

Diet of juvenile southern elephant seals reappraised by stable isotopes in whiskers

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ABSTRACT: Declines in marine predator populations have been attributed to anthropogenic activity and environmental change. Southern elephant seals *Mirounga leonina* are major consumers of biomass in the eastern region of the Southern Ocean and have been declining in numbers since the 1960s. Previous studies have identified evidence for habitat and diet partitioning over a range of spatial and temporal scales between juveniles and adults in the Macquarie Island population. We first analysed the stable isotopes (SI) of 6 entire vibrissae from a dead adult female southern elephant seal from Kerguelen Islands to determine moult and growth patterns. Secondly we analysed the SI from the vibrissae of 102 juvenile southern elephant seals to investigate diet. The results from the growth pattern analysis indicated that vibrissae do not grow or moult simultaneously. However, it is likely that at least part of the vibrissae will have been produced sometime during the most recent trip to sea and will give a broad indication of diet. The subsequent SI analysis confirmed that juveniles are consuming greater proportions of fish species, and identified myctophids as the primary component of juvenile diet. Myctophids are also consumed by king penguins *Aptenodytes patagonicus* which have greatly increased in numbers recently in the Macquarie Island area. This may have presented the juvenile southern elephant seals with increased competition and may influence survival.

KEY WORDS: Stable isotopes · Vibrissae growth patterns · Diet · Fish · Squid · Resource partitioning · Inter-specific competition

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INTRODUCTION

Marine predator population declines are caused by many different factors, including anthropogenic activity such as development and over-harvesting (Field et al. 2009). Other factors include natural variation in ecosystem composition that affects a populations' access to resources (Barbraud & Weimerskirch 2001, Nicol et al. 2008). These changes in the higher order predators and meso-predator abundances may lead to

large changes in ecosystem structure and stability and have in some cases lead to catastrophic ecosystem collapses (Estes et al. 1998, Myers et al. 2007). The Southern Ocean has demonstrated ecosystem perturbations due to climatic changes, mediated through variation in sea ice extent which impacts on overall productivity (Arrigo et al. 1998, McMahon & Burton 2005) at a range of spatial and temporal scales. Therefore it is likely that variation in resource availability will affect predator foraging success and may differen-

tially affect age, size or functional groups of a species (Field et al. 2007a).

Southern elephant seals *Mirounga leonina* are major consumers of Southern Ocean biomass (Bradshaw et al. 2003). Since the 1960s there has been a major decline in southern elephant seal numbers, the extent, timing and nature of which was subject to considerable intra-population variability (Hindell 1991, Hindell et al. 1994, McMahon et al. 2005). The reason for the decline has remained unclear, although a mounting body of evidence suggests that changing environmental circumstances may have played a major role (Hindell 1991, Hindell et al. 1994, McMahon & Burton 2005, McMahon et al. 2005, Field et al. 2007a). Indeed, demographic modelling has indicated that juvenile survival was lower in the declining populations compared to the stable or increasing populations implicating this as a factor influencing the population trends (Hindell 1991, Hindell et al. 1994, McMahon et al. 2005). Resource limitation due to environmental changes was subsequently suggested to be affecting younger age classes more than the older age classes.

There is a clear spatial separation between juvenile and adult southern elephant seal foraging strategies; as seals age they make fewer, longer trips to sea moving further from their natal islands (Field et al. 2005). The relative low rates of juvenile survival imply that this age group is experiencing some set of circumstances that is different to the adult component of the population and to that of juvenile seals from stable populations. A difference in diet between juveniles and adult seals was confirmed in a recent study comparing fatty acids (FA) in the blubber of juvenile and adult seals (Newland et al. 2009), which indicated that juvenile seals from Macquarie Island consumed predominantly fish, while the adults consumed more squid. However, the FA interpretation in that study was largely qualitative, and while suggesting that important age-based differences in diet exist, it did little to identify the specific details regarding diet which are required to interpret demographic differences.

Quantifying the naturally occurring carbon and nitrogen stable isotopes (SI) in animal tissues has become an increasingly important tool for gathering trophic and dietary information (Wada et al. 1987, Peterson & Fry 1987, Lajtha et al. 1995, Kelly 2000, Lewis et al. 2006). The utility of carbon and nitrogen isotopes in food web studies relies on the fact that the isotopic characteristic of these 2 elements found in the diet are incorporated into consumer tissues in predictable ways. When nitrogen is assimilated, the lighter ^{14}N is preferentially excreted and consumers become enriched in ^{15}N relative to their diet (DeNiro & Epstein 1978, Minagawa & Wada 1984, Hobson et al. 1996). This degree of enrichment is broadly pre-

dictable from one trophic level to the next, which allows $\delta^{15}\text{N}$ values to serve as indicators of the relative trophic position of a consumer (DeNiro & Epstein 1978, Hobson & Welch 1992, Davenport & Bax 2002).

As the primary process using ^{13}C is photosynthesis (McConnaughey & McRoy 1979, Tieszen et al. 1983, Hobson et al. 1996), carbon isotope ratios in marine systems are directly related to the source and thus location of primary production. This allows for a geographical interpretation of carbon isotope values, which can be utilised to indicate broad-scale foraging locations of animals in the marine environment (France 1995, Cherel & Hobson 2007).

Inert tissues such as hair, fur, vibrissae (whiskers), feathers and teeth differ fundamentally from other tissues (blood and muscle) because once the protein is incorporated it remains biologically unchanged, providing a long-term time series of isotope data representing the period of growth (Hobson & Clark 1992, Hobson et al. 1996, Hirons et al. 2001a, Kurle & Worthy 2002, Zhao & Schell 2004, Greaves et al. 2004). This temporal view is extremely valuable as many marine predators forage over large distances for long periods of time and exploit a variety of food sources, and therefore exhibit seasonal and long-term variations in diet (Hirons et al. 2001b, Cherel et al. 2009).

The vibrissae of pinnipeds are particularly useful for diet history studies using SI analysis (Hirons et al. 2001a, Zhao & Schell 2004, Greaves et al. 2004, Lewis et al. 2006, Cherel et al. 2009). However, in order to interpret these time series, information in the appropriate spatial and temporal context, knowledge of stable isotope assimilation rates, and vibrissae growth and moult characteristics are required (Hobson et al. 1996, Hirons et al. 2001a, Zhao & Schell 2004, Greaves et al. 2004, Lewis et al. 2006). Knowledge of growth rates are required to determine the timeframe of the dietary history contained in the vibrissae. Identification of vibrissae moult patterns is also important, as the timing of vibrissae replacement will mark the start of any dietary history. If the vibrissae moult and grow randomly then knowledge of the individual vibrissae history will be very important. In contrast, if vibrissae moult and grow synchronously all vibrissae may have a similar SI signature.

