). However, it is unclear to what extent these historic feeding grounds, or others, are used today. SRWs have been sighted near the Antarctic Peninsula and South Georgia (Hamner et al. 1988, Moore et al. 1999, Reilly et al. 2004), and 3 whales that were photo-identified on their nursery ground at Península Valdés have been photographed off South Georgia (Best et al. 1993). Satellite tags have shown that South African right whales apparently use 3 different feeding grounds, only one of which matches one of the IWC historic feeding grounds (south of 50° S and between 30° E and 10° W; Mate & Best 2008, Mate et al. 2011). More recently, SRWs tagged off Península
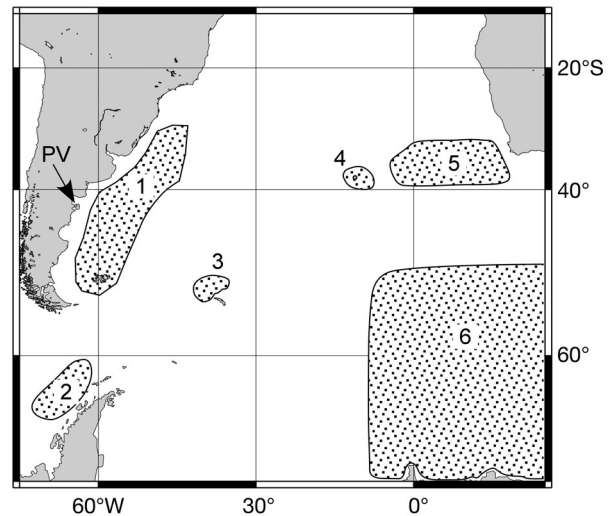

Fig. 1. South Atlantic and Atlantic sector of the Southern Ocean indicating the 6 historic southern right whale feeding grounds recognized by the International Whaling Commission (IWC 2001). (1) Offshore South America, (2) Antarctic Peninsula, (3) South Georgia, (4) Tristan da Cunha, (5) Cape Town-Tristan da Cunha (a band [30° to 40° S] of catches between Gough Island and South Africa), and (6) a diffuse area south of 50° S and between 30° E and 10° W. The location of Península Valdés (PV), Argentina, is also marked

Valdés visited the outer Patagonian Shelf east of Península Valdés and north of the Falkland/Malvinas Islands, the Scotia Sea near South Georgia/Islas Georgias del Sur and the South Sandwich Islands/Islas Sandwich del Sur, and the South Atlantic basin between 38 and 58° S (Zerbini et al. 2015, 2016). Apart from these regional sightings and preliminary telemetry data, little is known of the whales' current feeding distribution in the South Atlantic.

SRWs feed on krill (primarily *Euphausia superba*) and copepods. Individuals killed in the South Atlantic during an illegal hunt by Soviet whalers in the 1960s had stomachs full of unidentified euphausiids if taken south of 50° S, or calanoid copepods if taken north of 40° S, or mixtures of these 2 prey types if taken between 40° and 50° S (Tormosov et al. 1998). Hamner et al. (1988) observed right whales feeding on *E. superba* near the Antarctic Peninsula and South Georgia; the whales have also been observed to feed occasionally at the Península Valdés calving ground (Payne 1995, Sironi 2004, Hoffmeyer et al. 2010).

Skin isotopes as tracers of foraging ecology and migration

Regional variations in stable isotope ratios have been used to identify the feeding locations and migra-

tory patterns of many species of birds and mammals, including whales (Schell et al. 1989, Hobson 1999, Rubenstein & Hobson 2004, McMahon et al. 2013). This is possible because stable isotope ratios have predictable patterns of change across landscapes (Hobson 1999, Rubenstein & Hobson 2004, West et al. 2006). In marine ecosystems for example, carbon isotope ratios ($^{13}C/^{12}C$) decrease with increasing latitude, and more shallow waters have higher values compared to pelagic waters in both carbon and sulphur ($^{34}S/^{32}S$) isotope ratios (Peterson & Fry 1987, Fry 2006). The carbon isotope patterns are in part the result of temperature differences, CO_2 concentrations and differences in plankton species and metabolism (Peterson & Fry 1987, Fry 2006, McMahon et al. 2013, Magozzi et al. 2017), while the differences in sulphur reflect differences in the anoxic conditions of the waters and sources of sulphur (Peterson & Fry 1987, Fry 2006). A second characteristic of isotopes that makes them useful to track animal movements is that isotopes are incorporated directly from diet into animal tissues with varying degrees of discrimination. Some isotopes (e.g. carbon) reflect the diet without much change, while others (e.g. nitrogen) show considerable enrichment and are affected by variables such as nutritional stress and food quality (Deniro & Epstein 1981, Roth & Hobson 2000, McCutchan et al. 2003, Fuller et al. 2004). When incorporated into body tissues, nitrogen isotope ratios ($^{15}N/^{14}N$) increase an average of 3‰ per trophic level over the whole animal body (DeNiro & Epstein 1978, 1981, Peterson & Fry 1987, Kelly 2000). Not much is known about sulphur discrimination in animal tissues, although it is expected to be negligible or very small (Richards et al. 2003, Arneson & MacAvoy 2005). The stable isotope values recorded in an animal's tissues represent an integration of the food consumed anywhere from the last few hours or weeks (blood plasma or muscle) up to the animal's entire life (bone collagen), depending on the isotope turnover rate of the tissue that is analyzed (Rubenstein & Hobson 2004).

