

**Authors**

G J Greg Hofmeyr<sup>1,2</sup>, Marthán N Bester<sup>1</sup>, Steve P Kirkman<sup>1,3</sup>, Christian Lydersen<sup>4</sup> and Kit M Kovacs<sup>4</sup>

**Title**

Intraspecific differences in the diet of Antarctic fur seals at Nyrøysa,  
Bouvetøya

**Affiliations and addresses**

<sup>1</sup>. Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

<sup>2</sup>. Current address: Port Elizabeth Museum at Bayworld, P.O.Box 13147, Humewood 6013, South Africa

<sup>3</sup>. Current address: Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, South Africa

<sup>4</sup>. Norwegian Polar Institute, Polar Environmental Centre, 9296 Tromsø, Norway

**Corresponding author**

Greg Hofmeyr

Email            greg@bayworld.co.za

Tel                +27 41 584 0650

Fax                +27 41 584 0661

## ABSTRACT

Intraspecific differences in the diets of many species of pinnipeds are to be expected in view of the great differences in morphology, life history and foraging behaviour between the sexes of many species. We examined the diet of the Antarctic fur seal population at Bouvetøya, Southern Ocean to assess intersexual differences. This was made possible by the analysis of prey remains extracted from scats and regurgitations collected in areas used primarily by one or the other sex. The results indicate that both males and females feed primarily on Antarctic krill *Euphausia superba* with several species of fish and squid being taken, likely opportunistically given their prevalence. Significant differences were identified in the frequency of occurrence of otoliths in scats and the percentage numerical abundance of the major fish prey species in the diet. Adult males ate a smaller quantity of fish overall, but ate significantly more of the larger fish species. The greater diving capabilities of males and the fact that they are not limited in the extent of their foraging area by having to return regularly to feed dependant offspring may play a role in the differences found in the diets of males and females. Additionally, females might be more selective, favouring myctophids because they are richer in energy than krill. The absence of major differences in the diet between the sexes at this location is likely due to the high overall abundance of prey at Bouvetøya.

## KEYWORDS

Antarctic fur seal, diet, Southern Ocean, intersexual differences

## INTRODUCTION

Otariids are characterised by extreme sexual dimorphism (Lindenfors et al. 2002) with differences in body mass ranging from adult males being on average twice that of adult females in Hooker's sea lions *Phocarctos hookeri* to more than five times greater in Northern fur seals *Callorhinus ursinus* (Bininda-Emonds and Gittleman 2000). The life histories of the sexes also differ greatly, with females maturing earlier than males and living longer (Bester 1987; Butterworth et al. 1995; Lander 1981; McCann and Doidge 1987; Payne 1977; Trillmich 1987; Warneke and Shaughnessy 1985). The larger males have both a greater diving capacity than females, and generally forage at greater depths, and should be able to capture larger prey more easily (Meynier et al. 2008; Page et al. 2005b; Page et al. 2006; Staniland and Robinson 2008). Furthermore, adult female otariids are more restricted in the size of their potential foraging areas than males for a major portion of the year, because of the necessity of returning to a dependant pup during the nursing period which lasts many months (Meynier et al. 2008; Page et al. 2005b; Page et al. 2006; Staniland and Robinson 2008). These factors are likely to result in differences in the diets of males and females.

Antarctic fur seals *Arctocephalus gazella* are typical of otariids in their degree of sexual dimorphism with adult males being on average 4.2 times heavier than females (Boyd and Duck 1991; Lunn and Boyd 1993). Males of this species have a very different life history compared to females, with differences in their behaviour being particularly notable during the austral summer. From late October until early January adult males come ashore to defend territories (Bonner 1968; Duck 1990; Kerley 1983; Payne 1977), staying ashore for a little less than a month (Arnould and Duck 1997). A second peak in haulout numbers of males occurs in late January and early February, when they return to moult after a period at sea (Kerley 1983; Page

