



Intra-annual consistent diet of lanternfish and krill in adult female southern elephant seals *Mirounga leonina* from the South Georgia population

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ABSTRACT: Southern elephant seals *Mirounga leonina* are top predators in the Southern Ocean and significant consumers of mesopelagic mid-trophic level prey while spending most of the year foraging out at sea. Yet, there is still considerable uncertainty regarding variability in the dietary composition between individuals and over time. We ran a suite of mixing models using carbon and nitrogen stable isotope ratios from the vibrissae of 54 adult female southern elephant seals from the South Georgia population (2005–2009) and potential fish, squid, and krill prey. Our goals were to (1) estimate the dietary composition of this population as a whole, (2) compare the dietary composition of individuals between previously identified foraging strategies, and (3) quantify the degree of dietary consistency at the individual level throughout a long foraging migration. Models indicate that myctophid fish were the dominant prey item consumed (mean 45% of diet), followed by Antarctic krill and Antarctic jonasfish. However, there was considerable variability within and among groups of seals regarding specific prey items consumed and the degree of individual dietary specialization, possibly as a means of reducing intraspecific competition. Finally, our models provide evidence of most seals displaying dietary consistency throughout a foraging migration. These findings have important management implications for the South Georgia population in an uncertain future and highlight the need for more effective krill management along the western Antarctic Peninsula.

KEY WORDS: Stable isotopes · Mixing models · Krill · Lanternfish · Diet · Vibrissa · Elephant seals

1. INTRODUCTION

Understanding the diet and potential for adaptation in foraging behavior of a top predator can reveal underlying patterns of its biology and changes in prey availability (Xavier et al. 2013, Hindell et al. 2016, Spencer et al. 2017, Galicia et al. 2021). Many marine mammals undergo extensive movement patterns while foraging at sea and partake in aerobically de-

manding dives in pursuit of their prey (Hindell & McMahon 2000, Williams et al. 2000). Abundance and distribution of preferred prey species for marine mammals are driven by environmental processes, directly (e.g. sea ice for refugia) or indirectly (i.e. those that affect prey by influencing lower trophic level communities; Loeb & Santora 2015). These environmental processes are dynamic and may lead to changes in prey availability, requiring top predators

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to adapt their foraging strategies accordingly. Many species of marine mammals are able to alter their behavior to match the fine-scale distribution of potential prey species in at least 1 of 2 ways: (1) by changing foraging location geographically or vertically in the water column to exploit prey, and/or (2) by displaying behavioral plasticity to select and capture a variety of different prey species depending on what is more readily available (Hamilton et al. 2019). In this sense, marine mammals constantly incorporate ecological information through their foraging behavior. They are thus valuable candidates for use as sentinel species for ecosystem change; however, this requires extensive information on their diet and its plasticity.

Southern elephant seals *Mirounga leonina* are the largest pinnipeds and are important top predators across the Southern Ocean and sub-Antarctic waters (McConnell et al. 1992, Hindell 2018, Mestre et al. 2020). While there remains a large degree of uncertainty regarding their diet, previous studies have suggested that elephant seals consume multiple species of fish, particularly myctophids (lanternfish), and squid; however, there does appear to be considerable variation in diet through time, space, and by methodology (Daneri et al. 2000, Daneri & Carlini 2002, Bradshaw et al. 2003, Cherel et al. 2008, Newland et al. 2009, Bailleul et al. 2010). Additionally, more recent studies using stable isotope analysis have raised the possibility of juvenile southern elephant seals incorporating significant amounts of Antarctic krill *Euphausia superba* into their diets in the Marion Island and Macquarie Island populations (Walters et al. 2014, Lübcker et al. 2017). While the species could be described as a dietary generalist, there is likely considerable variation among individuals regarding the level of individual specialization, which may have arisen from the need to reduce intraspecific competition (Newland et al. 2009, Hückstädt et al. 2012).

Multiple methods have been employed to describe the diet of pinnipeds, including stomach content, scat, stable isotope, and fatty acid analyses, all of which come with caveats (Green & Burton 1993, Daneri et al. 2000, Daneri & Carlini 2002, Staniland 2002, Bradshaw et al. 2003, Field et al. 2007, Cherel et al. 2008). For example, relying on prey found in stomachs or scat overestimates the importance of certain prey species (e.g. squid, because beaks are harder to digest) while ignoring or severely underestimating the contribution of others (Cherel et al. 2008). Each diet sampling method also provides different temporal windows into individual and population behavior. Stomach content and scat analysis only identify prey representing an individual's most recent foraging

excursions, while stable isotope and fatty acid analysis provide data that are relevant for the period a given tissue was synthesized (e.g. days to entire lifetimes; Fleming et al. 2018, Teixeira et al. 2022). Southern elephant seals spend 8–10 mo of the year foraging at sea, potentially undergoing multiple shifts in diet and rendering a single synoptic characterization of diet inadequate.

It is necessary for researchers to incorporate dietary information of southern elephant seals at intervals dispersed throughout the entire course of their time spent foraging (up to 10 mo) to understand how these animals interact with and respond to a changing Southern Ocean. Elephant seal vibrissae grow continuously and are believed to be shed approximately once per year, usually during the molting period when seals are hauled out on land (Lübcker et al. 2016, McHuron et al. 2019). As a result, stable isotope ratios analyzed from incremental sections of the vibrissae provide a continuous time series of dietary information for the year (Lübcker et al. 2017). Carbon and nitrogen are most frequently used in foraging studies of animals, expressed in delta notation ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) as the ratio of heavy to light isotopes in a sample to the ratio of heavy to light isotopes in an internationally accepted standard (Fry 2006, Wolf et al. 2009, Kurle & McWhorter 2017). $\delta^{13}\text{C}$ in the ocean is driven primarily by patterns of primary production and, therefore, is closely linked with the foraging habitat of an animal (DeNiro & Epstein 1978, Fry 2006, Fleming et al. 2018). At the same time, $\delta^{15}\text{N}$ is an indicator of trophic position because $\delta^{15}\text{N}$ undergoes considerable increases with each incremental step up the food chain due to the preferential excretion of the isotopically lighter and less energetically costly ^{14}N (DeNiro & Epstein 1981, Gradinger 2009, de la Vega et al. 2019). When carbon and nitrogen ratios of potential prey species are included in analyses along with those of a focal consumer, relative prey contributions to the diet of the consumer can be estimated by using stable isotope mixing models (Stock & Semmens 2016a, Stock et al. 2018, Guerrero et al. 2021). For a difficult-to-study species such as the southern elephant seal, these models are currently the only feasible way to estimate diet over the course of an entire foraging season.

Hückstädt et al. (2012) used the movement and diving behavior of adult female southern elephant seals, paired with stable isotope analysis, to identify 8 distinct groups of seals based on unique foraging strategies. These strategies varied in their degree of pelagic versus benthic foraging, movement locations, dive behaviors, stable isotope ratios, and level of individ-

ual dietary specialization. Yet, no attempt was made to estimate specific prey items eaten, describe how prey selection differs between clusters, or elucidate potential changes in diet over time. Here, we extend this analysis to estimate dietary composition and behavioral plasticity in the diet of these same adult female elephant seals throughout a post-molt foraging trip (~8 mo). Isotope ratios from vibrissae of southern elephant seals collected during haul-out periods along the western Antarctic Peninsula (WAP) from 2005 to 2009 (see Hückstädt et al. 2012) were incorporated into Bayesian stable isotope mixing models along with a suite of potential fish, cephalopod, and krill prey species to examine foraging preferences of this Southern Ocean top predator. Specifically, we aimed to (1) examine dietary composition at the population level, (2) compare the dietary composition of previously identified groups of seals and how variations in foraging strategies may lead to different subsets of resources utilized, and (3) reveal patterns of prey selection at the individual level using 1 cm vibrissa segments representing discrete periods throughout the foraging season. These results will provide valuable data for understanding the prey selection of southern elephant seals and the capability of individuals to shift their diet in response to changing environmental conditions—an important predictor for the persistence of a species in the face of environmental change.