Measurements of stable isotope ratios from skin biopsies have been used to study the foraging ecology of free-ranging whales (Todd et al. 1997, Hooker et al. 2001, Ruiz-Cooley et al. 2004, Godard-Codding et al. 2011, Witteveen et al. 2012). The main difficulty is that isotopic discrimination and turnover rates cannot be estimated directly for the skin of large whales because controlled feeding experiments are not feasible. The isotopic offset between fin whale *Balaenoptera physalus* skin and potential prey has been estimated at 2.82‰ for $\delta^{15}N$ and 1.28‰ for $\delta^{13}C$ values (Borrell et al. 2012); these are similar to the average classic values for whole animals (~3‰ for nitrogen and 0 to 1‰ for carbon; Peterson & Fry 1987, Post 2002). The turnover interval for whale skin is thought to be between 1 mo (Todd et al. 1997) and several months (Ruiz-Cooley et al. 2004). This uncertainty in temporal integration is perhaps the largest source of error when using isotope ratios of skin to study a whale's diet and migration. However, skin is the only tissue that can easily be collected from large numbers of live whales using a minimally invasive procedure that yields samples large enough to be used for several different types of analyses (e.g. stable isotopes, DNA, fatty acids, trace elements).

In an attempt to identify the feeding locations currently used by the SRW population from Península Valdés, we analyzed stable carbon and nitrogen isotopes of skin samples in relation to published and unpublished isotopic values of euphausiids and copepods from different areas across the southwestern South Atlantic and the Atlantic sector of the Southern Ocean. Our use of published isotope data for different animal taxa has the purpose to broadly characterize the isotopic variability among historic feeding grounds. We also present preliminary stable sulphur isotope values from skin samples to test whether this extra tracer might provide additional information regarding feeding differences among whales. We investigated whether different age and sex classes appear to use these resources differently, and we also compared the stable isotopic values of SRWs to those of other predators from these same regions.

MATERIALS AND METHODS

Sample collection and analyses

Skin samples (n = 196) were obtained by biopsy darting live whales off Península Valdés, Argentina (42° 30′ S, 64° 00′ W) over 4 consecutive years (2003 to 2006) at the time of peak whale abundance (September and October) (Payne 1986). To avoid including re-sampled whales, individuals were photographed for later identification based on callosity patterns and other natural marks (Payne et al. 1983). Age classes (adults and juveniles) were determined primarily based on body size, and adult nursing females were recognized by the presence of calves. The genders of juveniles and single adults were determined whenever possible from observation of the genital area; otherwise, gender was later identified by PCR amplification and electrophoresis of Z*fx* and Z*fy* introns following Shaw et al. (2003).

After collection, skin samples were dried in an oven; no chemical preservative was used. Dried samples were ground to a fine powder and lipids extracted using Soxhlet extraction (2:1 chloroform: methanol) following Todd et al. (1997). Approximately 1 mg sample^{-1} was analyzed for carbon and nitrogen isotopes using a Carlo Erba 1108 elemental analyzer coupled to a Thermo Finnigan Delta S IRMS at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah. Sulphur (δ^{34}S) analysis was conducted at the Colorado Plateau Stable Isotope Laboratory (CPSIL), using a Costech ECS4010 elemental analyzer interfaced to a Thermo-Electron Delta Plus Advantage IRMS. The isotope ratios are expressed as δ^{13}C, δ^{15}N or δ^{34}S (‰) = $[(R_{sample} / R_{standard}) - 1] \times 10^3$, where R is ^{13}C/^{12}C, ^{15}N/^{14}N or ^{34}S/^{32}S for δ^{13}C, δ^{15}N or δ^{34}S, respectively. Standards were referenced to Vienna Pee Dee Belemnite (VPDB) for carbon, atmospheric air (AIR) for nitrogen and Vienna Canyon Diablo Triolite (VCDT) for sulphur isotopes. The reproducibility was 0.1, 0.2 and 0.2‰ for δ^{13}C, δ^{15}N, and δ^{34}S respectively, based on repeated analyses of laboratory standards. The δ^{13}C and δ^{15}N values of the SIRFER laboratory reference materials (2 glutamic acids) were +24.0 and +49.6‰ for UU-CN-1, −28.2 and −4.6‰ for UU-CN-2, respectively. These values were assigned after calibration against the international standards USGS40 and USGS41. The δ^{13}C and δ^{15}N values of a powdered keratin quality control material were −24.0 and +5.9‰, respectively, when calibrated against USGS40 and USGS41. For δ^{34}S values, CPSIL reported that data were normalized using 6 isotope standards: IAEA-S1 (−0.3‰), IAEA−S2 (22.7‰), IAEA−S3 (−32.6‰), IAEA−SO5 (0.5‰), IAEA−SO6 (−34.1‰) and NBS 127 (21.1‰). The internal working standard was bovine liver (NIST 1577b: 7.69‰), and as secondary standards mussel tissue (NIST 2976), oyster tissue (NIST 1566b), tomato leaves (NIST 1573a) and keratin (TCI chemical) were used.

Statistical analyses

Differences in isotope values among whales of different age–sex classes (adults, juveniles, males and females) and among whales sampled in different years (2003 to 2006) were evaluated using Kruskal-Wallis tests. Post hoc Dunn's multiple comparisons tests were used to detect groups that differ (Dunn 1964). Non-parametric Spearman's correlations (Sokal & Rohlf 1981) were used to test for associations between isotope ratios of different elements, and between isotope ratios and sampling years. In all tests, the threshold for significance was set at 0.05. Statistical analyses were conducted in R (R Core Team 2012).