et al. 2003). Adult females come ashore to pup during late November and in December (Bonner 1968; Duck 1990; Kerley 1983; Lunn and Boyd 1993; Payne 1977). They spend approximately a week ashore, during which time they give birth and subsequently mate (Boyd 1999; Duck 1990; Lunn and Boyd 1993). Following this time ashore they alternate between periods of 1-10 days at sea foraging and periods of 1-3 days ashore attending the pup (Boyd et al. 1991; Guinet et al. 2000) until the pup is weaned at approximately 4 months of age (Doidge et al. 1986; Kerley 1983; Payne 1979). Differences in foraging behaviour between the sexes have been shown to exist in this species; adult males at both South Georgia and Heard Island generally forage at different locations to females and dive deeper and for longer than females, and do so for a greater portion of the day (Boyd et al. 1998; Green 1997; Staniland and Robinson 2008). However, no studies have compared the diets of adult male and female Antarctic fur seals to explore the impacts of these observed differences in foraging behaviour of the sexes.

Bouvetøya (54° 26' S., 03° 24' E.) supports the second largest breeding population of Antarctic fur seals in the world, with some 15 000 pups born annually (Hofmeyr et al. 2005). The great majority of these seals haul out on a coastal platform known as Nyrøysa. During the breeding season, the largest breeding aggregations are found on a large, relatively flat section of beach known as Norstrand. This area, where the majority of pups are born, is referred to hereafter as the main colony (or abbreviated as MC). Norstrand is backed to the south and inland by rough slopes (hereafter SL), which are also occupied by seals. A second relatively flat beach, Sørstrand (abbreviated as SS), is found at the southern end of Nyrøysa. There is considerable sexual segregation in these terrestrial habitats, with adult females dominating MC, while adult males are far more numerous at SS; SL is a mixed site preferred by juvenile animals. This allows for the collection of scats that are likely produced by a particular sex. We used this opportunity to examine the differences in the diet between adult male and female Antarctic fur seals at Bouvetøya.

## METHODS

### *Fur seal numbers*

The proportion of Antarctic fur seals of the various age and sex classes was determined on four occasions at MC, and on five occasions each at SS and SL. Seals within an approximate four metre radius of each scat in each class were counted prior to disturbance. Each animal was assigned to one of five age and sex classes (adult male, adult female, subadult male, subadult, pup) by an experienced observer based on criteria detailed in Bester (1987)

### *Scat collection and analysis*

Scats were collected on seven occasions at approximately weekly intervals, starting on the 20<sup>th</sup> of December 2001 and ending on the 7<sup>th</sup> of February 2002. Collections took place at three different sites: MC, SL and SS (Figure 1). Only fresh, entire, undisturbed scats were collected. Scats were collected individually in plastic bags and kept at an ambient temperature of approximately 5° C. until mid February. Thereafter scats were kept frozen until processing.

Scats were thawed just prior to processing and then strained individually through a 0.5 mm aperture diameter sieve. Krill remains were noted but not retained since they were too heavily digested to be useful in

further analysis. Squid beaks seen during the straining process were removed. After straining, all remaining material was air dried or slow dried in an oven at temperatures of less than 50° C. All remaining squid beaks and all fish otoliths were then removed. Prey remains were identified under a dissecting microscope with the aid of Reid (1996), Smale et al. (1995), and Williams and McEldowney (1990). Prey remains were quantified using four measures: (1) percentage frequency of occurrence (% FO) recorded the proportion of scats containing squid beaks or otoliths of a particular prey species, or krill exoskeletons, (2) percentage numerical abundance (% NA) recorded the percentage of retained prey items of each species compared to the total number of retained prey items, (3) prey items per scat (PI/S) recorded the mean number of retained prey items (i.e. otoliths and squid beaks) per scat containing retained prey items, and (4) prey item length. For the latter, the diameters of uneroded otoliths were measured using a micrometer. Prey length and mass of the most commonly consumed prey species were reconstituted using regressions published in Williams and McEldowney (1990).

