

## DECADAL SHIFT IN FORAGING STRATEGY OF A MIGRATORY SOUTHERN OCEAN PREDATOR

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## ABSTRACT

Rapid anthropogenic environmental change is expected to impact a host of ecological parameters in Southern Ocean ecosystems. Of critical concern are the consequences of these changes on the range of species that show fidelity to migratory destinations, as philopatry is hypothesised to help or hinder adaptation to climate change depending on the circumstances. Many baleen whales show philopatry to feeding grounds and are also capital breeders that meet migratory and reproductive costs through seasonal energy intake. Southern right whales (*Eubalaena australis*, SRWs) are capital breeders that have a strong relationship between reproductive output and foraging success. The population dynamics of South Africa's population of SRWs are characterised by two distinct periods: the 1990s, a period of high calving rates; and the late 2010s, a period associated with lowered calving rates. Here we use analyses of stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope values from SRW biopsy samples ( $n = 122$ ) collected during these two distinct periods to investigate foraging ecology of the South African population of SRWs over a time period coincident with the demographic shift. We show that South African SRWs underwent a dramatic northward shift, and diversification, in foraging strategy from 1990s-2010s. Bayesian mixing model results suggest that during the 1990s, South African SRWs foraged on prey isotopically similar to South Georgia/Islands Georgias del Sur krill. In contrast, in the 2010s, South African SRW foraged on prey isotopically consistent with the waters of the Subtropical Convergence, Polar Front and Marion Island. We hypothesise that this shift represents a response to changes in preferred habitat or prey, e.g., the decrease in abundance and southward range contraction of Antarctic krill. By linking reproductive decline to changing foraging strategies for the first time in SRW, we show that altering foraging strategies may not be sufficient to adapt to a changing ocean.

*KEY WORDS* (6 – 10)

Southern right whale, cetacean, climate change, reproductive success, stable isotopes, foraging ecology, Southern Ocean, Bayesian mixing model, SIBER, indicator species

## 1. INTRODUCTION

Oceanic ecosystems are changing rapidly on a global scale due to a host of anthropogenic impacts (Bindoff et al., 2019). The most pronounced physical changes include increasing ocean temperatures, the southward shift of fronts in the Southern Ocean, ocean acidification and changes in seasonal sea-ice extents (Böning et al., 2008; Bracegirdle et al., 2008; Orr et al., 2005; Sokolov & Rintoul, 2009). The consequences of these physical changes on Southern Ocean food webs are complex (Constable et al., 2014), and are likely to have multifaceted ecological impacts on marine species, including physiology, phenology, behaviour, population densities and structure including migratory patterns, food web architecture and dynamics, and species ranges (Trathan et al., 2007). Of particular concern is the impact that such physical change will have on Antarctic krill (*Euphausia superba*), the dominant mid-trophic species in Southern Ocean food webs (Atkinson et al., 2004; Reid & Croxall, 2001). The southwest Atlantic sector of the Southern Ocean, which contains over 50% of Antarctic krill stocks, has seen a major reduction in Antarctic krill density from 1976 to 2003 (Atkinson et al., 2004) as well as a significant southward contraction in Antarctic krill over the past 90 years (Atkinson et al., 2019). Population models constructed by Murphy et al. (2007) indicate that a regional warming of 1°Celsius during the coming century could lead to a 95% reduction in the abundance and biomass of Antarctic krill in the southwest Atlantic Ocean.

Changes in krill availability can have profound negative impacts on krill predators in the Southern Ocean (Barbosa et al., 2012; Forcada et al., 2005; Forcada & Trathan, 2009; Fraser & Hofmann, 2003). Particularly disconcerting are the potential impacts on capital breeders; i.e., species relying on seasonal energy reserves for reproduction (see Jönsson, 1997), such as southern right whales (*Eubalaena australis*, hereafter SRW). SRWs consume large amounts of krill and copepods during the austral summer on high-productivity foraging grounds which are stored as blubber; sustaining migration, mating and calving during the remainder of the year (Lockyer, 2007). SRW mothers rely on their energy reserves to sustain themselves and their calves during lactation (Lockyer, 2007), losing up to 25% of their body volume during a few months (Christiansen et al., 2018). Sufficient energy reserves are thus crucial for both mother and calf survival (Lockyer, 2007).

The reproductive output of SRWs in Argentina (expected calving rate) and Brazil (observed calving rate) are correlated with krill abundance at a summer foraging ground off South Georgia (Islas Georgias del Sur), which, in turn, is linked to large-scale global climate drivers such as the El Niño–Southern Oscillation and the Southern Annular Mode (Leaper et al., 2006; Seyboth et al., 2016). Several studies have shown that reproduction is suppressed in cetaceans during periods of nutritional stress (Greene et al., 2003; Hlista et al., 2009; Lockyer, 1986; Reeves et al., 2001; Ward et al., 2009;

Williams et al., 2013), potentially the cause of lower reproductive output in Argentinean SRWs (Rowntree et al., 2013). If summer foraging and reproductive success are correlated in SRWs, then it follows that a decrease in SRW reproductive rates may be caused by reduced biological productivity at offshore foraging grounds.

SRWs show migratory fidelity to destinations, with long-term photo-identification and genotype studies showing philopatry to natal wintering grounds (i.e. Payne, 1986; Best, 1990; Bannister, 2001; Best, Brandão & Butterworth, 2001; Patenaude & Baker, 2001; Carroll et al., 2016). Furthermore, correlations between isotopic profiles ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), indicative of summer foraging grounds, and maternally-inherited mitochondrial DNA haplotypes support the hypothesis that SRW calves learn annual summer foraging destinations from their mothers during a prolonged period of parental care (Carroll et al., 2015; Valenzuela et al., 2009). This transmission of information alludes to the presence of migratory culture in SRWs, where culture is 'information or behaviour – shared by a population or subpopulation – which is acquired from conspecifics through some form of social learning' (Rendell & Whitehead, 2001, p.364). Culture is believed to have evolved as a highly adaptive strategy to pass valuable information between conspecifics (Keith & Bull, 2017). Such transmission of information can occur within generations (horizontally), or in this case, across generations (vertically) (Whitehead et al., 2004). It is important to note, however, that all behaviour is the result of interactions between genetics and the environment – a concept well illustrated by a network-based diffusion analysis by Allen et al. (2013), which allowed for the simultaneous consideration of ecological, social and genetic factors as drivers of learned behaviour in humpback whales (*Megaptera novaeangliae*).

Philopatry can be particularly advantageous in relatively stable environments (Keith & Bull, 2017), for example, in aiding individuals to find suitable foraging grounds in a vast ocean. However, on a species level, philopatry (assuming a degree of diversity) can also allow species to track changes in the environment (Kokko & Sutherland, 2001). For example, SRWs in the southwest Atlantic have been found to exhibit diverse foraging strategies (Valenzuela et al., 2018) which may allow the species to cope with potential productivity changes at some of their foraging grounds.

However, in the face of extremely rapid anthropogenic climate change (Bindoff et al., 2019), conserved decisions in SRWs brought about by migratory culture may prevent the exploitation of new feeding areas, and may even become maladaptive if conditions in many of the established foraging grounds become less optimal (Keith & Bull, 2017; Whitehead et al., 2004). In these instances, rapid anthropogenic climate change can lead to ecological traps (as defined by Keith & Bull, 2017; Schlaepfer et al., 2002), wherein environmental cues which individuals use to assess habitat quality become decoupled from the habitat's true quality, causing individuals to make maladaptive habitat choices. Nonetheless, innovation from individual SRWs, followed by horizontal cultural transmission, may

provide a highly effective method to facilitate adaptive behavioural changes in SRW populations (Keith & Bull, 2017; Whitehead et al., 2004).

Previous studies have inferred changes in South American SRW foraging success via inference from changes in their calving output and correlations with global climate indices (Leaper et al., 2006; Seyboth et al., 2016). More recently, the SRW population from Peninsula Valdés in Argentina has been shown to have a decreased growth rate between 2007 and 2016 (Crespo et al., 2019). Interestingly, the reproductive output of the South African SRW population is characterized by an initial period (1971 – 2006) with high calving rates (Brandão et al., 2010) followed by a second period during the late 2010s with reduced calving rates (Brandão et al., 2018; Vermeulen et al., 2018), and an associated decreased population growth rate (Brandão et al., 2018). Being capital breeders, an associated reduction in foraging success in South African SRWs may be assumed. We therefore aim to investigate temporal trends in their foraging strategies, using stable isotope analyses.

Stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios of skin biopsy samples have been widely used in the study of cetacean foraging ecology (Hooker et al., 2001; Ruiz-Cooley et al., 2004; Todd, 1997; Valenzuela et al., 2018; Witteveen et al., 2011), likely indicating where whales have foraged in the few months prior to sampling (Busquets-Vass et al., 2017). Stable isotope values (e.g.,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of tissue samples can thus serve as indicators of foraging grounds, as their signatures are incorporated directly from food sources into consumer tissues, with varying degrees of discrimination (Newsome et al., 2010), and their values have predictable patterns of change across terrestrial and marine systems (Graham et al., 2010; Hobson, 1999).

The isotopic composition of an organism can be used to quantify its 'isotopic niche' or ' $\delta$ -space' and can be used as a powerful tool to investigate the ecological niche of that organism (Newsome et al., 2007b). Isotopic niche space (range of isotopic values, defined as parts per mil or ‰) and niche area (area occupied in space characterised by two or more isotopes, ‰<sup>2</sup>) can reveal patterns of resource partitioning or variation in foraging strategies (e.g., Buelow et al., 2018; Das et al., 2017; Dehnhard et al., 2020; Mendes et al., 2018; Ryan et al., 2013). Additionally, assuming the isotopic composition of a system's baseline is known, isotopic mixing models can take these observations further by reconstructing the proportional diet of the consumer (Phillips et al., 2014; Stock et al., 2018), thus allowing further inference to be made into variation and specialisation of cetacean foraging strategies and foraging ground location (e.g., Witteveen et al., 2011).

Importantly in the context of marine megafauna foraging ecology, a significant latitudinal gradient in  $\delta^{13}\text{C}$  values of phytoplankton and zooplankton is found in the world's oceans, a pattern that is particularly accentuated in the Southern Ocean (Cherel & Hobson, 2007; Espinasse et al., 2019;

Magozzi et al., 2017; McMahon et al., 2013a). This gradient is partly due to processes driven by temperature variations (McMahon et al., 2013a), CO<sub>2</sub> concentrations (Peterson & Fry, 1987) and variations in the metabolism of the primary producer with latitude (Hobson et al., 2010). The latitudinal gradient is a well-established principle in top marine predator foraging ecology, it shows temporal stability across decades (Logan et al., 2020), and has proven an effective indicator of broad foraging habitats in both short (i.e.  $\leq 4$  years; e.g., Cherel & Hobson, 2007; Lübcker et al., 2017; Valenzuela et al., 2018) and long term studies (i.e.  $\geq 14$  years e.g., Logan et al., 2020; Mestre et al., 2020).

Here, we take this approach and assess the isotopic niche space and diet composition of South African SRWs sampled during a period with high calving rates (the 1990s) and during a period with reduced calving rates (the late 2010s). Should the stable isotope values of South African SRWs remain constant across time, then this would be indicative of consistent foraging strategies. Here, the population could be subject to an ecological trap, driven by the combination of being highly philopatric capital breeders showing fidelity to a foraging ground that has become suboptimal in an ocean experiencing change. Alternatively, should there be substantial changes in the isotopic values of South African SRWs across time, then we infer that the changes reflect alterations in foraging behaviour. This could be an indication of adaptation to changing oceanic conditions, but given the recent declines in reproductive output, the shift in foraging may have led to SRWs feeding in less productive regions or on less nutritious prey. Regardless, as long-lived, wide-ranging ocean predators, the response of SRWs to changing oceanic conditions will likely be indicative of broad-scale productivity changes in their foraging grounds in general.

## 2. Methods

### *2.1 Sample collection*

South African SRW skin biopsy samples (Table 1) analysed in this study are a mixture of previously collected (1990s, 2015, 2016) and recently collected samples (2019). The recently collected samples were obtained using small stainless steel biopsy darts deployed from a crossbow (Lambertsen, 1987) on SRWs in Walker Bay, Hermanus (34° 26' S, 19° 18' E) and in San Sebastian Bay, Witsand (34° 23' S 20° 52' E) (Figure S1) in September 2019 (close to the August SRW calving peak; Best, 1994). Samples were stored frozen until stable isotope analyses. Prior to obtaining a biopsy sample, individual whales were photo-identified based on natural markings (Payne et al., 1983) using a DJI phantom 4 pro drone (35 cm diameter, 1388 g, www.dji.com), thus avoiding re-sampling of whales. Age classes (unaccompanied adults/juveniles) were visually determined based on the size of individuals, and adult-nursing females (cows) were identified by the presence of calves. Previously collected samples

Table 1: Southern right whale skin samples used for isotopic analyses, shown by sampling year and age class: cows (adult-nursing females) and unaccompanied adults (males, non-nursing females, pregnant females, juveniles). Unknown age classes are non-calves.

Decade	Year	Sample size (n)	Sampling month					Age Class		
			July	August	September	October	November	Cows	Unaccompanied adults	Unknown
1990	1995	13	3	6	0	4	0	1	11	1
	1996	13	7	0	0	6	0	6	2	5
	1997	18	0	0	13	0	5	17	1	0
	Total	44	10	6	13	10	5	24	14	6
2010	2015	2	0	0	0	2	0	0	0	2
	2016	27	2	5	14	6	0	1	9	17
	2019	49	0	0	49	0	0	41	8	0
	Total	78	2	5	63	8	0	42	17	19
Summary		122	12	11	76	18	5	66	31	25

include those collected from free-ranging SRWs on South African coastal waters (Figure S1) from 1995 – 1997 (biopsy samples stored in dimethyl sulfoxide, DMSO; Best et al., 2003) and 2015 – 2016 (sloughed skin stored in ethanol; Carroll et al., 2020). The effect of DMSO storage is removed by lipid extraction (Burrows et al., 2014; Busquets-Vass et al., 2017; Newsome et al., 2018; Todd et al., 1997) and storage in ethanol has no effect on the isotopic composition of animal tissues (Hobson et al., 1997). Nevertheless, we assessed the C/N ratios of all samples to ensure that lipid extraction had normalized the C/N ratio across samples which were preserved differently.

### *2.2 Stable isotope analysis*

All skin samples underwent freeze-drying and lipid extraction following Todd et al. (1997). Approximately 0.5 – 0.6 mg of dried skin was weighed into tin capsules pre-cleaned with toluene. For the 1990s and 2015/16 samples, carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios were measured using a Costech 4010 elemental analyzer coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer at the Stable Isotope Biogeochemistry Laboratory (SIBL, Durham, UK). The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios of the 2019 samples were measured using an elemental analyser (Flash EA 1112 Series) coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system, housed at the Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria (Pretoria, South Africa). Analyses in all labs used the internationally accepted standards Vienna Pee Dee Belemnite (VPDB) for  $\delta^{13}\text{C}$ , and atmospheric nitrogen for  $\delta^{15}\text{N}$  (AIR); units are expressed as parts per thousand, or per mil (‰) to ensure comparability. Analytical precision for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the 1990 and 2015/16 samples were assessed via analyses of in-house and international reference materials for each daily run, which were stringently calibrated against international standards (e.g., USGS 40, IAEA 600, IAEA N2), and was measured to be  $\pm 0.1\text{‰}$  (SD) (Carroll et al., 2015). Analytical precision for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of the 2019 samples was monitored via routine analyses of in-house standards (Merck Gel:  $\delta^{13}\text{C} = -20.26\text{‰}$ ,  $\delta^{15}\text{N} = 7.89\text{‰}$ , C% = 41.28, N% = 15.29 and DL-Valine:  $\delta^{13}\text{C} = -10.57\text{‰}$ ,  $\delta^{15}\text{N} = -6.15\text{‰}$ , C% = 55.50, N% = 11.86), which were calibrated against international standards (NBS 22, IAEA-CH-3, IAEA-CH-6, IAEA-CH-7, IAEA N-1, IAEA N-2, IAEA NO-3), and was measured to be  $\pm 0.08\text{‰}$  (SD) for both carbon and nitrogen respectively.

### *2.3 Statistical analyses*

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for South African SRW skin samples ( $n = 122$ ) were plotted in R v3.6.3 (R Core Team, 2020) to visually inspect the data for any trends. Distributions of stable isotope values were assessed for normality using the Shapiro-Wilk test. Differences in stable isotope values of SRW skin samples grouped into (a) decade; (b) year; and (c) month of sampling, were assessed via Kruskal-Wallis



tests and post hoc Dunn's multiple comparisons tests (Dunn, 1964). Statistical analyses were conducted in R v3.6.3 (R Core Team, 2020).