Food web stable isotope ratios

Stable isotope values of copepods, euphausiids and marine vertebrate predators (fish, seabirds, pinnipeds and odontocetes) were primarily obtained from the literature (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m603p243_supp.pdf). We focused on studies reporting isotope values of copepods and euphausiids from historical whaling areas of the southwestern South Atlantic Ocean and the Atlantic sector of the Southern Ocean (from 20° E to 70° W), that reported both δ^{13}C and δ^{15}N values. The δ^{13}C and δ^{15}N values of predators were used as isotopic references to give context to our whale skin measurements and not as a comprehensive review of predators' trophic ecology, and thus perhaps represent an incomplete data set. We are aware that by combining these various sources of data we are incorporating a large amount of uncontrolled uncertainty, but these feeding areas have not all been studied equally. Thus, we combined the available information regardless of methodological differences and number of samples. The reader must be aware that each taxon is comprised of different species; for example, data for copepods include at least 13 different species and data for euphausiids include at least 7 species (Table S1). Furthermore, in several cases identification did not go beyond the family level. Thus, even within each taxon we are grouping different trophic levels. The data are comprised of a large temporal range (1986 to 2008), as well as different seasons (Table S1). The type of sample analyzed differed among publications, ranging from whole animal, to muscle, to blood or 'soft tissues'. The treatment of the sample also differed among publications, with some conducting lipid extraction and some not. Finally, the δ^{13}C and δ^{15}N values from the original publications also varied; some publications reported the entire data sets, while others only reported a few descriptive statistics (mean, standard deviations, minimum or maximum values; Table S1). In some cases data were only presented as graphs, so we extracted the isotope values from those plots, likely increasing the associated errors.

There was no temporal coincidence between the collection of whale samples (2003 to 2006) and prey samples, with the exception of zooplankton from

Uruguay that were collected in 2004 and 2005. The designation of geographical locations in Table S1 followed the original papers, but in some cases data were grouped in a particular region to help with visualization and analyses; for example, samples from the Weddell Sea, the Lazarev Sea and the African Quadrant were grouped into one area termed LAQW, and all samples collected near the Patagonian coast were termed PS (for Patagonian Shelf) regardless of their latitude. We analyzed euphausiids and copepods collected by surface tows with plankton nets off Uruguay and Peninsula Valdés, Argentina (Table S1). Carbon and nitrogen isotope analyses were conducted at SIRFER using the same methodology as explained for skin samples, except that lipids were not extracted from the plankton samples. Reported C/N ratios had an average of 4.5 ± 1.1 for these samples.

Mixing model

Linear isotope mixing models are useful to reconstruct the proportional contribution of different food sources to the diet of a consumer. Bayesian mixing models have the capability of calculating real distributions of proportional contributions in undetermined systems and incorporating uncertainty in the isotope values of sources and in the tissue isotope discrimination (Parnell et al. 2010). However, due to the characteristics of our data sources (explained above) and the fact that we do not know the specific trophic enrichment, the uncertainty components in our model are extremely underestimated. Furthermore, we have 2 isotope tracers and 7 food sources, which makes this a highly undetermined system. Thus, the following diet reconstruction should be taken as an exercise rather than a true and definitive estimate of SRW diet.

Reconstructions of diet and locations of feeding grounds were performed by estimating true probability distributions of relative contributions of potential prey to the isotope values of whale skin. These relative contributions were estimated by fitting linear mixing models in a Bayesian framework using the package SIAR for R (Parnell et al. 2010). The Bayesian approach implemented in SIAR uses multiple data points for the predator (individual whales), multiple potential food sources (defined as 7 different combinations of prey species and feeding grounds) and their isotopic variability (expressed as average ± SD), and trophic-level correction factors and their associated variability (average ± SD). Each model was run for 50 000 iterations, discarding the first 5000

iterations as burn-in, and without concentration dependence (assuming all sources of C/N are equal). No prior external information was added to guide the models. Trophic correction factors were 2.82 ± 0.3‰ for $\delta^{15}N$ and 1.28 ± 0.38‰ for $\delta^{13}C$ values (Borrell et al. 2012).

RESULTS

Stable isotope ratios of skin samples

The SRW skin samples collected at Península Valdés had an overall mean $\delta^{13}C$ of −20.8 ± 1.4‰ (range −23.9 to −17.2‰, n = 196), a mean $\delta^{15}N$ of 8.4 ± 2.1‰ (range 6.0 to 15.0‰, n = 196) and a mean $\delta^{34}S$ of 18.3 ± 0.7‰ (range 17.6 to 20.4‰, n = 27). Stable isotope values for each of the 196 individuals are presented in Table S2 in the Supplement. Carbon, nitrogen and sulphur distributions were not normal and were positively skewed (Shapiro-Wilk tests, p < 0.001; Figs. 2 & 3). Carbon and nitrogen distributions appeared to be multimodal (Fig. 2), with nitrogen values clearly falling into 3 main groups: a lower group with a mean $\delta^{15}N$ of 7.5‰ (range 6.0 to 9.5‰, n = 158), a middle group with a mean $\delta^{15}N$ of 10.5‰ (range 9.9 to 10.7‰, n = 8) and an upper group with a mean $\delta^{15}N$ of 12.8‰ (range 11.5 to 15.0‰, n = 30). When samples were separated by age and sex classes, the gaps became wider and the multimodal pattern became even more apparent (Fig. 2). Overall, there was a positive correlation between $\delta^{13}C$ and $\delta^{15}N$ values (Spearman's ρ = 0.7, p < 0.001, n = 196; Fig. 2) but no correlation between $\delta^{34}S$ values and either of the other 2 isotopes (p < 0.1, n = 27; Fig. 3).

