Extreme dietary specialisation in adult male southern elephant seals: determining variation between individual trophic diets

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ABSTRACT: Although dietary studies have provided important insights into the causes and ramifications of diet variation for the southern elephant seal (SES) (*Mirounga leonina*), adult males are comparatively underrepresented within that literature. Individual males can vary morphologically as well as behaviourally, leading to differences in their life history trajectories and outcomes. Therefore, to improve our understanding of the male diet, we sought to determine the degree of dietary variation between as well as within individuals from the West Antarctic Peninsula. Secondly, we investigated whether individual morphological traits, seasonality, and year influenced their dietary variation. Whiskers were sampled from 31 adult male seals and used to measure the bulk stable isotope nitrogen (δ^{15}N). We sequentially segmented each whisker to create a time series of datapoints for each individual, allowing us to compare δ^{15}N variation within each seal as well as assess variation between the seals. We then investigated the relationships between male dietary variation and body length, girth, season, and year. We found that adult male SESs maintained an extremely specialised diet. Variation between individuals was strongly correlated with their body size, with larger seals feeding higher up the trophic web. Interestingly, seasonality and year both influenced variation within the seals' diets, but only year was seen to influence the variability between seals. We discuss the possible causes and ramifications of dietary specialisation for the SES and highlight the need for combined tracking and stable isotope investigations to improve our understanding of the ontogeny of the seals' dietary specialisation.

KEY WORDS: Marine mammal · Diet specialisation · Individual variation · Sex-specific variation · West Antarctic Peninsula · Nitrogen · Stable isotope analysis · Southern Ocean

1. INTRODUCTION

Variation in the diets of individuals can influence their life history, survivability, and reproductive success. This kind of individual-level variation can lead to shifts in a population's structure and distribution as well as impact their evolutionary fitness and adaptive capacity (Bolnick et al. 2003). Diet is influenced by ecological, physiological, and environmental drivers. For instance, factors such as age and sex

are known to impact the intra- and inter-individual variation in population diet, but other variables such as breeding stage, resource competition, or seasonal fluctuations can result in dietary variation between individuals of the same age and sex (Bolnick et al. 2003, Rossman et al. 2015, Knox et al. 2019). Dietary differences can alter an individual's exposure to pathogens (Johnson et al. 2009), predation risk (Beltran et al. 2021), and competition pressures (Araújo et al. 2008), all of which can affect the longevity and survivability of the individual. Therefore, it is important to understand the degree of dietary variation among individuals of a population and determine its influence on population ecology.

From terrestrial to aquatic and marine environments, individual dietary specialisation (IDS) is found across a broad range of species and is influenced by individual-level physiological, behavioural, and environmental differences (Bolnick et al. 2003, Franco-Trecu et al. 2014, Robertson et al. 2014, Jordaan et al. 2019, Herath et al. 2021). It indicates how unique an individual's diet is in relation to the rest of the population, and as variation in diet can influence population ecology (Bolnick et al. 2003), it can be used to understand which individuals within the population may be vulnerable to current or predicted changes within their ecosystem (Johnson et al. 2009). IDS is defined as the ratio of between-individual component (BIC) and within-individual component (WIC) compared to the total diet of the studied population (also known as total niche width) (Roughgarden 1972, Bolnick et al. 2002). IDS is commonly applied in ecological research as a measure of similarity or difference between groups or individuals of a given population. Data is often pooled and used to highlight dietary differences between age and sex groups within or between populations (Bolnick et al. 2003, Newsome et al. 2009, Hückstädt et al. 2012b, de Lima et al. 2019, Lewis et al. 2022). Unfortunately, not many of these studies have examined whether there are differences between individuals within those sub-groupings, likely because the impact of the variation is hard to tease apart, and sample size is often relatively small when working with wild or remote species. Dietary variation, though, is seen between individuals of the same age and sex and has provided interesting insights into the ramifications of diet on factors such as differences in reproductive success (Balme et al. 2020).

Studies using individual-level data have provided valuable insights into the diet variability between southern elephant seal (SES) age and sex cohorts (Gallon et al. 2018). Chaigne et al. (2013) found that although both sexes have similar diets as weanlings

and juveniles, as males age they continue to expand their feeding habits, whereas females do not. Hückstädt et al. (2012b) continued to further our understanding of the importance of dietary differences in SESs by looking at the degree of specialisation within adult females. Hückstädt et al. (2012b) found that females were a population of specialists, feeding at different trophic levels from one another even though they were of a similar age and from the same colony. Comparatively, adult males are underrepresented in these kinds of dietary studies, including those based on traditional stomach or scat analysis methods (Green & Burton 1993, Daneri et al. 2015). While adult male SES dietary specialisation has not been explicitly tested, Lewis et al. (2006) did report substantial variation both within as well as between individual male nitrogen stable isotope (δ^{15}N) values. Intriguingly, this variability in nitrogen levels was not related to male age and size, and Lewis et al. (2006) theorised that males were likely specialising and that something other than age was leading to this dietary variability.

The relatively limited dietary information available for adult male SESs from Isla 25 de Mayo/King George Island comes from the examination of food remains obtained by stomach flushing techniques (Daneri et al. 2015). Cephalopod prey was mainly represented by the teuthids *Psychroteuthis glacialis* and *Moroteuthopsis* (formerly *Kondakovia*) *longimana* and octopodids of the genera *Pareledone* and *Adelieledone*, whereas the fish diet included mainly the myctophid *Gymnoscopelus nicholsi* and, in minor proportions, the nototheniids *Gobionotothen gibberifrons* and *Pleuragramma antarctica* (Daneri et al. 2015). Adult male SESs are significantly larger than adult females, often migrating to and utilising different foraging zones as well as feeding on different prey compared to females (Tosh et al. 2009, Daneri et al. 2015, Gallon et al. 2018, Campagna et al. 2021). However, a greater emphasis needs to be placed on developing our understanding of individual male diet, as variation in movement and behaviour between individual males during their foraging phases may also lead to differences in diet. Individual males from the same colony are known to migrate across large distances and to different feeding grounds (Campagna et al. 1999, Tosh et al. 2009, Zhang et al. 2016, Hindell et al. 2020), which could result in different energetic demands for individuals during this time. Across the Southern Ocean, significant variation in resource productivity is closely tied to oceanographic features which can influence the type, quality, and abundance of prey available (Ichii et al. 2020). Along with this,

SESs exhibit strong inter-annual foraging site fidelity, returning each year to the same grounds to feed (Rita et al. 2017) and display area-restricted search behaviours while foraging (Hindell et al. 2016, Campagna et al. 2021, Arce et al. 2022). While both of these behaviours are fairly common, together they may increase an individual's familiarity with not only their foraging site but also the movements of their prey, leading to an improved capacity to exploit a preferred food resource and thereby increasing the potential for specialisation.

Individual males' diets and the degree of variation within and among them may also differ based on the individual's boldness or personality. Preliminary work by Allegue et al. (2022) found that bolder SES individuals were selecting different foraging habitats, and while personality was not assessed for SESs, Herath et al. (2021) showed that dietary breadth and quality were related to personality in the common brushtail possum *Trichosurus vulpecula*.

Along with these behavioural variables, morphological differences are also known to influence adult male SESs. Males are heavily reliant on their body length and mass to support their breeding and recovery efforts. Male body size plays an important role during the breeding season, with larger males more likely to out-compete smaller males during the highly competitive period (McCann 1981, Modig 1996). The breeding season lasts 2–3 mo, in which males continually fast and can lose up to 52 % of their body mass (Galimberti et al. 2007). In the following months, males feed to recover their losses and prepare for the following breeding season, but any variation between or even within those individuals' diets could result in differing recovery results. Therefore, in order for us to understand how or if diet influences individual male life history, we first need to develop an understanding of the baseline differences between individual diets and determine what factors could be influencing any variation between as well as within those individuals' diets.

To develop this baseline for the male SES, we utilised $\delta^{15}N$ stable isotope analysis (SIA). Nitrogen SIA can be performed on a variety of different biological materials (e.g. blood, skin, bone, dentine, keratin) and is used as a proxy for diet, which is particularly beneficial when direct observation of what the individual is consuming is not feasible (often the case for marine mammals) (Kernaléguen et al. 2015, Lübcker et al. 2016, Botta et al. 2018, Walters et al. 2020, Botha et al. 2023). As multiple tissues can be used to extract dietary information, it is a versatile method that has been well reported throughout the literature for many species (Hobson et al. 1996, Newsome et al. 2010). In particular, whiskers provide a relatively stable, keratinous matrix that allows for time-series modelling to increase the length of time in which dietary information can be extracted (Rogers et al. 2016). Therefore, through the use of nitrogen SIA, this study determines the level of dietary specialisation of adult male SESs, along with developing an understanding of the degree of dietary variation within and between the individuals' diets. By increasing our baseline knowledge of dietary variation between and within males, and by exploring key factors that could impact this variability, we can bring our understanding of male diets closer in line with that of female SESs. In doing so, we hope to create a clearer foundation, which will allow adult male SESs to be incorporated in greater depth into SES population ecology and behavioural studies in the future.

2. MATERIALS AND METHODS

Adult male SESs (n = 31) from Isla 25 de Mayo/King George Island, West Antarctic Peninsula (WAP; 62.2336° S, 58.6987° W) were sampled during the breeding season (October and November) in 2006 (n = 7), 2007 (n = 11), and 2013 (n = 13). Individuals were identified through the ongoing tagging program conducted on the population by the Argentinian Antarctic Division.

