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RESEARCH ARTICLE

Age-related shifts in the diet composition of southern elephant seals expand overall foraging niche

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Abstract Southern elephant seals are important apex predators in a highly variable and unpredictable marine environment. In the presence of resource limitation, foraging behaviours evolve to reduce intra-specific competition increasing a species' overall probability of successful foraging. We examined the diet of 141 (aged 1–3 years) juvenile southern elephant seals to test the hypotheses that differences between ages, sexes and seasons in diet structure occur. We described prey species composition for common squid and fish species and the mean size of cephalopod prey items for these age groups. Three cephalopod species dominated the stomach samples, *Alluroteuthis antarcticus*, *Histioteuthis eltaninae* and *Slosarczykovia circumantarcticus*. We found age-related differences in both species composition and size of larger prey species that probably relate to ontogenetic changes in diving ability and haul-out behaviour and prey availability. These changes in foraging behaviour and diet are hypothesised to reduce intra-specific food competition concomitant with the increase in foraging niche of growing juveniles.

Introduction

The distribution of biological resources within the Southern Ocean is highly variable, unpredictable and patchy at several spatial and temporal scales (El-Sayed 1988; Constable et al. 2003). Spatial and temporal variation in the physical oceanographic factors provide a diversity of habitats that influence the distribution, structure and abundance of ecological communities (Lutjeharms 1990; Rodhouse and White 1995; Arrigo et al. 1998; Constable et al. 2003). In recent years, our understanding of primary production and energy flow through the lower trophic levels of the marine food web in this region have improved greatly (Arrigo et al. 1998; Constable et al. 2003); however, there is still a significant lack of information regarding energy flow through the mid-order organisms (Rodhouse and White 1995) that are important prey sources for predators such as seabirds, pinnipeds and cetaceans.

As juveniles, individuals need to grow rapidly to maximise their lifetime reproductive fitness. This is more pronounced in polygamous species that show pronounced sexual dimorphism and where reproductive success in one sex (generally males) is highly variable (Trivers 1985; Clinton 1994). Phenotypic plasticity in growth patterns combined with ontogenetic differences in behaviour may reduce competition for resources and the negative effects of environmental variation (Pianka 1981; Polis 1984; Schoener 1986; Post

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and Parkinson 2001; Bolnick et al. 2003). The end result will be ontogenetic niche shifts (Woodward and Hildrew 2002), and ultimately resource partitioning of total niche width of the species attributed to the age/size structure of the population (Warren 1996; Williams and Martinez 2000; Bolnick et al. 2003). As such, a reduction in intra-specific competition by resource partitioning has been observed for many species (Polis 1984) over a range of spatial scales, especially where food resources may be limited due to intra- and inter-annual variation in productivity (Perry 1996; Kato et al. 2000; Wikelski and Wrege 2000; Bowen et al. 2002), though there have been few detailed studies of larger marine predators. Therefore, in an unpredictable environment it is likely that predator species will display ontogenetic niche shifts that will reduce competition and maximise foraging success for each age class (Van Valen 1965; Takimoto 2003; Field et al. 2005a).

The southern elephant seal (*Mirounga leonina*) is an apex predator of the pelagic open-ocean system. This species has a circumpolar distribution, is a wide-ranging, deep-diving predator that spends more than 80% of its annual cycle at sea (Le Boeuf and Laws 1994). They are major consumers of biomass, primarily squid and fish (Boyd et al. 1994; Bradshaw et al. 2003; Hindell et al. 2003). The population of *M. leonina* at Macquarie Island in the Pacific sector of the Southern Ocean has been declining since 1950 for reasons that are still unclear (Hindell et al. 1994), although it has been suggested that this species is susceptible to changes in the availability of prey (Hindell et al. 1994; Guinet et al. 1999; Slip and Burton 1999; McMahon et al. 2003, 2005). In particular, juvenile survival, which has been suggested to be influenced by ontogenetic changes in morphology, behaviour and foraging experience, appears to be one of the driving factors in the decline and population change in general (McMahon et al. 2003; Hindell et al. 1994).

Recent studies have demonstrated that there is an ontogenetic change in diving and foraging capacity in elephant seals, and though their complex physiology is not completely understood as the animals age and increase in body size, their ability to dive longer and deeper also increases (Le Boeuf et al. 1996; Slip 1997; Stewart 1997; Irvine et al. 2000; Le Boeuf et al. 2000; Field et al. 2004, 2005a). Elephant seals are also highly sexually dimorphic as adults (although less so as juveniles); however, gender differences in energy use by juveniles relating to the requirements for moulting and sexual development have been demonstrated (Field et al. 2005b). Thus, it is likely that juvenile elephant seals should demonstrate shifts in diet structure as they age towards adulthood.

Previous studies of southern elephant seal diet (Rodhouse et al. 1992; Green et al. 1998; Slip 1995; van den Hoff 2004) have identified that they are opportunistic generalist feeders with a broad foraging niche (Whitehead et al. 2003), with geographical (Green et al. 1998; Danieri et al. 2000) and seasonal (Piatkowski et al. 2002; Bradshaw et al. 2003) differences in diet composition. However, no one has addressed the hypothesised change in diet composition within the juvenile years.