2. MATERIALS AND METHODS

2.1. Seals

All animal sampling procedures were conducted under US NMFS Permit No. 87-1851-00 and were approved by the Institutional Animal Care and Use Committee (IACUC) at the University of California Santa Cruz. Details regarding original data collection, including study site, experimental design, and stable isotope analysis, have been previously described by Hückstädt et al. (2012). In short, data from 54 southern elephant seals sampled during the molt haul out (January–February) during 2005 ($n = 5$), 2006 ($n = 12$), 2007 ($n = 11$), 2008 ($n = 11$), and 2009 ($n = 15$) are included here. All sampling took place on Livingston Island, South Shetlands, Antarctica. The most basal segment was removed due to differences in C:N ratios (Hückstädt et al. 2012). Vibrissa samples ($n = 614$) were cleaned, cut into 1 cm segments, and labeled by length before carbon and nitrogen bulk stable isotope analysis. Maximum lengths ranged from 6 to 15 cm,

depending on the individual. The first segment (length 1) was the proximal section of the vibrissae closest to the skin and, therefore, represents the most recent period of growth. In contrast, the distal segment represents the oldest period of growth. Vibrissae growth rates for southern elephant seals are unknown, although McHuron et al. (2019) found that for northern elephant seals *Mirounga angustirostris*, vibrissae growth was approximately 10 ± 12 d per every half centimeter. However, this estimate had a significant range, from 2 to 65 d of growth represented per half centimeter (McHuron et al. 2019).

Results from Hückstädt et al. (2012) grouped seals into 8 distinct clusters based on foraging strategies and biotelemetry data. Most clusters showed a primarily shelf-based foraging strategy; in contrast, individuals from Cluster 1 displayed a largely pelagic foraging strategy, and individuals in Clusters 2 and 8 displayed a mix of shelf-based and pelagic foraging (Hückstädt et al. 2012). Importantly, Cluster 6 consisted of just 1 individual, an outlier that fed in a small geographic area in the Drake Passage. For this study, these clusters remain the same and are used as a basis for interpreting subsequent mixing model analyses. Moving forward, all remaining methods from this current study are novel.

2.2. Prey

Carbon and nitrogen isotope values for a suite of prey species potentially consumed by southern elephant seals foraging near and within the Antarctic Polar Front were collected from the published literature (Polito et al. 2011a,b, 2013, Seco et al. 2016). Isotope ratios from a total of 13 potential prey species are included here. They are made up of 1 species of krill (Antarctic krill *Euphausia superba*), 3 species of cephalopod (glacial squid *Psychroteuthis glacialis*, giant warty squid *Moroteuthis longimana*, and smooth hooked squid *Filippovia knipovitchi*), and 9 species of fish (Antarctic silverfish *Pleurogramma antarcticum*, grey rockcod *Lepidonotothen squamifrons*, Bolin's lanternfish *Protomyctophum bolini*, Antarctic lanternfish *Electrona antarctica*, Nichol's lanternfish *Gymnoscopelus nicholsi*, Antarctic jonasfish *Notolepis coatsoorum*, dusky rockcod *Trematomus newnesi*, electron subantarctic lanternfish *E. carlsbergi*, and mackerel icefish *Champscephalus gunnari*). All prey included in mixing model analyses were collected within the temporal scope of the study period (2005–2009). Lipid was extracted from fish and krill samples, but not squid, before isotope analysis (Seco et al. 2016). Fish

and krill lipid extraction was performed with an 8 h soak in a 1:1 petroleum-ether:ethyl-ether mixture (Polito et al. 2011a,b, 2013). Isotope data for the 3 squid species were taken from beaks, so a mathematical correction was applied to make ratios reflective of digestible soft parts by adding 4.7‰ $\delta^{15}\text{N}$ and subtracting 0.6‰ $\delta^{13}\text{C}$ (Cherel & Hobson 2005, Kim et al. 2012).

2.3. Mixing models

Mixing models were run using the package 'MixSIAR' (Stock & Semmens 2016a, Stock et al. 2018) in R (Version 4.3.2, R Core Team 2023). 'MixSIAR' uses a Bayesian framework to estimate the relative proportions of multiple sources (prey) to the diet of a consumer (southern elephant seals). Prey data were incorporated into the models as means \pm SD, and consumer data were included as raw values. As ratios of both carbon and nitrogen stable isotopes change from source to consumer, it is important to use an accurate estimate for the magnitude of this change, known as the trophic discrimination factor (TDF; Hobson et al. 1996, Newsome et al. 2010). Estimates of TDF for southern elephant seals are unavailable; therefore, we used surrogate species with similar ecology and physiology. We used mean pinniped TDFs specific to the transfer of fish muscle to seal vibrissae that were estimated for harbor seals *Phoca vitulina*, harp seals *Pagophilus groenlandicus*, and ringed seals *Pusa hispida*, as well as more conservative estimates of TDF standard deviations from southern elephant seals (average between the 3 species of $3.2 \pm 0.3\%$ for $\delta^{13}\text{C}$ and $2.8 \pm 0.3\%$ for $\delta^{15}\text{N}$; Hobson et al. 1996, Beltran et al. 2016, Lübcker et al. 2017). The high degree of fractionation for carbon is consistent with previous studies of mammalian hair, a similar keratinous and metabolically inert tissue (Nakamura et al. 1982, Tieszen & Boutton 1988).

A limitation of mixing models, including the Bayesian models used here, is that the inclusion of too many sources (i.e. prey) can confound results and impede the ability to differentiate accurately between sources. Carbon and nitrogen ratios of sources must be significantly different for a clear distinction of the prey contribution. Therefore, prey species were pooled together when necessary, considering the similarities in their ecology and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios (Phillips et al. 2005; Table S1 in the Supplement at www.int-res.com/articles/suppl/m753p175_supp.pdf). New means and SD were calculated for a total of 7 sources that were subsequently included in mixing models: Antarctic krill, cod icefish (notothens; *L. squamifrons*, *T. newnesi*,

C. gunnari, *P. antarcticum*), Antarctic lanternfish, squid (*P. glacialis* and *M. longimana*), lanternfish (myctophids; *P. bolini*, *G. nicholsi*, *E. carlsbergi*), smooth hooked squid, and Antarctic jonasfish. Permutational multivariate analyses of variance (PERMANOVA) and pairwise comparisons (Anderson & Walsh 2013) were used to ensure all source groups had significantly different ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Note that Antarctic lanternfish was not combined into the larger lanternfish group because of differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, possibly due to biogeography (Fig. 1). A critical assumption of Bayesian mixing models used to ensure correct diet estimation is that all consumer data, when plotted in carbon and nitrogen isospace, must fall within the mixing polygon created by the source means \pm SD after being corrected for TDF (Fig. 1). Using methods from Smith et al. (2013), we removed a total of 11 consumer datapoints which did not satisfy the point-in-polygon assumption from further analyses (leaving $n = 603$ vibrissae segments; Fig. 1). Excluded datapoints came from multiple individuals, yet no one individual had all datapoints removed. Therefore, we were still left with a total of 54 individuals.