2.1. Approvals and permits

Fieldwork in 2006 and 2007 was conducted in accordance with Taronga Zoo Animal Care and Ethics protocol (ACEC approval number 4a/04/06) and permits approved by the Dirección Nacional del Antártico in accordance with the Scientific Committee on Antarctic Research (SCAR) Code of Conduct for Animal Experiments and terms of Annex II of the Protocol on Environmental Protection to the Antarctic Treaty. Fieldwork in 2006 and 2007 was conducted under the Antarctic Seals Conservation Regulations permit number 06-07-2810 to T. L. Rogers. Fieldwork in 2013 was conducted in accordance with the SCAR Code of Conduct for Animal Experiments and the provisions of Article 3 and Annex II of the Protocol on Environmental Protection to the Antarctic Treaty, the Convention for the Conservation of Antarctic Seals to H. Bornemann.

Access to the Antarctic Specially Protected Area No. 132 (former SSSI-13), Potter Peninsula, Isla 25 de

Mayo/King George Island, South Shetland Islands, was approved by the Dirección Nacional del Antártico, Buenos Aires, Argentina (Toma, Intromisión Perjudicial e Introducción de Especies), PERMISO (Segun Art 3, Anexo II del Protocolo de Madrid, Ley 24.216), and PERMISO (Según Art 7, Anexo V del Protocolo de Madrid, Ley 25.260).

Permits to export seal whiskers via Germany to Australia were granted under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and permits issued by the German Federal Agency for Nature Conservation (BfN, permit nos. IFS00001/16 and W-05115/16) to H. Bornemann The permits issued by the Australian Government Department of Environment and Heritage Environment Protection and Biodiversity Act 1999 were under numbers PWS P700022 and 2007-AU-471237 to T. L. Rogers.

2.2. Sample collection

Seals were lightly sedated using 1.3 mg kg^{-1} zolazepam:tiletamine (Zoletil® 100, Virbac), administered intramuscularly (Higgins et al. 2002, Carlini et al. 2009, Bornemann et al. 2013).

For each seal, the longest whisker was plucked (intradermal section included) from the posterior row. Morphological information was collected with standard length measured as a straight line from the tip of the nose to the end of the tail while the seal lay ventrally and at full extension, and girth was measured dorsally from the posterior crease of the pectoral flipper across the body to the opposite corresponding location (Bell et al. 1997). Immobilisation dose rates including the length and girth of the 2013 collection are available at https://doi.pangaea.de/10.1594/PANGAEA.833216.

2.3. Whisker modelling

Total whisker length was obtained by stretching each whisker straight and taking the measurement to the nearest 0.5 mm. To remove contaminants and lipids, individual whiskers were then cleaned using an ultrasonic bath; initially with 150 ml of ultrapure water for 20 min, then in 150 ml of 2:1 chloroform: methanol solution for a further 20 min (Lewis et al. 2006). All whiskers were dried for 24 h after the final bath.

To account for the non-linear growth of the SES whiskers (Lübcker et al. 2016), we applied a modified discrete von Bertalanffy growth equation developed in Hall-Aspland et al. (2005) and Rogers et al. (2016). The equation calculates the non-linear growth of the whisker over time from the distal (oldest growth point) to the proximal end (newest growth point) (see Text S1 in the Supplement at www.int-res.com/articles/suppl/m725p185_supp.pdf for equation details). From this, we modelled a series of time points that were relative to the length of the whisker. Using these time points, a growth model was generated, and individual whiskers were sectioned, with each section representing approximately 8 ± 1 d to ensure temporal independence between each sampling point along the whisker.

Analysis was run on a subsection of each whisker segment. The subsection was taken from the leading edge of each segment (closest to the face of the seal). The remaining fragment of that segment was used as a 'buffer' to ensure substantial time was left between each point used in our analysis. As fasting can influence the nitrogen values (Lübcker et al. 2020), datapoints from October and November were removed to ensure samples were representing the males' foraging period. The analysed subsections were each weighed (0.35 ± 0.08 mg) and enclosed in a tin capsule (Thermo Scientific 25208000 tin capsules 10 × 10 mm, catalogue number 36-102-5620).

The whisker samples were combusted in an elemental analyser (Flash 200 Organic Elemental Analyser, Thermo Scientific), where δ^{15}N and carbon stable isotope (δ^{13}C) values were determined using a continuous flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific) at the Bioanalytical Mass Spectrometry Facility, University of New South Wales (UNSW) Sydney, Australia. Results are presented using standard delta notation in parts per thousand (‰). δ^{15}N and δ^{13}C values were corrected to atmospheric N_2 (air) and Vienna Pee Dee Belemnite (VPDB), respectively (Bond & Hobson 2012). International reference standards USGS40 (δ^{15}N$_{AIR}$ = −4.52 ± 0.06‰; δ^{13}C$_{VPDB-LSVEC}$ = −26.39 ± 0.04‰) and USGS41a (δ^{15}N$_{AIR}$ = 47.55 ± 0.15‰; δ^{13}C$_{VPDB-LSVEC}$ = 36.55 ± 0.08‰) (Qi et al. 2003, 2016) were used to correct instrumental drift and measurement errors. The ratio of carbon:nitrogen (C:N) values for the whisker segments ranged from 2.82 to 3.77 (n = 322, mean ± SD: 3.2 ± 0.09). The theoretical C:N ratio for keratin is 3.4, with an acceptable range between 2.9 and 3.8 having been developed on human hair (O'Connell & Hedges 1999). Therefore, to reduce contamination or analysis bias, values that fell outside the recommended range were removed (n = 318, 3.2 ± 0.08; Fig. S1).

2.4. Statistical modelling

All statistics were performed in R version 4.0.1 (2020-06-06).

To assess the response of nitrogen to our explanatory variables, we used a generalised additive model of location scale and shape (GAMLSS) (Rigby & Stasinopoulos 2005). To estimate the mean and variance of $\delta^{15}N$ values as a function of explanatory variables, a log-normal response family for both the mean and variance of $\delta^{15}N$ was used (Stasinopoulos et al. 2018). This approach allowed us to investigate not only the relationship between mean $\delta^{15}N$ and our explanatory variables but also the relationship between specialisation (variability of $\delta^{15}N$) and our explanatory variables. For both the mean and variance formula, explanatory variables included standard length and girth, which were log transformed to normalise their values, as well as year and a random effect for seal ID. Results are reported with estimate (estimate), standard error (SE), and p-value (p).

Seasonality, which is where the average $\delta^{15}N$ or variability of $\delta^{15}N$ has periodicity, was also accounted for in both the mean and variance models with the inclusion of cyclical terms $\sin(2\pi date/365)$, and $\cos(2\pi date/365)$ (Stolwijk et al. 1999). An exponential correlation structure (using 'corExp' from 'nlme') on the residuals accounted for temporal autocorrelation (Texts S2 & S3). The model and our measured datapoints were temporally aligned using date stamps generated from the modified discrete von Bertalanffy growth equation above.

Model assumptions were checked using a wormplot (a de-trended QQ-plot of the normalized quantile residuals, recommended when using the GAMLSS) (van Buuren & Fredriks 2001). The elliptical curve indicates the point-wise confidence bands of 95%.

2.5. Specialisation

We calculated the specialisation ratio of individuals by comparing the WIC in log-$\delta^{15}N$ with the population variation in log-$\delta^{15}N$, where the population was defined to be those seals observed in the same year ($n_{2006} = 7$, $n_{2007} = 11$, $n_{2013} = 13$). We calculated the average and confidence interval of the specialisation ratio across the whole population. We estimated the individual seal variation in log-$\delta^{15}N$ by refitting the GAMLSS model. Seal ID remained a fixed effect in the variance formula, and the explanatory variables

of girth, standard length, and seasonality were omitted from the variance formula. The seal-level intercepts in the variance model characterise the variability per seal.

We estimated the population-level variation per year by calculating a weighted variance of all nitrogen values, with weights inversely proportional to the number of observations per seal in that year. As some individuals had more datapoints than others due to variation in whisker length, we used a weighted variance so that each seal is considered an equal member of the population. Based on the specialisation index outlined in Bolnick et al. (2003) and Hückstädt et al. (2012b), we categorised individuals as extreme specialists when their specialisation ratio was <0.2; specialists if they fall between 0.2 and 0.5; and generalists if their ratio was >0.5. Once the specialisation ratio was calculated, we then regressed this ratio against standard length, girth, and seasonality to assess if they had any association with specialisation.

3. RESULTS

Adult male SES $\delta^{15}N$ values ranged from 10.2 to 17.3‰ and $\delta^{13}C$ ranged from −23.7 to −18.2‰ (Fig. 1, Table S1). Males ranged from 3.8 to 4.8 m in length and 2.95 to 4.25 m in girth. Time represented by the whiskers was 112 ± 25 d from June to October within their respective sampled years (Figs. S2 & S3).

3.1. Inter-individual variation in nitrogen

There was a strong positive correlation between male variation in $\delta^{15}N$ and their body size. Variation between male $\delta^{15}N$ corresponded with differences in their standard length (GAMLSS: estimate: 0.614, SE: 0.046, p < 0.01; Fig. 2A) and girth (GAMLSS: estimate: 0.395, SE: 0.024, p < 0.01; Fig. 2B) (Tables S2 & S3), with longer and wider males having a higher $\delta^{15}N$.