Whales from different age and sex classes showed significant differences in $\delta^{13}C$ (Kruskal-Wallis [K-W] χ^2 = 9.3, p < 0.05) and $\delta^{15}N$ (K-W χ^2 = 20.7, p < 0.001) but not in $\delta^{34}S$ (K-W χ^2 = 3.0, p = 0.4). Adult female $\delta^{15}N$ values (median 7.4‰, range 8.1‰, n = 143) were significantly lower than those of juvenile females (median 8.2‰, range 6.3‰, n = 24) and juvenile males (median 8.6‰, range 8.3‰, n = 20; p < 0.05 for both comparisons; Fig. 2). Juvenile male $\delta^{13}C$ values (median −20.3‰, range 4.4‰) were significantly higher (p < 0.05) than the values in both female age classes (median and range for adults: −21.1 and 5.9‰; juveniles: −21.4 and 4.2‰; Fig. 2). Adult males showed medians and ranges that did not differ from any other class for either isotope (median and range for $\delta^{15}N$: 8.6 and 6.3‰, for $\delta^{13}C$ −20.5 and 5.8‰; Fig. 2a). However, this group had a small sample size of n = 9.
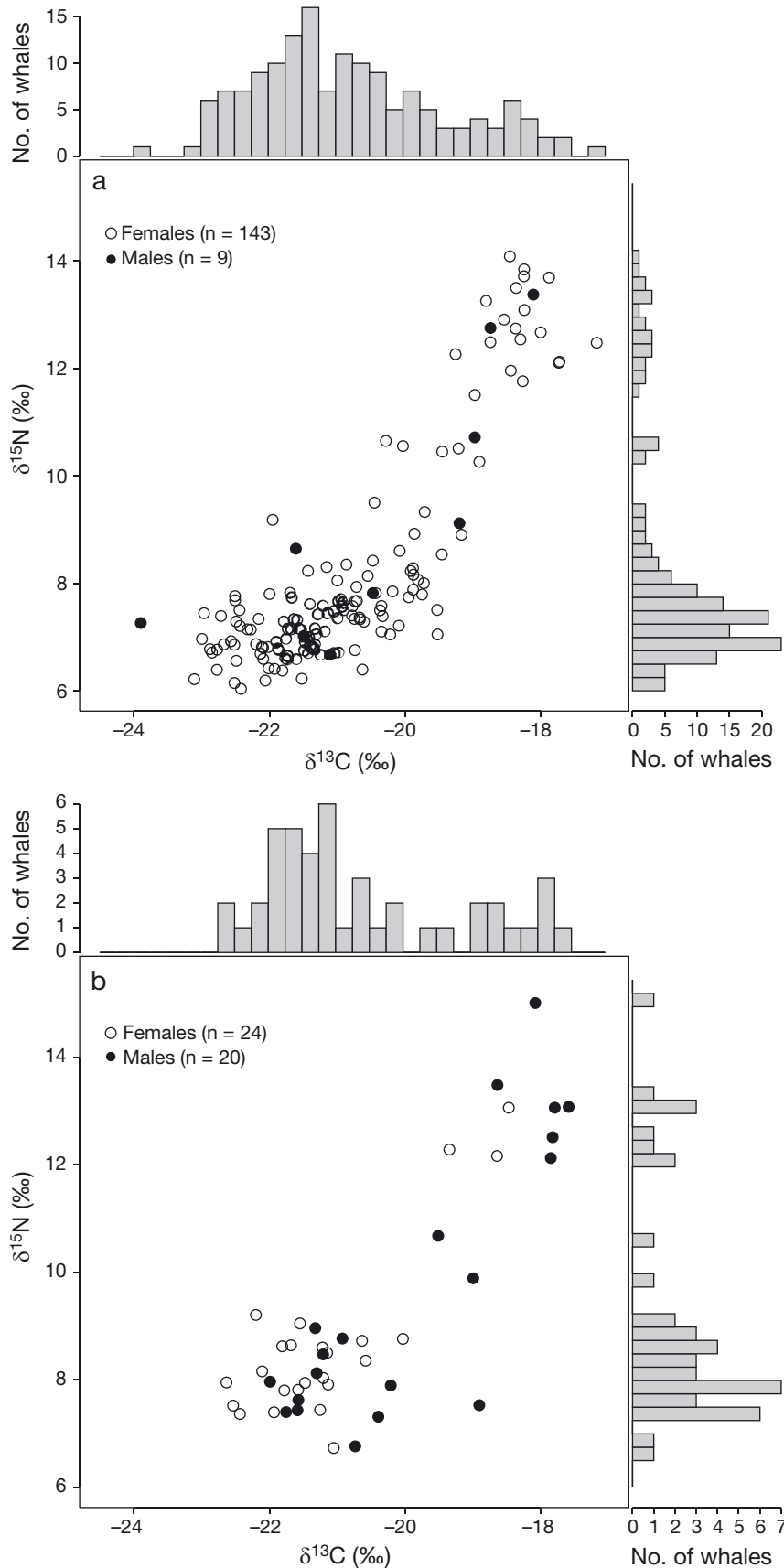
Skin samples collected in different years showed significant differences in $\delta^{13}C$ (K-W χ^2 = 19.7, p < 0.001) and $\delta^{15}N$ (K-W χ^2 = 12.4, p = 0.006) but not in $\delta^{34}S$ (K-W χ^2 = 6.8, p = 0.08). Post hoc Dunn's multiple comparisons tests indicated that the $\delta^{13}C$ and $\delta^{15}N$ values for the year 2006 ($\delta^{13}C$ = −20.1‰, $\delta^{15}N$ = 8.2‰, n = 50; Fig. 4) were higher than for any other year ($\delta^{13}C$ = −21.3‰, $\delta^{15}N$ = 7.4‰ for the other 3 yr combined; Fig. 4).