#### *2.4 Southern right whale isotopic niche space*

We estimated, and examined trends in, the isotopic niche space (‰) of South African SRWs sampled during the two decades via the Stable Isotope Bayesian Ellipses (SIBER) package (version 2.1.4) in R (Jackson et al., 2011). Bivariate ellipses were used to delineate isotopic niche space ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  value 95% confidence interval ellipses) for SRWs sampled in the 1990s and 2010s respectively, and the total isotopic niche space for the sampled population. Bayesian standard ellipses areas ( $\text{SEA}_B$ ) were plotted using the SIBER routine to show niche overlap. Niche area and overlap ( $\%^2$ ) were estimated based on 1,000,000 Markov chain Monte Carlo (MCMC) iterations, after 100,000 burn-ins, implemented in rjags (Plummer, 2018).  $\text{SEA}_B$  were fitted to the data using a vague normal prior on the means and a vague Inverse Wishart prior on the covariance matrix of the sample (Jackson et al., 2011). Convergence was assessed using the Gelman & Rubin (1992) scale reduction factor with values below 1.1 indicating convergence.

#### *2.5 Dietary reconstruction*

To further our understanding of South African SRW foraging ecology, we estimated the proportional composition of South African SRW diet using isotopic mixing models. This was done in two parts: the compilation of a reference zooplankton dataset and the running of mixing models.

##### *2.5.1 Zooplankton stable isotope values*

SRWs feed on copepods and krill (Tormosov et al., 1998), and those that winter in South African waters are thought to have at least three summer foraging grounds (Figure 1; Best, 2007). However, these locations are based largely on illegal Soviet catch data (Tormosov et al., 1998) and Townsend's (1935) charts of open boat whaling catches, and their use by the contemporary population is not certain (Best, 2007). Contemporary information from satellite tags deployed on SRWs in South Africa in 2001 revealed that the Subtropical Convergence (STC), the Polar Front (PF) and the west coast of South Africa are likely important for South African SRW foraging (Mate et al., 2011).

Given the remote location of foraging grounds of South African SRWs (see Figure 1), preventing the direct sampling of prey, we obtained  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of likely prey taxa from the SRWs' assumed historical and contemporary foraging grounds (Figure 1; Best, 2007) from the literature (Table S1), as done in other studies using mixing models to estimate diet composition in marine mammals (i.e. Lübcker et al., 2017; Valenzuela et al., 2018). However, to account for the uncertainty in contemporary foraging grounds, additional published data was acquired for areas known to serve as feeding grounds for SRWs in the Southwest Atlantic Ocean (acquired from Valenzuela et al., 2018). The geographical

locations (Table S1) correspond to sampling locations in the original study. All zooplankton samples underwent lipid extraction or had a lipid correction model applied to their  $\delta^{13}\text{C}$  values (Table S1). Zooplankton stable isotope data from broad overlapping oceanographic regions were grouped together to aid the data visualization and analyses. For example, the area code 'Far South' (FS) consists of zooplankton collected at 55°S, 65°S, the Lazarev Sea, and the Weddell Gyre (Figure 1). The remaining prey sources were grouped to represent the *Polar Front* (PF), *Scotia Sea* (SS), *Subtropical Convergence* (STC), *west coast of Namibia* (Nam), the *west and south coasts of South Africa* (SA), *South Georgia* (SG) and *Marion Island* (MI; Figure 1, Table S1).

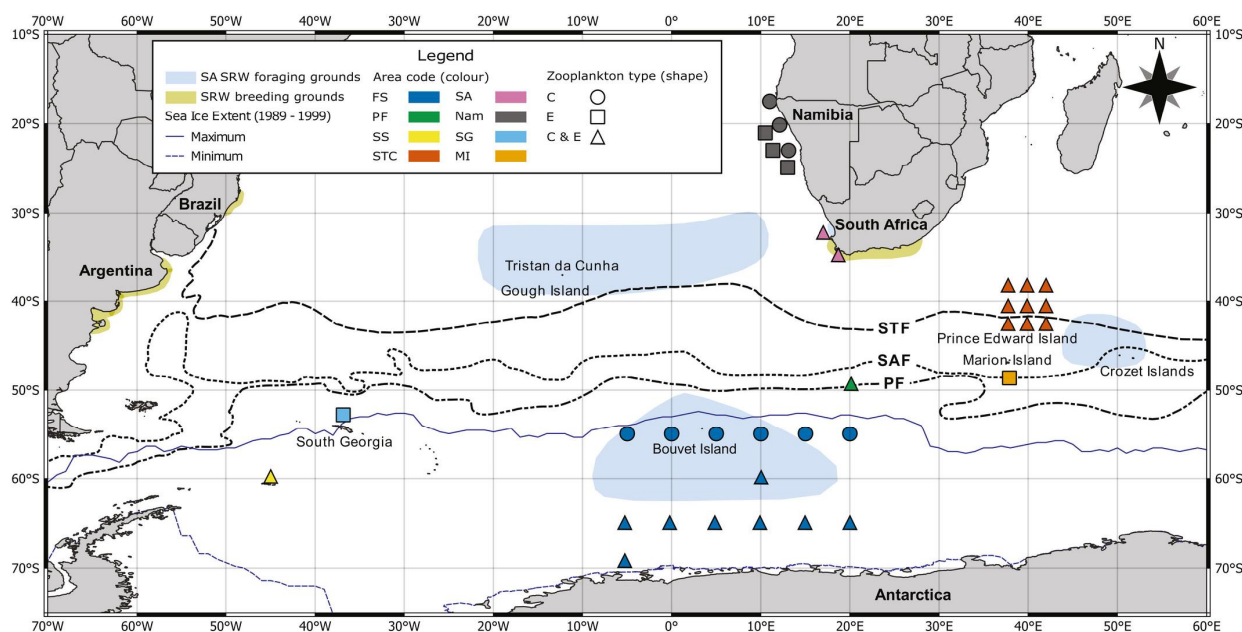


Figure 1 Map of the South Atlantic, Southwest Indian, and Southern Ocean, with blue shading indicating the summer foraging grounds of the South African population of southern right whales, as suggested by Best (2007); yellow shading: the major winter breeding grounds of southern right whales within the map extent; circles, squares and triangles: the locations of zooplankton samples acquired from the literature and whose stable isotope profiles are used in this study, organized by area and prey source codes: Far South (FS), Polar Front (PF), Scotia Sea (SS), Subtropical Convergence (STC), west and south coasts of South Africa (SA), west coast of Namibia (Nam), South Georgia (SG), Marion Island (MI); copepods (C), euphausiids (E); positions of the Subtropical Front (STF), Subantarctic Front (SAF), Polar Front (PF) (Orsi & Harris, 2019); and the minimum and maximum sea ice extents for the period of 1989 – 1999 (Smith & Jacka, 2003).

### 2.5.2 Bayesian mixing models

Bayesian stable isotope mixing models, implemented in R using the MixSIAR package (version 3.1.10) (Stock & Semmens, 2016a), were used to estimate the proportional composition of prey (i.e. sources) to the diet of South African SRWs. Adopting a Bayesian mixing model approach overcomes certain limitations of linear mixing models, and allows for the estimation of proportional contributions of diet

in undetermined systems (i.e. more sources than isotopes) while incorporating uncertainties in the isotopic values of sources and trophic enrichment factors (TEFs) (Parnell et al., 2010).

Amongst several other important considerations (see Phillips et al., 2014), mixing models with more than seven prey sources are unlikely to yield precise and interpretable results (Stock et al., 2018), and mixing models cannot differentiate between sources with similar isotopic signatures (Phillips et al., 2014). Thus, isotopically similar copepod and euphausiid sources from the same region (see area codes in Figure 1) were grouped (Phillips et al., 2014).  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  value means and SD of the various source groups were then acquired from source distributions which we calculated via weighting the means of each taxon by sample size (Phillips et al., 2014). We scrutinized isotope mixing polygons (isospaces) to ensure that the sources from each geographic region (see area codes in Figure 1) were sufficiently isotopically dissimilar, and as a result, we assessed two mixing models with slightly different combinations of sources. The mixing models assessed employed multiple data for the consumer (individual whales,  $n = 122$ ), mean  $\pm$  SD and sample size for each potential source (Table S2), and TEFs with their associated isotopic variability (i.e. mean  $\pm$  SD).