#### *Regurgitation collection and analysis*

Subsamples of fresh regurgitations, comprising almost exclusively of entire krill, were collected opportunistically. Each regurgitation sample was collected in a plastic bag, with care being taken to avoid crushing the contents. Regurgitations were transferred into a plastic vessel containing 70 % alcohol within a few hours of collection and stored in these containers until analysis. The krill species was identified following Kirkwood (1982). Whole individual krill were measured using the total length from anterior margin of the eye to the posterior tip of the telson (Morris et al. 1988). Due to the subsampling of regurgitations and the paucity of prey other than krill being found, no numerical counts of prey items were completed for these samples.

## RESULTS

A total of 210 scats were collected over the seven weeks of sampling, 70 from each location. 108 regurgitations were collected from MC, 42 from SS and none from SL.

#### *Fur seal numbers*

For determining age and sex class distribution of seals, a total of 306 animals excluding pups were counted at MC, 152 at SL and 166 at SS. The distribution of these categories varied significantly between sites (Figure 2,  $G_H = 375.4$ ,  $df = 6$ ,  $p < 0.01$ ). MC was dominated by adult females (60.5 % of seals, excluding pups) while SS was dominated by adult males (86.7 %). A more even distribution between age and sex categories was found at SL, with the dominant age classes being immatures (44.1 %) and adult females (30.3 %).

#### *Frequency of occurrence*

All scats collected at MC, 98.6 % from SL and 97.1 % from SS contained krill exoskeletons (Figure 3). There was no significant difference in % FO of krill between the sites ( $X^2 = 2.03$ ,  $df = 2$ ,  $p > 0.05$ ). Otoliths were found in 55.7 % of scats from MC, 50 % of scats from SL, and only 24.3 % of scats from SS; these differences are statistically significant ( $X^2 = 16.0$ ,  $df = 2$ ,  $p < 0.01$ ). Approximately twice as many scats from

SL (20 %) contained squid beaks compared to MC (11.4 %) or SS (10.0 %), but these differences were not statistically significant ( $X^2 = 2.03$ ,  $df = 2$ ,  $p > 0.05$ ).

#### *Prey items per scat*

The mean PI/S was 9.6 ( $\pm 12.3$ ) for MC, 7.6 ( $\pm 12.3$ ) for SL and 7.8 ( $\pm 7.1$ ) for SS. These values were not significantly different (Kruskal-Wallis:  $H(2, N=96) = 1.34$ ,  $p = 0.51$ ). When considered independently, no significant difference was found between locations in either the mean number of otoliths per scat containing otoliths (Kruskal-Wallis:  $H(2, N=91) = 3.02$ ,  $p = 0.22$ ) or the mean number of squid beaks per scat containing squid beaks (Kruskal-Wallis:  $H(2, N=29) = 1.22$ ,  $p = 0.54$ ).

#### *Numerical abundance*

Non-krill prey items retained for identification (N=812) were primarily fish otoliths (92.6 %), with the remainder being squid beaks (7.4%). The species identity of all but 22 otoliths and 17 squid beaks was established. Twelve species of fish were identified. Together the three most common fish species contributed almost nine tenths of the % NA of non-krill prey items from all sites on Nyrøysa: *Electrona antarctica* (62.2 %); *Gymnoscopelus nicholsi* (13.2 %); and *G. braueri* (11.1 %). The remains of two species of cephalopods were identified in the scats; *Brachioteuthis riisei* was the most common squid, comprising 4.8 % to the total non-krill prey, while *Moroteuthis knipovitchi* comprised 0.6 % (Table 1).