Therefore, in this study, we examine the diet of juvenile southern elephant seals for intra-specific and seasonal differences that may result from variation in at-sea behaviour. Furthermore, we address the complex question of whether the previously observed seasonal differences in metabolic rate within the juvenile age classes are a function of variation in prey species abundance or whether it is variation due to physiological limitations. We hypothesise that (1) as juvenile seals age and grow, they are able to dive deeper and travel farther from Macquarie Island, they may be able to exploit larger prey and/or increase number of species available to them as a function of prey spatial variation; (2) seasonal differences in at-sea behaviour and haul-out patterns may also affect prey availability and hence diet composition; and (3) there may be sexual differences in the diet selected due to the different metabolic requirements of males and females (Field et al. 2005b). Finally, where intra-specific differences have been found, we have calculated the minimum sample required to find a difference using a novel approach that can be used for future lavaging studies.

Methods and materials

From September 1999 to September 2000, 141 known age juvenile southern elephant seals (McMahon et al. 2003) were stomach lavaged during their annual haul-out periods as they returned ashore at Macquarie Island (158°57′E, 54°30′S; Fig. 1). Juvenile seals were determined as being between 1 and 4 years old, and are referred to as 1-, 2- or 3-year-old seals. Seals caught between the start of September and the end of February were regarded as having been caught during summer and those caught between March–August represent those caught in winter.

Sample collection

The beaches on and near the northern isthmus of the island were searched daily for marked individuals

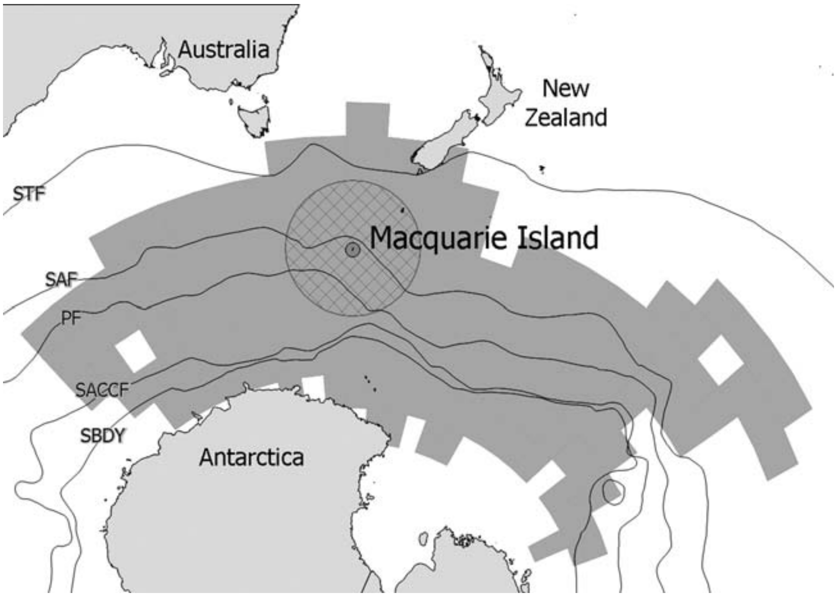

Fig. 1 The known foraging range of juvenile southern elephant seals from Macquarie Island shown as shaded in *grey* (adapted from Field et al. 2004), and the possible area the seal may have used within 7 days (700 km) of returning to haul-out shaded within the *hatched circle*, using 100 km day^{-1} as a daily rate of travel (adapted from Field et al. 2004)

returning ashore that day. As the seals returned to the island for either their mid-year (winter) or moult (summer) haul-out, they were caught by placing a canvas bag over the seal's head (McMahon et al. 2000) and anaesthesia was administered intravenously using prescribed doses (Field et al. 2002) of a combined 1:1 mixture of tiletamine and zolazepam (Telazol®, Forte Dodge, Castle Hill, NSW, Australia).

Once anaesthetised, the seals were weighed (± 1 kg), measured (± 10 mm) and lavaged (Slip 1995). The regurgitant was filtered through a 1-mm sieve to retrieve the stomach contents. The lavage procedure was repeated three times to remove the bulk of the stomach contents. The filtered stomach contents were then placed into a storage jar and filled with 70% ethanol until the contents were sorted and the prey items identified.

To test for age and sex differences in size (mass) of seals that were lavaged, which may attribute to dietary differences, we used a two-way general linear models (GLM) and the ANOVA function in the R package (Ihaka and Gentleman 1996) to describe the relationships between age and sex on seal mass.

In preparation for sample sorting and identification, the stomach contents were flushed with fresh water and placed in a sorting tray. From the stomach samples, the presence of fish otoliths, eyes and bones, squid mouthparts (consisting of an upper and lower beak), penn and eyes, crustaceans and other invertebrates, parasitic worms, sediment and plastic particles were identified. Lower squid beaks were identified to the lower taxa possible, using voucher specimen collections (from Malcolm Clarke held at the Australian Antarctic Division) and descriptions in Clarke (1986), and the lower rostral lengths (LRL) measured to ± 0.01 mm. *Slosarczykovia circumantarcticus* (Cherel et al. 2004) was previously mis-identified as *Brachioteuthis picta* (Rodhouse et al. 1992), *Mastigoteuthis* sp. (Green et al. 1998) and *Chiroteuthis* sp. (Slip 1995) until correctly identified as a separate genus by Lipinski (2001). Fish otoliths were also identified to genus or species level where possible using a voucher collection (from Dick Williams held at the Australian Antarctic Division) and the descriptions in Williams and McEldowney (1990). Most otoliths showed significant erosion (Williams and McEldowney 1990) and only one pair could be measured.