The proportional contribution of each potential source to the diet of South African SRWs was estimated by running three MCMC chains, each comprising 3,000,000 iterations of which the first 1,500,000 iterations were discarded. Sampling (during the last 1,500,000 iterations) was conducted at every 500th iteration. Potential sources had uniform (i.e. assumed non-informative) prior distributions. As suggested by Stock & Semmens (2016b), a process  $\times$  residual error structure was implemented. TEFs used were  $1.28 \pm 0.38\text{‰}$  for  $\delta^{13}\text{C}$  values and  $2.82 \pm 0.3\text{‰}$  for  $\delta^{15}\text{N}$  values (Borrell et al., 2012). Model convergence was assessed via the Gelman & Rubin (1992) scale reduction factor with values less than 1.1 indicating convergence and the Geweke test, a two-sided z-test comparing the mean of the first part of the chain with the mean of the second part (Stock & Semmens, 2016a). Finally, different mixing models were assessed using the widely applicable information criterion (WAIC) and approximate leave-one-out cross-validation (LOO) (Stock et al., 2018; Vehtari et al., 2017).

## 2. Results

### *2.1 Stable isotope ratios of skin samples*

SRW skin biopsy samples collected in South Africa over the period of 1995 – 2019 had an overall mean  $\delta^{13}\text{C}$  of  $-21.98 \pm 1.89\text{‰}$  (range  $-25.95$  to  $-16.28\text{‰}$ ,  $n = 122$ ) and a mean  $\delta^{15}\text{N}$  of  $7.12 \pm 1.03\text{‰}$  (range  $5.01$  to  $12.19\text{‰}$ ,  $n = 122$ ). Samples collected in the 1990s had a mean  $\delta^{13}\text{C}$  of  $-23.76 \pm 1.17\text{‰}$  (range  $-25.95$  to  $-20.46\text{‰}$ ,  $n = 44$ ) and a mean  $\delta^{15}\text{N}$  of  $7.14 \pm 0.43\text{‰}$  (range  $6.46$  to  $7.94\text{‰}$ ,  $n = 44$ ). Samples collected in 2010s had a mean  $\delta^{13}\text{C}$  of  $-20.98 \pm 1.43\text{‰}$  (range  $-23.61$  to  $-16.28\text{‰}$ ,  $n = 78$ ) and a mean  $\delta^{15}\text{N}$  of  $7.12 \pm 1.25\text{‰}$  (range  $5.01$  to  $12.19\text{‰}$ ,  $n = 78$ ; see Supporting Information 1 for full dataset).

The  $\delta^{13}\text{C}$  distribution of the combined dataset did not significantly violate the assumption of normality (Shapiro–Wilk  $W$ -test:  $n = 122$ ;  $p > 0.05$ ; Figure 2), while the  $\delta^{15}\text{N}$  distribution of the combined dataset were significantly non-normal (Shapiro–Wilk  $W$ -test:  $n = 122$ ;  $p < 0.001$ ; Figure 2). Visual inspection of isotope values suggests substantial isotopic differentiation between SRW skin biopsies collected in 1995, 1996 and 1997 compared to 2015, 2016 and 2019 (Figure 2).

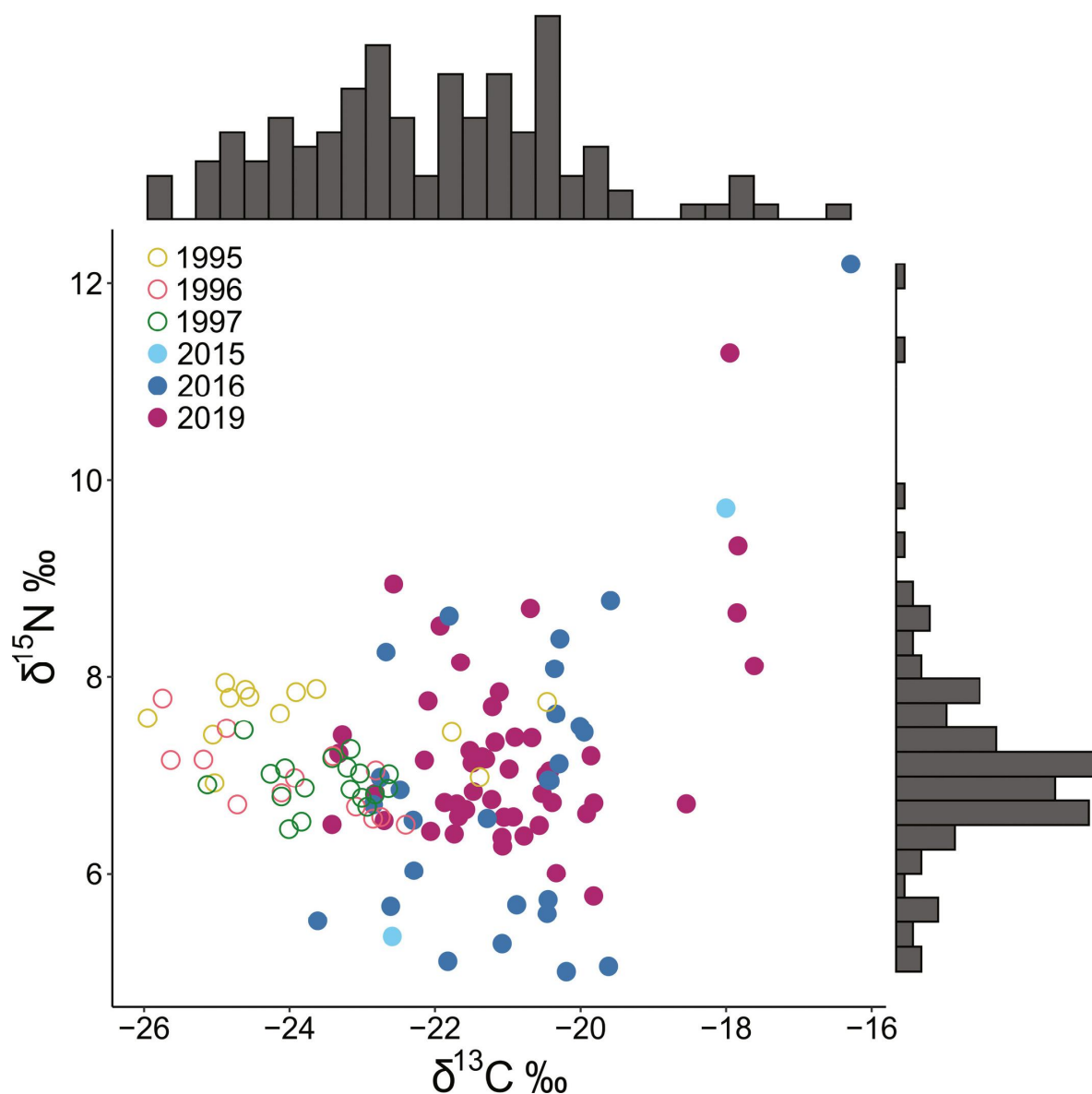


Figure 2  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from 122 southern right whale skin biopsy samples collected over the period of 1995 – 2019. Values are grouped by the year (colour) and decade (1990's are open circles, 2010's are filled circles) of sample collection. Frequency distributions of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are shown as marginal histograms.  $\delta^{13}\text{C}$  values are normally distributed (Shapiro-Wilk test:  $n = 122$ ;  $P > 0.05$ ), while  $\delta^{15}\text{N}$  values are not normally distributed (Shapiro-Wilk test:  $n = 122$ ;  $P < 0.001$ ).

Skin samples collected in different decades (1990 and 2010) show significant differences in  $\delta^{13}\text{C}$  values (Kruskal-Wallis [K-W]  $\chi^2 = 66.3$ ,  $p < 0.001$ ; Figure S2: see Supporting Information 2 for all R code used in the analysis) but not in  $\delta^{15}\text{N}$  values (K-W  $\chi^2 = 1.79$ ,  $p > 0.05$ ; Figure S2). Skin samples collected in different years show significant differences in  $\delta^{13}\text{C}$  (K-W  $\chi^2 = 66.5$ ,  $p < 0.001$ ; Figure 3) and in  $\delta^{15}\text{N}$  (K-W  $\chi^2 = 12.7$ ,  $p < 0.05$ ; Figure 3). Post hoc Dunn's multiple comparisons tests indicated that  $\delta^{13}\text{C}$  values for the years 2019, 2016 and 2015 were all significantly higher than the  $\delta^{13}\text{C}$  values for the years 1995, 1996 and 1997 (Figure 3; Table S3, Table S4). Post hoc Dunn's multiple comparisons tests indicated that  $\delta^{15}\text{N}$  values for the year 1995 were significantly higher than the  $\delta^{15}\text{N}$  values for the years 1996, 1997, 2016 and 2019 (Figure 3; Table S3, Table S5).