Percentage numerical abundances of the four most common prey species (*E. antarctica*, *G. nicholsi*, *G. braueri* and *B. riisei*) were compared between sites while grouping the % NA of all other species and unidentified remains as “other”. Differences in the distribution of non-krill prey species between sites (Figure 4) were significant ( $G_H = 50.9$ ,  $d.f. = 10$ ,  $p < 0.01$ ). *E. antarctica* was the dominant non-krill prey at all locations making up two thirds of the non-krill part of the diet at both MC (62.9 %) and SL (69.0 %), but only approximately half of the non-krill prey at SS (47.7 %). The second most common fish species was *G. nicholsi* which occurred at similar levels in the diet at all sites (12.3 % at MC, 12.5 % at SL and 16.8 % at SS). *G. braueri* occurred at similar relative abundance levels at MC (13.3 %) and SS (19.5 %), but few were found at SL (3.6 %). *B. riisei* was the fourth most common species for both MC (3.4 %) and SS (4.7 %), while this species was more common than *G. braueri* at SL (7.2 %). All other species (*E. carlsbergi*, *G. bolini*, *G. piabilis*, *Krefflichthys andersoni*, *Metelectrona ventralis*, *Protomyctophum tenisoni*, *P. choriodon*, *Lepidonotothen larseni*, *Notolepsis coatsi* and *Moroteuthis knipovitchi*) were found only in small amounts ( $\leq 2\%$ NA).

#### *Reconstituted length and mass of prey remains*

Regurgitations, and therefore measurements of krill, were only acquired from MC and SS. Only Antarctic krill *Euphausia superba* were found in regurgitations. The mean ( $\pm$  SD) body length of krill from MC was  $51.0 \pm 4.9$  mm, while that from SS was  $51.4 \pm 3.7$  mm. No significant difference in length was found between these two sites (Kolmogorov-Smirnov,  $n_1 = 108$ ,  $n_2 = 42$ ,  $p > 0.05$ ).

Otolith lengths were compared within each of the three species found in large enough sample sizes at more than one site. No difference was found between the three sites in otolith lengths of *E. antarctica* (Kruskal-

Wallis:  $H(2, N = 268) = 2.41, p = 0.30$ ) or *G. nicholsi* (Kruskal-Wallis:  $H(2, N = 78) = 1.54, p = 0.46$ ). Since only nine *G. braueri* otoliths were found at SL, this site was excluded from comparisons for this species. No difference was found between the lengths of otoliths at MC and SS for *G. braueri* (Kolmogorov-Smirnov,  $n_1 = 28, n_2 = 25, p > 0.05$ ).

The mean reconstituted length for *E. antarctica* at all sites was 81.0 mm ( $\pm 8.9$ ) while the mean reconstituted mass was 7.5 g ( $\pm 2.6$ ). For *G. braueri* the values for these measurements were 83.1 mm ( $\pm 10.4$ ) and 5.3 g ( $\pm 2.2$ ) while for *G. nicholsi* they were 125.2 mm ( $\pm 10.3$ ) and 23.6 g ( $\pm 6.2$ ).

## DISCUSSION

Many marine vertebrates inhabiting the Southern Ocean feed primarily on Antarctic krill, including most populations of Antarctic fur seals (Caseaux et al. 1998; Daneri 1996; Daneri and Coria 1992; Daneri and Coria 1993; Daneri et al. 1999; Osman et al. 2004; Reid 1995; Reid and Arnould 1996). Only the small Antarctic fur seal populations living in the Indian section of the Southern Ocean, which comprise less than 1 % of global abundance (Hofmeyr et al. 2005), have diets dominated by fish and squid (Green et al. 1989; Green et al. 1991; Klages and Bester 1998; Makhado 2008). The diet of Antarctic fur seals at Bouvetøya in the austral summer of 2001/02 was clearly dominated by Antarctic krill, as was the case in the summers of 1996/97 and 1998/99 (Kirkman et al. 2000; Klages et al. 1998). A number of species of fish and cephalopods are also consumed at this location, but they form a minor part of the diet and are likely eaten opportunistically (Kirkman and Bester 1999). Despite this, differences between the sexes in the composition of their diets might well be important in indicating differences in the foraging behaviour (Kirkman and Bester 1999).