Stable isotope values in the food chain

Overall, zooplankton and predators (excluding whales) from northern and coastal areas of the Patagonian Shelf (PS) and Uruguay tended to have higher $\delta^{13}C$ and $\delta^{15}N$ values than those from colder waters such as the Southern Ocean (Table S1, Fig. 5). The isotope values of copepods and euphausiids from PS were significantly higher than those from the Southern Ocean (*t*-tests, p < 0.001 for both isotopes; Fig. 5a). Zooplankton samples from Uruguay were intermediate and had a large isotopic range (Fig. 5a). Predators from the PS and Southern Ocean were also isotopically distinct from each other (*t*-tests, p < 0. 001 for both distributions) and there was a large gap in the isotopic distribution between these 2 regions (Fig. 5b). The only animals from PS that did not differ isotopically from the Southern Ocean were king penguins *Aptenodytes patagonicus* sampled on the Malvinas/Falkland Islands and 2 cold-water odontocetes (*Lagenorhynchus cruciger* and *Pho-*

Fig. 2. $\delta^{15}N$ and $\delta^{13}C$ values from 196 southern right whale skin samples collected from (a) adults and (b) juveniles off Península Valdés. Frequency distributions of $\delta^{15}N$ and $\delta^{13}C$ are shown as marginal histograms. Isotope values are not normally distributed (Shapiro-Wilk test, p < 0.001) and appear to be multimodal, especially for nitrogen
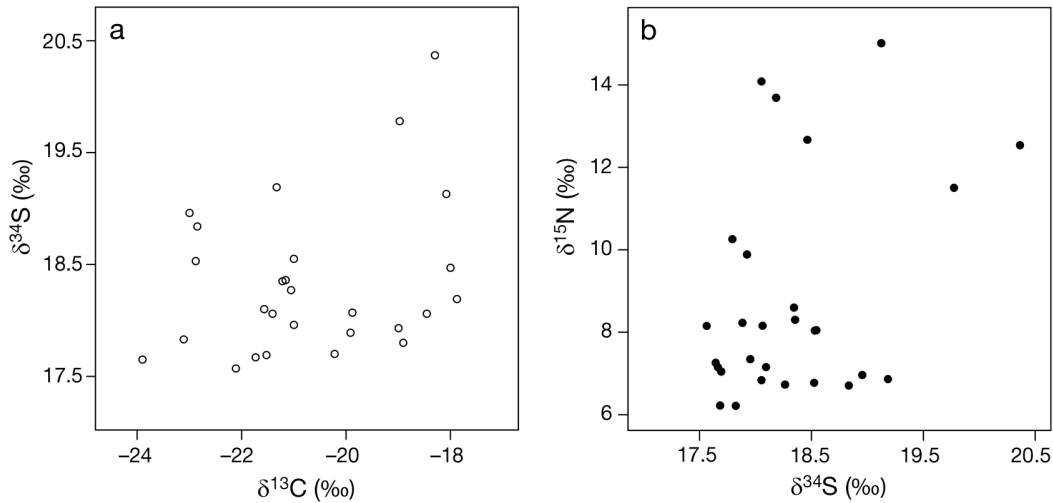
Fig. 3. Sulphur ($\delta^{34}S$) values from 27 skin samples of southern right whales in relation to (a) $\delta^{13}C$ and (b) $\delta^{15}N$ values. No correlations between sulphur isotope values and carbon or nitrogen values were found. The sulphur isotope distribution is not normal (Shapiro-Wilk test, p < 0.001)

coena dioptrica) that stranded on the coast of Tierra del Fuego, in southern Patagonia (Table S1, Fig. 5b).

When corrected for trophic enrichment (2.82‰ for $\delta^{15}N$ and 1.28‰ for $\delta^{13}C$), SRW isotope ratios overlapped with ratios for zooplankton from several locations in the western South Atlantic and the Southern Ocean, including the PS, the Polar Front and South Georgia (Fig. 5a). Different groups of right whales clustered with values from different regions. Whales with the lowest $\delta^{13}C$ and $\delta^{15}N$ values clustered with zooplankton from the Polar Front, Scotia Sea and South Georgia, and whales with the highest isotope values clustered with zooplankton from the PS.
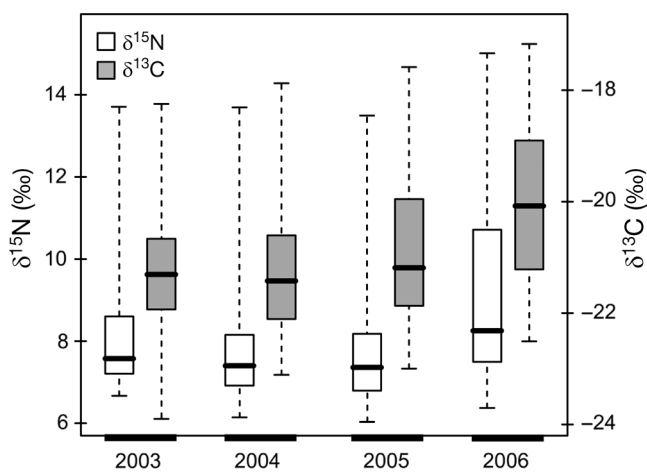

Fig. 4. Stable isotope values from southern right whale skin samples by year of collection. Boxplots represent the median, 25th to 75th percentiles, minimum and maximum values. $\delta^{15}N$ values are shown in open boxes; $\delta^{13}C$ values in grey boxes

Whales with intermediate values did not cluster with any single food source in particular (Fig. 5a).

SRW skin samples showed $\delta^{15}N$ values similar to those of other predators sampled in the Southern Ocean, while their $\delta^{13}C$ values were intermediate (Fig. 5b). The isotope ratios of the predators in Fig. 5b were derived from a variety of tissues that were subject to different treatments, and this heterogeneity may be a source of experimental error.