The overall aim of this study was to assess the validity of using SI in vibrissae for foraging studies of juvenile southern elephant seals. More specifically we aimed to (1) explore the potential of vibrissae SI analysis as a means of quantifying diet trends and differences in southern elephant seals, (2) assess vibrissae growth patterns of juvenile southern elephant seals using SI analysis, (3) describe seasonal, sex and age variations in SI signatures of juvenile southern elephant seal vibrissae.

MATERIALS AND METHODS

This study had 2 components: the first was an assessment of southern elephant seal *Mirounga leonina* vibrissae growth dynamics based on multiple entire (root–tip) vibrissae collected simultaneously from a single individual found dead at Isles Kerguelen. The second component uses this information to design a sampling regime for 102 vibrissae collected from juvenile seals from Macquarie Island in 2000, for the purpose of identifying the relative trophic position and diet of the seals.

Vibrissae growth dynamics. Study area and sampling: An adult female southern elephant seal was accidentally killed by a tractor at Isles Kerguelen on 22 January 2005. The seal was healthy and near the end of its annual moult at the time of death. A total of 29 entire vibrissae (i.e. root–tip) were plucked from the right side of the seal's face within one hour of death. Each vibrissa was weighed and measured. Six vibrissae of similar length and weight were chosen for subsequent analysis to maximize any possible similarities between vibrissae age and growth rate. We used these vibrissae to address several key questions regarding vibrissae growth dynamics: (1) Do all vibrissae moult at the same time and grow at the same rate? If this were the case, isotopic signatures would be similar along the length of all the vibrissae. (2) What period of time do the vibrissae grow over? Adult female southern elephant seals make 2 annual migrations from their breeding and moulting sites at Isles Kerguelen (Bailleul et al. 2005). As these migrations traverse quite different water masses, and assuming continual growth at sea, there should be a detectable change in the $\delta^{13}\text{C}$ values along the vibrissae. The number of $\delta^{13}\text{C}$ cycles would be indicative of the number of migrations made during the vibrissae life.

Vibrissae preparation: Prior to sample analysis, each vibrissa was soaked in a bath of 2 parts chloroform and 1 part methanol for 2 min then rinsed in the same mixture. This was repeated 3 times. Any remaining residue on vibrissae was scrubbed off with a small scrubbing brush and the soaking process repeated. After washing, the vibrissae were placed in an oven at 60°C for 72 h. Once washed and dried, the vibrissae were sectioned into approximately 2 mm sections (ranging in mass from 0.5–2.2 mg). This represented a trade-off between the number of sections (and hence the temporal resolution attainable for the isotopic time series) and the size of the sample.

Sample analysis: A total of 116 sections from the 6 vibrissae (DC2, DD2, DD3, DF4, DG4, E4), with a mean of 21 ± 3.5 (SD) sections per vibrissae was used

for SI analysis (Table 1). Each section was analysed using an Isoprime continuous-flow isotope-ratio mass spectrometer (Micromass). Results are presented in the usual δ notation relative to Pee Dee Belemnite (PDB) and atmospheric N_2 (air) for ^{13}C and ^{15}N , respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors $<0.15\%$ and $<0.20\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Stable isotope analysis was performed by the Environmental Biology Group, Research School of Biological Sciences, Australian National University (ANU).

Dietary assessment of juvenile vibrissae SI signatures. Study area and animals: The seals used in this study were marked as pups on the isthmus breeding colony at Macquarie Island (McMahon et al. 2006). We used 102 animals, 51 females and 51 males, sampled from 1999 to 2000 for a previous study that examined stomach contents (Field et al. 2007b) (Table 2).

Juvenile southern elephant seals have 2 distinct annual haul-out periods; the moult haul-out that occurs during the summer and the mid-year haul-out which occurs in the winter. Juvenile seals sampled between the start of September and end of February were caught during the summer moult haul-out, and therefore had vibrissae grown predominantly during the winter time at sea. This interpretation was based on the results of the whisker growth described in the previous section. Juveniles sampled from March to August represent seals caught during their mid-year winter haul-

Table 1. *Mirounga leonina*. The length, weight and number of sections of 6 vibrissae (DC2, DD2, DD3, DF4, DG4, E4) collected from a post-moult adult female at Isles Kerguelen in 2005

| Vibrissae ID | Length (mm) | Weight (mg) | Number of sections |
|---------------|----------------|----------------|--------------------|
| DC2 | 74 | 25.0 | 22 |
| DD2 | 60 | 14.9 | 16 |
| DD3 | 77 | 30.6 | 25 |
| DF4 | 70 | 23.9 | 24 |
| DG4 | 72 | 25.6 | 22 |
| E4 | 65 | 19.6 | 18 |
| Mean \pm SD | 70.0 \pm 6.2 | 23.3 \pm 5.4 | 21.2 \pm 3.5 |

Table 2. *Mirounga leonina*. Number of juveniles sampled for stable isotope (SI) analysis in each age (1, 2, 3 yr olds) and sex class, as well as the season/haul-out (summer 1999, winter 2000) that each seal was sampled in

| Age (yr) | — Female — | | | — Male — | | | Total |
|------------------------|------------|----|----|----------|----|----|-------|
| | 1 | 2 | 3 | 1 | 2 | 3 | |
| Summer (1999) moult | – | 4 | 10 | – | 12 | 9 | 35 |
| Winter (2000) mid-year | 20 | 15 | 2 | 15 | 9 | 6 | 67 |
| Total | 20 | 19 | 12 | 15 | 21 | 15 | 102 |

out, and had vibrissae that were predominantly grown during the summer period at sea. Juvenile seals were aged between 1 and 4 yr old, had no breeding experience, and are referred to as 1, 2, or 3 yr olds.

Each day the beaches of the isthmus were searched for seals as they returned to the island. Newly arrived seals were then caught, restrained with a canvas bag over their heads (McMahon et al. 2000a) and the anaesthesia was administered intravenously using a commercially available 1:1 mixture of tiletamine and zolazepam (Telazol, Forte Dodge, Castle Hill, NSW, Australia) at prescribed dose rates (Field et al. 2002). Vibrissae samples were taken while seals were sedated. A large vibrissa was cut at the base (part closest to the face) with a small pair of wire cutters and placed in a labeled air-tight glass vial.