Year also influenced variability between the individual male $\delta^{15}N$ values. On average, there was less variation between individual male seals in 2006 (n = 7) than in 2007 (GAMLSS 2007: estimate: 0.028, SE: 0.006, p < 0.01, n = 11) and 2013 (GAMLSS 2013: estimate: 0.051, SE: 0.006, p < 0.01, n = 13). There was no significant difference between $\delta^{15}N$ values in 2007 and 2013. Season had no influence on mean $\delta^{15}N$ values between males.
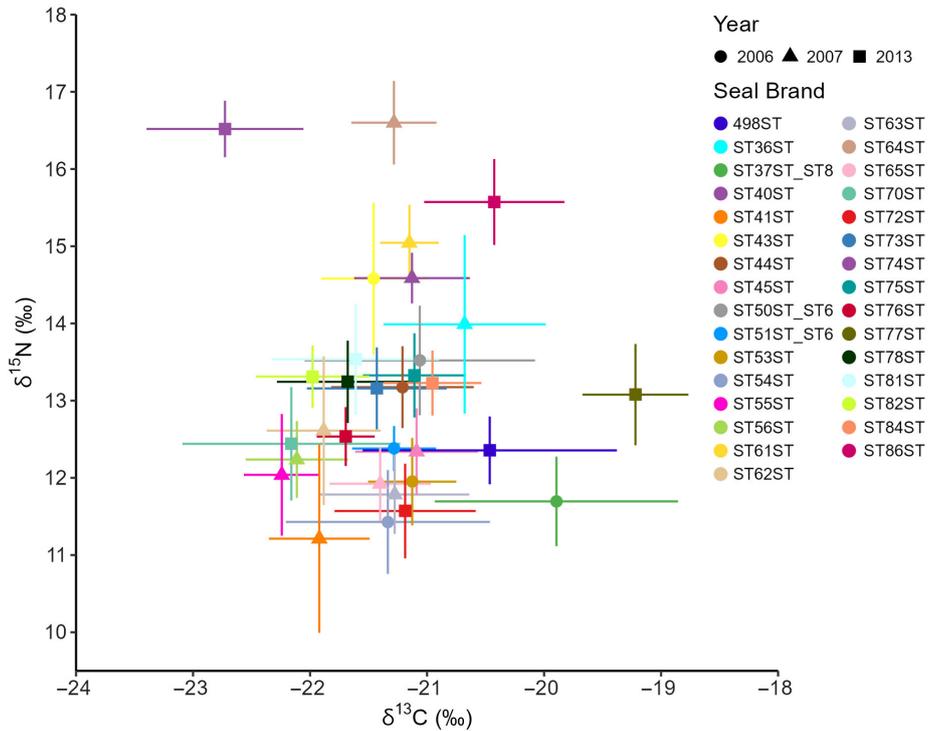
Fig. 1. Stable isotope biplot indicating the mean (points) ± SD (whiskers) of $\delta^{13}C$ and $\delta^{15}N$ values of the adult male southern elephant seal. Shapes: sampled year groups; colour: individual seals
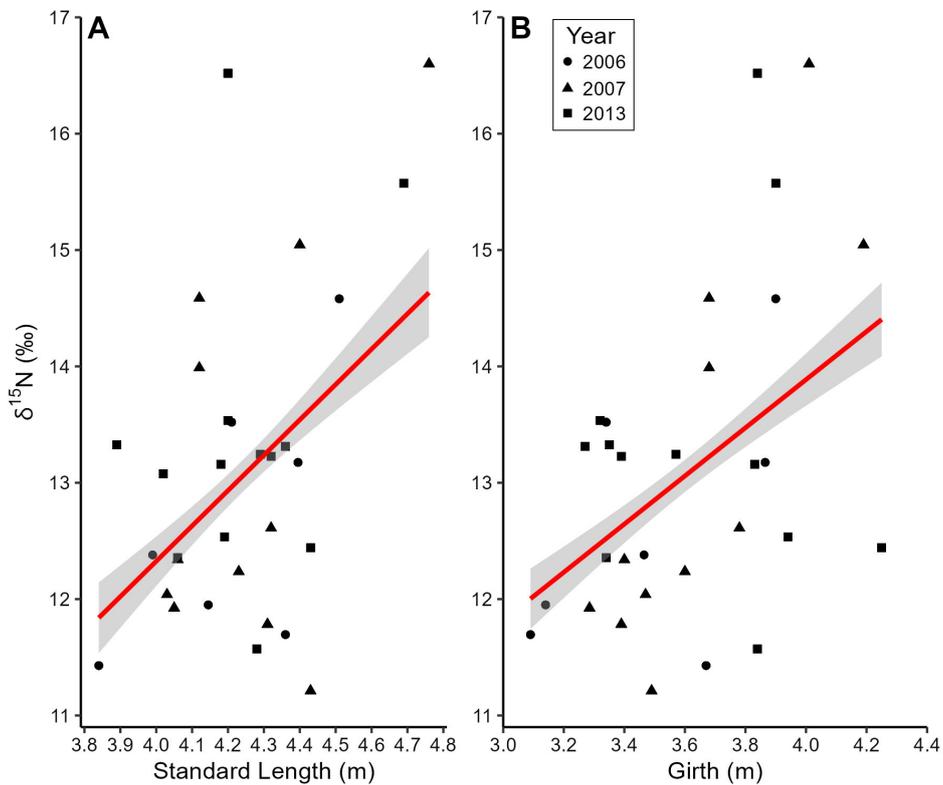

Fig. 2. Adult male southern elephant seal nitrogen stable isotope analysis values: positive correlation between the mean $\delta^{15}N$ values in response to individual seals' (A) standard length (n = 31; GAMLSS: estimate: 0.614, SE: 0.046, p < 0.01) and (B) girth (n = 31, GAMLSS: estimate: 0.395, SE: 0.024, p < 0.01). Grey shading: 95% confidence interval
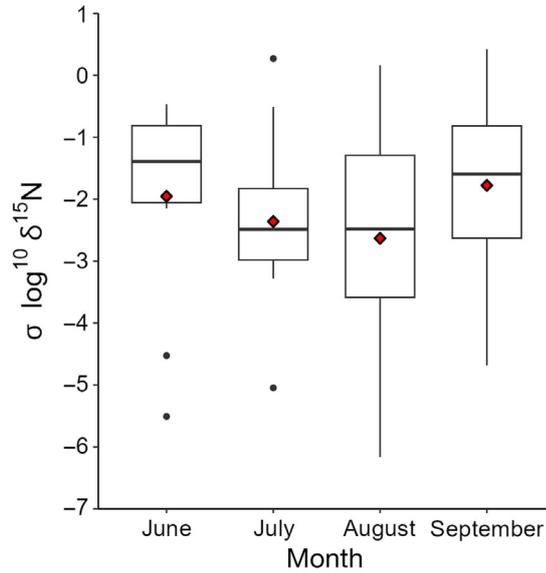
Fig. 3. Variation within male southern elephant seal nitrogen across the months leading into breeding season. Greater variation within the seals' $\delta^{15}N$ values was seen in June (n = 13) and September (n = 31) compared to samples from July (n =19) and August (n =31). Bold horizontal line: median $\delta^{15}N$ for each month; box: interquartile range (IQR), with the upper and lower quartiles marked by the box's edge; whiskers: minimum and maximum non-outlier data points within 1.5 times the IQR from the edges of the box; individual points beyond the whiskers: outliers; red diamonds: mean within-individual variation each month

3.2. Intra-individual variation in nitrogen

Seals had more variation within their diets in June (n = 13) and September (n = 31) compared to July (n = 19) and August (n = 31) (Fig. 3), with the seasonality terms sin (GAMLSS: estimate: 1.528, SE: 0.263, p < 0.01) and cos (GAMLSS: estimate: 1.468, SE: 0.251, p < 0.01) showing a strong positive correlation between the intra-individual variation in $\delta^{15}N$ values.

Comparing the WIC between the years, individuals sampled in 2013 (GAMLSS: estimate: −0.392, SE: 0.108, p < 0.01; Fig. 4) had less variability in their $\delta^{15}N$ values compared to the 2006–2007 cohorts. There was also no relationship between the seals' within-individual $\delta^{15}N$ values and their standard length or girth.

