Antarctic fur seals foraging in the Polar Frontal Zone: inter-annual shifts in diet as shown from fecal and fatty acid analyses

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ABSTRACT: We studied the dietary preferences of Antarctic fur seals *Arctocephalus gazella* from Cap Noir, Îles Kerguelen, foraging in the Antarctic Polar Frontal Zone (PFZ) in February of 1998, 1999 and 2000. Scats were collected and analyzed for remaining prey hard parts in each of the 3 years, and in 1999 and 2000, the fatty acid (FA) composition of fur seal milk samples was also examined for longer-term dietary preferences. Scat analyses revealed that seals foraged primarily on fish and some squid in all 3 years with 25 species of fish being taken during the study. Myctophid fish accounted for an average of 94% by number of all fish consumed with 3 species, *Gymnoscopelus nicholsi*, *G. piabilis* and *Electrona subaspera*, forming the core diet. Inter-annual differences in dietary species composition were apparent, however, with the presence of the mackerel icefish *Champsocephalus gunnari* in 1998 and the myctophid *Protomyctophum tenisoni* in 1999 accounting primarily for the differences observed between years. While reconstituted prey biomass per scat was similar between years, scats from 1998 represented less energy per gram than those from 1999 and 2000. This study highlights the usefulness of using FA signature analysis to confirm longer-term shifts in dietary intake of fur seals using milk samples. Polyunsaturated fatty acids (PUFAs) were significantly more prevalent in the 1999 milk samples, which were also lower in overall lipid content (43% vs 53%). *G. nicholsi,* a particularly oily fish, occurred in higher proportions in the diet in 2000, perhaps explaining the higher incidence of monounsaturated fatty acids (MUFAs) in this year and the generally higher lipid levels present in milk samples. The inter-annual variation in the diet of Antarctic fur seals confirmed by these 2 techniques lends support to the hypothesis that previously identified variations in oceanographic conditions surrounding Îles Kerguelen in 1998, 1999 and 2000 affect the availability of fur seal prey resources.

KEY WORDS: Myctophid · Fatty acid · Kerguelen · Lipids · Fish · Squid · *Arctocephalus gazella*

INTRODUCTION

The Southern Ocean ecosystem is strongly influenced by the movement of several strong currents, most notably the Antarctic circumpolar current, and coupled climatic anomalies such as the Antarctic circumpolar wave (White & Peterson 1996). While primary production is relatively low in open parts of the Southern Ocean (Hempel 1985), frontal regions may form

discrete areas of biological enhancement (Lutjeharms et al. 1985). Studies of zooplankton communities in the vicinity of the Antarctic Polar Frontal Zone (PFZ) have identified regions of high productivity that vary at a range of spatial and temporal scales (Pakhomov et al. 1994, Pakhomov & Froneman 2000, Hunt et al. 2001). Consequently, the ecosystem also supports a very high biomass of vertebrate predators such as otariid seals, penguins and seabirds, which are limited in their distribution by their ability to travel from breeding sites while provisioning their offspring. Antarctic fur seals

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raise a single pup over a 4 mo lactation period from December to March during which they spend time foraging at sea followed by periods ashore suckling their pup (Doidge et al. 1986). As central place foragers, they are limited in their prospecting range by the fasting constraints of their young; consequently, oceanographic variation within their foraging range could affect the species composition of prey available to them.

The Antarctic krill *Euphausia superba* comprises a large part of the zooplankton biomass in the Southern Ocean (Schnack 1985), providing a food source for a large proportion of marine predators south of the Antarctic Polar Front (PF), particularly in the vicinity of the Scotia Sea (Croxall et al. 1985, Reid 1995, Reid & Arnould 1996). Many sub-Antarctic predators however, such as king penguins, Antarctic fur seals, large pelagic fish and several species of squid (Sabourenkov 1991, Cherel & Ridoux 1992, Rodhouse & White 1995, Bost et al. 1997, Cherel et al. 1997, Goldsworthy et al. 1997, Green et al. 1997, González & Rodhouse 1998, Moore et al. 1998), depend primarily on mesopelagic fishes of the family Myctophidae (lanternfishes) which represent the second largest and most widely distributed biological resource in Antarctic waters (Sabourenkov 1991), with many species being circumpolar in distribution (Hulley 1990).