Sample analysis: The 102 vibrissae that we collected were cut into a total of 4309, 0.5 mg sections, 41 ± 10 (mean \pm SD) sections per vibrissae. The sections from each vibrissa were numbered sequentially, starting at the base. In light of the results of vibrissae growth analyses (see Results), these numbers were used to randomly select a single section from each vibrissa.

Statistical analysis: A series of general linear models (GLMs) were used to examine the importance of 3 covariates (*season, age and sex*) on variation of SI values. The response variable, either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ was modelled with combinations of the 3 covariates. Model selection was based on Akaike's information criterion corrected for small samples (AIC_c , Burnham & Anderson 2002). Specific model comparisons were based on the information-theoretic evidence ratio (ER) which is equivalent to the AIC_c weight (w) of the full model divided by the weight of the null model ($w\text{AIC}_c$). Higher ER values indicate higher likelihoods of the tested model relative to the null (Burnham & Anderson 2002). All statistical analyses were done in R version 2.6.0 (R Development Core Team 2004).

RESULTS

Vibrissae growth

The 6 vibrissae collected from the adult female had a length of 70.0 ± 6.2 mm (all values mean \pm SD) and a weight of 23.3 ± 5.4 mg. The number of sections analysed along each vibrissa was 21.2 ± 3.5 . The $\delta^{13}\text{C}$ values ranged from -21.6 to -18.1 ‰. The $\delta^{15}\text{N}$ values ranged from 8.9 to 11.6‰ (a difference of 2.7‰). This indicates that during the time that the seal grew these vibrissae the prey items varied by almost a complete trophic level. There also appeared to be co-variation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; as $\delta^{13}\text{C}$ decreased $\delta^{15}\text{N}$ increased (Fig. 1).

Synchrony of moult and growth rate

The 6 vibrissae exhibited a range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values along their lengths, and there was also considerable variation among the vibrissae (Fig. 1). This clearly demonstrates that all vibrissae on this individual did not moult at the same time or grow at the same rate. The vibrissae DD2 and DD3 were nonetheless very similar with respect to both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, indicating they had similar growth histories. A third, E4, was also similar, although in this case the distal portions of the vibrissa differed from the other 2 as the $\delta^{13}\text{C}$ values indicated that some segments appeared to have grown when the seal was further north. This was the longest vibrissa of those sampled and the differences at the distal end may indicate that this vibrissa was somewhat older than the others and incorporated a longer time series of isotopic information.

Period of growth for vibrissae

To quantify the period of growth for vibrissae, we examined the $\delta^{13}\text{C}$ signature along the vibrissae. Given that adult female southern elephant seals range widely throughout the Southern Ocean, the $\delta^{13}\text{C}$ in the vibrissae should contain signatures from several distinctive water masses (Field et al. 2001, Bailleul et al. 2005). Therefore, the 2 annual foraging trips that elephant seals make to feed (post-breeding and post-moult) might be expected to be identifiable as cycles within the $\delta^{13}\text{C}$ signatures along the vibrissae (Cherel et al. 2009). In fact, none of the vibrissae we sampled showed multiple cycles in $\delta^{13}\text{C}$ along their lengths (Fig. 2). However, the 3 most similar vibrissae (DD2, DD3 and E4), which appeared to be growing over the period leading up to the seals moult showed clear partial cycles, providing evidence that these vibrissae did represent tissues produced during the previous migration.

The other 3 vibrissae (DC2, DF4 and DG4) had quite different isotopic profiles. In particular the basal sections had $\delta^{13}\text{C}$ values of -20.4 , -21.0 and -20.7 ‰, respectively (compared to the mean for DD2, DD3 and E4 of -21.5 ± 0.1 ‰). These vibrissae also had divergent $\delta^{15}\text{N}$ values: 11.6, 10.6 and 11.1‰, respectively (compared to the mean for DD2, DD3 and E4 of 10.3 ± 0.2 ‰). This confirms that the vibrissae are not moulted synchronously, and suggests that vibrissae do not grow continuously, as there were different basal values. It is likely that the distal ends of vibrissae are continually abraded while at sea (and possibly on land), and that occasionally a vibrissa is completely lost. When this happens a new vibrissa is likely to be grown immediately, and continue to grow until the functional length