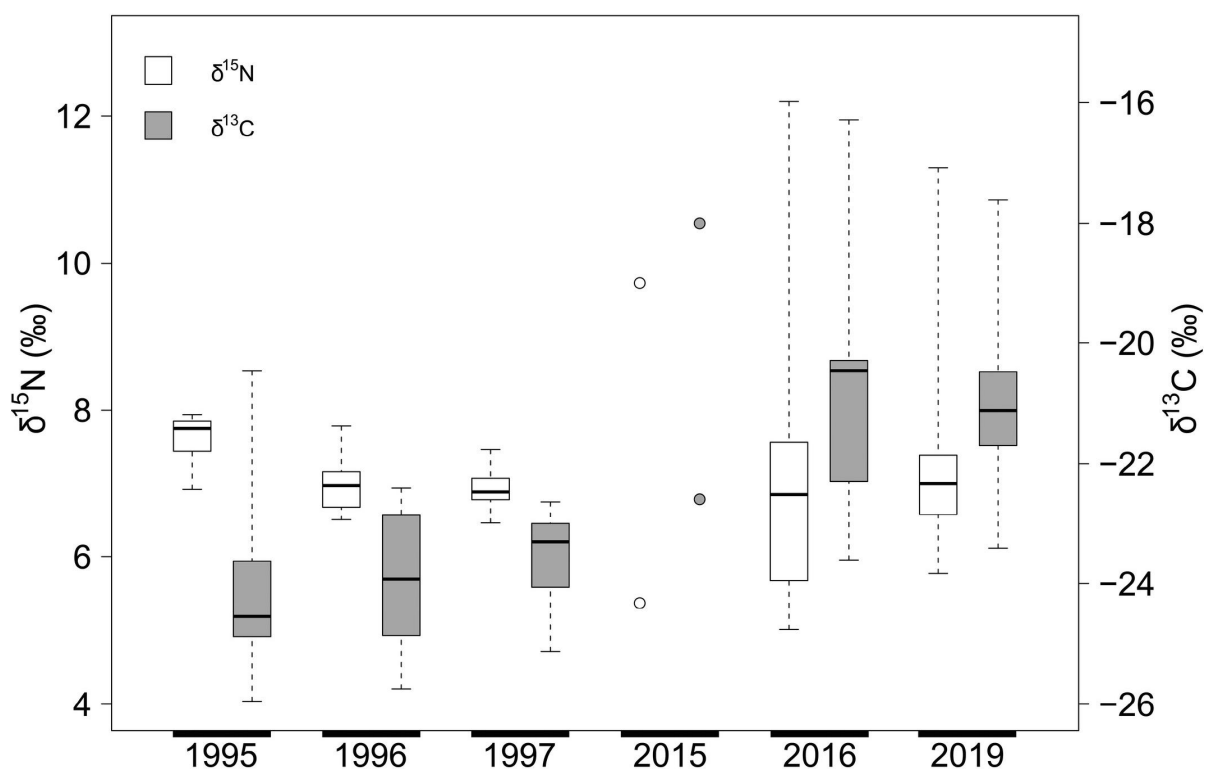


Figure 3 Stable isotope values ( $\delta^{13}\text{C}$  &  $\delta^{15}\text{N}$ ) from 122 southern right whale skin biopsy samples grouped by year of collection: 1995 ( $n = 13$ ), 1996 ( $n = 13$ ), 1997 ( $n = 18$ ), 2015 ( $n = 2$ ), 2016 ( $n = 27$ ), and 2019 ( $n = 49$ ). Boxplots represent the median, 25th and 75th percentiles, minimum and maximum values.

Skin samples collected in different months within the decade of 1990 show significant differences in  $\delta^{15}\text{N}$  (K-W  $\chi^2 = 11.2$ ,  $p < 0.05$ ; Figure S3) but not in  $\delta^{13}\text{C}$  values (K-W  $\chi^2 = 1.9$ ,  $p > 0.05$ ; Figure S3). Post hoc Dunn's multiple comparisons tests indicated that  $\delta^{15}\text{N}$  values for the month of September were lower than the  $\delta^{15}\text{N}$  values for the months of July and August (Figure S3; Table S6, Table S7). Skin samples collected in different months within the decade of 2010 show no significant differences in  $\delta^{15}\text{N}$  (K-W  $\chi^2 = 6.7$ ,  $p > 0.05$ ; Figure S4) nor in  $\delta^{13}\text{C}$  values (K-W  $\chi^2 = 3.1$ ,  $p > 0.05$ ; Figure S4).

### 3.2 Southern right whale isotopic niche space

The SIBER assessment of the South African SRW samples collected in two different decades indicated a substantial expansion and shift in the isotopic niche space of SRWs sampled in the 2010 decade (Figure 4).  $SEA_B$  modes of the 1990 and 2010 SRW samples were  $1.69\text{‰}^2$  and  $4.84\text{‰}^2$ , respectively (Figure 4).

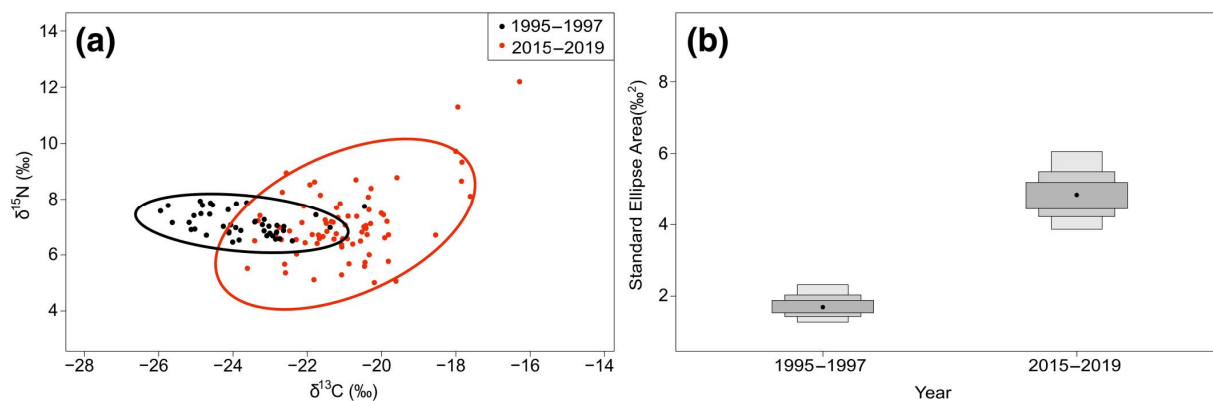


Figure 4 Variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in southern right whale skin biopsy samples ( $n = 122$ ) categorised by decade of collection. (A) 95% CI bivariate ellipses of southern right whale skin biopsy samples collected in 1995 – 1997 (black dots) and in 2015 – 2019 (red dots), demonstrating a significant isotopic niche shift and expansion in South African southern right whales in the 2010 decade. (B) Central tendency and measures of uncertainty (50%, 75% and 95% credible intervals, black dot is the mode of each distribution) of Bayesian standard ellipses areas ( $SEA_B$ ) for southern right whale skin samples collected in 1995 – 1997 and in 2015 – 2019.

### 3.3 Dietary estimations

Overall, zooplankton from coastal areas (Nam & SA) and the STC tended to have higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than those from colder waters further south (Figure S5). When corrected for trophic enrichment (TEF  $1.28\text{‰}$  for  $\delta^{13}\text{C}$  and  $2.82\text{‰}$  for  $\delta^{15}\text{N}$ ; Borrell et al., 2012), SRW skin isotope ratios overlapped with ratios for zooplankton from several locations, including South Georgia, the PF, Marion Island, the STC and coastal Africa (Figure S5).

Sources from the west coast of Namibia and sources from the STC could not be differentiated by mixing models, and thus, given the lack of evidence for South African SRWs making use of coastal Namibia as a foraging ground (Best, 2007; Mate et al., 2011), we excluded this source from the mixing model source pool. All sampled areas in which both prey types were present, apart from the PF, had isotopically similar signatures for copepods and euphausiids (Figure S5). Thus, to account for the isotopic dissimilarity between copepods and euphausiids from the PF, we ran two different mixing models in MixSIAR. The first mixing model ( $M1$ ) had 7 sources, each source being a combination,

where possible, of copepods and euphausiids from the same region (Figure 5). The second model (*M2*) also had 7 sources, but here with copepods and euphausiids from the PF separated (Figure S6). Mixing model *M2* could not differentiate between copepods from the PF and euphausiids from South Georgia (see Figure S5), so euphausiids from South Georgia were excluded from mixing model *M2* (Figure S6).