3.3. Individual specialisation

Most adult male SESs were extreme specialists (65 %: 20 of 31 individuals), feeding on less than 20 % of their population's $\delta^{15}N$ range. Of the remaining 11 individuals, 10 were specialists (32 %) and 1 fed more broadly as a generalist (3 %) (Fig. 2). The overall specialisation ratio average was 0.18, with a confidence interval for the total population (n = 31) of 0.135–0.233.
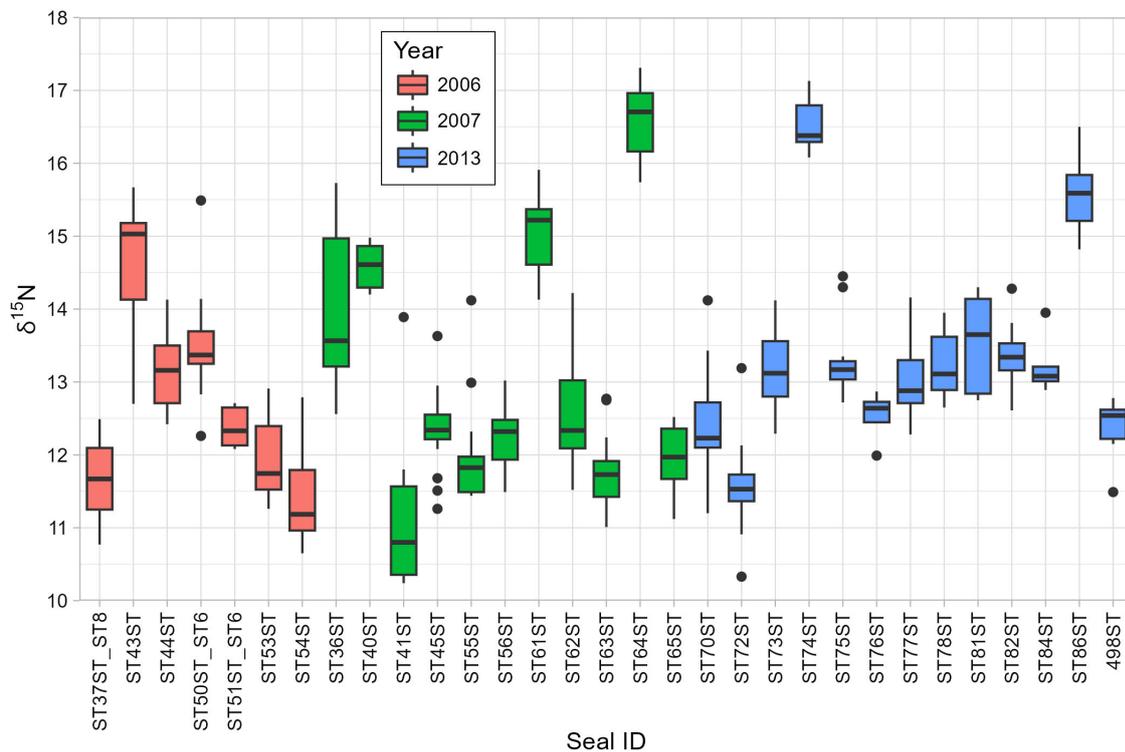

Fig. 4. Individual seal $\delta^{15}N$ variation. Greater variation within the seals' $\delta^{15}N$ values was seen in 2006 (n = 7) and 2007 (n = 11) compared to seals sampled in 2013 (n = 13) who showed less variation within their diets. Boxplot parameters as in Fig. 3
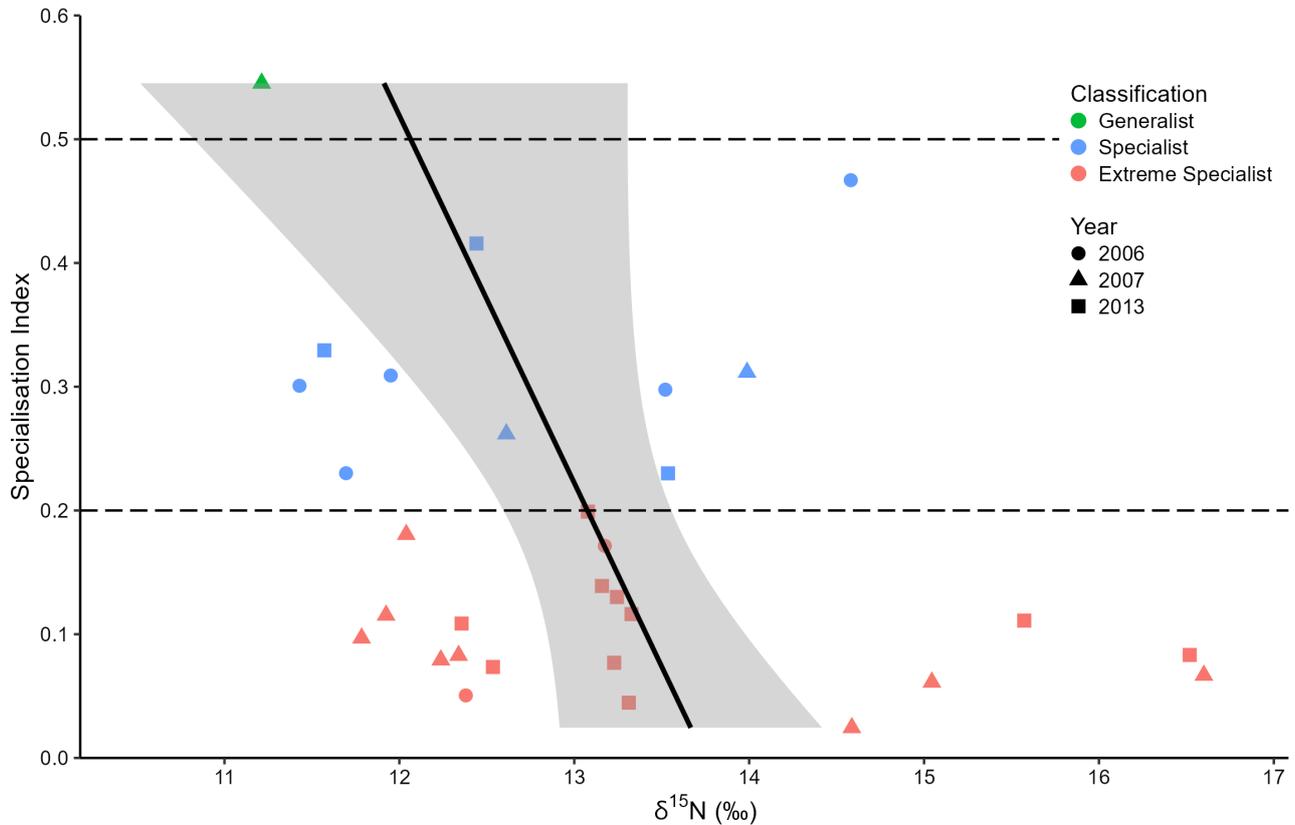
Fig. 5. Male southern elephant seal individual dietary specialisation values. There is a negative linear relationship between specialisation and mean $\delta^{15}N$ value (GLM: estimate: −0.726, SE: 0.281, p = 0.016) for adult male southern elephant seals ($n_{individual}$ = 31). Horizontal dashed lines delineate the categories of extreme specialist (n = 20; 65%), specialist (n = 10; 32%), and generalist (n = 1; 3%). Grey shading: 95% confidence interval (0.135–0.233). Shapes represent the year the individual was sampled

The generalised linear model identified that $\delta^{15}N$ was the only variable correlated with specialisation. Therefore, a higher $\delta^{15}N$ was associated with a lower specialisation ratio, which corresponds to greater individual specialisation (GLM: estimate: −0.673, SE: 0.256, p = 0.014; Fig. 5, Table S4). Standard length and girth did not have a significant relationship with specialisation.

4. DISCUSSION

Here, we have shown that adult male SES diet varies significantly between individuals. The variation in $\delta^{15}N$ was correlated with the seals' body size, with larger and longer males feeding at a higher trophic level than smaller individuals. We also found that dietary variation was occurring within the individuals' diets over time. This variation did not follow any detectable trend, with some seals having more dietary variation in spring while other seals had more variation in their winter diet. Based on this individual-level data, we were able to determine that adult

male SESs maintain extremely specialised diets, whereby individuals, regardless of their body size, feed on a narrow subsection of the population's total possible trophic diet. These results improve our understanding of the individual-level diet of adult male SESs and the factors that may be contributing to this variability.

4.1. Male inter-individual variation

The $\delta^{15}N$ values varied between males based on their body size. We found that larger male seals were feeding at a higher nitrogen level than smaller conspecifics. Within certain ecosystems or even consumer groups, a higher nitrogen value can be indicative of a higher trophic position, and for the marine system, larger prey items are generally higher up in the trophic food web (Cherel et al. 2010, Potapov et al. 2019). These larger, higher-trophic prey items can provide more energy per successful feed, but they are often more energetically costly to capture, handle, and digest (Meyers et al. 2021).

Although extremely large marine mammals (e.g. baleen whales over 11 000 kg) consume very small prey such as krill, copepods, or small fish (Tucker & Rogers 2014), for many marine species including seals, as their body size increases so too does the body size of their optimal prey (Bowen et al. 2002, Brose et al. 2006, Tucker & Rogers 2014). This has previously been shown by Slip (1995), who found that while squid species such as the *Gonatus antarcticus* were consumed by SESs of all age classes, smaller, often juvenile seals ate smaller prey, and by Daneri et al. (2015), who found a positive relationship between the size of the seal and its prey (the Antarctic glacial squid *Psychroteuthis glacialis*). Here, it may be that for smaller seals, the greater energetic output required to capture and process larger prey may not confer the same advantage it does for larger seals, making it a less beneficial option (Dalponti et al. 2018). Gape size can also be a limiting factor for marine mammals such as seals, as it can dictate the size and type of prey that they can capture and handle. Two common feeding strategies that seals have been recorded using are suction feeding, whereby they swallow their prey whole, and pierce feeding, in which they use their teeth to secure prey (Kienle & Berta 2016, Kienle et al. 2020). Based on their cranial and mandibular structure, the SESs likely use the suction method to capture prey (Kienle & Berta 2016), and although this feeding method is thought to be more energetically efficient, there may be a prey-size point at which they switch feeding techniques (Kienle & Berta 2016). Kienle et al. (2020) found that when prey length was greater than 80% of the Hawaiian monk seals' head length, it would switch from suction feeding to pierce feeding, as it was a faster feeding strategy but was only used on small to medium size prey. Our larger SESs could either be specialised foragers, using the piercing method and pursuing larger prey more frequently than their smaller counterparts, or larger males may be innately more capable of foraging on proportionally larger prey items using suction feeding, or a mixed technique, which may be leading to their higher average nitrogen values.