As the number of factors that can be incorporated into MixSIAR is limited to 2, a total of 8 mixing models were run separately, 1 per foraging cluster (previously determined by Hückstädt et al. 2012). For each run, diet was estimated for every seal using individual ID (fixed factor) and vibrissa length (1 cm segments) as a random factor nested within individual ID. Hückstädt et al. (2012) found no effect of year on elephant seal isotope ratios. As a result, the effect of year was not considered in mixing models due to uneven temporal coverage of both elephant seal and prey data (results not shown). All models used the process \times residual error structure (Stock et al. 2018) and consisted of 3 Markov chain Monte Carlo (MCMC) chains, each with a length of 3 000 000 iterations, a burn-in of 1 500 000, and a thinning rate of 500. This left us with a total of 9000 posterior draws. To account for uncertainties regarding southern elephant seal diet and the limitations of relying on stomach and scat analyses, and to prevent unnecessary biases, all models were run with non-informative Dirichlet priors (Swan et al. 2020). Model convergence was validated using the Gelman-Rubin and Geweke diagnostic tests (Geweke 1991, Gelman et al. 2004, Stock & Semmens 2016b, Guerrero & Rogers 2020). Gelman-Rubin diagnostics indicated strong convergence of the 3 MCMC chains for each of the 8 mixing models. As the Gelman-Rubin diagnostic is arguably a more robust indicator of model convergence than the Geweke diagnostic, we were more lenient with allowing some chains to have higher-

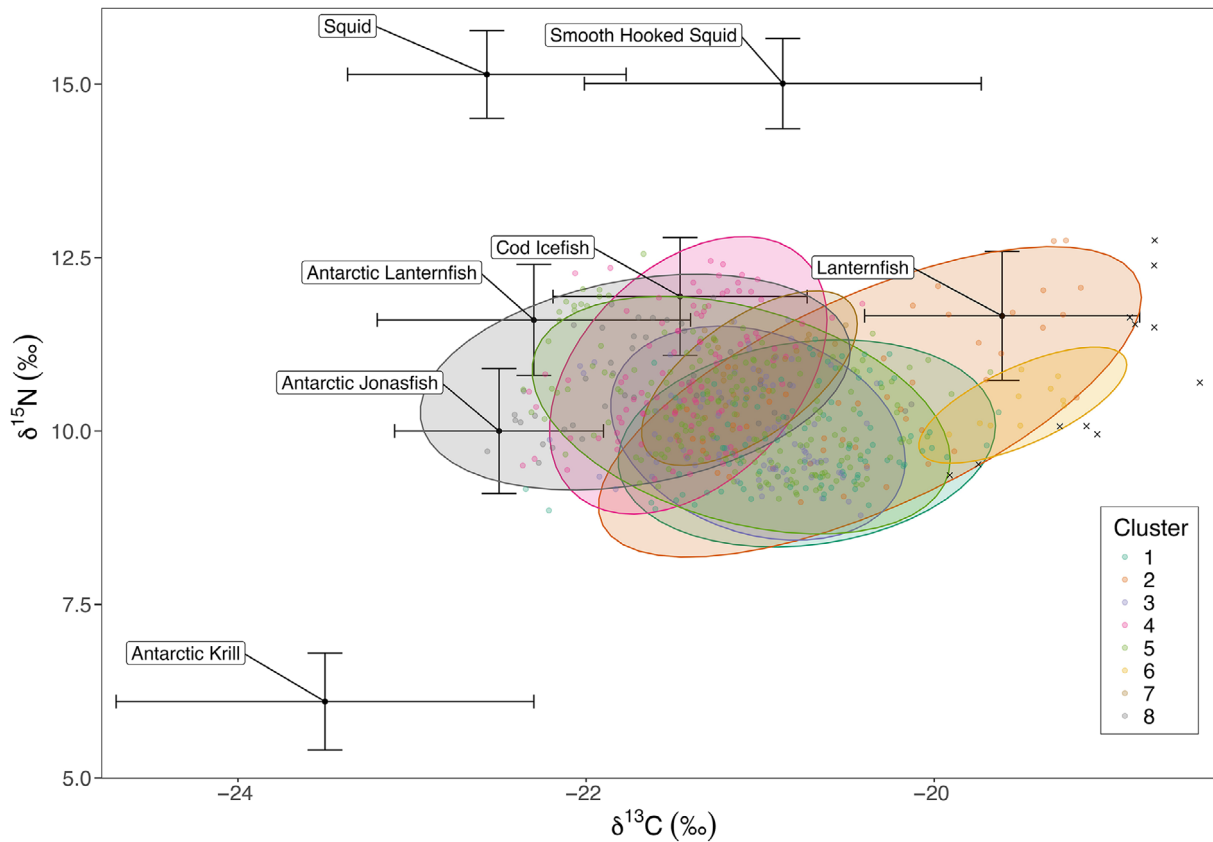


Fig. 1. Mixing plot showing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each vibrissa segment from every included elephant seal and means \pm SD for the 7 included source groups. Color corresponds to previously identified clusters based on seal foraging behavior. All sources are plotted after being corrected for trophic discrimination factors. Ellipses encompass approximately 95% of all datapoints per cluster (n = 603). Black 'Xs' denote points outside of the mixing polygon which were removed from analyses (n = 11)

than-ideal values for the latter test. There were also 2 instances in which pairs-plots indicated strong negative correlations between prey types of $>|0.8|$, and both were only marginally highly correlated (-0.81 between Antarctic jonasfish and Antarctic krill for both Clusters 4 and 7; Fig. S1). These 2 prey types therefore cannot be unambiguously estimated for Clusters 4 and 7, and results for these 2 clusters, as well as the overall population level results, should be interpreted with some caution. All mixing model results are reported as mean proportions of the posteriors \pm SD.

2.4. Dietary specialization and dissimilarity

From the mixing model results, a specialization index was calculated for each vibrissa length of all individuals as the distance in Euclidean space between a hypothetical consumer feeding on all prey items evenly and the predicted diet of each individual (Newsome et al. 2012, Cabrol et al. 2021). Values ranged from 0 to 1, where 0 is indicative of a perfect

generalist and 1 a perfect specialist. A multivariate homogeneity groups dispersion analysis was then run using the 'vegan' package in R (Oksanen et al. 2022) and estimated dietary proportions to quantify dissimilarity in diet of individuals within and between the 8 foraging clusters. Diet estimates from mixing models were used to calculate the distance between each individual vibrissa segment and the centroid of the corresponding cluster in Euclidean space. Multidimensional scaling was used for visualization (Kruskal & Wish 1978).

2.5. Individual-level temporal analysis

Each seal underwent further analysis to elucidate changes in diet over the course of a foraging season at the individual level. First, the top 2 prey items identified by mixing models (lanternfish and Antarctic krill) were selected so that all individuals would be analyzed based on the same 2 sources. Posterior draws for these sources at all vibrissae lengths were pulled, and data

were combined into 3 time periods, each representing approximately one-third of a seal's foraging excursion (hereafter referred to as 'periods'). To compare relative changes in the contribution of each prey source, posterior distributions from each of the 3 time periods per prey source per individual were compared to one another, with 3 comparisons made per prey source: 1st versus 2nd period, 2nd versus 3rd period, and 1st versus 3rd period. As elephant seal vibrissae do not exhibit linear growth rates or similarity in growth rates between individuals, combining isotope data into approximate thirds of a foraging season is perhaps the most unbiased method of time-stamping our dietary results (Lübcker et al. 2016, McHuron et al. 2019).