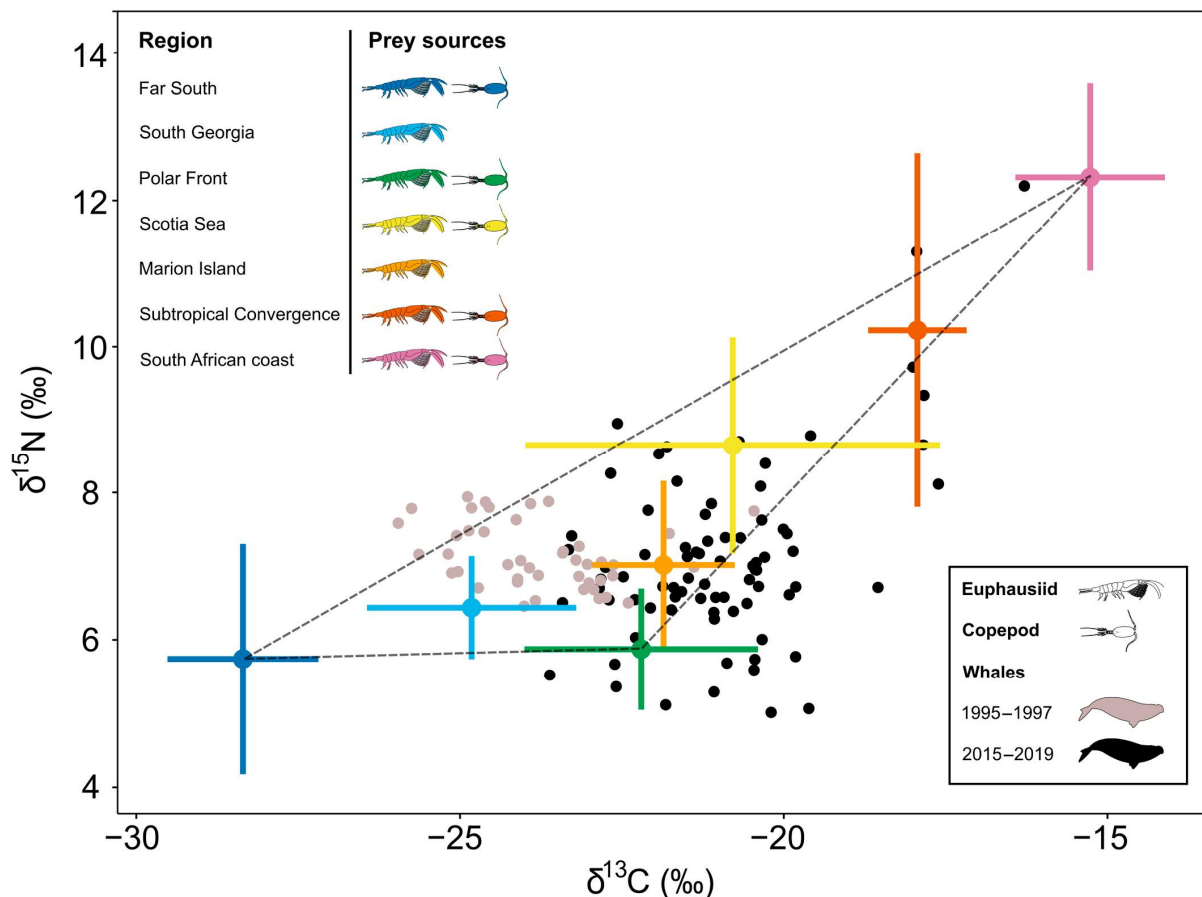


Figure 5 MixSIAR isotope mixing polygon (isospace) for mixing model 1 (*M1*) illustrating source (prey groups) and southern right whale isotope signatures.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of southern right whale skin biopsy samples are grouped by decade (1990: grey dots, 2010: black dots). Each source is corrected for trophic level. The error bars in the sources correspond to the standard deviations calculated from data in Table S1. Sources are colour-coded by region and prey source composition is indicated by euphausiid and copepod clipart. See Table S2 for uncorrected prey source statistical summaries.

LOO statistics provide a strong weighting preference for mixing model *M1* over *M2*, thus, the graphical results for mixing model *M2* can be found in the supplement (Figure S6 and S7, Table S9). Mixing model *M1* estimated that euphausiids from South Georgia contribute 43% (median, with 95% Bayesian credible intervals: 25% – 59%, see Table S8) to the diet of SRWs sampled in the 1990 decade (Figure 6). Smaller dietary contributions to the 1990 decade were estimated with copepods and

euphausiids from Far South (FS) contributing 16% (5% – 27%) and euphausiids from Marion Island contributing 14% (1% – 27%) (Figure 6). Dietary contributions estimated for SRWs sampled in the 2010 decade by *M1* were complex, with the presence of three bimodal posterior distributions representing two distinct potential outcomes (Figure 6). Specifically, the diets of the SRWs sampled in the 2010 decade either comprised primarily of euphausiids from Marion Island (78%, 0 - 91%) or both copepods and euphausiids from the PF (7%, 0% – 34%) and STC (4%, 0% – 63%). All remaining sources used in model *M1* had potential contributions of <10%.

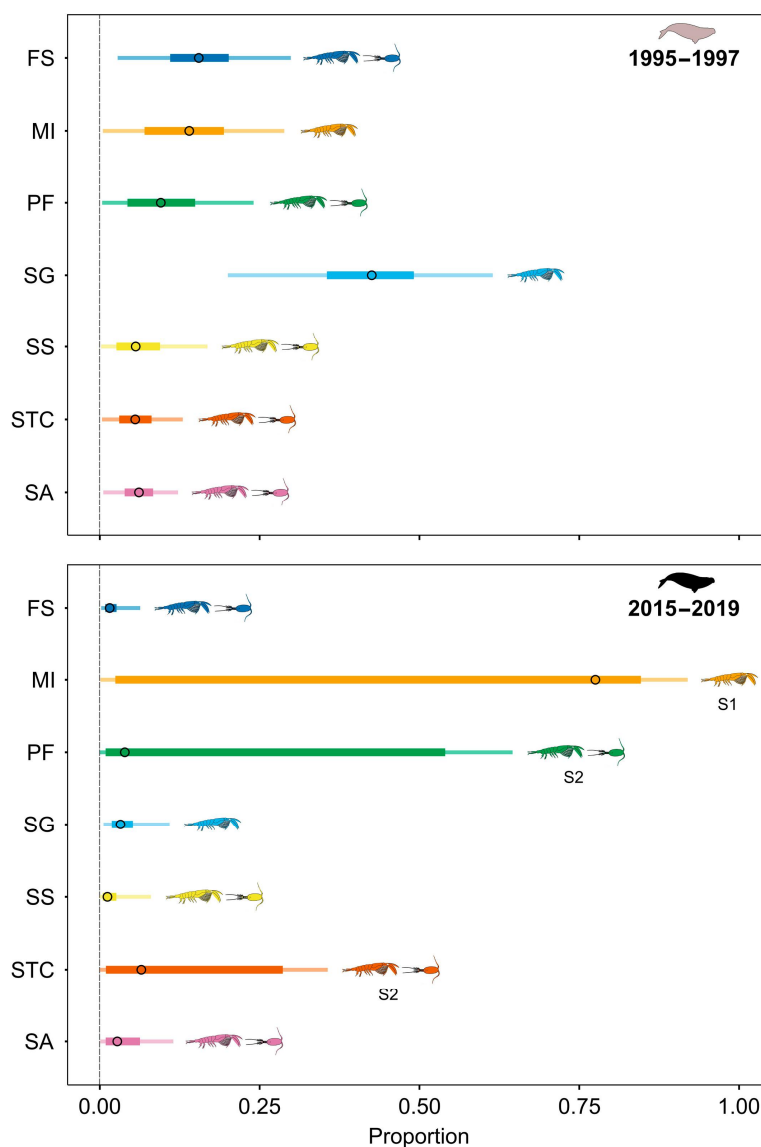


Figure 6 MixSIAR model outputs for mixing model *M1* showing estimates (median, 50% and 95% credibility intervals) of diet composition for South African southern right whales (SRW) sampled in 1995 – 1997 and 2015 – 2019. FS is Far South, MI is Marion Island, PF is Polar Front, SG is South Georgia, SS is Scotia Sea, STC is Subtropical Convergence, SA is west and south coasts of South Africa, and euphausiids and copepods are represented by clipart. The two distinct mixing model potential outcomes for SRWs sampled in 2015 – 2019 are indicated by S1 and S2.