Mixing models and diet reconstruction

Results from the SIAR modelling are presented as supplemental information (Figs. S1 & S2, Tables S3 & S4 in the Supplement). As stated in the 'Materials and methods', the large uncertainty in isotope values of sources and trophic enrichments, added to the large number of sources and only 2 isotope tracers make this model an exercise rather than a true quantification of proportional contribution to the whales' diet. With that in mind, we ran 2 different models in SIAR. In the first model (M1), the whales were divided into 3 groups based on the clear multimodal distribution of $\delta^{15}N$ values as described above: group 1 ($\delta^{13}C$ = −18.3 ± 0.5, $\delta^{15}N$ = 12.9 ± 0.8, n = 30), group 2 (−19.4 ± 0.5, 10.5 ± 0.3, n = 8) and group 3 (−21.3 ± 0.9, 7.5 ± 0.7, n = 158). In the second model (M2), given the large isotopic range of the lower group and the positive covariation of $\delta^{13}C$ and $\delta^{15}N$ values (Spearman's ρ = 0.45, p < 0.001), the data were analyzed by hierarchical clustering using Euclidian distances with K = 4, and each of the 4 resulting clusters was selected as a new group for the second model
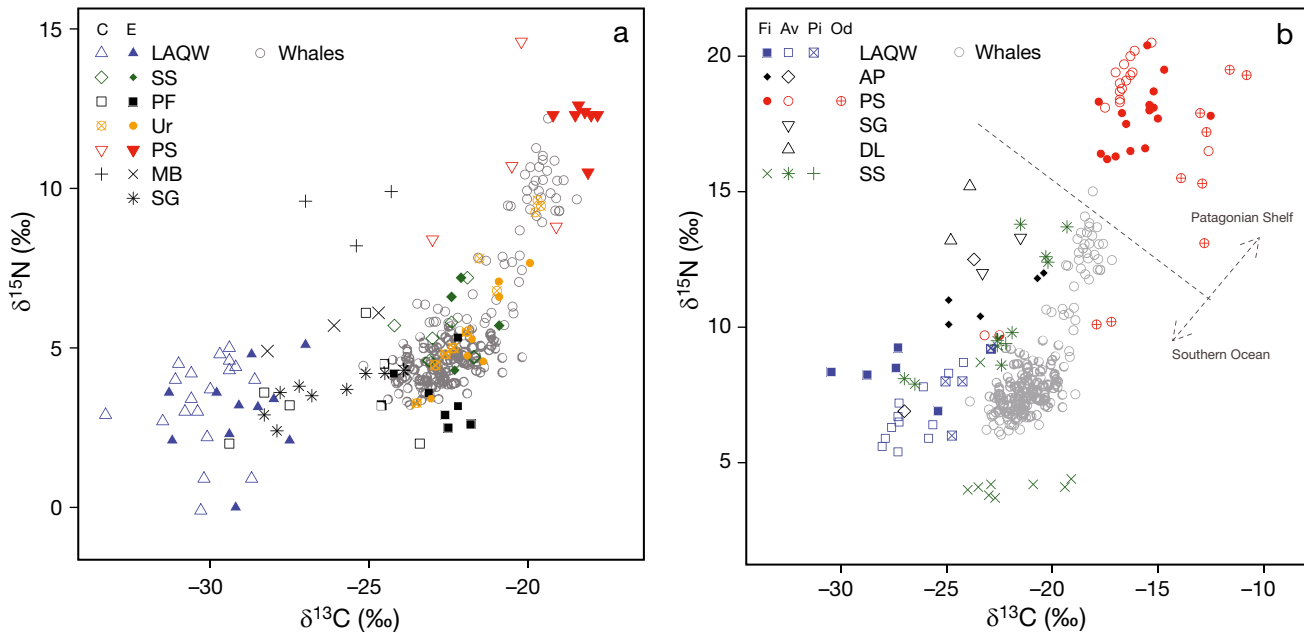
Fig. 5. Stable carbon and nitrogen values of southern right whales (SRW) and (a) their prey and (b) other predators from the South Atlantic and Southern Ocean. The δ13C and δ15N from skin samples are corrected for trophic level in (a) and not corrected in (b). Copepod (C), Euphausid (E), Fish (Fi), Aves (Av), Pinniped (Pi) and Odontocete (Od) values are from Table S1 in the Supplement. Samples are from Uruguay (Ur), Patagonian Shelf (PS), South Georgia (SG), Scotia Sea (SS), Marguerite Bay (MB), Antarctic Peninsula (AP), Polar Front (PF), Draunning Maud Land (DL) and a large area that includes the Lazarev Sea, the American and African quadrants and the Weddell Sea (LAQW)

(Figs. S1 & S2). In M2, groups 1 and 2 were the same as in M1, while group 3 was split into group 3a (δ13C = −20.2 ± 0.5, δ15N = 8.0 ± 0.6, n = 42) and group 3b (−21.7 ± 0.6, 7.3 ± 0.7, n = 116). In both models we used 7 food sources extracted from Table S1; their means and standard deviations are summarized in Table S3 and Fig. S1.

Results from the SIAR modelling are presented in Fig. S2 and Table S4. In agreement with the results drawn from the graphical exploration of the data, whales in group 1 obtained their largest contribution from euphausiids from the PS and their second largest contribution from the Polar Front (PF). Group 2 obtained relatively equal contributions from 3 sources: PS, PF and the Scotia Sea (SS). The whales in group 3 (under model M1) appeared to obtain most of their nutrition from PF euphausiids, followed by SS. Under model M2, group 3a relied mainly on PF euphausiids, followed by PS. Group 3b also relied mainly on PF samples, but used 2 secondary sources in equal proportions: South Georgia (SG) and SS.