When the number of 1 cm vibrissa segments for an individual was not evenly divisible by 3, more segments were included in the earlier periods as elephant seal vibrissae grow at faster rates early on after they are shed before slowing to an asymptotic length (Lübcker et al. 2016, McHuron et al. 2019). Additionally, any individual with more than 12 vibrissa segments had all lengths >12 included in the 1st period. For example, for an individual with a maximum vibrissa length of 9 cm, periods consisted of lengths 1–3 (3rd period), 4–6 (2nd period), and 7–9 (1st period), with the larger numbers corresponding to earlier periods of growth. If an individual had a maximum length of 15 cm, periods consisted of lengths 1–4, 5–8, and 9–15. Last, if an individual had a maximum length of 10 cm, periods consisted of lengths 1–3, 4–6, and 7–10 (Table S2).

To determine the extent of dietary consistency, or lack thereof, at the individual level throughout the foraging season, we calculated the Bhattacharyya coefficient (BC) for each comparison using the package 'dispRity' (Guillermé 2018). BC calculates the probability of overlap between 2 distributions, where 0 indicates no overlap, and 1 indicates complete overlap. Previous studies using stable isotope mixing models have treated any BC of <0.6 as indicative of a significant difference in diet (Catry et al. 2009, Bond & Diamond 2011, Swan et al. 2020); for this study, we used the same threshold. Individuals from Clusters 4 and 7 were excluded from this analysis, as mixing models were not able to differentiate between Antarctic krill and Antarctic jonasfish.

3. RESULTS

Mean (\pm SD) $\delta^{13}\text{C}$ along all analyzed vibrissae lengths was $-21.03 \pm 0.68\text{‰}$ and ranged from -22.65 to -18.47‰ . Mean $\delta^{15}\text{N}$ was $10.35 \pm 0.83\text{‰}$ and

ranged from 8.79 to 12.75‰. When ratios were averaged together by cluster, a visual inspection of trends over time (from the distal to proximal ends of vibrissae) for $\delta^{13}\text{C}$ showed either an overall decrease (e.g. Clusters 2 and 8) or remained relatively consistent (Fig. S2). A similar pattern was observed for $\delta^{15}\text{N}$, with values either declining over the vibrissae lengths or remaining consistent; however, a declining trend was more common for $\delta^{15}\text{N}$ than for $\delta^{13}\text{C}$ (Fig. S2).

3.1. Population-level diet

At the population level, the lanternfish group was the dominant food source (approximately 45% of diet, by mean). The remaining sources, in decreasing order of importance, were both Antarctic krill and Antarctic jonasfish (together representing up to 34% of diet), followed by cod icefish and Antarctic lanternfish. In contrast, smooth hooked squid and squid had only marginal values (<7% of total diet; Fig. 2). Detailed means \pm SD are reported in Table 1.

3.2. Cluster-level diet and specialization

As expected, diet varied between previously identified foraging clusters and between individuals within foraging clusters (Fig. 3). The lanternfish group was an important prey source for all clusters, with Antarctic krill remaining important for most. Antarctic jonasfish was also important for several clusters, particularly Cluster 4 (note the Cluster 4 model could not distinguish between Antarctic jonasfish and Antarctic krill) and Cluster 8. Cluster 8 was the only cluster in which lanternfish was not the dominant component of diet, but instead was surpassed by Antarctic jonasfish. Both the cod icefish group and smooth hooked squid were predicted to contribute to diet in Cluster 4, and Antarctic lanternfish was at least somewhat important for individuals from Cluster 5. Estimated proportions of all 7 sources can be found in Table 1.

Results from the multivariate homogeneity groups dispersion analysis highlight within- and between-cluster dispersion (Fig. 4). Each point represents a 1 cm vibrissa segment; the closer 2 points are in space, the more similar is the diet selection. Clusters 4, 5, and 3 occupied the most space, as variability among individuals in these clusters was high. Additionally, individuals from Cluster 4 were clearly distinct from the rest of the clusters, likely driven by the relatively low influence of the lanternfish group in diet as well as the inclusion of cod icefish and smooth hooked

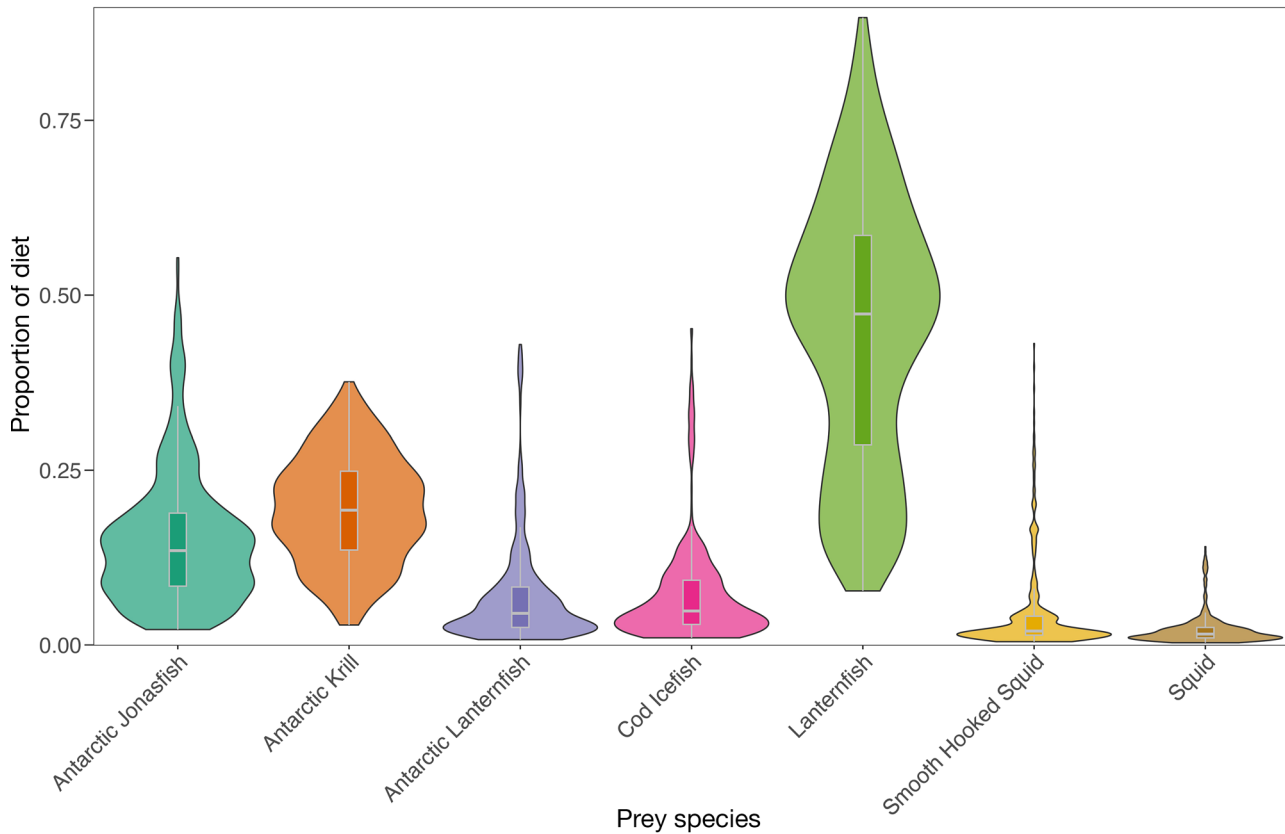


Fig. 2. Mixing model results for the entire population of 54 individual elephant seals, with no regard to cluster. Box and violin plots were made from mean values of prey estimates from each individual vibrissa length. Boxes show first and third quartiles, medians (horizontal lines), and maximum and minimum values no greater than 1.5 times the interquartile range (whiskers)

squid (Fig. 4). Individuals from Cluster 5 displayed a wide range of dietary preferences. Some individuals shared more similarity in diet with Clusters 1 and 2, the diets of which were driven by the highest proportions of lanternfish, followed by Antarctic krill and Antarctic jonasfish, with low contribution from other sources. In contrast, some individuals in Cluster 5

were more similar to individuals from Cluster 8, with diet dominated by Antarctic jonasfish and then lanternfish (59% of diet together). Cluster 5 individuals also displayed the largest range of specialization index of all the clusters (Fig. 5).