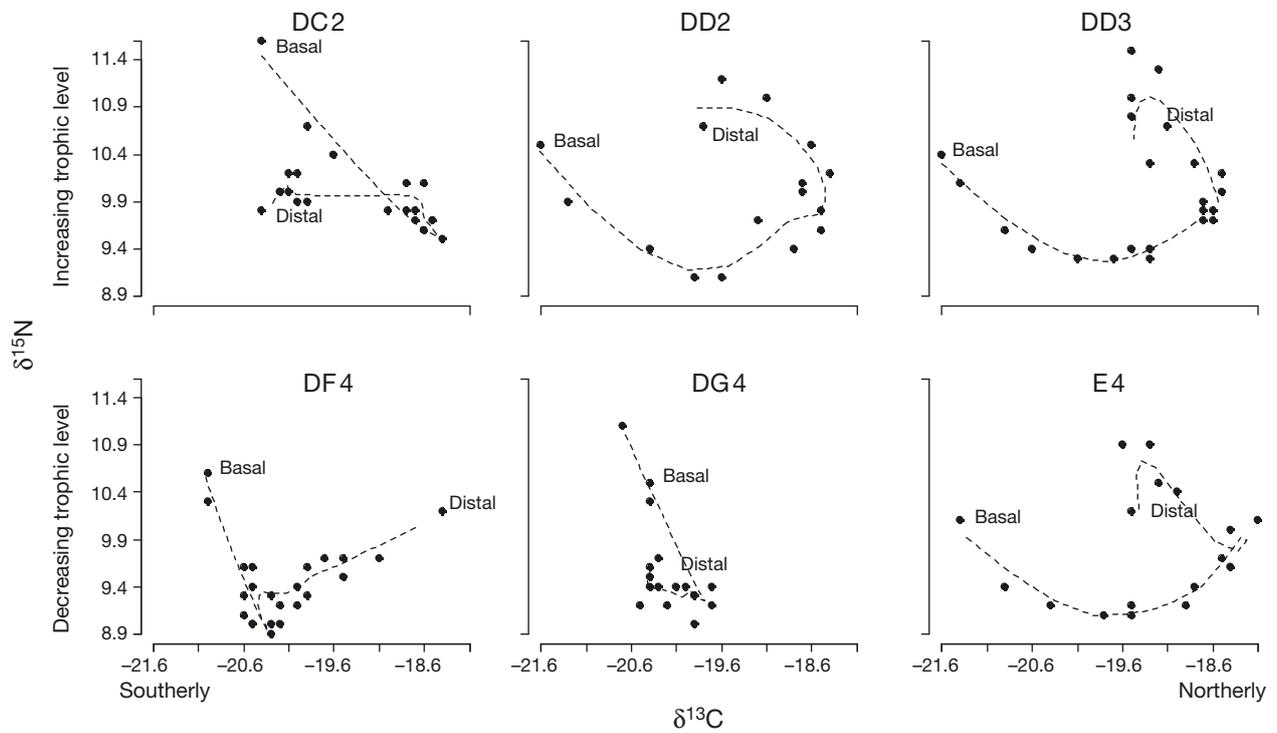


Fig. 1. *Mirounga leonina*. $\delta^{13}\text{C}$ plotted against $\delta^{15}\text{N}$ values for each segment along the length of 6 individual vibrissa obtained from an adult female located at Iles Kerguelen. The dotted line represents a smoothed line using a Lowess smoothing algorithm

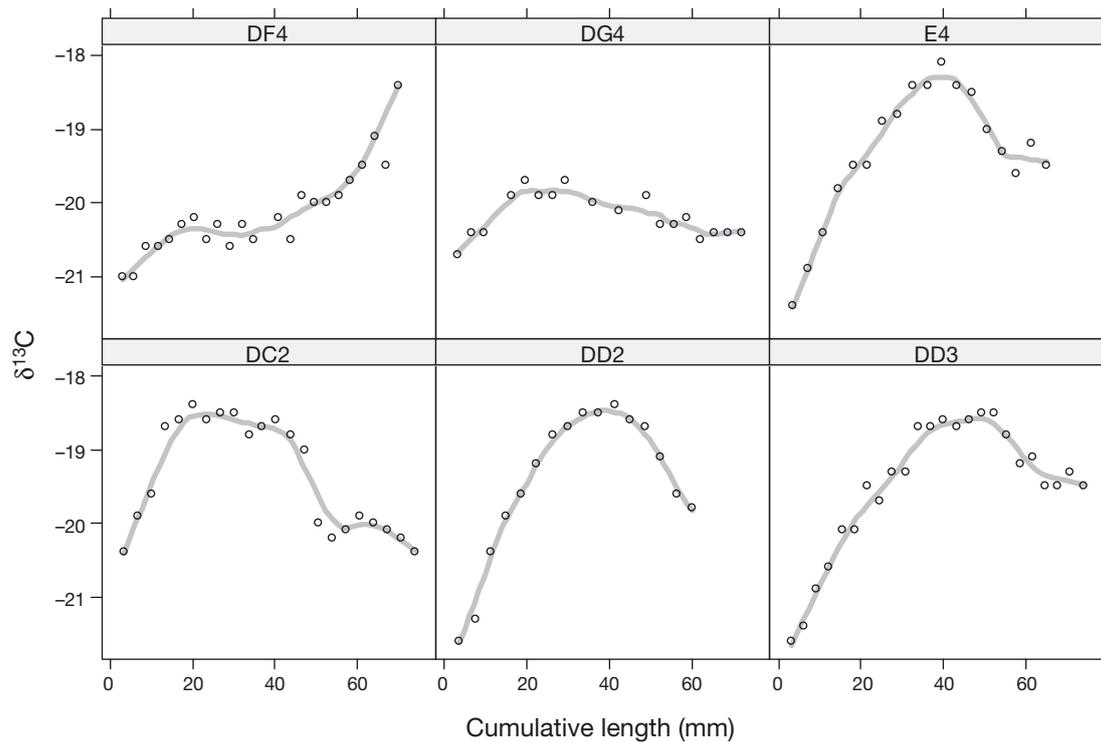


Fig. 2. *Mirounga leonina*. The sequence of $\delta^{13}\text{C}$ values along the length of each of 6 individual vibrissa obtained from an adult female located at Iles Kerguelen. The grey line represents a smoothed line using a Lowess smoothing algorithm

is attained. After this the vibrissae may grow more slowly to maintain their functional length in the face of slow distal abrasion, or perhaps not at all.

As the growth of vibrissae is episodic and the timing and rate of this growth is dependent on each vibrissa's individual moult and abrasion history, randomly selected vibrissae cannot be attributed with any certainty to a particular period of the seals migratory phase. However, it is likely that at least part of the vibrissae will have been produced sometime during recent trips to sea and will give a broad indication of the diet for that age group. The base of each vibrissa should represent the previous trip to sea even if it is newly formed, given that the energy for this would come from the fat stores which would have been acquired during the time at sea.

Stable isotope (SI) assessment of diet

From the above, it is clear that different vibrissae from the same seal can represent different foraging histories and therefore that vibrissae collected at random from juvenile seals could have grown at any point in the previous foraging trip. We therefore constrained our subsequent study to a broad-scale investigation of trophic level and foraging location by analysing one randomly selected 2 mm section from each of the vibrissae of the 102 juvenile seals. In doing so, the only assumption we make regarding age and time of growth of each sub-sample is that it was produced some time in the preceding 6 mo.

Vibrissae $\delta^{13}\text{C}$ values (mean \pm SD) from these seals ranged from -23.0 to -17.7‰ ($-20.3 \pm 1.0\text{‰}$). The $\delta^{15}\text{N}$ values ranged from 8.7 to 13.8‰ ($11.0 \pm 1.3\text{‰}$) (Fig. 3). The range of 5.3‰ for the $\delta^{13}\text{C}$ indicates that sub-samples were grown while the juveniles were foraging in widely dispersed water masses. The range of 5.1‰ for the $\delta^{15}\text{N}$ indicates that the juvenile seals foraged on prey from different trophic levels most likely including crustaceans, fish and squid (Cherel et al. 2009).