Although the results should be interpreted with caution, since the sites MC and SS were only dominated by, and not exclusively inhabited by, particular sex and age classes, this study indicates that the diet of Antarctic fur seals at Bouvetøya differs between the sexes when prey other than krill are considered. During the summer of 2000/2001 adult males consumed fewer fish than females, with half as many scats at the male dominated site containing otoliths compared to scats at other sites. The mean number of otoliths did not differ, however, between scats that contained these items at male and female dominated sites. While three species of fish comprised most of the non-krill prey at all sites, the relative numbers of these species differed significantly between the sexes. Reconstituted individual prey mass showed that adult males ate proportionately more of the larger species (*G. nicholsi*), which had a mean body mass three and five times that of the other two fish species.

Other studies have also reported intersexual differences in the diet of other species of pinnipeds, both among otariids (Castley et al. 1991; Lewis et al. 2006; Meynier et al. 2008; Page et al. 2005b; Page et al. 2006; Trites and Calkins 2008) and phocids (Beck et al. 2005; Beck et al. 2007; Breed et al. 2006; Field et al. 2007). Differences between the diets of males and females have been ascribed to three factors: (1) reducing dependence on prey species where individuals might face competition from the other sex (Breed et al. 2006; Castley et al. 1991; Field et al. 2007; Lewis et al. 2006; Page et al. 2005b; Page et al. 2006), (2) different dietary requirements of males and females (Beck et al. 2007; Breed et al. 2006; Page et al. 2005a; Page et al.

2005b), and (3) different foraging capabilities of males and females (Beck et al. 2007; Field et al. 2007; Page et al. 2005a; Page et al. 2005b; Page et al. 2006). These hypotheses are not mutually exclusive and all three might play a role at Bouvetøya.

While it is possible that adult males feed further from Bouvetøya than the more restricted adult females to avoid competing with them, it seems unlikely that intersexual competition is a major factor at this site. The population of Antarctic fur seals at Bouvetøya increased rapidly until the mid 1990's, suggesting that prey was abundant (Hofmeyr et al. 2005). Pup production has stabilized during the five years prior to the collection of scats for this study. However, this is numerical levelling off is likely a reflection of habitat-mediated density-dependent pup survival, rather than prey availability, as the mean duration of foraging trips at this colony by adult females is short (Biuw et al. 2009) and the growth rates of pups (Norwegian Polar Institute, unpublished data) are similar to, or higher than, those of Antarctic fur seals at other sites (Croxall et al. 1988; Doidge et al. 1986; Kirkman et al. 2003; Walker and Boveng 1995), while beach space is clearly limited, and has declined due to recent land-slides.

Most of the fish prey caught by Antarctic fur seals at Bouvetøya are small myctophids, which are more energy dense (5.6 – 8.0 kJ/g) than Antarctic krill (4.2 – 4.35 kJ/g) (Cherel and Ridoux 1992; Clarke and Prince 1980; Doidge and Croxall 1985; Guinet et al. 1996). Because they are larger, male fur seals require a greater absolute energy input than females and are therefore expected to either consume more food or consume higher quality food (Beck et al. 2007). One would therefore expect males to select myctophids. Adult male New Zealand fur seals *A. forsteri* have a more specialized diet than adult females and eat prey with a higher energy content (Page et al. 2005a). Lactating females, however, must provision not only themselves but also dependant offspring; adult female fur seals are known to have an elevated feeding rate during lactation, which is estimated to be 1.6 times that of non-lactating adult females in northern fur seals *Callorhinus ursinus* (Perez and Mooney 1985). Lactating adult females also require a considerable protein intake when provisioning pups (Page et al. 2005a) which might be a factor in the bias towards selection of myctophids by females which have a higher protein content than krill (Clarke and Prince 1980). Adult female Antarctic fur seals might follow the same pattern as grey seals, in which adult females select prey species of a higher quality than those selected by males (Beck et al. 2007). On the other hand, the small but significant difference in consumption of energy rich myctophids might possibly simply reflect a difference in foraging habitats of the sexes around Bouvetøya.