The Southern Ocean has a diverse and abundant selection of protein-rich prey spread both vertically and horizontally. Larger body size can provide a greater swimming and diving advantage for air-breathing marine mammals, which may be another factor influencing why we found that larger seals are consuming higher nitrogen prey. Vertical prey assemblage (prey type and prey size) varies based on light, temperature, and predation risk, and therefore can influence the dive behaviours of predators (Plötz et al. 2002, Watanabe et al. 2003, Guinet et al. 2014, Ichii et al. 2020). Larger prey species have been shown to avoid predation by remaining deeper in the water column (Ichii et al. 2020). Larger seals are capable of performing deeper or longer dives without exceeding their aerobic limit, due to their greater oxygen-storing capacity (Halsey et al. 2006b, Hayward et al. 2016). And while Lasch et al. (2023) found that the largest male SESs from Marion Island were diving deeper and for longer periods at a time, even if larger seals do not dive deeper (McIntyre et al. 2012), their larger oxygen stores allow those individuals to find and remain at the optimum foraging depth for longer bouts (Halsey et al. 2006a). Although longer and deeper dives often require greater recovery time at the surface (Boyd & Croxall 1996), extending search and capture time within a productive prey patch may increase their probability of encountering higher-value prey items (Weise & Costa 2007). It may also be used as a way to reduce inter- or intra-specific resource competition, as Weise et al. (2010) found that larger male Californian sea lions undertook longer dives and exploited deeper waters compared to smaller conspecifics, likely in order to either reduce competition or increase their foraging profitability. Interestingly, within the Potter Peninsula colony, resource competition may be increasing. Negrete et al. (2022) identified that between 2008 and 2018, female numbers increased by 64.5% at a rate of 5% yr^{-1}; the authors hypothesised that these fluctuations in population density may be in response to changes in the inter-annual winter sea ice extent, whereby in years of low sea ice, more ice-free beaches are accessible and females may not be returning to their natal breeding beaches. Instead, they are remaining closer to and breeding near their more southerly foraging areas, which may be increasing resource competition in the region. This is concerning, as the accelerated warming occurring across the WAP could also impact key SES prey species such as the Antarctic silverfish *Pleuragramma antarctica*, whose recruitment and abundance of larvae are linked to sea ice (Corso et al. 2022). The increase in SES numbers coupled with the decreased sea ice duration (Stammerjohn et al. 2008a) and the reduction in prey abundance may therefore compound dietary resource competition for the SES.

Year was also associated with variability in nitrogen between the male seals. In 2006, nitrogen values were on average lower than in 2007 and 2013. Nitrogen may differ from year to year due to fluctuations in the baseline nutrient levels (Murphy et al. 2007a).

These fluctuations are often linked to seasonal or yearly atmospheric and oceanographic events changing ice melt intensity and the strength and concentration of nutrient mixing from deep ocean upwellings (Stammerjohn et al. 2008b, Santamaría-del-Ángel et al. 2021, St John Glew et al. 2021). Changes in the biogeochemical cycles can influence primary and secondary productivity which are associated with shifts in the recruitment and abundance of key prey groups such as krill or the Antarctic silver-fish *P. antarctica* (Murphy et al. 2007a,b, Steinke et al. 2021, Corso et al. 2022). As most male SESs were extremely specialised, they may be more responsive to these kinds of environmentally driven shifts in their food web due to their extremely narrow trophic feeding niche. The crabeater seal, another highly specialised Southern Ocean predator, was also found by Hückstädt et al. (2012a) to have significant inter-annual variation in their nitrogen trophic level and prey consumption. The authors suggested that the variation was likely linked to climatic variables impacting their prey resources in different years. It is possible that the variation we detected between years is a reflection of the random sampling of extremely specialised feeders and not the population's response to changing environments or behaviour. As Hückstädt et al. (2012a) also found similar results in their study on the extremely specialised crabeater seal, which was also conducted over 3 sampling years, it would be worthwhile for future research to increase the number of sampling years to strengthen our understanding of this trend that has now been seen in 2 separate phocid species.

4.2. Male intra-individual variation

These large-scale atmospheric and oceanographic events could also be influencing the variation within individual diets, as we also found that there were seasonal shifts within the diets of the individual seals. Variation within diet may indicate changes in resources or the individual's ability to access certain prey items within the highly seasonal Antarctic ecosystem. Seasonal oceanographic features known as polynyas (large patches of open water surrounded by ice) result in highly productive areas that support an abundance of high-quality prey (Maqueda et al. 2004). Though polynyas are detectable year-round, they go through 'active' ice-production phases during the winter months and 'inactive' or post-polynya phases once the sea ice has melted (Maqueda et al. 2004, Malpress et al. 2017). Seals that remain within

the polynyas during the winter months are thought to be taking advantage of not just the open water access that the polynyas provide within the winter fast ice but also the prolonged secondary productivity phase that is associated with polynya zones (Labrousse et al. 2018). Labrousse et al. (2018) found that half of the SESs sampled from the Kerguelen Island population exploited the polynyas for just a short period and left before the winter ice set in, whereas other seals remained within the polynyas across the entire winter period. This preferential difference in either staying or leaving the highly productive zone likely results in a diet shift and could therefore increase the level of variation within those diets. This was also reflected in the findings of Arce et al. (2022), who reported that seals that remain within these polynyas improve their body condition more rapidly due to the highly productive nature of the polynya as well as a reduction in the seals' search efforts.

In addition to these seasonally driven localised zones, regional shifts in the nitrogen isotope baseline also occur, though it is seen across a larger and less defined area. By creating an isoscape based on zooplankton sampled along the west of Antarctica, Brault et al. (2018) found that spatial shifts in the regional $\delta^{15}N$ were strong, with areas such as the Ross Sea and Amundsen Sea having significantly higher $\delta^{15}N$ compared to the WAP, the Polar Front Zone, and the Antarctic Continental Zone. With these differences likely driven by increased iron inputs from glacial melts, large polynyas, and extensive continental shelves (Brault et al. 2018), these regional differences in $\delta^{15}N$ may lead to variation within the seals' diets as they move through different regional zones across their 8–10 mo foraging migration. The other possibility may be that the seal is not eating different prey items over time, but as the $\delta^{15}N$ baseline shifts between the regions, so too might the $\delta^{15}N$ value of its prey, thereby reflecting not so much a change in diet or what the seal is actually consuming across time but instead represent a change in the regional baseline of the food web that the seal is migrating through. As nitrogen isotopic values can vary between seasons within the same geographic region (St John Glew et al. 2021), caution should be exercised when interpreting isoscapes in relation to studies such as ours. As isoscapes require a vast amount of fine-scale data, currently many are limited to representing a static snapshot of a specific region's seasonal isoscape (Brault et al. 2018). That being said, as more data is collected and more comprehensive isoscapes are developed for different regions at different times, their application to isotopic data

interpretation will be critical in untangling differences between baseline shifts and dietary variation in migrating species.

Although carbon was not included in the model for this study, it too can provide valuable insight into the potential movement and foraging locations of the individuals. Carbon isotopes can be used as a tool to understand where highly migratory species go, and when tracking information is unavailable, it can be used to identify likely feeding habitats for top consumers such as the Antarctic fur seal *Arctocephalus gazella* (Walters et al. 2020). Here, the adult male SES $\delta^{13}C$ ranged from −23.7 to −18.2‰ (Table S1). Again, looking at the spatial isoscape compiled by Brault et al. (2018), for $\delta^{13}C$ they found that values decreased with increasing latitude, with the highest zooplankton $\delta^{13}C$ values being found across the Polar Front Zone and the Antarctic Continental Zone (both −24.2 ± 0.9‰), and the lowest $\delta^{13}C$ values being found in the Ross Sea and the Antarctic Zone (−27.5 ± 1.6 and −27.1 ± 0.7‰ respectively). Our carbon values indicate that our seals are likely feeding in the lower, more southerly regions, but as the sampling efforts of Brault et al. (2018) were restricted to the austral summer periods and our seals' carbon values represent the winter and spring seasons, a more closely related isoscape would allow a more accurate comparison of our seals' potential foraging movements. As previously discussed for $\delta^{15}N$ isotopic baselines, the $\delta^{13}C$ baseline also varies both temporally and spatially, and any interpretation of migratory movements based solely on $\delta^{13}C$ should be discussed with caution (McMahon et al. 2013). Future studies would benefit from combining and comparing satellite tracking data with stable isotope data as done by Walters et al. (2014) and Walters et al. (2020) to better understand how carbon and nitrogen shift for individuals in relation to their known migratory path.

4.3. Individual specialisation

Individual adult male SESs maintain an extremely specialised diet in the months leading up to their breeding period. In using the BIC and WIC values, we were able to determine the males' degree of dietary specialisation. Our results have expanded on previous observations made by Gallon et al. (2018), and particularly Lewis et al. (2006), who found that individual male $\delta^{15}N$ values showed consistency across time. Nitrogen was associated with specialisation, with seals who fed at a higher nitrogen level more likely to have a lower specialisation ratio. Body size, however, did not show any strong relationship with specialisation in male SESs. We found that males of any size were specialising at their trophic nitrogen level.