Calculations of dietary specialization throughout the course of a foraging season by cluster reveals further

Table 1. Mean \pm SD proportion of diet for each of the 7 prey sources. Asterisks indicate strong negative correlation between prey sources, indicating that models failed to distinguish between them. Cluster indicates previously identified groups of elephant seals from Hückstädt et al. (2012)

	Antarctic jonasfish	Antarctic krill	Antarctic lanternfish	Cod icefish	Lanternfish	Smooth hooked squid	Squid
Global	0.150 \pm 0.094*	0.194 \pm 0.076*	0.070 \pm 0.074	0.072 \pm 0.071	0.449 \pm 0.191	0.044 \pm 0.063	0.022 \pm 0.022
Cluster 1	0.128 \pm 0.055	0.223 \pm 0.060	0.019 \pm 0.008	0.024 \pm 0.010	0.585 \pm 0.095	0.012 \pm 0.004	0.008 \pm 0.003
Cluster 2	0.054 \pm 0.024	0.161 \pm 0.080	0.017 \pm 0.004	0.023 \pm 0.006	0.724 \pm 0.111	0.013 \pm 0.003	0.008 \pm 0.002
Cluster 3	0.124 \pm 0.080	0.241 \pm 0.055	0.041 \pm 0.019	0.052 \pm 0.022	0.505 \pm 0.100	0.022 \pm 0.008	0.015 \pm 0.005
Cluster 4	0.197 \pm 0.072*	0.189 \pm 0.084*	0.042 \pm 0.016	0.178 \pm 0.107	0.214 \pm 0.091	0.154 \pm 0.087	0.026 \pm 0.023
Cluster 5	0.135 \pm 0.083	0.190 \pm 0.076	0.129 \pm 0.102	0.048 \pm 0.029	0.452 \pm 0.171	0.019 \pm 0.012	0.026 \pm 0.026
Cluster 6	0.086 \pm 0.002	0.221 \pm 0.015	0.057 \pm 0.000	0.071 \pm 0.001	0.493 \pm 0.014	0.045 \pm 0.001	0.027 \pm 0.000
Cluster 7	0.145 \pm 0.025*	0.144 \pm 0.063*	0.074 \pm 0.016	0.106 \pm 0.018	0.461 \pm 0.065	0.042 \pm 0.007	0.026 \pm 0.004
Cluster 8	0.328 \pm 0.099	0.117 \pm 0.029	0.094 \pm 0.022	0.101 \pm 0.029	0.259 \pm 0.121	0.047 \pm 0.021	0.053 \pm 0.027

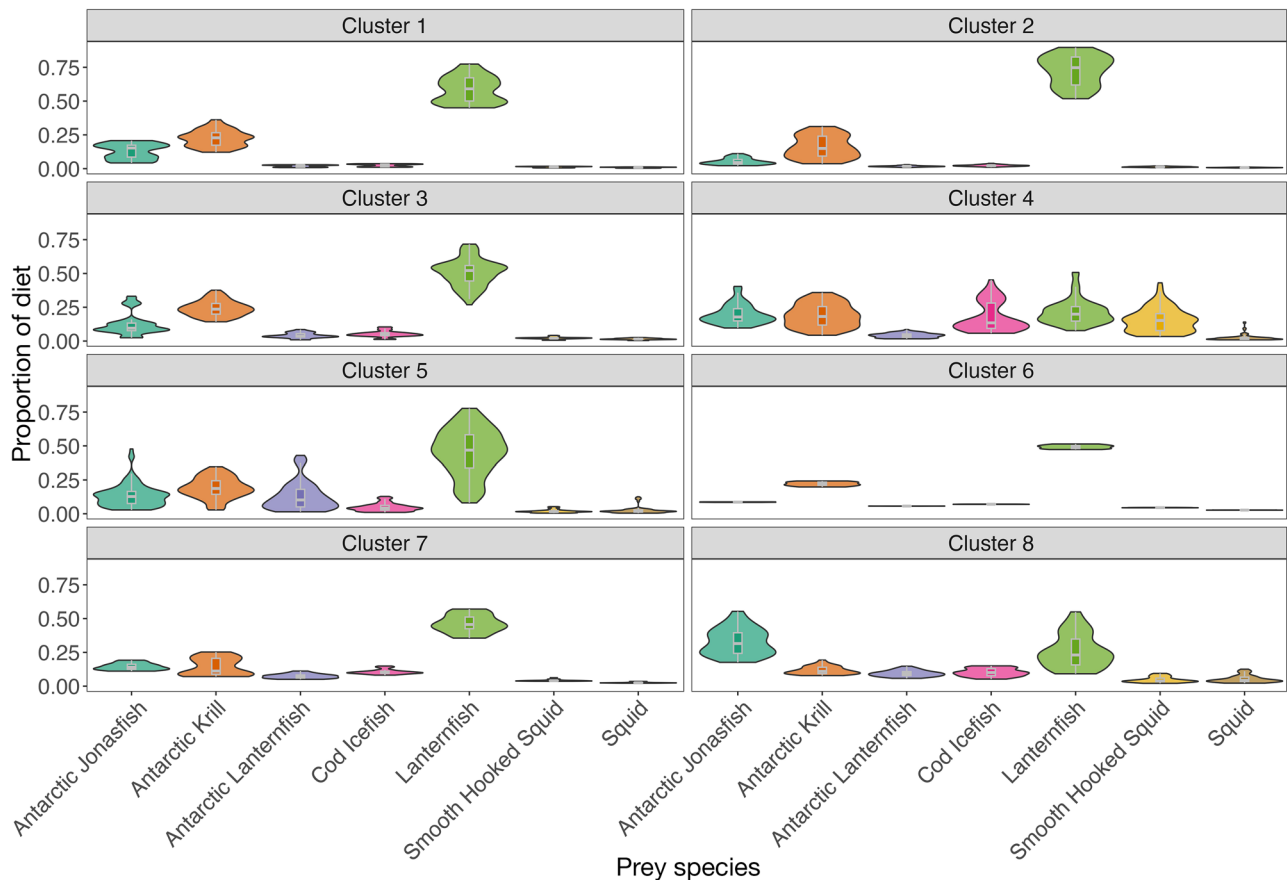


Fig. 3. Mixing model results for each of the 8 clusters. Box and violin plots were made from mean values of prey estimates from each individual vibrissa length. Box plot description as in Fig. 2

patterns in the data. Specialization index ranged from 0.16 to 0.88. Individuals varied in their estimated degree of dietary specialization both within and between clusters (Fig. 5). For example, individuals from Cluster 2 had the highest degree of specialization, followed by Cluster 1. Clusters 4 and 8 had the lowest degrees of specialization, and Clusters 3, 5, 6, and 7 were intermediary (note that Cluster 6 consists of only 1 individual, thus we cannot speak on within-group variability, only within-individual). Of these, Clusters 3 and 5 displayed high within-cluster variability in dietary specialization, with individuals ranging from generalist to specialist (Fig. 5). Estimates of dietary specialization remained more or less consistent for most individuals over the length of the vibrissae; however, a marked decrease in specialization toward a more generalist diet can be seen in individuals from Clusters 2, 5, and 8 (Fig. 5).