Statistical analysis—general differences in the prey

To test for overall differences in general prey types (presence/absence), statistical comparisons were made between different sex, age and season groups using ANOSIM analyses on Bray–Curtis dissimilarity matrices (Primer-e, PML, Plymouth, UK) using 999 permutations. Where significant differences between the main effects were found, the differences in prey type (presence/absence) were described using similarity of percentages analyses, SIMPER (Primer-e, PML, Plymouth, UK).

Intra-specific differences in prey species abundance

Common prey species were defined as only those species that were found in (5% of the samples). To test for intra-specific and seasonal differences in the abundance of prey, we used non-parametric multivariate tests (ANOSIMs and SIMPER, as above) that allowed robust analysis of combined prey species data. These tests are limited in their ability to perform multiple interactions between group variables, so in order to test our main hypothesis (i.e. that there are age differences in the diet of juvenile seals) we needed to control for the potential effects of season and gender. Therefore, based on three a priori decisions, we used a hierarchical approach (Fig. 2), first testing for the effect of sex, then controlling for season and finally for age effects by removing any possible confounding interactions that may occur. Due to the limited number of individual seals lavaged in some of the groups, comparisons were only made where we had more than five individuals in each group.

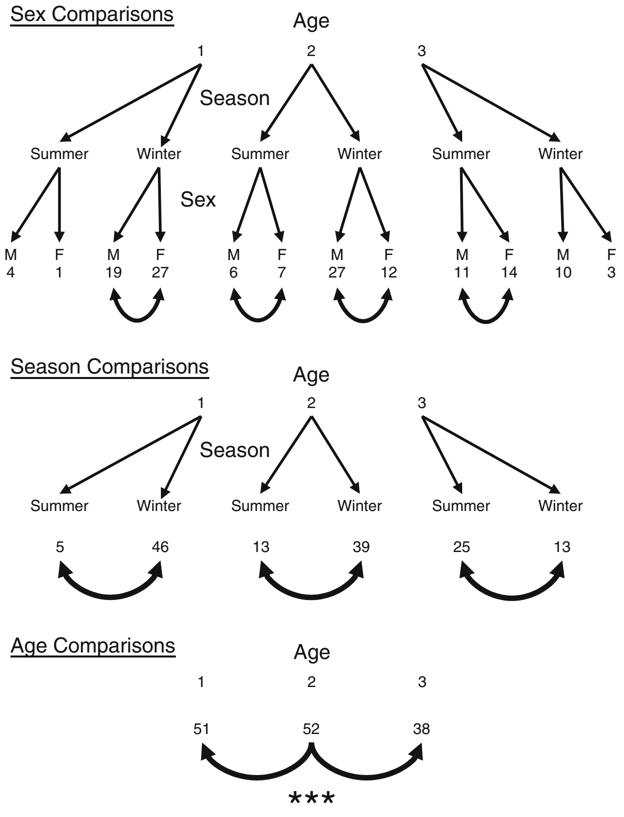

Fig. 2 The hierarchal statistical design used in this study to exclude potential confounding effects of sex and season. Comparisons were restricted to groups with >5 stomach samples and are indicated with *double-headed arrows*. The *numbers* below each of the tested groups indicate the number of samples and the connecting *arrows* show the tested comparisons. *Asterisk* indicates the level of significance (P) of each test where (* >0.05, ** >0.005 and *** >0.001)

Size of prey

Squid size is known to vary throughout the year. Therefore, we compared the mean LRL of the of those common prey species that occurred in all age and sex groups during a limited time (from 22 April 2000 to 19 May 2000) in winter to reduce the influence of variation prey size due to these temporal growth patterns of the individual squid species. Using a one-way linear model in the R package (Ihaka and Gentleman 1996) there were no significant difference in the mean LRL for any of the six common species during this winter observational period. To examine differences in the size of squid eaten by different aged and sex groups, we used two-way GLM and the ANOVA function in the R package (Ihaka and Gentleman 1996).

Minimum sample requirement

As a guide for future diet studies using stomach lavaging in this species, we determined the minimum number of samples required to detect significant age differences in the abundance of prey in their diet. We reasoned that after a number of samples have been compared for each age group, the addition of further samples will not increase the probability of finding a difference between age groups. We took two samples at random from each age group and compared the groups using an ANOSIM. We repeated this 1,000 times, and calculated the number of times that the ANOSIM found a significant difference. We then increased the number of samples taken from each age group by 1 and repeated the process. This was repeated until we reached maximum number of samples within an age group. We were then able to plot the probability of finding a difference at the 5% significance level ($\alpha = 0.05$) between age groups against the number of samples required from each age group.