While the juveniles foraged at different trophic levels and in different areas of the Southern Ocean there was evidence to suggest that this changed with age and season (Fig. 4). The differences in $\delta^{13}\text{C}$ were best described by the *age + season* GLM, which explained 13% of the total deviance (%DE) (Table 3). This model ($w\text{AIC}_c = 0.72$) fitted the data approximately 3 times better than the next best model, *age + season + sex* ($w\text{AIC}_c = 0.25$). The GLM relating $\delta^{15}\text{N}$ to the same

factors also found that the *age + season* model provided the best fit (Table 3). Although this model had a relatively low %DE (6.4%), it still had an improved fit ($\text{ER} = 2.7$) of around 3 times that of the next best model, and 3.5 times greater than the null model, indicating that there was moderate support for its selection.

The mean $\delta^{13}\text{C}$ values were lower in winter than in summer indicating that the seals moved relatively further south during winter. Also, the $\delta^{13}\text{C}$ values tended to decrease with age, indicating that older seals ventured farther south than the younger ones. Similarly, the $\delta^{15}\text{N}$ also changed with age and season, in this case the seals were taking prey from a higher trophic level during summer months, and when younger.

DISCUSSION

In this study, we compared stable isotopes values to demonstrate ontogenetic changes in both diet and foraging locations in juvenile southern elephant seals. This has been previously demonstrated in studies using tracking data and stomach contents (Field et al. 2007a,b). However, for the first time, our results from

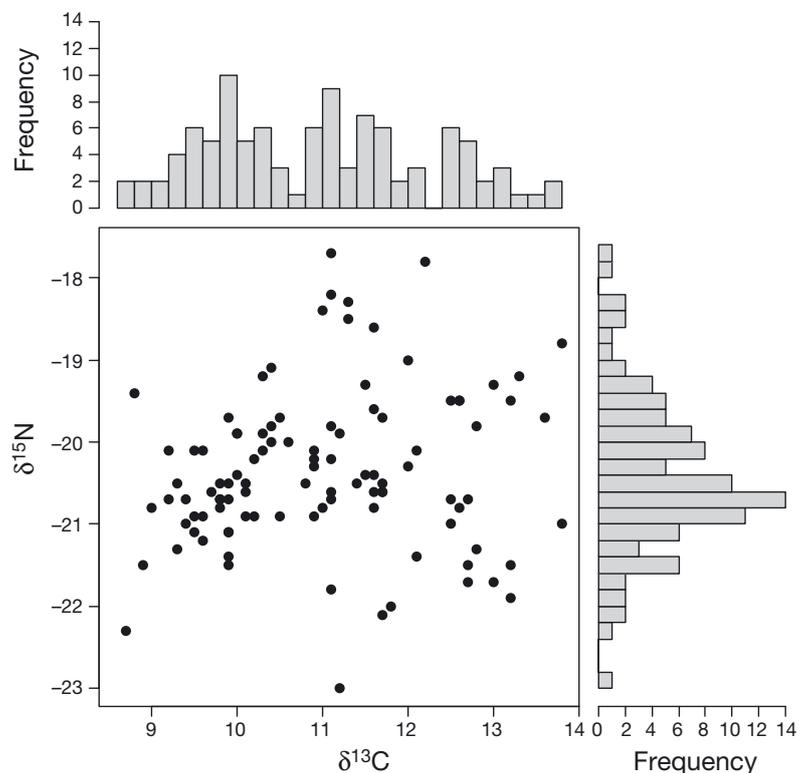


Fig. 3. *Mirounga leonina*. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the vibrissae of 102 juveniles from Macquarie Island. Each point represents a randomly selected 2 mm section along the length of each vibrissa. Also shown are marginal frequency distributions for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

Table 3. *Mirounga leonina*. Generalised linear model selection results of isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) from a randomly selected 2 mm section of vibrissae from 102 individual juvenile southern elephant seals. The models related the isotope values to the sex and age of the individual, and the season (summer or winter) in which the vibrissa was collected and the null model (1). The models are ranked in order of Akaike weights ($w\text{AIC}_c$). k: number of estimated parameters; LogL: maximized log-likelihood of the model; AIC_c : selection criteria; ΔAIC_c : difference between the model's AIC_c value and the minimum AIC_c value; %DE: percent deviance explained by the model

| Model | k | LogL | AIC_c | ΔAIC_c | $w\text{AIC}_c$ | %DE |
|--|---|----------|----------------|----------------------|-----------------|--------|
| $\delta^{13}\text{C}$ related to | | | | | | |
| <i>Age + season</i> | 4 | -133.415 | 275.242 | 0.000 | 0.719 | 12.903 |
| <i>Age + sex + season</i> | 5 | -133.358 | 277.340 | 2.099 | 0.252 | 13.001 |
| <i>Age</i> | 3 | -138.648 | 283.540 | 8.299 | 0.011 | 3.492 |
| 1 | 2 | -140.460 | 285.042 | 9.800 | 0.005 | 0.000 |
| <i>Season</i> | 3 | -139.422 | 285.089 | 9.847 | 0.005 | 2.016 |
| <i>Age + sex</i> | 4 | -138.648 | 285.708 | 10.466 | 0.004 | 3.492 |
| <i>Sex + season</i> | 4 | -139.345 | 287.103 | 11.862 | 0.002 | 2.162 |
| <i>Sex</i> | 3 | -140.445 | 287.135 | 11.893 | 0.002 | 0.030 |
| $\delta^{15}\text{N}$ related to | | | | | | |
| <i>Age+season</i> | 4 | -166.195 | 340.802 | 0.000 | 0.413 | 6.425 |
| <i>Age+sex+ season</i> | 5 | -166.087 | 342.799 | 1.998 | 0.152 | 6.622 |
| <i>Season</i> | 3 | -168.397 | 343.038 | 2.236 | 0.135 | 2.296 |
| 1 | 2 | -169.581 | 343.284 | 2.482 | 0.119 | 0.000 |
| <i>Age</i> | 3 | -169.271 | 344.786 | 3.984 | 0.056 | 0.608 |
| <i>Sex</i> | 3 | -169.388 | 345.021 | 4.220 | 0.050 | 0.378 |
| <i>Sex+season</i> | 4 | -168.313 | 345.038 | 4.236 | 0.050 | 2.456 |
| <i>Age+sex</i> | 4 | -169.021 | 346.453 | 5.652 | 0.024 | 1.094 |

the SI analysis suggest that juvenile southern elephant seals *Mirounga leonina* from Macquarie Island are consuming a diet of predominantly myctophid fish. Quantifying and describing the diet of juvenile seals is important because the decrease in population size at this location was likely the result of factors affecting juveniles (Hindell 1991, Hindell et al. 1994, McMahon & Burton 2005, McMahon et al. 2005). Food and energy intake are vital as any changes in the availability and quality of food will affect energy acquisition and ultimately survival (McMahon et al. 2000b, McMahon et al. 2003).