3.3. Individual-level temporal analysis

After excluding individuals from Clusters 4 and 7, we were left with a sample size of $n = 44$ seals. Ap-

proximately 1/3 of these individuals ($n = 16$) had a $BC < 0.6$ for at least one comparison (Table 2). In every such instance, the proportion of lanternfish consumed decreased over time while the proportion of krill increased. Importantly, in all but 1 individual (SE09-13) the low BC values were associated with the first period (1st – 2nd and 1st – 3rd). SE09-13 was the only seal to have a marked difference in diet between the last 2 periods of foraging (Table 2). Fig. 6 displays broad temporal changes in predicted diet over the course of the foraging season.

4. DISCUSSION

Our examination of the dietary composition and intra-annual variability of southern elephant seals that molt at the WAP (part of the South Georgia population) agrees with previous reports of the importance of lanternfish in the diet of adult females (~50% of diet; Daneri et al. 2000, Daneri & Carlini 2002, Bradshaw et al. 2003, Cherel et al. 2008, Newland et al. 2009, Bailleul et al. 2010). However, our models indi-

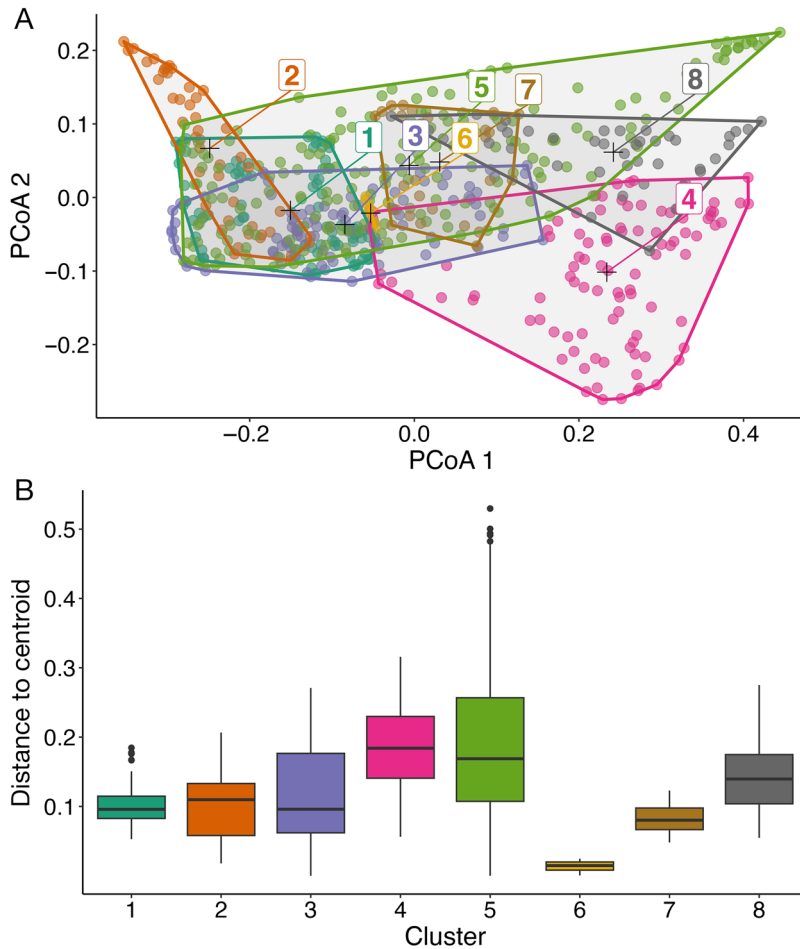


Fig. 4. Results from the multivariate homogeneity group dispersion analysis. (A) Multidimensional scaling used for visualizing dissimilarity among clusters. Color and number correspond to foraging cluster. Each individual point in the figure is for a single 1 cm vibrissa segment. (B) Distance to centroid. Boxes show first and third quartiles, medians (horizontal lines), and maximum and minimum values no greater than 1.5 times the interquartile range (whiskers). Points beyond the whiskers are outliers

cated that squid contributed only marginally to seal diet, contradicting previous studies based on scat and stomach content analyses (Daneri et al. 2000, Field et al. 2007). Scat and stomach content analyses, however, are biased toward overestimating hard parts of prey (e.g. squid beaks) and are only reflective of recently ingested prey, which are in turn often biased toward high local prey abundance. Recent studies on female northern elephant seals, combining video cameras and accelerometers, found that individuals feed primarily on myctophid fish and not squid, despite earlier evidence from stomach contents in favor of a squid-heavy diet (Yoshino et al. 2020, Adachi et al. 2021). Bailleul et al. (2010) found similar results for female (juvenile and adult) and juvenile male southern elephant seals from the Kerguelen Islands; the authors argued that squid species were

largely absent from diet based on stable isotope analysis and that seals were instead relying heavily upon mesopelagic fish. Additionally, after mathematically correcting squid beak $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to represent the whole body, $\delta^{15}\text{N}$ of the 3 species of squid were similar to, or even higher than, elephant seal $\delta^{15}\text{N}$. If squid were an important dietary source, we would expect the elephant seals included here to have considerably higher $\delta^{15}\text{N}$ due to fractionation and the tendency for a consumer to have enriched $\delta^{15}\text{N}$ relative to its diet. Thus, our results provide further support for this hypothesis, indicating that squid might represent an important opportunistic prey, but are not consistently eaten by southern elephant seals along the WAP.

Our models indicated that Antarctic krill was an important dietary component for these seals. Elephant seals are not known to be significant consumers of krill, although a previous study of southern elephant seals in the Indian sector of the Southern Ocean using stable isotope mixing models found krill to be an important dietary component of juveniles (Lübcker et al. 2017). Similarly, Walters et al. (2014) compared ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from first-year juvenile elephant seals from Macquarie Island to potential prey sources and inferred krill to be important in diet, noting that juveniles had lower

$\delta^{15}\text{N}$ compared to adults. We propose that elephant seals that forage over the continental shelf of the WAP may be an important and largely unaccounted-for consumer of krill. While unknown, it is not surprising. This is congruent with the ecological significance of krill along the WAP as a prey item supporting large populations of fish, cephalopods, birds, and marine mammal species, including pinnipeds (Lowry et al. 1988, Friedlaender et al. 2006, Trivelpiece et al. 2011, Trathan & Hill 2016, Hückstädt et al. 2020, Krause et al. 2020). Our study also provides evidence for krill-feeding by adult females, not just juveniles. However, it should be noted there is a possibility that fish consumed by seals may have already had krill in their stomachs, and that this secondary consumption could have at least partially affected our model results. Additionally, mixing models for Clusters 4 and 7 were