Adult female Antarctic fur seals dive mostly during the late afternoon and night, taking advantage of the diurnal, vertical migration of krill (Biuw et al. 2009). This pattern is similar to what has been observed at South Georgia (Boyd et al. 1998; Staniland and Robinson 2008). Adult males at South Georgia, however, dive mostly during the day; their deeper diving capabilities are thought to allow them to reach krill at the increased depths that they inhabit during daylight hours. It is likely that adult male Antarctic fur seals at Bouvetøya are similarly less restricted in their vertical and temporal foraging habitat than females. In addition, males should also be less restricted in their horizontal foraging habitat, since they do not have to return frequently to the colony to feed dependent pups. Exploiting a marine environment that is generally inaccessible to females may therefore result in different fish encounter rates between males and females.

Ultimately, it is not known why males do not select the most energy rich prey available at Bouvetøya, especially since they face fewer restrictions to their foraging behaviour than do females. Further research on intersexual dietary differences of Antarctic fur seals at Bouvetøya, both from traditional scat analysis and from fatty acid studies, in addition to studies of foraging behaviour, is required to shed light on this observation.

Trites and Calkins (2008) found that the diets of Steller sea lions of different sex and age classes differed sufficiently from one another to prohibit using scats from sites inhabited by bachelor males as a proxy for the diet of all age classes combined, and therefore for calculating the estimated food consumption for the entire population. This is not a concern at Bouvet, however, because the diets of all age and sex classes other than pups are heavily dominated by krill; Kirkman et al. (2000) estimated that krill formed some 97.5 % of diet by biomass at this site in the 1998/99 summer. This value would not change appreciably if the diets of adult males and adult females were calculated separately. It is, on the other hand, possible that the dominance of krill and high overlap between the diet of the sexes will change in future years. Greater competition in years with higher food stress might force a change in the diet of one or both sexes.

Future changes in diet are likely given the recent decline in the abundance of Antarctic krill (Atkinson et al. 2004). While no commercial fishing for krill has taken place in waters around Bouvetøya over the last ten years (CCAMLR 2009), the possible effects of future fishery activities (Constable et al. 2000) and climate change (Thompson and Solomon 2002; Turner et al. 2005) are important. Differences in the diet of male and female seals mean that indicators of change in prey populations may be more discernible in one or the other sex. This supports further monitoring of the diet of the two sexes separately where possible. Furthermore, while the foraging behaviour of adult females is monitored at various sites as part of the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) Ecosystem Monitoring Programme (CEMP; (Agnew 1997; CCAMLR 2004; Constable et al. 2000), the differences in the ways that males and females exploit their marine environment indicate that the foraging behaviour of males should also be monitored.

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#### ETHICAL STANDARDS

The experiments reported on in this publication comply with current Norwegian and South African law.

#### CONFLICT OF INTEREST

We declare no conflict of interest in the completion of this study.



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## CAPTIONS

**Fig. 1 a** Outline of Bouvetøya showing the location of Nyrøysa, the Antarctic fur seal *Arctocephalus gazella* breeding rookery. **b** Location of scat collection sites on Nyrøysa. MC, SL and SS are abbreviations for sites known as the Main Colony, the Slopes and Sørstrand respectively.

**Fig. 2** Percentage of different age and sex categories of Antarctic fur seals *Arctocephalus gazella* found at three different locations at Nyrøysa, Bouvetøya, December 2001 – February 2002. MC, SL and SS are abbreviations for locations known as the Main Colony, the Slopes and Sørstrand respectively. Seals aged less than one year are excluded here.

**Fig. 3** Percentage frequency of occurrence (% FO) of the remains of prey in the scats of Antarctic fur seals *Arctocephalus gazella* at three locations on Nyrøysa, Bouvetøya, December 2001 – February 2002. MC, SL and SS are abbreviations for locations known as the Main Colony, the Slopes and Sørstrand, respectively.