Vibrissae growth

Vibrissae are particularly useful in studies of foraging ecology of marine mammals as they represent a time line of foraging history (Zhao & Schell 2004, Greaves et al. 2004, Cherel et al. 2009). In some circumstances, such as when the vibrissae are collected from animals that have also been satellite tracked, this time line can be given a spatial context, potentially enabling spatially explicit representation of broad-scale dietary patterns. However, in order to interpret the spatial and temporal context of diet from stable isotope signatures along vibrissae the growth history of

the vibrissae needs to be known (Hirons et al. 2001a, Zhao & Schell 2004, Greaves et al. 2004). If growth rate is continuous, stable isotopes will be constantly integrated into the continuously growing vibrissae, leaving a permanent dietary time line. Alternatively, if a vibrissa's growth period is longer than a year, annual behaviours, such as moulting, will be identifiable in the carbon stable isotope signatures as seals return to shore. This could then be used to calibrate a specific time and place of a particular section of vibrissae growth.

However, the results from our SI analysis of 6 entire vibrissae, collected simultaneously from the same seal, indicated that these individual vibrissae had different formation and growth histories. Some appeared to have been grown in the few months prior to collection, but others had patterns consistent with them being somewhat older, suggesting asynchronous growth patterns. As there were no multiple

cycles in the ^{13}C data for any whisker. This suggests that the growth period of the vibrissae is relatively quick and occurs during a single trip to sea. Consequently our results indicate that vibrissae collected from seals, while containing valuable information regarding diet and foraging location, lack the resolution to temporally place the foraging activities with certainty. These results were also indicated by Greaves et al. (2004) who found that the vibrissae of grey seals *Halichoerus grypus* had asynchronous moult and growth patterns, as well as Hirons et al. (2001a) with harbor seals *Phoca vitulina* and Steller sea lions *Eumetopias jubatus*. Ling (1966) found that southern elephant seals do not shed their vibrissae during the annual moult but that they are replaced irregularly instead. He later implies that because vibrissae seem to function as individual sensory organs, replacement based on loss or damage may be more of an advantage than moulting all vibrissae seasonally (Ling 1977). Surprisingly, our isotopic data are not in agreement with the results from Lewis et al. (2006) who found that 3 vibrissae from 1 individual southern elephant seal had similar SI signatures along their length; but this is likely to be a sampling artefact.

The SI profiles of the basal sections indicated growth had not been continuous, with the most recent component of 3 of the vibrissae having signatures from dis-

tant water masses. This variation may occur because either vibrissae are sometimes moulted at sea, or more likely, they are continuously worn down and broken and growth takes place whenever and for as long as is needed to produce a functional vibrissa. A number of vibrissae were missing from the muzzle at the time of collection, indicating that the seal did not have its complement of vibrissae at the time of its death, suggesting that vibrissae are continuously broken and re-grown.

Vibrissae, as we have shown, provide a powerful non-invasive way to assess diet and foraging location, but in order to be a useful tool in assessing diet and foraging zones we need to be able to quantify growth rates i.e. add a temporal component. One way to get accurate estimates of growth is to incorporate a marker into the vibrissae at a known time, much the same way that tetracycline is used as a marker for assessing growth rates (Garshelis & Noyce 2006). In studies of wild animals it is possible to use 'natural bio-markers', and in our study we used the cyclic pattern of migration to identify cycles in $\delta^{13}\text{C}$, as the animals moved in and out of different water masses. None of the 6 vibrissae exhibited such a cycle, indicating that none contained a growth record corresponding to even a single migration, the most recent of which was the 70 d post-breeding cycle. This finding concurs with the notion of vibrissae being replaced opportunistically as required while the seals are at sea.

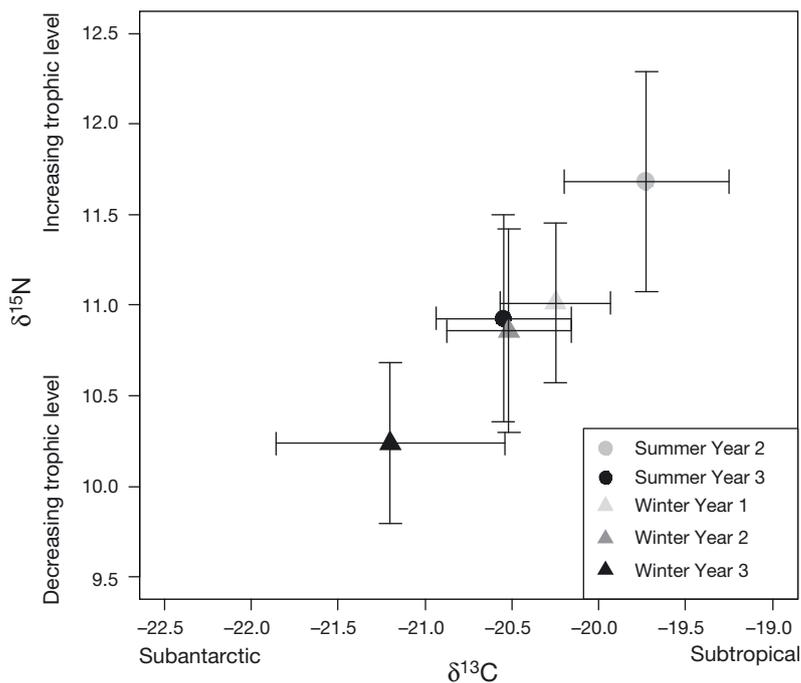


Fig. 4. *Mirounga leonina*. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (means \pm 1 SE) from vibrissae of juveniles from Macquarie Island for each age class (1, 2 and 3 yr old), as well as the different seasons (summer, winter)