Results

During their annual moult, as the seals returned in the austral summer, the mean body mass ($\bar{X} \pm \mathrm{SD}$) of juvenile male and female seals ranged from 200 ± 42 kg for 1-year olds, 256 ± 36 kg for 2-year olds and 350 ± 38 kg for 3-year olds. In winter, during their mid-year haul-out, each of the age groups had increased in mass, where mean masses were 210 ± 29 kg for 1-year olds, 316 ± 47 kg for 2-year olds and 438 ± 92 kg for 3-year olds. Overall, the mass of the seals increased significantly between each age group ($F_{(3,123)} = 87.063$, $P > 0.001$) and though male seals were slightly larger than females in each age group they were not significantly different ($F_{(1,123)} = 3.796$, $P = 0.054$).

Overall diet composition

Squid remains were found in all 141 samples and fish remains in 107 samples (76%). The remains of *Gammarid* sp. and *Hyperid* sp. Amphipods were also found in 17% of the stomach samples, although these were partially digested and could not be identified further. The occurrence (presence/absence) of squid and fish remains in the overall diet composition (Table 1) was unaffected by seal age and sex, and season [*Age*: Global $R = 0.009$, significance level of sample statistic (SSS) = 17.3%, number of permuted statistics (NPS) $\leq 0 = 172$; *Sex*: Global $R = -0.007$, SSS = 85.7%, NPS $\leq 0 = 856$; *Season*: Global $R = -0.009$, SSS = 63.6%, NPS $\leq 0 = 635$; Table 1]. Also noteworthy was that no plastic particles were found in any of the samples.

Table 1 The frequency of occurrence of overall diet composition from the stomach contents of juvenile southern elephant seals from Macquarie Island from September 1999 to September 2000

	n	Squid remains	Fish remains	Crustacean	Worms	Sediment
All seals						
Overall	141	100.00	75.89	17.73	85.82	68.79
Females	64	100.00	79.69	20.31	81.25	64.06
Males	77	100.00	72.73	15.58	89.61	72.73
Summer	43	100.00	76.74	6.98	90.70	37.21
Winter	98	100.00	75.51	22.45	83.67	82.65
1 year						
Overall	51	100.00	82.35	27.45	84.31	78.43
Females	28	100.00	92.86	39.29	85.71	82.14
Summer	1	100.00	100.00	0.00	100.00	100.00
Winter	27	100.00	92.59	40.74	85.19	81.48
Males	23	100.00	69.57	13.04	82.61	73.91
Summer	4	100.00	75.00	25.00	75.00	0.00
Winter	19	100.00	68.42	10.53	84.21	89.47
2 year						
Overall	52	100.00	75.00	17.31	86.54	69.23
Females	19	100.00	73.68	5.26	73.68	57.89
Summer	7	100.00	71.43	0.00	85.71	28.57
Winter	12	100.00	75.00	8.33	66.67	75.00
Males	33	100.00	75.76	24.24	93.94	75.76
Summer	6	100.00	100.00	0.00	100.00	50.00
Winter	27	100.00	70.37	29.63	92.59	81.48
3 year						
Overall	38	100.00	68.42	5.26	86.84	55.26
Females	17	100.00	64.71	5.88	82.35	41.18
Summer	14	100.00	64.29	7.14	85.71	35.71
Winter	3	100.00	66.67	0.00	66.67	66.67
Males	21	100.00	71.43	4.76	90.48	66.67
Summer	11	100.00	81.82	9.09	100.00	45.45
Winter	10	100.00	60.00	0.00	80.00	90.00

Squid and fish taxa

Fifteen squid and 17 fish taxa were found, excluding combined genera groups where individual species were identified, within the diet samples (Table 2). The most abundant squid species found in the samples were *A. antarcticus* (~60% of samples), *Slosarczykovia circumantarctica* (~68%) and *Histioteuthis eltaninae* (~80%). Of the fish taxa identified, two genera of Myctophidae were most common, *Electrona* and *Gymnoscopelus* species, and were found in ~11 and ~9% of the samples, respectively. All taxa are known to have either sub-Antarctic or Antarctic distributions (Clarke 1986; Rodhouse et al. 1992; Slip 1995; van den Hoff 2004).

Prey species abundance differences

In each of the four comparisons between sexes (controlling for sample size, season and age, Fig. 2), there were no significant differences in the abundance of prey species between male and female juvenile seals (*1-year olds in winter*: Global $R = 0.069$, SSS = 6.2%, NPS $\leq 0 = 61$; *2-year olds in summer*: Global $R = 0.064$, SSS = 18.8%, NPS $\leq 0 = 187$; *2-year olds in winter*: Global $R = 0.077$, SSS = 15.2%, NPS $\leq 0 = 151$; *3-year olds in summer*: Global $R = -0.008$, SSS = 48.4%, NPS $\leq 0 = 483$). Because there was no sex effect, we pooled the data and tested for a difference between the seasons for each age group. Again, there were no significant seasonal differences within each age group (*1-year olds*: Global $R = 0.102$, SSS = 22.4%, NPS $\leq 0 = 223$; *2-year olds*: Global $R = -0.014$, SSS = 52.0%, NPS $\leq 0 = 519$; *3-year olds*: Global $R = 0.054$, SSS = 17.6%, NPS $\leq 0 = 175$). Because there were no sex or season effects, we pooled all our data to determine if there were significant differences in prey abundance among 1-, 2- and 3-year-old seals. Our analysis showed that there were significant differences observed between the 1-year olds and 2- and 3-year olds (Global $R = 0.148$, SSS = 0.1%, NPS $\leq 0 = 0$; Fig. 3). The three most common species in all the three age groups (accounting for ~80% of the diet) were *A. antarcticus*, *S. circumantarctica* and *H. eltaninae*, although they occurred in different proportions (Table 3). From the SIMPER analyses, five species accounted for ~70% of the dissimilarity between 1-year-old seals and the 2- and 3-year olds. These species in order of importance were *H. eltaninae* (>20%), *S. circumantarctica* (>20%), *A. antarcticus* (>10%), the combined lantern fish taxa of *Electrona* sp. (~7%) and *Psychroteuthis glacialis* (~6%), whereas 1-year-old seals had greater numbers of *S. circumantarctica* and