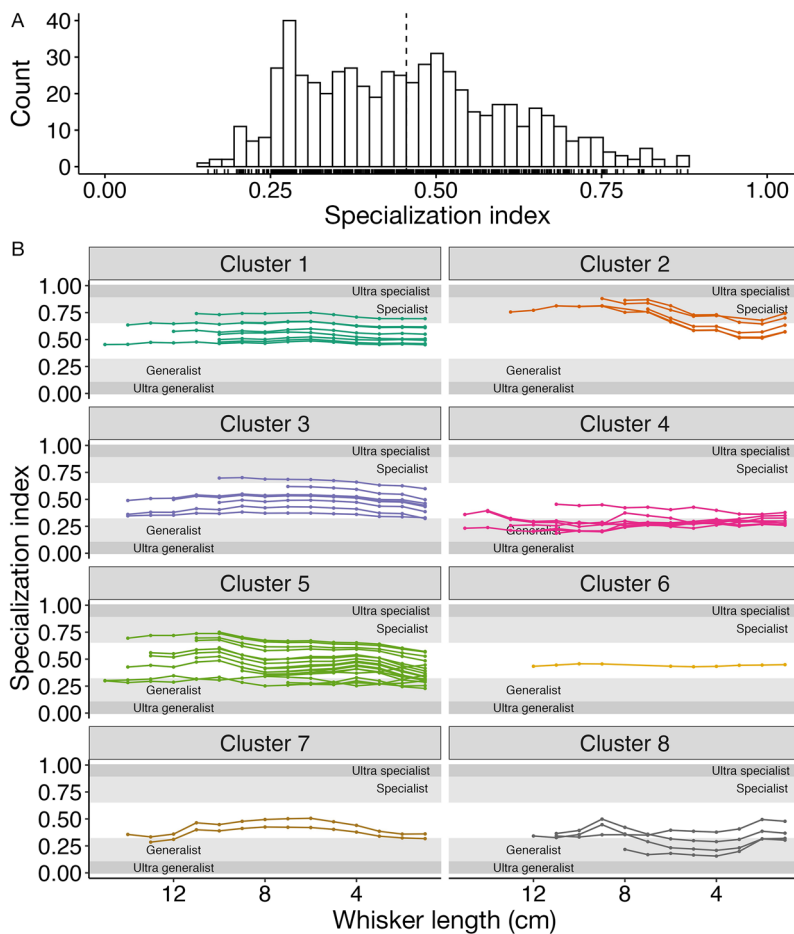


Fig. 5. Specialization index calculated for each vibrissa length for every individual elephant seal as the distance in Euclidean space between each modeled datapoint and a hypothetical consumer that eats every prey item equally. (A) Distribution of counts for every datapoint. The vertical dotted line indicates the mean value. (B) Estimated dietary specialization over time, where every line represents one individual. Note that time moves from left to right as vibrissa length decreases. Color corresponds to cluster

not able to distinguish between krill and Antarctic jonasfish as sources; nonetheless, krill were still predicted to be an important dietary source for other clusters and the strong negative correlation between the 2 sources for Clusters 4 and 7 likely does not affect our overall conclusions.

Unfortunately, we are unable to speculate as to why certain clusters varied in their dietary composition and degree of specialization. In conjunction with findings from Hückstädt et al. (2012), there do not appear to be many clear correlations between our dietary results and previously identified foraging strategies (e.g. pelagic versus shelf foragers, diving behaviors, isotopic variability). Notably, Cluster 2 was found to be the most generalist cluster from Hückstädt et al. (2012) based on variability in isotope ratios; based on our mixing model results, individuals

from Cluster 2 exhibited the most specialist foraging strategies of all included in our analyses (Fig. 5). Instead, we highlight here that mixing models and subsequent analyses support the idea that southern elephant seals that forage along the WAP vary in their diet selection and degree of individual specialization, possibly due to the need to reduce intraspecific competition (Bolnick et al. 2003, Hückstädt et al. 2012). Our results highlight the importance of considering diversity and the degree of individual plasticity in the foraging strategies of southern elephant seals and underscore the importance of taking into account individual strategies when addressing the ecological role of marine top predators in their ecosystems, instead of a 'one size fits all' approach.

Our mixing model results suggest that approximately two-thirds of elephant seals included in this study maintained a consistent diet, preferentially feeding on the same set of prey sources throughout the year (Fig. 4). However, because nearly all observed dietary shifts were found to be driven by differences in the first period of a foraging season, and because in every case the lanternfish group decreased in diet while krill increased, we believe that there is possibly a fasting signal affecting our results. This is further corroborated by a decreasing trend in $\delta^{15}\text{N}$

over vibrissae lengths (Fig. S2). If earlier periods of vibrissae growth happen on land while seals are fasting, $\delta^{15}\text{N}$ may be artificially inflated. After leaving the molt haul-out and resuming foraging, the decrease in seal $\delta^{15}\text{N}$ would explain the predicted shift from lanternfish to Antarctic krill, a lower trophic level organism. Such a fasting signal could also mean that our estimated proportion of krill in diet is conservative. Additionally, if fasting affected our results, the comparison we should focus on is between the 2nd and 3rd foraging periods, after the fasting signal disappears. In this case, all seals included in our analyses, with the notable exception of SE09-13, likely remained consistent in diet over the foraging season. This supports other studies documenting that southern elephant seals have a high level of consistency in foraging strategies. For example, 6 elephant seals included

Table 2. Bhattacharyya coefficients (BC) for the 16 elephant seals that displayed a significant dietary shift during the foraging season (BC < 0.6). All values of BC < 0.6 are in **bold**. Coefficients were calculated between each of the 3 periods of a foraging season and for the proportion of lanternfish and Antarctic krill in the diet. Trend indicates whether prey was increasing or decreasing in diet (dashes indicate no change for that prey group). Cluster indicates previously identified groups of seals from Hückstädt et al. (2012)

Individual	Cluster	Prey	1 st to 2 nd period	2 nd to 3 rd period	1 st to 3 rd period	Trend
SE05-05	2	Lanternfish	0.27	0.86	0.12	Decrease
		Antarctic krill	0.32	0.96	0.36	Increase
SE07-02	2	Lanternfish	0.73	0.61	0.24	Decrease
		Antarctic krill	0.65	0.71	0.41	Increase
SE06-04	3	Lanternfish	0.97	0.65	0.55	Decrease
		Antarctic krill	0.92	0.83	0.63	—
SE08-04	3	Lanternfish	0.99	0.72	0.69	—
		Antarctic krill	0.9	0.78	0.57	Increase
SE08-13	3	Lanternfish	0.93	0.67	0.45	Decrease
		Antarctic krill	0.9	0.76	0.48	Increase
SE09-08	3	Lanternfish	0.69	1	0.71	—
		Antarctic krill	0.75	0.91	0.55	Increase
SE07-09	5	Lanternfish	0.8	0.77	0.42	Decrease
		Antarctic krill	0.62	0.92	0.43	Increase
SE07-13	5	Lanternfish	0.7	0.77	0.36	Decrease
		Antarctic krill	0.52	0.91	0.37	Increase
SE08-11	5	Lanternfish	0.88	0.75	0.48	Decrease
		Antarctic krill	0.5	0.98	0.46	Increase
SE08-12	5	Lanternfish	0.81	0.75	0.43	Decrease
		Antarctic krill	0.59	0.95	0.47	Increase
SE09-04	5	Lanternfish	0.7	0.77	0.32	Decrease
		Antarctic krill	0.62	0.7	0.27	Increase
SE09-05	5	Lanternfish	0.73	0.82	0.39	Decrease
		Antarctic krill	0.69	0.76	0.33	Increase
SE09-07	5	Lanternfish	0.61	0.65	0.2	Decrease
		Antarctic krill	0.55	0.61	0.14	Increase
SE09-13	5	Lanternfish	0.93	0.55	0.74	Decrease
		Antarctic krill	0.89	0.96	0.98	—
SE06-02	8	Lanternfish	0.58	0.94	0.43	Decrease
		Antarctic krill	0.98	0.98	0.95	—
SE06-06	8	Lanternfish	0.84	0.79	0.49	Decrease
		Antarctic krill	0.99	0.95	0.97	—

in this data set were resampled a year after initial sampling, and all but 1 had similar ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between years (Hückstädt et al. 2012). Additionally, female southern elephant seals tagged on Macquarie Island displayed strong site fidelity between years while foraging in the Pacific sector of the Southern Ocean (Bradshaw et al. 2004), and similar findings of foraging consistency have also been reported in other species of pinnipeds globally. These include gray seals *Halichoerus grypus* showing individual consistency in vibrissae stable isotope ratios, Australian sea lions *Neophoca cinerea* displaying consistency in foraging locations and trophic position of prey consumed, leopard seals *Hydrurga leptonyx* predictably switching from a diet dominated by krill and fish during the spring to a more energy-dense and mammal-dominated diet after arrival to a fur seal colony in the summer, and northern elephant seals showing site

fidelity to foraging locations and migratory corridors, among others (Simmons 2008, Lowther et al. 2011, Hernandez et al. 2019, Krause et al. 2020). Foraging site fidelity and employing consistent foraging strategies likely result in significant fitness payoffs, though changing environmental conditions may have adverse effects (Abrahms et al. 2018).