**Fig. 4** Percentage numerical abundance (% NA) of squid beaks and fish otoliths recovered from the scats of Antarctic fur seals, *Arctocephalus gazella*, collected at three locations on Nyrøysa, Bouvetøya, December 2001 – February 2002. MC, SL and SS are abbreviations for sites known as the Main Colony, the Slopes and Sørstrand, respectively.

**Table 1** Prey species identified from remains recovered in the scats of Antarctic fur seals *Arctocephalus gazella* from three different sites at Nyrøysa, Bouvetøya, from December 2001 – February 2002. MC, SL and SS are abbreviations for sites known as the Main Colony, the Slopes and Sørstrand, respectively.

FIGURES

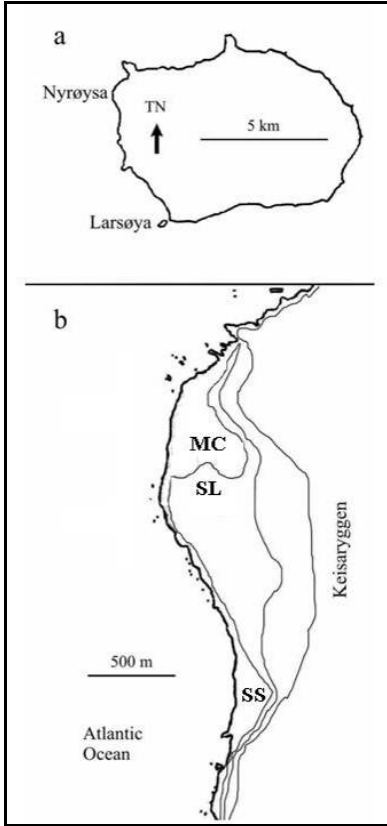


Fig. 1

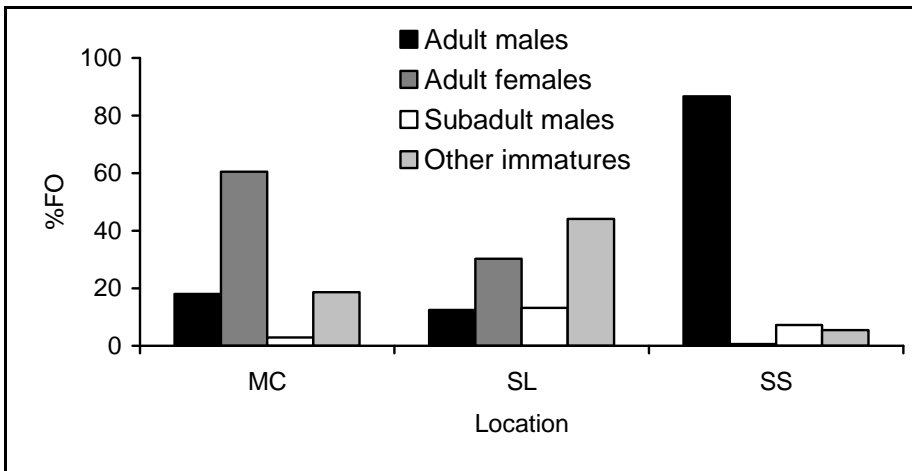


Fig. 2

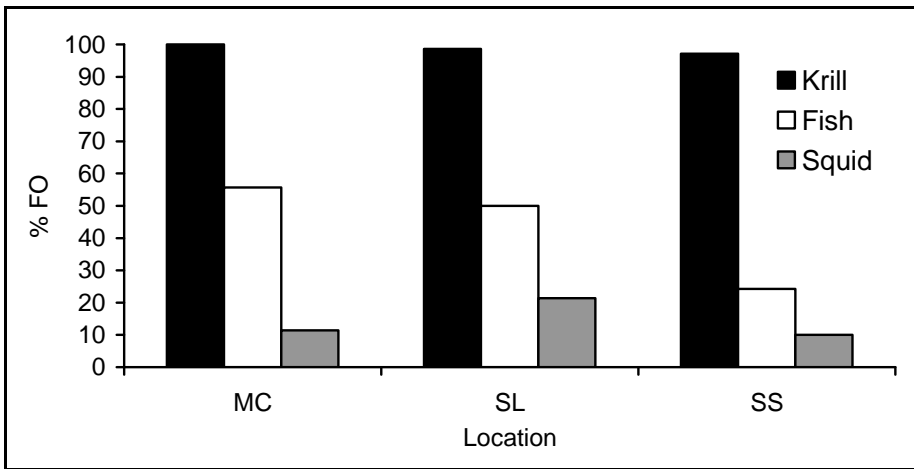


Fig. 3

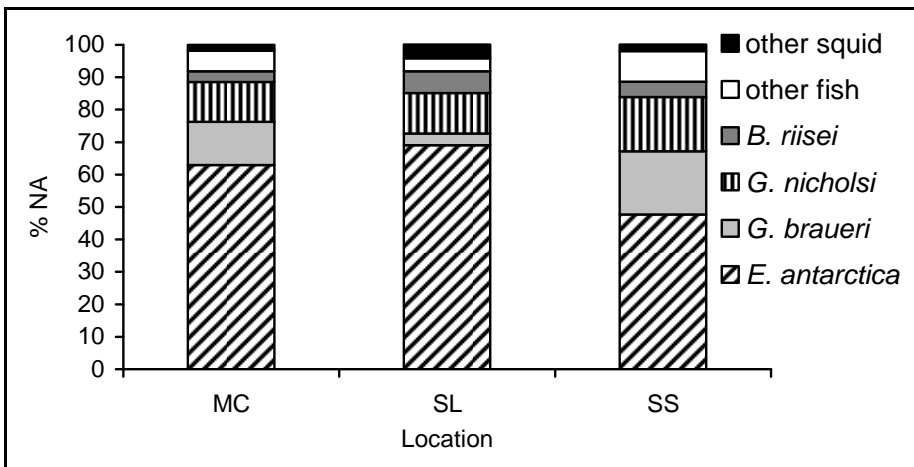


Fig. 4

Table 1

	Percentage frequency of occurrence			Percentage numerical abundance		
	MC	SL	SS	MC	SL	SS
Krill species						