Mixing model *M2* estimated that copepods and euphausiids from Far South (FS) contribute 33% (24% – 42%) to the diet of SRWs sampled in the 1990 decade. Smaller dietary contributions to the 1990 decade were estimated with euphausiids from Marion Island contributing 21% (11% – 32%) and copepods from the PF contributing 17% (3% – 31%) (Figure S7, Table S8). For SRWs sampled in the 2010 decade, only a single source, euphausiids from Marion Island, were estimated to substantially contribute to SRW diet, with a contribution of 84% (72% – 93%) (Figure S7). All remaining sources used in model *M2* had potential contributions of <10%.

#### 4. DISCUSSION

The detection of changes in marine megafauna population dynamics and foraging ecology provides insight into how anthropogenic change can influence natural systems (e.g., Davis et al., 2017, 2020; Fleming et al., 2016). Here, we used stable isotope analyses of skin biopsy samples to investigate long-term shifts in foraging ecology of South African SRWs. Results show that the population has recently shifted and diversified its foraging strategies, suggesting that their previously productive foraging grounds have changed over time. Considering the vast oceanic range of SRW foraging grounds, our findings point toward large-scale ecosystem changes in the Southern Ocean. This is perhaps not surprising, given the unprecedented impacts of recent climate change on Southern Ocean physical features, which in turn, have driven regional changes on all levels of Antarctic marine food webs (see Rogers et al., 2020 and references therein). The shift in foraging strategies is also concurrent with a time period associated with lowered reproductive output in the South African SRW population (Brandão et al., 2018; Vermeulen et al., 2018). As highly migratory capital breeders, SRWs have a strong relationship between foraging success and their reproductive output (Leaper et al., 2006; Lockyer, 2007; Seyboth et al., 2016), therefore, questions arise on their recent success in foraging.

##### *4.1 Decadal shift in southern right whale isotope values*

Results of this study demonstrate a significant shift in  $\delta^{13}\text{C}$  and a broadening of  $\delta^{15}\text{N}$  values (Figure 3) of SRW skin biopsy samples over the period 1995 – 2019. SRWs sampled in the 1990-decade have lower  $\delta^{13}\text{C}$  values than the 2010-decade, and their reconstructed diet consists predominantly of prey sources from regions with isotopic signatures similar to euphausiids from South Georgia. Our findings for the 1990-decade are supported by isotopic data from 11 South African SRW baleen plates collected from 1963 – 1994 (Best & Schell, 1996), which suggested foraging occurred predominantly south of the STC. In contrast, SRWs sampled in the 2010-decade, with higher  $\delta^{13}\text{C}$  values in skin, likely foraged further north, in regions with isotopic signatures similar to those found at the STC, PF and Marion Island. While the shift in diet is clear, the mixing model found two possible outcomes for the 2010-decade between which it could not distinguish: (1) euphausiids from Marion Island; or (2) copepods

and euphausiids from the PF and STC. Despite the model converging, these two scenarios are potentially confounded as Marion Island is located between the PF and STC along an isotopic gradient, rather than being discrete isotopic regions. Prey sources from the STC are isotopically discrete from those collected at Marion Island and the PF (Figure 5); and despite post hoc tests indicating isotopic similarity between sources from the PF and Marion Island, the mixing model results do not suggest that the two regions are isotopically equivalent. Additionally, whaling records, photo-identification, and satellite tagging data reveal that both Marion Island and the PF represent likely foraging grounds used by South African SRWs (IWC, 2013; Mate et al., 2011; Smith et al., 2012). Therefore, prey sources from Marion Island, the PF, and STC were retained in the mixing model.

The mixing models presented here reveal that a northward shift in the foraging of South African SRWs has likely occurred recently. The findings of Tormosov et al. (1998), which show that SRWs mostly feed on krill when south of 50°S, and copepods when north of 40°S, suggest that the northward shift in foraging presented here is likely accompanied by an increasing proportion of copepods in the diet of SRWs. Further work using microchemical markers or information from offshore movements of satellite-tagged SRWs would allow further inference to be made into South African SRW foraging ecology and diet composition. Fatty acids are widely used to assess the foraging ecology of marine mammals (e.g., Budge et al., 2008; Haug et al., 2017; Herman et al., 2005; Hooker et al., 2001; Marón et al., 2020; Olsen & Grahl-Nielsen, 2003) and they are known to undergo little biochemical change when passed up the food chain (Iverson, 2009). Similarly, compound-specific isotope analyses of amino acids have been proven a valuable tool in top predator foraging ecology (e.g., Nelson et al., 2018; Pomerleau et al., 2017; Zupcic-Moore et al., 2017) as it provides information about essential amino acids which are preserved unchanged through the food chain (Larsen et al., 2013). Incorporating compound specific analyses and *a priori* narrowing likely foraging grounds with satellite tag work into the Bayesian mixing model approach would further amplify the ecosystem baseline signals, inform model prior distributions (see Moore & Semmens, 2008), and would ultimately permit more accurate estimation of diet composition in SRWs.

The evidence for a shift in foraging strategy in South African SRWs presented here, occurred between a period characterised by rapid population growth (1990-decade; Brandão et al., 2010) and one characterised by an increase in calving intervals and decreased growth rate (2010-decade; Brandão et al., 2018; Vermeulen et al., 2018). It is unlikely that this suboptimal reproductive output and the shift in foraging strategy we present could have occurred coincidentally, given: (1) SRWs are capital breeders, which rely on accumulated energy reserves for successful reproduction (Lockyer, 2007); (2) periods of suppressed reproduction have been shown to occur during periods of nutritional stress in cetaceans (Greene et al., 2003; Hlista et al., 2009; Lockyer, 1986; Reeves et al., 2001; Ward et al., 2009;

Williams et al., 2013); and (3) the reproductive output of SRWs in Argentina and Brazil have been found to respond to fluctuations in krill abundance (Leaper et al., 2006; Seyboth et al., 2016). These concurrent events thus suggest not only a shift in foraging strategy but also a decreased foraging success in the 2010-decade.

Alternatively, the shift in foraging strategy in South Africa's population of SRWs may be related to SRW population recovery. A higher density of SRWs in the last decade could lead to more intra-specific competition for potentially shrinking prey sources, thus resulting in a fraction of the population having suboptimal foraging success, and potentially explaining the lowered reproductive output seen in South Africa. However, the mechanisms by which SRWs will respond to approaching their carrying capacity are not yet fully understood and the data to test this idea are not available. Furthermore, the pre-exploitation, global historical SRW population size has been estimated to consist of 101,882 individuals (95% posterior probability 88,282 – 123,780; Jackson et al., 2008), while the most recent estimate of global abundance indicates a population size of approximately 13,611 SRWs (IWC, 2013), thus, the global population does not appear close to full recovery.

Had the foraging strategy of South African SRWs remained constant during the 1990s and 2010s, then further investigation into the hypothesis of an ecological trap may be warranted, whereby SRWs may be making maladaptive habitat choices based on former reliable environmental information (Schlaepfer et al., 2002), leading to poor body condition and suboptimal reproductive output. However, we provide evidence for the inverse: SRWs appear to have shifted and potentially diversified their foraging strategies, possibly making use of anomalously high productivity at the STC (Del Castillo et al., 2019), yet still displaying suboptimal reproductive output. Although it is intuitive to suggest that diversification in foraging may provide some degree of resilience to large-scale oceanic changes (see Cartwright et al., 2019) – our results, combined with the increase in calving intervals and decreased population growth rate (Brandão et al., 2018; Vermeulen et al., 2018), suggest that the potential foraging plasticity provided by diversifying foraging strategies may in fact not be sufficient to ensure continued foraging success, and therefore successful reproduction, in South African SRWs.

The shift in foraging strategy could be linked to an increase in productivity in the region between the STC and PF: the Sub Antarctic Zone; hereafter SAAZ. Over the period 1987 – 2018, Del Castillo et al. (2019) found strong increases in surface chlorophyll concentrations in the Pacific, Atlantic and Indian sectors of the Southern Ocean, particularly in the SAAZ. Furthermore, since approximately 2010, winter months in the Atlantic region of the SAAZ have seen extremely high chlorophyll concentrations, characteristic of summer month concentrations (Del Castillo et al., 2019). We hypothesize that this expansion of productivity in the SAAZ into winter, has resulted in year-round high productivity at

specific SRW foraging grounds. Given the high productivity in the SAAZ, South African SRWs may not need to migrate to foraging grounds south of the PF. Alternatively, they may still migrate to foraging grounds south of the PF, but also take advantage of high productivity in the SAAZ on their northwards migration. How this may have led to an apparent decreased foraging success remains to be determined.