Table 2 The frequency of occurrence (FoO) of squid and fish prey taxa identified from the stomach contents of juvenile southern elephant seals from Macquarie Island

Prey taxa							
Squid taxa	FoO (%)	*n* samples	*n* beaks	Fish taxa	FoO (%)	*n* samples	*n* otoliths
Alluroteuthis antarcticus[a]	59.86	85	406	*Krefftichthys anderssoni*[a]	0.70	1	1
Brachioteuthis sp.[a]	38.03	54	90	*Protomyctophum choriodon/normani*	0.70	1	1
Slosarczykovia circumantarctica[a]	67.61	96	468	*Electrona* sp.[a] (all sp. combined)	11.27	16	174
Galiteuthis glacialis[a]	25.35	36	54	*Electrona carlsbergi*[a]	3.52	5	13
Gonatus antarcticus[a]	40.85	58	123	*Electrona subaspera*[a]	0.70	1	2
Histioteuthis eltaninae (B1)	79.58	113	945	*E. carlsbergi/E. subaspera*	4.23	6	61
Histioteuthis atlantica (B3)	4.93	7	7	*Gymnoscopelus* sp.[a] (all sp. combined)	9.86	14	83
Kondakovia longimana[a]	12.68	18	42	*Gymnoscopelus bolini*[a]	3.52	5	17
Martialia hyadesi[a]	38.03	54	115	*Gymnoscopelus braueri*[a]	1.41	2	2
Moroteuthis ingens[a]	14.08	20	25	*Gymnoscopelus nicholsi*[a]	0.70	1	2
Moroteuthis knipovitchi[a]	38.73	55	136	*Gymnoscopelus piabilis*[a]	0.70	1	4
Moroteuthis sp.[a]	11.27	16	20	*Icichthys australis*[a]	3.52	5	5
Philidoteuthis boschmai	1.41	2	2	*Paradiplospinus gracilis*[a]	0.70	1	1
Psychroteuthis glacialis[a]	34.51	49	191	*Bathylagus* sp.[a]	0.70	1	1
Taonius pavo	14.08	20	27	*Phosichthys argenteus*	0.70	1	1
Unidentifed species	24.65	35	55	*Magnisudis prionosa*[a]	0.70	1	3
				Nototheniid type	0.70	1	12
				Dissostichus eleginoides[a]	0.70	1	2
				Ebinania macquariensis?	0.70	1	1
				Unidentifed species	13.38	19	149
				Unidentifed species (probably myctophidae)	18.31	26	949

[a] Squid and fish species that are found at or south of the Antarctic Polar front

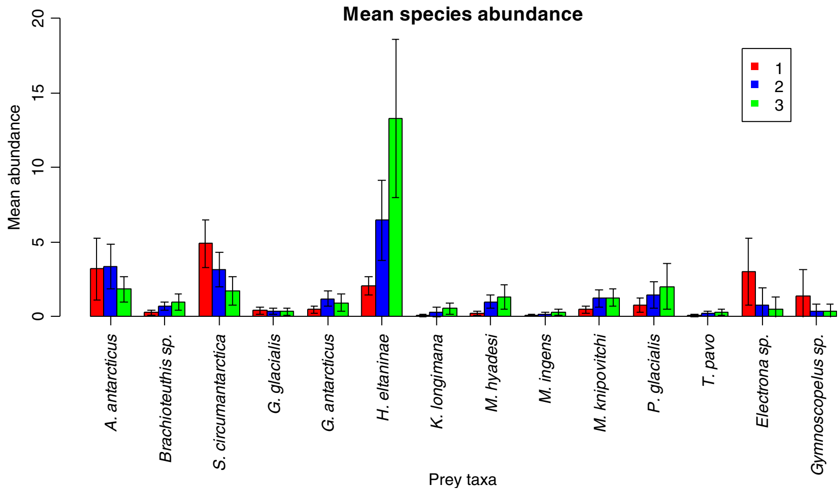

Fig. 3 The species abundance ($\bar{X} \pm 2$ SE) for the common prey species for 1-, 2- and 3-year-old southern elephant seals from Macquarie Island

Electrona sp., but less *H. eltaninae* and *P. glacialis* than 2- and 3-year olds.

Size of squid prey

Lower rostral lengths of the seven squid species found in the diet of all 97 juvenile seals in winter were compared among the three age groups. There were significant differences for only two of the prey species (Fig. 4) in the size of beaks found, with older seals taking larger *Martialia hyadesi* (ANOVA; $F_{(2,38)} = 3.24$, $P = 0.050$). Sex differences (Fig. 5) in size of prey between male and female seals were found for only one prey species, *M. hyadesi*, where males had larger beaks in their samples (ANOVA; $F_{(1,39)} = 6.63$, $P = 0.014$).