As adult male SESs of any size can develop and maintain a highly selective diet, dietary specialisation in the SES may be related to its tendency to develop foraging site fidelity early in life. Individuals will often return each year to the same feeding grounds, which can increase their familiarity with the area and its prey patch distribution (McIntyre et al. 2017). This long-term familiarity with the regional oceanographic and bathymetric features may improve the foraging efficiency of these individuals, and could reduce the energetic costs of specialising on specific prey found within their foraging zone (Bradshaw et al. 2004). Authier et al. (2012) also found that individuals who developed a stable foraging strategy early in life were more likely to live longer, making it through to adulthood. Reasonably, this stable foraging strategy coupled with the early development of foraging site fidelity may increase the likelihood of these males becoming highly specialised foragers regardless of their size.

High levels of individual specialisation within a population can also be driven by resource availability. To reduce resource competition, individuals from the same population may select different and sometimes even subpar food options to avoid conflict or energetically risky foraging behaviours (Svanbäck & Bolnick 2007, Johnson et al. 2009, Tinker et al. 2012, van Overveld et al. 2018). At present, competition for food resources between SESs is still poorly understood; therefore, we cannot determine whether their high level of dietary specialisation is in response to resource competition. Lewis et al. (2006) suggested, however, that a specialist diet could help the male SESs of Peninsula Valdes reduce competition and avoid some of the trophic diet overlap occurring between other SES males as well as the South American sea lion *Otaria flavescens*. More specifically to our study region, though, Tosh et al. (2009) and James et al. (2012) found that after the moult season in 2000, the majority of Potter Peninsula male SESs remained near the WAP region, preferring to forage along the continental shelf, or continued to move into the Weddell Sea. McIntyre et al. (2014) also found that after moult season in 2010, most males moved north along the WAP towards the Scotia Sea, with 2 individuals moving south towards the Bellingshausen Sea. Of the 13 males that were sampled in 2013, their post-breeding movements were tracked, showing that most individuals (9 of 13) travelled further south along the WAP

(Bornemann et al. 2014b,c,d,e,h,i,j,l) and only 4 of 13 travelled north into the Scotia Sea (Bornemann et al. 2014a,f,g,k) (Fig. S4 and Table S5). Unlike other SES colonies, females in the WAP region deviate from the norm and remain feeding along the WAP continental shelf instead of heading north and away from the encroaching ice sheets during the winter (Hindell et al. 2016, Labrousse et al. 2017). Currently, as more females seem to be remaining further south for longer periods, likely due to the warming climate (Negrete et al. 2022), valuable food resources and key foraging grounds may be under increasing pressure, which may lead to changes in diet and the need to specialise. As nitrogen was shown to vary between years, influencing BIC, we felt it valuable to only compare the seals' specialisation ratio within their sampling year. While that did make for a relatively small sample population, our average and confidence intervals show good precision. In the future, though, larger sample populations would reduce any measurement errors and improve our understanding of the long-term consistency of male dietary specialisation.

Thus, through analysing the bulk $\delta^{15}N$ values of these adult male SESs at an individual level, we have been able to further develop our understanding of the variability in diets between as well as within these individuals. We have highlighted that males maintain an extremely specialised trophic-level diet over the months leading up to the breeding season, and that their morphology is correlated with the variation between individual $\delta^{15}N$ values. We have also shown that both seasonality and year need to be considered when looking at dietary variation. Future works would benefit from increasing the sample size to make the analysis of year more robust, and as this work continues to build on the foundational knowledge of male SES diets, it would be instructive to incorporate groups of males from other colonies around the Southern Ocean to explore whether males from different regions are also following the trends shown in this study. Our results underpin a plea for long-term investigations following SES individuals over several years in combined tracking and/or stable isotope investigations complemented with dietary studies based on traditional methods in order to improve our understanding of the ontogeny of the seals' dietary specialisation.

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Text S1: Modified Discrete von Bertalanffy Equation

Discrete von Bertalanffy equation (Hall-Aspland et al. 2005).

$$(Tp - Tp-1) = (Lp - Lp-1)k(La - Lp-1)$$

where (Tp – Tp-1) denotes the time in days represented between points p and p-1; (Lp – Lp-1) is the length of a segment between points p and p-1; k is the growth coefficient; and La is the asymptotic length, calculated from maximum whisker length of the population plus 1%.

The growth coefficient k was calculated using the following equation (Hall-Aspland et al. 2005):

$$k = -ln[1 - l(t)La] \, t(l)$$

where l(t) is the population's maximum whisker length in millimetres; and t(l) is the maximum period of time a whisker could represent (365 days) (Lübcker et al. 2016).
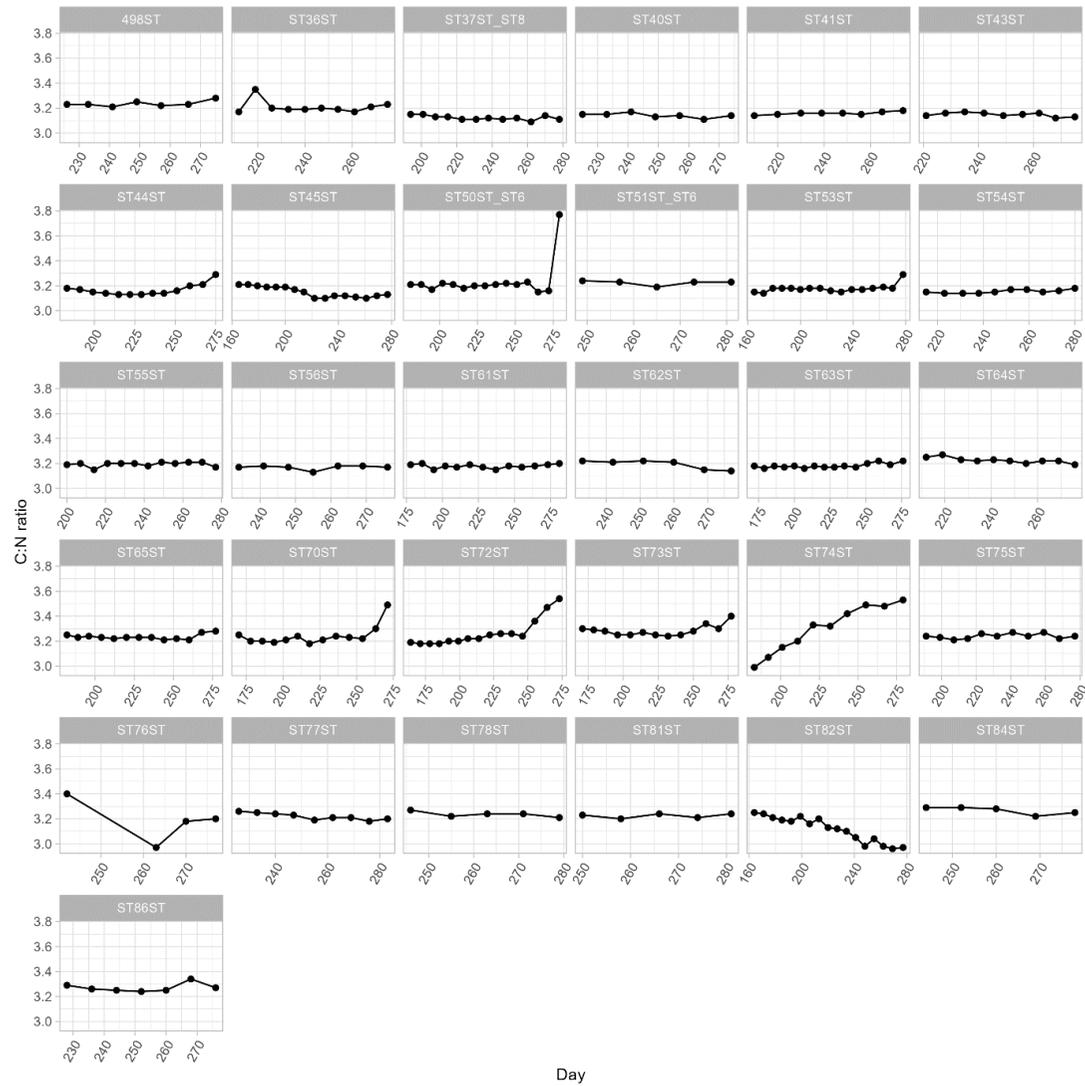
Fig. S1. Atomic C:N ratio per seal. X axis represents days (along the length of each seals whisker). Y axis represents the carbon:nitrogen ratio.

2

Table S1. Summary table of individual seals.