<i>Euphausia superba</i>	100	98.6	97.1	unknown	unknown	unknown
Fish species:						
<i>Electrona antarctica</i>	47.1	35.7	20.0	62.9	69.0	47.7
<i>Electrona carlsbergi</i>	2.9	1.4	0	0.5	0.7	0
<i>Gymnoscopelus nicholsi</i>	14.3	15.7	10.0	12.3	12.5	16.8
<i>Gymnoscopelus braueri</i>	8.6	7.1	5.7	13.3	3.6	19.5
<i>Gymnoscopelus bolini</i>	1.4	0	2.9	0.3	0	2.0
<i>Gymnoscopelus piabilis</i>	0	0	1.4	0	0	1.3
<i>Gymnoscopelus</i> spp.	4.3	0	0	1.0	0	0
<i>Krefflichthys andersoni</i>	0	1.4	0	0	0.4	0
<i>Metelectrona ventralis</i>	0	1.4	0	0	0.7	0
<i>Protomyctophum tenisoni</i>	0	1.4	0	0	0.4	0
<i>Protomyctophum choriodon</i>	1.4	0	0	0.3	0.4	0
<i>Lepidonotothen larseni</i>	2.9	0	0	1.0	0	0
<i>Notolepsis coatsi</i>	1.4	0	1.4	0.5	0	1.3
Unidentified otoliths	7.1	5.7	2.9	2.6	1.8	4.7
Squid species:						
<i>Brachioteuthis riisei</i>	8.6	15.7	8.6	3.4	6.8	4.7
<i>Moroteuthis knipovitchi</i>	1.4	2.9	1.4	0.3	1.1	0.7
Unidentifiable squid beaks	7.1	7.1	1.4	1.6	2.8	1.3
Total non-krill prey items	57.1	52.9	27.1	100	100	100