Table 3 The mean abundance and percentage contribution of the common prey taxa in the diet of 1- 2- and 3-year-old southern elephant seals

Age	1		2		3	
Species	Mean abundance	% Contribution	Mean abundance	% Contribution	Mean abundance	% Contribution
Alluroteuthis antarcticus	3.14	9.3	3.38	17.53	1.84	6.41
Brachioteuthis sp.	0.29	1.11	0.73	3.63	0.97	1.73
Slosarczykovia circumantarcticus	4.67	54.65	3.15	17.67	1.74	3.6
Galiteuthis glacialis	0.41	1.99	0.38	0.71	0.34	0.35
Gonatus antarcticus	0.47	2.85	1.21	4.29	0.95	1.51
Histioteuthis eltaninae	2.04	19.73	6.46	44.54	13.29	74.25
Kondakovia longimana	0.08	0.01	0.33	0.21	0.55	0.54
Martialia hyadesi	0.24	0.41	1.02	3.61	1.32	4.12
Moroteuthis ingens	0.08	0.04	0.17	0.25	0.32	0.39
Moroteuthis knipovitchi	0.45	1.62	1.23	4.5	1.29	3.34
Moroteuthis sp.	0.2	0.4	0.15	0.1	0.05	0
Psychroteuthis glacialis	0.75	3.19	1.46	2.29	2.03	3.15
Taonius pavo	0.08	0.03	0.21	0.16	0.32	0.51
Electrona sp.	3.69	3.66	0.81	0.41	0.53	0.03
Gymnoscopelus sp.	1.45	0.99	0.38	0.09	0.37	0.07

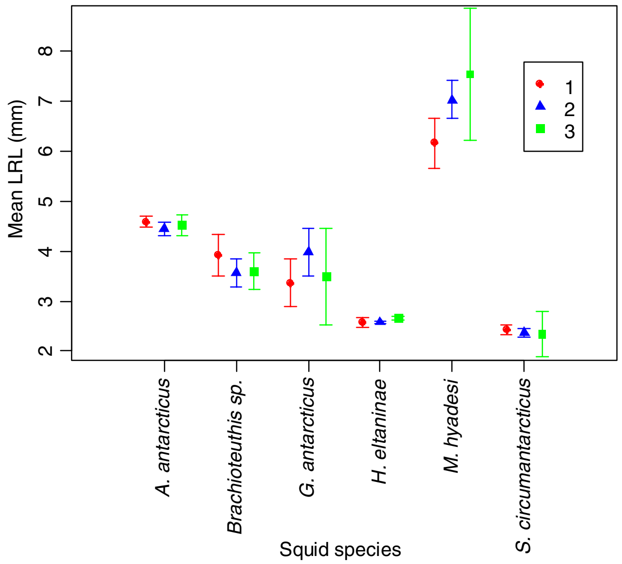

Fig. 4 Differences in LRL $(\bar{X} \pm 2\,\mathrm{SE})$ for the common squid species found in the stomachs of 1-, 2- and 3-year-old southern elephant seals from Macquarie Island

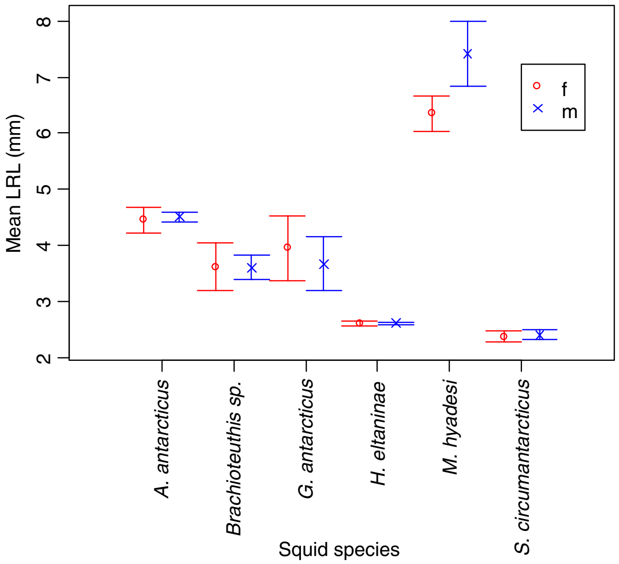

Fig. 5 Differences in LRL $(\bar{X} \pm 2\,\mathrm{SE})$ for the common squid species found in the stomachs of male and female southern elephant seals from Macquarie Island

Minimum sample required

There was a clear asymptote in the curve for the number of samples needed to find a significant difference (randomised ANOSIM; Fig. 6). After including 13 random samples from each age group, the probability of finding a significant difference ($SSS < 0.05$) between the groups was 95%. By comparing 15 samples there was a 99% probability of finding a significant difference.