#### *4.2 Cetaceans as indicators of large-scale oceanic changes*

Identifying species that may be useful for elucidating the links between physical environmental change and the ecological responses of top marine predators can provide insight into ecological dynamics and inform predictions for future responses of marine top predators in the face of rapid anthropogenic climate change (Fleming et al., 2016). However, the foraging and migratory responses of cetaceans to climate change appear context dependant.

Spatial and/or temporal mismatches between the life history or phenology of krill-dependant species and their prey availability, and thus their migratory habits, may be key to understanding the effects of climate change on the survival and reproduction of baleen whales (Tulloch et al., 2019). There is some evidence suggesting substantial flexibility in baleen whale migration. For example, gray whales (*Eschrichtius robustus*) have begun to respond to warming by remaining in Arctic areas over winter (Moore et al., 2007), and Spitsbergen's bowhead whales (*Balaena mysticetus*), unlike larger bowhead whale populations, have recently been found to forage and overwinter in cold, sea-ice associated waters. Dietary flexibility has also been documented; Fleming et al. (2016) found that the diet of humpback whales between 1993 and 2012 in the California Current System (CSS), inferred from isotope data, shifted with available prey resources in response to climate variability, indicating that the species is a promising indicator for ecosystem dynamics in the CSS. Indeed, the North Atlantic right whale (*E. glacialis*), closely related to the SRW, has shown changes in its seasonal distribution in recent years, likely linked to changing prey resources (Davis et al., 2017). This acoustic study, and a more recent one studying North Atlantic right whales, humpback, sei (*Balaenoptera borealis*), fin (*B. physalus*), and blue whales (*B. musculus*), showed distributional changes in all species that suggested they were keeping pace with environmental changes in the North Atlantic (Davis et al., 2020).

However, historic whaling records and more than 15 years of satellite-derived data have shown that humpback whale migrations in the southwest Atlantic have not changed during dynamic oceanographic and geomagnetic conditions (Horton et al., 2020). Furthermore, Abrahms et al. (2019) found that both long-term memory and resource tracking play vital roles in blue whale migrations, suggesting that other highly migratory species may struggle to adapt to climate change. What is clear from these examples, as well as the results we present, is that we are seeing differences in baleen

whale responses to climate change, and these differences tend to be correlated to poor population recovery. Indeed, although capital breeders like right whales may have some advantage given that their life history strategy decouples environmental productivity at their wintering breeding grounds from reproductive success, their reliance on foraging in some of the most rapidly changing parts of the world (Jansen et al., 2020; Rogers et al., 2020) seems to limit this benefit.

#### 4.3 Caveats

Our study has several assumptions common to stable isotope analyses: first, stable isotope values in the ecosystem (isotope baseline) have not changed enough over the time period of our study to influence the results; second, the prey dataset and TEF lead to an accurate reconstruction of diet; and thirdly, we are only detecting shifts over the period of integration of isotopes into the whales' skin.

The accurate interpretation of stable isotope values of a consumer requires an understanding of the spatial and temporal variation in isotopic compositions of food web baselines (Magozzi et al., 2017). Disentangling whether a change in a consumer's stable isotope values represents a shift in foraging behaviour or a shift in isotopic baseline is challenging (McMahon et al., 2013b). However, the increase in  $\delta^{13}\text{C}$  in South African SRWs is unlikely to be due to ecosystem baseline changes, as it is both substantial and in the opposite direction to the general trend of decreases in oceanic baseline  $^{13}\text{C}$  values (de la Vega et al., 2019; Hanson et al., 2009; Lorrain et al., 2020; Mestre et al., 2020; Newsome et al., 2007a). Specifically,  $\delta^{13}\text{C}$  values are known to decline by approximately  $-0.1$  to  $-0.2\text{‰}$  per decade (Sonnerup et al., 1999) due to ocean absorption of anthropogenic carbon emissions i.e. the Suess effect (Suess, 1955). As a result, several studies have detected decreases in marine predator  $\delta^{13}\text{C}$  values that could not be attributed to shifts in foraging strategies, but rather to changes in abiotic conditions and/or other biotic components of the Southern Ocean (i.e. Suess effect or changes in biological productivity: de la Vega et al., 2019; Hanson et al., 2009; Lorrain et al., 2020; Mestre et al., 2020; Newsome et al., 2007a; Quillfeldt et al., 2010). However, these studies have shown a small magnitude of change in  $\delta^{13}\text{C}$  (e.g.,  $-1.4\text{‰}$  from 2004 – 2017 for elephant seals in Mestre et al. 2020; and  $-1.8\text{‰}$  for three tuna species from 2000 – 2015 in Lorraine et al. 2020) in the direction of the Suess effect, compared with the mean increase in  $\delta^{13}\text{C}$  we present for South African SRWs from  $-23.76\text{‰}$  in the 1990s to  $-20.98\text{‰}$  in the 2010s (i.e.,  $+2.78\text{‰}$ ). Finally, recent work (e.g., Logan et al., 2020) suggests temporal stability in isotopic latitudinal gradients across decades in the Southern Ocean isoscape, thus supporting this supposition.

The isotopic dietary reconstruction presented here relies on the accurate representation of South African SRW prey isotopic values and that the TEF used accurately reflects the isotopic enrichment from SRW prey to SRW skin. We included a carefully vetted copepod and euphausiid dataset (i.e., data

were lipid-extracted or lipid normalised) available for regions of the South Atlantic Ocean, the southwest Indian Ocean and the Southern Ocean which South African SRWs may utilize as summer foraging grounds (Table S1). This approach has some limitations and sources of variance (for more details, please see Valenzuela et al., 2018). Nevertheless, this approach is commonly used in mixing models, as it represents the best available data (Lübcker et al., 2017; Valenzuela et al., 2018). Similarly, we used a TEF calculated for fin whale skin (Borrell et al., 2012) as to the best of our knowledge, a species-specific TEF has not been calculated for SRWs. This TEF ( $1.28 \pm 0.38\text{‰}$  for  $\delta^{13}\text{C}$  and  $2.82 \pm 0.3\text{‰}$  for  $\delta^{15}\text{N}$ ) is similar to the average values for whole animals ( $\approx 3\text{‰}$  for nitrogen and 0 to  $1\text{‰}$  for carbon; Peterson & Fry, 1987), and has previously been used in mixing models to reconstruct blue, sei, fin (Silva et al., 2019) and SRW diet (Valenzuela et al., 2018).

The timing of isotopic integration is also an important consideration in this and other isotope ecology studies. For whale skin, integration is thought to be approximately 3 - 5 months (Busquets-Vass et al., 2017), and so samples collected in the austral winter represent foraging in autumn or late summer. The 1990-decade data presented here, baleen plate analysis (Best & Schell, 1996) and historical whaling data (Smith et al., 2012) all suggest that higher latitude foraging grounds were visited later in summer and into autumn, prior to the northward migration. The work presented here suggests that the STC and PF, rather than foraging grounds further south, are now visited by SRWs prior to the northward migration. However, we cannot rule out that higher latitude foraging grounds are visited in spring or early summer, as the isotopic signatures would no longer be present in the whale skin; modern baleen whale plates would provide further information on this. Furthermore, it is important to acknowledge that SRWs may have subtly different isotopic signatures in their skin despite having visited the same foraging grounds. This can be a result of visiting foraging grounds in a different order, having different levels of foraging effort at each location, or by spending different amounts of time at each foraging ground. This is a limitation of many isotope studies on marine mammals and other vagile marine predators.

## 5. CONCLUSION

Stable isotope analyses reveal that the South African population of SRWs underwent a significant northward shift, and diversification, in foraging strategy from the 1990s to 2010s. This shift could represent a strategy to cope with changes in preferred prey or habitat, a positive sign that the species could potentially adapt to changing resources. However, the concurrent decline in reproductive success suggests the shift could also be a suboptimal foraging strategy. This contributes to the growing body of evidence that responses to climate change is context and species dependent in cetaceans but highlights how shifting foraging strategies may not be sufficient to cope with a changing environment.

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## DATA SHARING AND ACCESSIBILITY

The whale skin isotope data is available in Supporting Information 1 and R code used in the analysis is available in Supporting Information 2. All Supplementary Figures and Tables are in Supplementary Material.

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