DISCUSSION

Stable isotope ratios in skin samples indicate that Patagonian right whales currently use several differ-

ent feeding areas. Carbon and nitrogen isotope ratios were non-normally distributed over the population as a whole, indicating a non-homogenous food source (Hobson & Schwarcz 1986). The whales in groups with the highest and middle isotope values (groups 1 and 2) appear to rely largely on 2 distinct food sources, as suggested by the normal distribution of values and the lack of correlation between carbon and nitrogen isotopes within each group. The group with lowest isotope ratios (group 3) may consist of whales that rely largely on a single more or less homogenous food source, or a continuum of feeding sources, or at least 2 end-members, as indicated by the large isotopic range, the positive correlation between δ13C and δ15N values and the large size of this group. If all physiological aspects are assumed to be equal among the sampled whales, then the isotopic distribution of the whales' skin would appear to represent at least 3 different feeding sources. However, it is not clear whether these sources correspond to the feeding grounds where whales feed first, or longest, or most recently, or to mixtures of several places, because we do not yet understand how time-varying isotopic inputs are integrated in right whale skin (Todd et al. 1997, Ruiz-Cooley et al. 2004).

Sulphur isotope ratios were within the range expected for pelagic ecosystems (Peterson & Fry 1987,

Fry 2006). The lack of correlation with carbon and nitrogen isotopes suggests that the potential feeding sources are from areas with homogenous sulphur isotope signatures. The 2 samples with the highest $\delta^{34}S$ values came from the middle of the $\delta^{15}N$ distribution (whales in group 2), which may indicate a different food source with a more benthic or coastal contribution (Peterson & Fry 1987, Fry 2006).

The isotopic patterns detected among the species and regions analyzed here provide a whale-based view of the western South Atlantic and Southern Ocean food webs. A more in-depth representation of the trophic relationships within food webs from the regions mentioned here can be found in the original papers listed in Table S1 in the Supplement. The zooplankton data surveyed here serve as a reference to assign groups of whales to potential feeding grounds. Unfortunately, the large isotopic uncertainty in the food sources prevents us from explicitly assigning whales to specific narrower geographic areas. However, our interpretation of the location of potential feeding grounds is substantiated on the established geographic distribution of isotope values in the South Atlantic and Southern Ocean. There is a clear latitudinal decline of $\delta^{13}C$ values in the southwest South Atlantic and Southern Ocean, which has been seen in phytoplankton as well as in zooplankton samples (Cherel & Hobson 2007, Quillfeldt et al. 2010, McMahon et al. 2013, Magozzi et al. 2017). This carbon isotope gradient is, in part, the result of temperature differences, dissolved CO_2 concentration and differences in phytoplankton metabolism (Peterson & Fry 1987, McMahon et al. 2013, Magozzi et al. 2017). Furthermore, in our study area there are dramatic isotopic contrasts between water masses (e.g. an steep change in $\delta^{13}C$ values of particulate organic matter [POM] across the Drake Passage; Cherel & Hobson 2007, Quillfeldt et al. 2010, Magozzi et al. 2017). In our assembled data set (Table S1) we have seen non-overlapping isotope distributions and a large isotopic separation between animals (zooplankton and vertebrates) from the Patagonian shelf and from the Southern Ocean (as a whole), suggesting the existence of 2 isotopically distinct food webs (Forero et al. 2005, Quillfeldt et al. 2010, McMahon et al. 2013, Magozzi et al. 2017). Thus, assigning whales to these large regions or provinces, as suggested by Magozzi et al. (2017), is possible. On the other hand, assigning whales to sub-regions within the Southern Ocean is not that straightforward due to the noisy nature of the zooplankton data compiled here.

Because a whale cannot have simultaneous contributions from prey species geographically separated by large distances, the interpretation of a mixed isotope signal in whale skin provides a combination of dietary and migratory information. Considering the potential migratory patterns, those whales with the lowest isotope values may represent a segment of the population that travels and feeds primarily in higher latitudes of the Southern Ocean (e.g. PF and SG) and, while migrating towards Península Valdés, consumes prey with a higher isotope signature. The whales with the highest isotope values may tend to stay primarily on the PS (or areas with similar high $\delta^{13}C$ and $\delta^{15}N$ values), probably moving from north to south along the shelf break following seasonal changes in productivity (Romero et al. 2006). The isotope values of whales in the middle of the distribution are more difficult to interpret, as they could represent a truly mixed signal or an unknown and unsampled food source. For this intermediate group, the SIAR results describe a segment of the population with similar proportions from 3 feeding areas: PS, SS and PF. Even with the many sources of uncertainty, the overall results of the SIAR modelling agree with this interpretation and are consistent with a hypothesis that whales consume prey in at least 3 feeding grounds, or more likely, that they may have at least 3 different migratory patterns.

The scenarios of habitat use and migration of SRWs are supported by isotopic data from baleen plates and other non-isotope data. Rowntree et al. (2008) and Valenzuela et al. (2010, 2011) reported that the $\delta^{13}C$ and $\delta^{15}N$ values of baleen plates from adults and calves showed 3 different isotope profiles, with up to 8 annual foraging cycles for adults, probably associated with different migratory patterns. They found some baleen that contained annual cycles with only high $\delta^{13}C$ values reflecting northerly, warmer waters, some baleen that contained only low $\delta^{13}C$ values reflecting southern, colder waters, and some baleen that contained both high and low isotope values in their annual foraging cycles (Rowntree et al. 2008, Valenzuela et al. 2010, 2011).