Seal brand	Seal ID	Year	Nitrogen mean (‰)	Nitrogen sd	Carbon mean (‰)	Carbon sd	Specialisation classification	Specialisation ratio	Standard length (m)	Girth (m)	Whisker segment count
ST36ST	SES06-02	2007	13.99	1.15	-20.68	0.69	Specialist	0.31	4.12	3.68	10
ST37ST_ST8	SES06-03	2006	11.70	0.58	-19.89	1.04	Specialist	0.23	4.36	3.09	12
ST40ST	SES06-06	2007	14.59	0.33	-21.13	0.49	Extreme Specialist	0.02	4.12	3.68	7
ST41ST	SES06-07	2007	11.21	1.22	-21.92	0.43	Generalist	0.55	4.43	3.49	8
ST43ST	SES06-09	2006	14.58	0.98	-21.46	0.45	Specialist	0.47	4.51	3.9	9
ST44ST	SES06-10	2006	13.17	0.53	-21.21	0.61	Extreme Specialist	0.17	4.4	3.865	13
ST45ST	SES06-11	2007	12.34	0.56	-21.09	0.52	Extreme Specialist	0.08	4.06	3.4	16
ST50ST_ST6	SES06-18	2006	13.52	0.71	-21.06	0.99	Specialist	0.30	4.21	3.34	15
ST51ST_ST6	SES06-20	2006	12.38	0.29	-21.28	0.36	Extreme Specialist	0.05	3.99	3.465	5
ST53ST	SES06-22	2006	11.95	0.57	-21.13	0.38	Specialist	0.31	4.15	3.14	16
ST54ST	SES06-23	2006	11.43	0.67	-21.34	0.87	Specialist	0.30	3.84	3.67	10
ST55ST	SES06-24	2007	12.04	0.79	-22.24	0.32	Extreme Specialist	0.18	4.03	3.47	12
ST56ST	SES06-25	2007	12.24	0.50	-22.11	0.44	Extreme Specialist	0.08	4.23	3.6	7
ST61ST	SES06-30	2007	15.04	0.49	-21.15	0.25	Extreme Specialist	0.06	4.4	4.19	13
ST62ST	SES07-01	2007	12.61	0.96	-21.88	0.49	Specialist	0.26	4.32	3.78	6
ST63ST	SES07-02	2007	11.78	0.51	-21.28	0.64	Extreme Specialist	0.10	4.31	3.39	15
ST64ST	SES07-03	2007	16.60	0.54	-21.28	0.36	Extreme Specialist	0.07	4.76	4.01	10

ST65ST	SES07-04	2007	11.92	0.48	-21.40	0.43	Extreme Specialist	0.12	4.05	3.285	13
ST70ST	CAR2013_sel_m_03	2013	12.44	0.73	-22.16	0.93	Specialist	0.42	4.43	4.25	13
ST72ST	CAR2013_sel_m_05	2013	11.57	0.61	-21.19	0.60	Specialist	0.33	4.28	3.84	15
ST73ST	CAR2013_sel_m_08	2013	13.16	0.53	-21.43	0.60	Extreme Specialist	0.14	4.18	3.83	13
ST74ST	CAR2013_sel_m_09	2013	16.52	0.36	-22.73	0.67	Extreme Specialist	0.08	4.2	3.84	10
ST75ST	CAR2013_sel_m_10	2013	13.33	0.54	-21.11	0.44	Extreme Specialist	0.12	3.89	3.35	11
ST76ST	CAR2013_sel_m_11	2013	12.54	0.38	-21.70	0.25	Extreme Specialist	0.07	4.19	3.94	4
498ST	CAR2013_sel_m_12	2013	12.36	0.44	-20.46	1.09	Extreme Specialist	0.11	4.06	3.34	7
ST77ST	CAR2013_sel_m_13	2013	13.08	0.66	-19.22	0.45	Extreme Specialist	0.20	4.02	2.94	9
ST78ST	CAR2013_sel_m_14*	2013	13.24	0.53	-21.68	0.60	Extreme Specialist	0.13	4.29	3.57	5
ST81ST	CAR2013_sel_m_19*	2013	13.54	0.72	-21.61	0.71	Specialist	0.23	4.2	3.32	5
ST82ST	CAR2013_sel_m_20	2013	13.31	0.40	-21.98	0.48	Extreme Specialist	0.04	4.36	3.27	17
ST84ST	CAR2013_sel_m_22	2013	13.23	0.42	-20.95	0.42	Extreme Specialist	0.08	4.32	3.39	5
ST86ST	CAR2013_sel_m_24*	2013	15.57	0.56	-20.43	0.60	Extreme Specialist	0.11	4.69	3.9	7

Text S2. Model response and explanatory variables for the GAMLSS mu model to test the mean.

GAMLSS Mu link function:

Nitrogen (δ^{15}n) ~   log(length) +

log(girth) +

sin (2 * date * pi/365) +

cos (2 * date * pi/365) +

year +

random (seal ID) + re (random = ~1 | seal ID,

correlation = corExp (form = ~date | seal ID),

control = lmeControl (return Object = TRUE),

family = LOGNO())

Table S2. Table summarising the results of the GAMLSS model for mean. Bold with asterisks (*) indicates significance.

GAMLSS Mu
Coefficients:

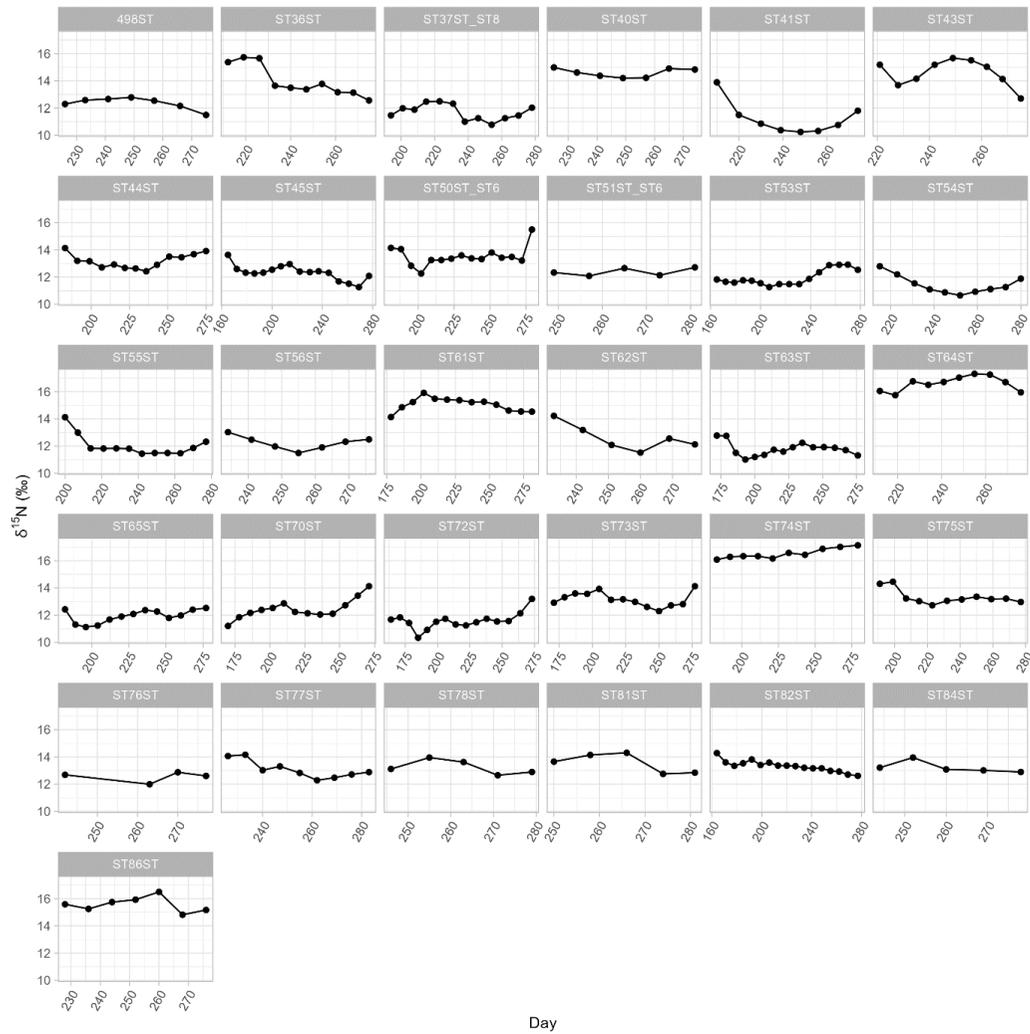|	Estimate	Std. Error	t value	P.value
(Intercept)	1.141	0.065	17.587	**< 0.001 ***
Log Length	0.614	0.046	13.249	**< 0.001 ***
Log Girth	0.395	0.024	16.638	**< 0.001 ***
Sin	0.007	0.014	0.503	0.615
Cos	-0.020	0.014	-1.49	0.138
Year2007	0.028	0.006	4.32	**< 0.001 ***
Year2013	0.051	0.006	8.953	**< 0.001 ***

Fig. S2. Stable isotope nitrogen (δ¹⁵N) whisker plot. Each plot represents an individual seal with day on the x axis and nitrogen (δ¹⁵N) on the y axis.

Text S3. Model response and explanatory variables for the GAMLSS sigma link model to test variance.

A) GAMLSS Sigma link function

Nitrogen (δ^{15}n) ~   log(length) +

log(girth) +

sin (2 * date * pi/365) +

cos (2 * date * pi/365) +

 year +

random (seal ID) +

family = LOGNO()

Table S3. Table summarising the results of the GAMLSS model for variance. Bold with asterisks (*) indicates significance.