Foraging characteristics of juvenile southern elephant seals

Analysing the isotopic signatures from the tissues of marine predators is an effective tool for gathering information on their foraging characteristics over long time scales. The $\delta^{13}\text{C}$ isotopic signature provides insight into the particular water masses the predators have fed in while the $\delta^{15}\text{N}$ isotopic signatures reveal the trophic level of the prey that was consumed. The $\delta^{13}\text{C}$ values identified from juvenile southern elephant seals in the current study ranged from -23.0 to -17.7 ‰. However, there is 3.2% enrichment in carbon between diet and vibrissae (Hobson et al. 1996), which needs to be taken into account when interpreting observed $\delta^{13}\text{C}$ values. By doing so, the $\delta^{13}\text{C}$ values of prey probably ranged between -26.2 to -20.9 ‰ indicating that seals foraged on prey throughout the Southern Ocean, from high-Antarctic to sub-Antarctic waters, with no evidence for any seal forage zones north of the Subtropical Front. The majority of seal prey had values between -24 to -23 ‰ (after accounting for the enrichment factor), and were therefore associated with waters south of the Antarctic Polar Front (APF), which was confirmed by a previous tracking study of the seals sampled here (Field et al. 2005). These seals travelled predominantly to the southeast and southwest of Macquarie Island, with a few travelling northwest. Yearlings travelled up to

2296 km from Macquarie Island, ranging from 126°E to 165°W and 41°S to 66°S . The 2 yr olds travelled up to 5076 km away, ranging from 115°E to 122°W and 44°S to 72°S . The 3 yr olds travelled up to 4084 km away from the island and ranged between 105°E to 123°W and from 43°S to 72°S (Field et al. 2005).

The mean $\delta^{15}\text{N}$ values indicated that the juvenile seals fed from several trophic levels, ranging from secondary consumers (i.e. crustaceans, zooplankton-feeding fish or squid) to higher level predatory fish and squid species. The stomach contents collected from these same individuals (Field et al. 2007b) showed that squid beaks were the predominant items retained in the seals stomachs (found in 100% of stomachs), while otoliths were found in 60 to 100% of stomachs depending on age class (Field et al. 2007b). The number of otoliths decreased as the seals aged; otoliths were found in 82% of 1 yr old stomachs, 75% of 2 yr olds and 68% of 3 yr olds (Field et al. 2007b). Of the fish species identified from the seals stomachs, myctophids had the highest level of occurrence (56%) compared to the other fish (22%) (Field et al. 2007b). These findings are consistent with

the $\delta^{15}\text{N}$ values as both squid and fish species can span this range of trophic levels. The few low $\delta^{15}\text{N}$ values suggest some juveniles were feeding mainly on crustaceans for part of their migration (Cherel et al. 2008). This is a new finding for elephant seals, but is consistent with the diet of some migrating Antarctic fur seals *Arctocephalus gazella* from Crozet (Cherel et al. 2009).

Comparisons with other predators

On average, the nitrogen levels of juvenile southern elephant seals were higher than the crustacean feeding macaroni penguins *Eudyptes chrysolophus*, southern rockhopper penguins *Eudyptes chrysocome chrysocome* and Adélie penguins *Pygoscelis adeliae* (our Fig. 5; Cherel & Hobson 2007, Cherel et al. 2007, 2008). Nitrogen from the juvenile vibrissae was more similar to the fish- and squid-eating emperor penguins *Aptenodytes forsteri* at the higher nitrogen levels ($\sim 12.5\%$) (Cherel & Hobson 2007, Cherel et al. 2007). On average, however, juvenile southern elephant seal $\delta^{15}\text{N}$ levels were almost identical to king penguins *Aptenodytes patagonicus* and Antarctic fur seals

(Cherel et al. 2008, 2007). King penguins and Antarctic fur seals also had similar $\delta^{13}\text{C}$ values to the juveniles indicating they were foraging in a broadly similar area and consuming prey of comparable trophic status. Both king penguins and Antarctic fur seals are known to eat the crustacean-feeding myctophids (Cherel et al. 2007). This finding is also consistent with previous stomach content analysis of these elephant seals (Field et al. 2007b). However, quantifying the contribution of myctophids to predator diets is problematic because myctophids are themselves crustacean predators putting them at the level of secondary and tertiary consumers (Cherel et al. 2010), a position shared with a number of squid species in the region, thus making it difficult to differentiate diet on the basis of SI analysis alone.

Comparison with fatty acids

The results from FA data from the same elephant seals used in this study indicated that the individuals most likely consumed a diet of predominantly fish (our Fig. 6; Newland et al. 2009). Having therefore eliminated squid as potential prey, we were then able to identify myctophids as the likely predominant prey species using SI analysis. Myctophids have been previously identified as the predominant fish component of the diet of these juvenile seals based on stomach content analysis (Field et al. 2007b). Although a very common component of the marine community in sub-Antarctic and Antarctic waters, myctophids have not been previously considered to be important in the diet of elephant seals. Instead, squid have been regarded as the primary prey of all age classes of elephant seals. This idea was recently challenged by Cherel et al. (2008) who suggested that adult females ate primarily myctophids, at least in the weeks and months prior to hauling out for their moult. Indeed, the corrected isotopic values of juvenile elephant seals from Macquarie Islands are almost identical to that of adult females from Kerguelen Islands ($\sim 10.0\%$), thus strongly suggesting a myctophid-based diet for both juvenile seals and adult females. This was in agreement with Bradshaw et al. (2003) who suggested that some adult females ate primarily fish, depending on the time of year or foraging location. Clearly, more isotopic data on adult females (and males) are needed to further clarify the prey of elephant seals at Macquarie Island.