Specialization at the individual level and consistently choosing among a subset of preferred prey likely increases foraging success and efficiency for individuals, while at the same time reducing intraspecific competition (Bolnick et al. 2003, McHuron et al. 2018, Carneiro et al. 2017). However, in contrast to our mixing model results, a previous study investigating the diet of southern elephant seals using fatty acid analysis mixing models found that individuals from Macquarie Island exhibited temporal shifts in prey selection (Bradshaw et al. 2003). Yet, it should be

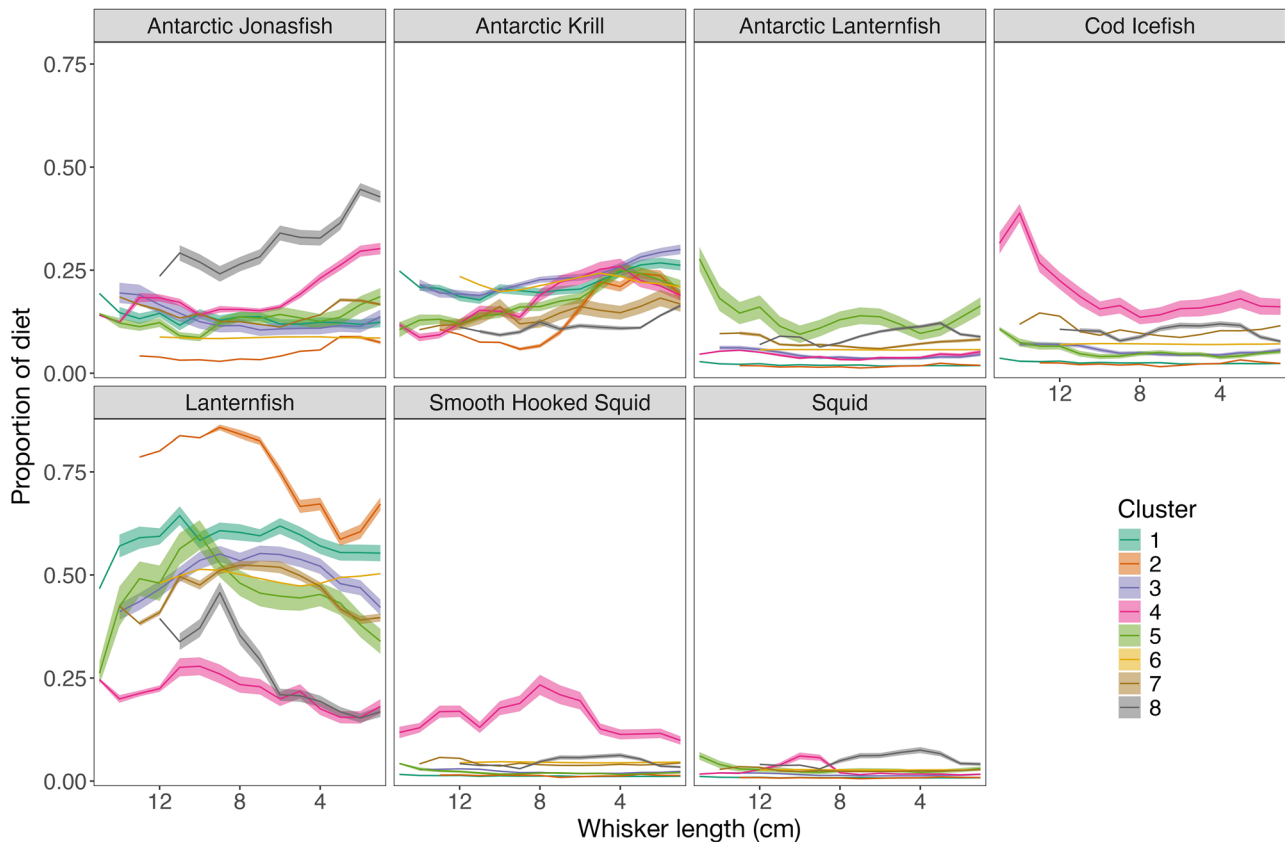


Fig. 6. Mean \pm SD of dietary composition of elephant seals over time, based on individual 1 cm vibrissae lengths. Note that time moves from left to right. Color corresponds to cluster

noted that the seals from Macquarie Island forage in open waters of the Southern Ocean (unlike seals in this study, which largely forage on waters over the continental shelf) and have experienced a population decline in recent decades, making it likely that those seals have been affected by additional stressors such as changing environmental conditions and competition for resources (McMahon et al. 2005, Hindell et al. 2017, Volzke et al. 2021). Additionally, time scales covered by repeat sampling of blubber in consecutive seasons (from Bradshaw et al. 2003) versus vibrissae are much different, and fatty acid analysis has higher resolution for prey selection than stable isotope analysis. Nonetheless, our study provides evidence that southern elephant seals from this population are consistent in their prey selection over a foraging migration in the Southern Ocean.

Using mixing models to elucidate the dietary contributions of prey for an obscure predator such as southern elephant seals in the Southern Ocean comes with some limitations. The fish and cephalopod community of the Southern Ocean is diverse, and only a handful of potential prey species for southern elephant seals could be included here

(Griffiths 2010). The prey species included in our models were limited to published values from potential prey that were collected in the same approximate locations (WAP and surrounding subantarctic islands) and approximate time frame as the seal samples (2005–2009). Stable isotope ratios vary over space and time in the marine ecosystem. Therefore, controlling for this variability in consumer and source $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ is essential. Several studies have shown some degree of spatial and temporal variability in isoscapes of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the Southern Ocean and specifically the WAP (Brault et al. 2018, Seyboth et al. 2018, Walters et al. 2020, St John Glew et al. 2021). However, given the large migratory range of adult female elephant seals included here, as well as limitations in the availability of prey data, we are unable to more precisely match consumer and prey data in space and time and must assume isotopic homogeneity for our analyses. Lastly, any segments of vibrissae grown during the prolonged fasting on land would be enriched in ^{15}N (Hückstädt et al. 2012); due to uncertainties regarding vibrissae growth timelines, we included all but the most basal segment of each vibrissa, which was

removed from analyses due to having a higher lipid content than the rest of the segments.

We provide additional support for the importance of myctophid fish in the diet of adult female southern elephant seals from the South Georgia population, as well as the importance of Antarctic krill. In addition, we identified at least some dietary variability between seals from previously identified foraging clusters. Finally, our models show a substantial degree of individual dietary consistency throughout a foraging migration, where elephant seals likely remain faithful to their dietary preferences. Yet, given that the WAP region is one of the most rapidly warming areas of the ocean (Ducklow et al. 2013), foraging flexibility may be assumed to be ecologically beneficial. These findings thus have important management implications for southern elephant seals in a rapidly changing Southern Ocean and underscore the importance of krill management along the WAP as an important strategy for yet another krill consumer.

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