Discussion

Southern elephant seals are deep-diving opportunistic, generalist feeders, and this particular foraging strategy may have evolved as a result of the dynamic and unpredictable seasonal and spatial distribution and abundance of target prey within the Southern Ocean. This species shows a high degree of dimorphism, with adult females and males being at least 10 and 100 times greater in mass than newborns. Assuming that re-

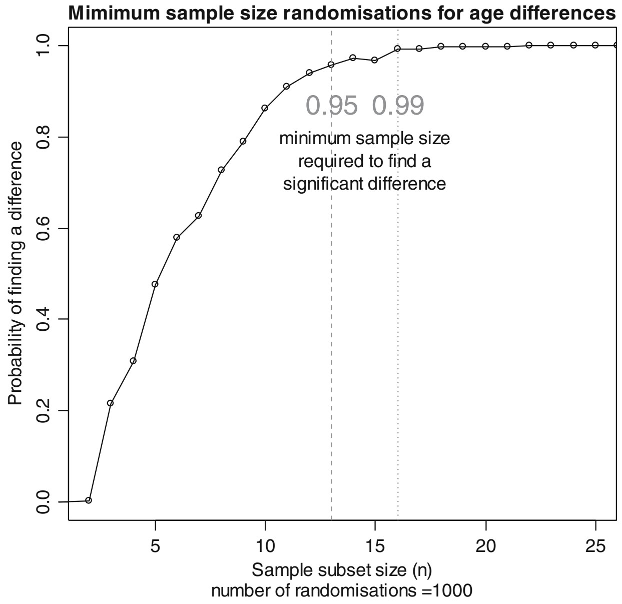

Fig. 6 The minimum number of samples required to find a significant difference ($P > 0.05$ and > 0.01) among 1-, 2- and 3-year-old southern elephant seals using a randomised selection of samples from our data

sources are limiting, however, one might expect that behavioural shifts among different 'ecological' species or sub-groups within the species would lead to a reduction in intra-specific competition for food resources (Polis 1984; Bolnick et al. 2003; Takimoto 2003; Field et al. 2005a). There are clear differences in diet among the 1-, 2- and 3-year-old seals, in terms of both species abundance and prey size, but no sex or season effect. These differences are most likely due to an increased diving ability, with increased body size and foraging range as the seals grow. The similarity in body size between same age male and females may be the primary reason for no sexual differences in the diet. Furthermore, a lack of a sex difference indicates that these dietary changes are not driven by differing metabolic requirements between the sexes (Field et al. 2005b). Therefore, dietary changes appear to be a function of ontogenetic changes in foraging capacity and range, regulated by physiological limitations and seasonal haul-out patterns (Field et al. 2005a). However, with a lack of information on prey distribution, the real reasons for age differences remain unclear.

As with many other species (Adams 1996; Wikelski and Wrege 2000; Spina 2000), an increase in size with age influences the ability of an individual to obtain prey and expand its foraging niche (Polis 1984; Radloff and Du Toit 2004). As seals grow, there are changes in the physiological diving abilities that allow older, larger individuals to dive deeper and longer (Le Boeuf et al. 1996; Burns 1999; Hindell et al. 1999; Irvine et al. 2000). Thus, older individuals that can remain at deeper depths longer have greater access to deeper-dwelling species. Our results show a clear change in the composition of diet among juvenile seals. The older seals have greater proportions of the larger squid in their samples (*Kondakovia longimana*, *M. hyadesi*, *Moroteuthis ingens* and *Moroteuthis knipovitchi*), which may not have been available to the smaller individuals. Indeed, there is some evidence for pelagic cephalopods that older and larger individuals are capable of more extensive vertical migrations (Jackson 1993; Arkhipkin and Bjørke 1999).

However, there was no difference in the size of most other prey species ingested. Therefore, differences in prey composition among age groups could also be due to variation in foraging range that appears to be regulated, in part, by variation in seasonal haul-out patterns according to age (Field et al. 2005a). This regulation appears to occur independently of dispersal capacity, because different age classes demonstrate similar rates of travel (Field et al. 2005a). Although our results only represent the diet as the seals return to the island, it appears that variation in foraging and haul-out behaviour in conjunction with modification of diet composition all contribute to a general reduction in intra-specific competition for this wide-ranging Antarctic marine predator.

Other studies of elephant seal diet have shown differences between juveniles and adults (Green et al. 1998; Slip 1995), although the nature of these differences were inconsistent. Slip (1995) found that juveniles were different from both male and female adults, while Green et al. (1998) found only differences between juveniles and adult females that could not be readily explained. Only one other study has specifically tested for differences among size/age classes, but the results were inconsistent and no trends were found (Rodhouse et al. 1992).