The distribution of catch positions of right whales in the 1800s and 1900s (Townsend 1935, Tormosov et al. 1998, IWC 2001), modern sightings (IWC 2001) and recent preliminary satellite telemetry data (Zerbini et al. 2015, 2016) also support the idea of different foraging–migratory patterns. SRWs killed in the South Atlantic during 1960s had stomachs full of euphausiids south of 50° S, calanoid copepods when taken north of 40° S, and a mixture of these 2 prey types when taken between 40° and 50° S (Tormosov

et al. 1998). The continental shelf off the eastern coast of South America (from southern Brazil to the Malvinas Islands) was a rich whaling ground, with a marked seasonality of catch positions; the whales were caught in northern areas from October to January and in southern areas from February to May. South Georgia was also an important whaling ground and continues to be an important SRW feeding area, where they are the most frequently sighted large whale species (Moore et al. 1999, IWC 2001).

In addition, it is possible that the SRWs from Península Valdés use an unknown feeding area. The stable isotope values of prey that were used in our study include only 4 of the 6 historic feeding areas recognized by the International Whaling Commission (IWC 2001) for the South Atlantic and the Atlantic sector of the Southern Ocean: the Antarctic Peninsula, SG, the PF (area 6 in Fig. 1) and the southern coast of South America. However, the samples representing the latter are from a small number of locations off Patagonia, and may not accurately represent the entire isotopic range of the whales' historic feeding ground. We have no copepod or euphausiid samples from other areas where whales formerly concentrated during the feeding months, such as the waters of the subtropical convergence or the area where right whales were killed illegally by Soviet whalers in the 1960s, near the confluence of the Malvinas and Brazil currents (Tormosov et al. 1998). Furthermore, satellite tags revealed that right whales of South Africa use 3 different feeding grounds as well, but only one of these corresponds to a recognized historic feeding ground (Mate & Best 2008, Mate et al. 2011).

Age segregation on feeding grounds has not been reported for baleen whales. The significant isotopic differences among age–sex classes could indicate physiological differences or different foraging strategies. Two factors could explain higher $\delta^{15}N$ values in juveniles than adults. First, juveniles may not have fully developed baleen plates (Schell et al. 1989). Best & Schell (1996) speculated that the postweaning pause in body growth detected in SRWs and bowheads may occur because juvenile baleen plates are not efficient filters. If juveniles cannot capture all sizes of prey (Mayo et al. 2001), then the isotope ratios incorporated could be biased toward the largest zooplankton stages and species. Schmidt et al. (2003) found that the $\delta^{15}N$ values of Antarctic copepods increased significantly with body size, and that Antarctic krill juvenile stages tended to have lower $\delta^{15}N$ than adults. Second, juvenile right

whales grow rapidly (Whitehead & Payne 1981, Best & Schell 1996) and maintain higher activity levels on the calving ground than lactating females (Sironi 2004). Both growth and increased physical activity have been proposed to increase the nitrogen isotope ratios in animal tissues (Kelly 2000). Recently Zerbini et al. (2015, 2016) proposed a differential use of the water column by juveniles and adults; however, this speculation was based on only a few dive profiles and more data are needed to see whether this is also a factor affecting the whales' isotope values.

The interannual differences in the overall distribution of $\delta^{13}C$ and $\delta^{15}N$ values detected in this study could be explained as a response to changes in the isotopic composition of the whales' food sources, or resulting from changes in foraging strategy. Interannual variations in the isotopic composition at the base of food webs produced by temperature anomalies may be responsible for the higher isotope ratios detected in 2006 (Peterson & Fry 1987, Druffel & Griffin 1999, Brix et al. 2004). Higher $\delta^{13}C$ values of primary producers could be attributed to a decrease in CO_2 solubility and change in the rate of carbon fixation as a response to warmer waters (Rau et al. 1989). However, it is also possible that prior to the 2006 calving season, food was not abundant in areas with normally low isotope values, causing the whales to switch to prey with higher isotopic values. A change in the abundance of Antarctic krill has affected the foraging strategies of other marine predators in the vicinity of South Georgia (Trathan et al. 2006). Because right whales calve predominantly at 3 yr intervals, the calving cohort present at Península Valdés in 2003 should have been present again in 2006; however, their isotope ratios differed. A longer time series of isotope-ratio samples from this population could greatly improve our understanding of yearly variations in foraging opportunities and the whales' responses to those challenges.

Similar changes have not been reported for whales in the Southern Hemisphere, but recently Pomerleau et al. (2017) documented significant differences in the $\delta^{13}C$ values of bowhead whale *Balaena mysticetus* skin (bulk and essential amino acids) sampled in West Greenland, over a period of 7 yr. They did not find differences in $\delta^{15}N$ values across years. They attributed these differences to changes in the carbon at the base of the food web, rejecting possible changes in trophic level or food source (Pomerleau et al. 2017). In our case, without additional information such as more tagged animals, amino-acid-specific isotope analyses or an extended

isotopic baseline, all the above explanatory hypotheses remain untested.

CONCLUSIONS

Different groups of SRWs that calve off Península Valdés use diverse food sources characterized by differential proportions of prey items from several regions. We detected isotopic differentiation between age classes, which could result from physiological or anatomical processes (e.g. higher metabolism or incompletely developed baleen), as well as from foraging in different areas on different prey. Interannual variability in mean carbon and nitrogen values may be caused by feeding in different areas, or ecological or physical changes affecting isotope sources. More data will be needed to distinguish among these hypotheses. We detected a large separation of isotope ratios in zooplankton from the PS and Southern Ocean that seems to explain a similar separation previously described among other predators from both areas. The data suggest that SRW skin integrates isotope values over a large geographic range and possibly over a long period of time. A better understanding of the skin turnover rate will allow mixing models to better estimate the proportions of food consumed and time spent on different feeding grounds, permitting the inference of long-range migratory patterns.

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