B) GAMLSS Sigma
Coefficients:

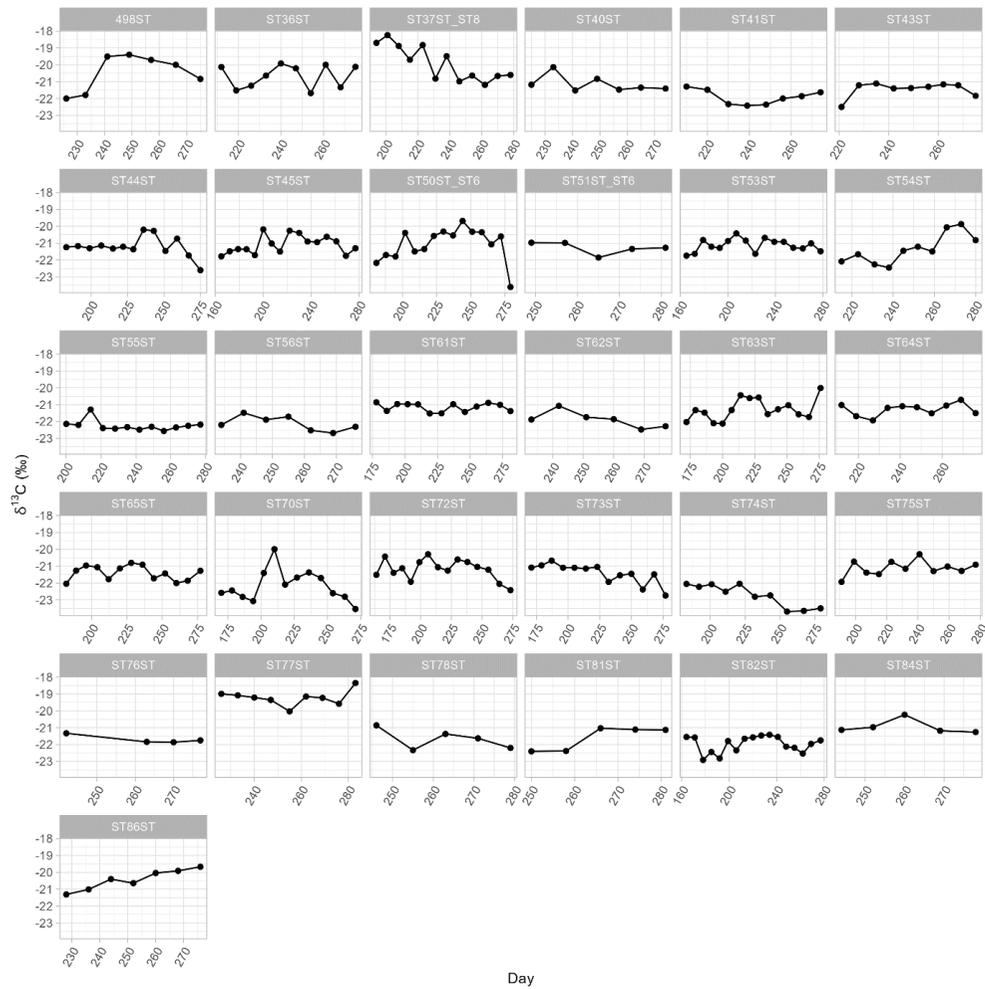|	Estimate	Std. Error	t value	P.value
(Intercept)	-1.305	1.291	-1.011	0.313
Log length	0.008	0.957	0.008	0.993
Log Girth	0.060	0.511	0.117	0.907
Sin	1.528	0.263	5.821	**< 0.001 ***
Cos	1.468	0.251	5.843	**< 0.001 ***
Year2007	-0.036	0.110	-0.328	0.744
Year2013	-0.392	0.108	-3.622	**< 0.001 ***

Fig. S3. Stable carbon isotope (δ¹³C) whisker plot. Each plot represents an individual seal with day on the x axis and carbon (δ¹³C) on the y axis.

Table S4. Individual specialisation generalised linear model. Bold with asterisks (*) indicates significance.

Specialisation GLM
Coefficients:

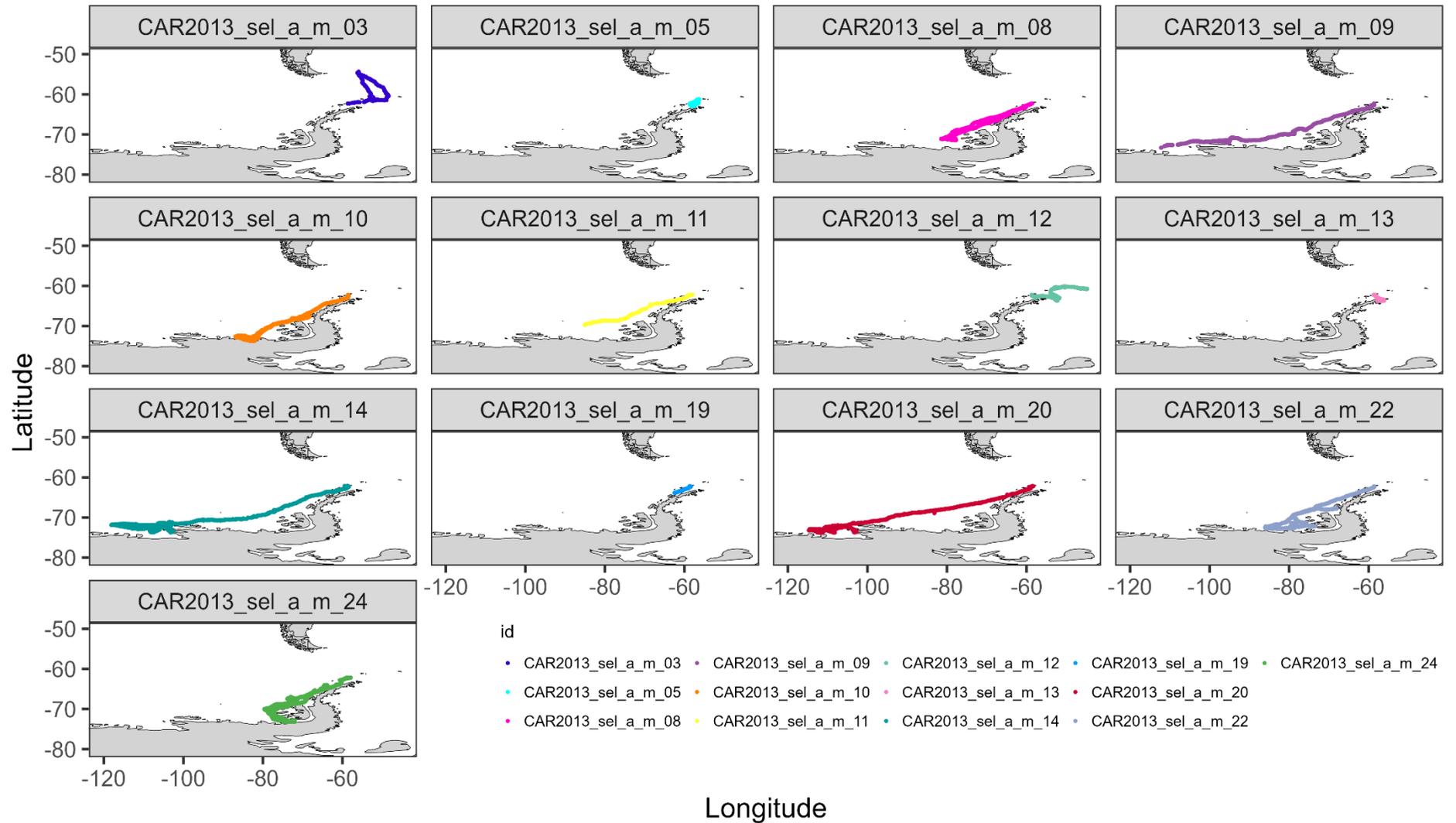|	Estimate	Std. Error	t value	P.value
(Intercept)	0.4827	0.7413	0.651	0.5204
Log Nitrogen	-0.6734	0.2558	-2.633	**0.0138***
Log Girth	0.2115	0.2986	0.709	0.4847
Log Length	0.8055	0.5511	1.462	0.1554

Fig. S4. Map showing the tracks of the 13 seals sampled in 2013 after breeding season (id represents the seals individual identification number). See table S9.2 for links to each individual's metadata.

Table S5. The citation and metadata for the 13 seals tracked after breeding season in 2013.

Seal ID	Citation and link to individual seal specific metadata
CAR2013_sel_a_m_03	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_03 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833592
CAR2013_sel_a_m_05	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_05 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833593
CAR2013_sel_a_m_08	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_08 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833594
CAR2013_sel_a_m_09	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_09 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833595
CAR2013_sel_a_m_10	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_10 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833596
CAR2013_sel_a_m_11	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_11 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833601
CAR2013_sel_a_m_12	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_12 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833597
CAR2013_sel_a_m_14	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_14 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833599
CAR2013_sel_a_m_13	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_13 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833598
CAR2013_sel_a_m_15	Bornemann, Horst; Schröder, Michael; Hellmer, Hartmut H; Márquez, María Elba Isabel; Rogers, Tracey; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_15 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833600
CAR2013_sel_a_m_16	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_16 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833602
CAR2013_sel_a_m_17	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_17 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833603
CAR2013_sel_a_m_18	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_18 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833604
CAR2013_sel_a_m_19	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_19 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833605

CAR2013_sel_a_m_20	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_20 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833606
CAR2013_sel_a_m_21	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_21 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833607
CAR2013_sel_a_m_22	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_22 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833608
CAR2013_sel_a_m_23	Bornemann, Horst; Rogers, Tracey; Márquez, María Elba Isabel; Daneri, Gustavo Adolfo; Mennucci, Jorge Augusto; Bester, Marthán Nieuwoudt (2014): At surface behaviour at location on spot of southern elephant seal CAR2013_sel_a_m_23 from King George Island. Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Bremerhaven, PANGAEA, https://doi.org/10.1594/PANGAEA.833609
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