Three species dominated the diet, although there were distinct differences between the different age groups. The diet of 1-year-old seals was dominated by *S. circumantarctus*, a small muscular squid (to around 150 mm; Lipinsky 2001) with a broad Southern Ocean distribution (Cherel et al. 2004). In contrast, the 2- and 3-year olds' diets were dominated by the slightly smaller *H. eltaninae* (to around 100 mm; Voss et al. 1998), which has a sub-Antarctic distribution (Cherel et al. 2004). Furthermore, the diet of 2-year olds, though not statistically significantly different from that of 3-year olds, was intermediate between the younger and older seals. Although little is known about the distribution of the main prey species, there is the potential that temporal and spatial movements of the prey species could influence the diet of the seals. All common prey species were found in the diets of all age groups throughout the year, and there were no seasonal differences in prey species abundance from our ANOSIM and SIMPER analyses. Therefore, although we do not discredit that there may be some variation in prey species abundance, it would seem likely that the differences we have observed are due to the different feeding strategies of the juvenile seals through differences in prey availability. Availability could be influenced by whether they are a solitary or schooling species, or by the relative costs of catching prey (for example, a slow swimming species verses a cryptic fast swimming species). For the larger squid species commonly found in the diet of the different age groups in winter, *M. hyadesi* (around 400 mm; Roper et al. 1984), the size of prey also increased with age. Only the larger seals may have been able to forage deeper and catch these larger prey, thereby increasing the range of prey sizes available and their foraging niche (Jackson et al. 2004; Radloff and Du Toit 2004). However, also important is the increase in the abundance of *H. eltaninae* as the seals get older. The reasons for this increase are unclear but, as with the increase in larger squid, are most likely due to the distribution of the prey species, which at present is unknown but could be inferred from fine scale studies of the seals diving and foraging behaviour.

There is a suite of methods available for the determination of diet, including direct and indirect observation, genetic sampling (Symondson 2002; Jarman et al. 2002), fatty acid signature analyses (Brown et al. 1999; Bradshaw et al. 2003; Iverson et al. 2004), stable isotope analyses (Iverson et al. 2004; Hooker et al. 2001), and through the study of remains in faecal and stomach contents (Santos et al. 2001). All these methods have advantages and disadvantages, but it is only through the direct analysis of prey remains that can we determine both species identity and ecological information (such as size structure) about the prey. Furthermore, our use of a novel approach to determine the minimum sample required to find a difference has given greater confidence to our results and provides some guidance for future studies using this technique to minimise disturbance and the impact of dietary studies.

In our study, we lavaged the stomachs of the seals as soon after their return as possible, however, these samples are only representative of their foraging as they return to Macquarie Island (Fig. 1) and not their entire foraging areas. Elephant seals have a rapid rate of digestion (~13 h; Krockenberger and Bryden 1994), although hard parts of the prey may be retained in the stomach for over 7 days (Tollit et al. 1997). Therefore, our samples are likely to have come from within 700 km of the island, using 100 km day^{-1} as the rate of travel by juvenile seals (Field et al. 2005a). This was reflected in the reduced abundance of Antarctic species in their diets. The results may also over-estimate the presence of prey with larger hard parts due to differential digestive rates (Daneri and Carlini 2002). Furthermore, some of the prey remains in our samples may have been from secondary ingestion (Arnett and Whelan 2001). From the few diet studies of squid found in the Southern Ocean (Phillips et al. 2003), it is clear that they are voracious predators that eat fish and squid and show seasonal differences in their diet.

Squid and fish, including some commercially taken species (Burton and van den Hoff 2002), are the main prey of southern elephant seals (Rodhouse et al. 1992; Green et al. 1998; Slip 1995; Danieri et al. 2000; Piatkowski et al. 2002; Bradshaw et al. 2003; van den Hoff et al. 2003; van den Hoff 2004), although the variation in their relative proportions is less well-known (Santos et al. 2001) for ecological and methodological reasons (Bradshaw et al. 2003). As in other diet studies of Macquarie Island juvenile elephant seals (1–4 years old, Green et al. 1998; 1-year olds, van den Hoff 2004), squid are the primary prey, however, the occurrence of fish remains found in our study (all age groups ~76%) were higher than in previous studies where fish were found in only 10% of samples (Green et al. 1998). This difference is likely to be due to the inter-annual variability in the availability of fish prey as suggested by Danieri et al. (2000).

Compared to previous studies (Green et al. 1998; van den Hoff 2004), the fish component of our juvenile diet sample contained many more fish species from pelagic, demersal and benthic habitats, including the Patagonian Toothfish (*Dissostichus eleginoides*) and the *Ebinania macquariensis*, an endemic benthic species only found around Macquarie Island (Williams 1988). The main difference, however, is the dominance of the squid *S. circumantarcticus*, which contributed ~55% of the total number of beaks in our samples, but only ~6% in Green et al. (1998). Other differences include a reduction in *H. eltaninae* (~12% compared to ~20% in our study) and *A. antarcticus* and *M. knipovitchi* (~30 and 12%, respectively, compared to 9 and 1.6%, respectively, in our study). These species are all commonly found south of the Polar Front (except *H. eltaninae*), therefore, these differences may result from a change in prey species availability among years due to inter-annual variation in the position or strength of water mixing at the Polar Front (Antonelis et al. 1994).

Although our data only represent the end of the foraging trip, there were clear age-related differences in diet, though it still remains unclear as to the proportions of fish and squid that are eaten while farther away at sea. As the stomach contents are likely to have been collected in broadly similar geographic regions (and there was no evidence of seasonal changes in diet composition), these differences must relate to some intrinsic difference in the seals (i.e. size; Radloff and Du Toit 2004). The intra-specific differences in diet composition linked with the increased foraging ranges with age (Field et al. 2005a) provide further evidence to support the hypothesis that ontogenetic niche expansion acts to reduce intra-specific competition. However, the diet composition varies with age and spatially, which needs to be addressed using the suite of dietary tools currently available to gain a better understanding of the dynamic ecological niche of this apex predator.

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