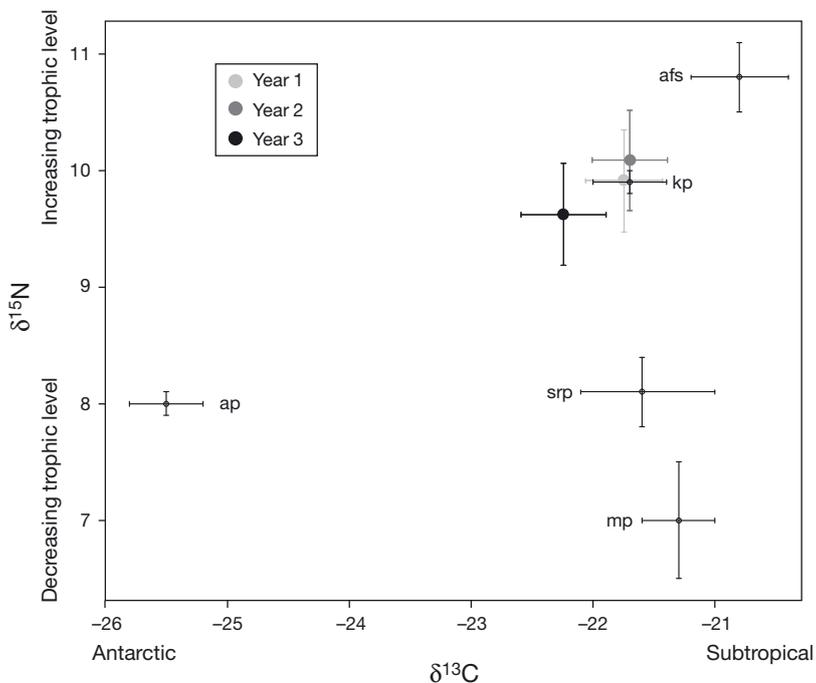


Fig. 5. *Mirounga leonina*. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (means \pm 1 SE) for the age (1, 2 and 3 yr old) and season (summer, winter) groups of juveniles from Macquarie Island, plotted with values for other sub-Antarctic predators from Iles Kerguelen: kp = king penguin, afs = Antarctic fur seal, srp = southern rockhopper penguin, mp = macaroni penguin. Also shown are Adélie penguins (ap) from Terre Adélie. Data from Cherel et al. (2008)

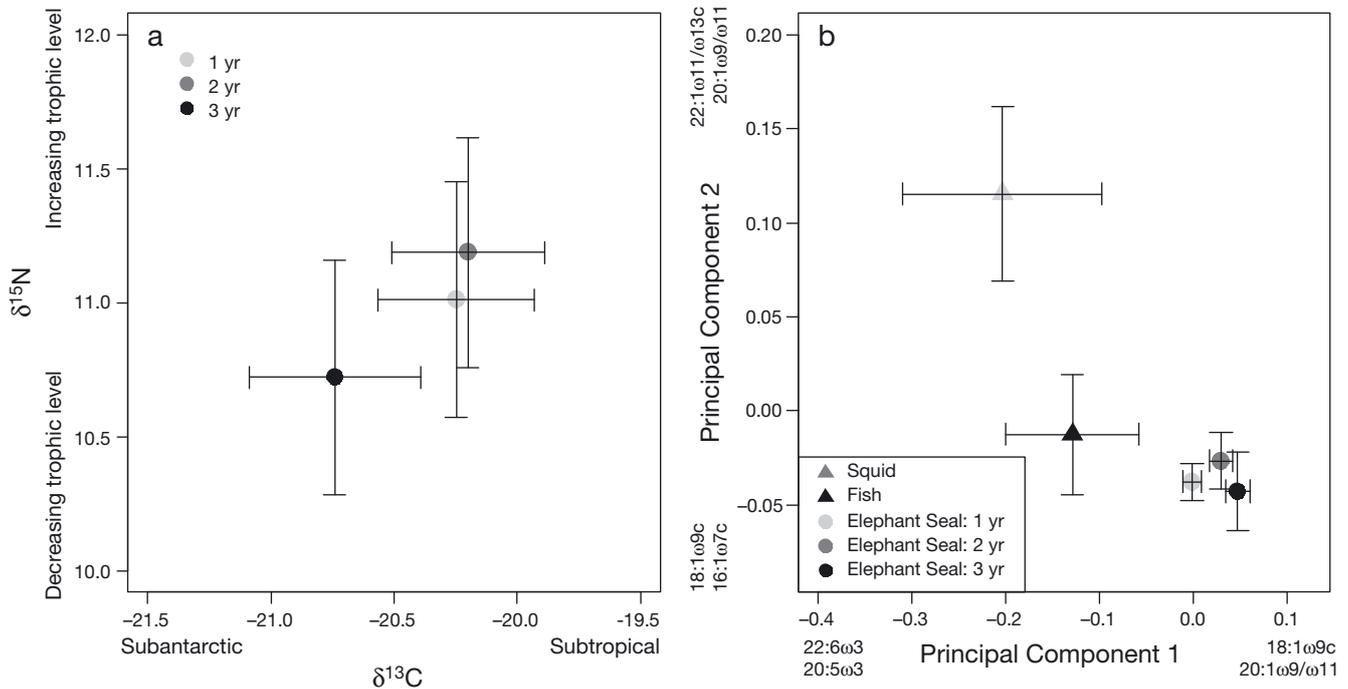


Fig. 6. *Mirounga leonina*. A comparison of 2 different biochemical markers from the tissues of southern elephant seals from Macquarie Island expressed as means (\pm SE) for each age class. (a) Stable isotopes in the vibrissae of juveniles. (b) The first 2 principal components of an analysis of 21 fatty acids of juveniles, including potential fish and squid prey (see Newland et al. 2009 for full details).

Implications for demographics of southern elephant seals

The southern elephant seal population in the Indian and Pacific Oceans declined precipitously between the 1960s and 2000s, for reasons that appear to be due to environmental factors disrupting food supply (Weimerskirch et al. 2003, McMahon & Burton 2005, McMahon et al. 2005). Previous studies have identified the juveniles of these populations as being particularly vulnerable to these environmental factors contributing to the declines (Hindell 1991, Hindell et al. 1994, McMahon & Burton 2005, McMahon et al. 2005).

Stable isotope signatures of juveniles were similar to other myctophid consumers including king penguins and fur seals. King penguin numbers have increased dramatically over the last 80 yr, while fur seal populations have slowly increased, which may result in increased inter-species competition for myctophids (Rounsevell & Copson 1982). Both king penguins (Kooyman et al. 1982, Moore et al. 1999) and southern elephant seals (Slip 1997, Irvine et al. 2000) are known to dive to great depths as they forage. In addition foraging ranges also overlap, with maximum distances of king penguins being 865 to 1984 km while juvenile southern elephant seals forage over average distances of 1432 to 2283 km (Bost et al. 2004, Field et al. 2007a). Thus if juvenile seals are consuming primarily the

same prey as penguins, and given that there has been a 78 fold increase in the Macquarie Island penguin population from 1930 (3400 birds) to 1980 (218 000 birds), and that new colonies are currently being established on the island (van den Hoff et al. 2009), it follows that there must have been a concurrent increase in competition for resources between seals and penguins. This may mean that seals need to dive deeper and forage further from Macquarie Island to gain greater access to vertically migrating prey across a wider distribution, and away from areas of higher abundance (Pakhomov et al. 1996). Thus, resource depletion through competition may be playing a role in the decrease in seal populations by reducing survival of newly weaned and juvenile seals (McMahon et al. 2000b, McMahon et al. 2003).

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