The Kerguelen Archipelago in the southern Indian Ocean is the summer breeding location of seabirds and seals, which in 1985 were estimated to consume approximately 462000 t myctophids yr^{-1} (Guinet et al. 1996), equating to 26% of all prey consumed. Two of the primary consumers, Antarctic fur seals *Arctocephalus gazella* and king penguins *Aptenodytes patagonicus,* have increased in number by up to 7-fold in this vicinity over the last 35 yr (Jouventin et al. 1982, Bester & Roux 1986, Guinet et al. 1996, Chamaillé-Jammes et al. 2000) and consequently, annual consumption rates are now undoubtedly considerably higher than the 1985 estimate. Abundant and predictable prey resources are a necessary requirement to support growing predator populations. The Kerguelen Archipelago is within close proximity of the PF, lying in the southern part of the PFZ (Park & Gambéroni 1997), which is defined as the zone between the sub-Antarctic Front (SAF) to the north and the PF to the south (Klyausov 1990, Park et al. 1993). The productive waters of the PFZ, where Antarctic krill are absent, are likely to influence the foraging and breeding success of predators at Îles Kerguelen (Bocher et al. 2001).

Myctophids, associated with deep Antarctic waters throughout their life cycles (Kozlov & Tarverdiyeva 1989), dominate the ichthyofauna within the southern PFZ near the Kerguelen Archipelago, with many species invading the surface layer at night (Duhamel et al. 2000) to feed on diurnally migrating meso- and macro-zooplankton. The general location of the ACC in this sector of the southern Indian Ocean is relatively stable owing to the influence of bottom topography (Park & Gambéroni 1995); however, movements of the PF by several degrees of latitude between years occur intermittently (see Moore et al. 1999). Thus, the relative proximity of the Kerguelen Archipelago to the PF provides an opportunity to examine inter-annual variation in the diet of predators with respect to the effects of changing oceanographic features. Accordingly, we aimed to document the diet of Antarctic fur seals breeding at Îles Kerguelen over 3 yr, with a larger aim of examining possible differences in diet with reference to variation in oceanographic conditions and foraging behavior of fur seals, which will be examined in a future paper.

The majority of pinniped and particularly otariid diet studies have assessed prey composition by identifying hard parts, such as fish otoliths and squid beaks, remaining in feces (Green et al. 1990, Daneri & Coria 1992, Reid & Arnould 1996, Cherel et al. 1997) and/or regurgitates (Goldsworthy 1992, Fea & Harcourt 1997, Kirkman et al. 2000). This method carries with it many biases in terms of the retention, digestion and erosion of prey hard parts. In feeding trials of several species of otariids, the recovery rates of otoliths have been found to be only 2 to 63% (Dellinger & Trillmich 1988, Gales & Cheal 1992, Fea & Harcourt 1997, Lake 1997), while a study of Antarctic fur seals identified high individual variability in recovery rates (0 to 90%; Staniland 2002) often with a complete absence of smaller fish otoliths (da Silva & Neilson 1985). In addition, hard parts actually retrieved from scats may only represent the ingestion of prey during the previous feeding bout (Helm 1984, Jobling & Breiby 1986, Staniland 2002). Several indirect methods are now being used to provide dietary information in addition to the conventional fecal analyses. Lipids, particularly fatty acids (FAs), may function as dietary indicators by comparing FA signatures of prey items and consequent comparison with predator tissues that are high in lipid, such as milk (Iverson 1993, Iverson et al. 1997, Brown et al. 1999) and adipose tissue (Raclot et al. 1998, Kirsch et al. 2000, Walton et al. 2000). This technique is based on the principle that unique arrays of FAs can be transferred largely unaltered up the food chain from prey to predator (Iverson et al. 1997, Raclot et al. 1998).

A secondary aim of the study was to compare dietary changes estimated by conventional scat analysis with the findings of signature FA analysis of fur seal milk samples. FA are derived primarily from immediate dietary intake (Iverson et al. 1997) and may represent dietary intake over a longer time span than scat analyses. Therefore, our secondary aim is to assess the usefulness of FA signature analysis (Iverson 1993) of fur seal milk in identifying longer-term dietary preferences than possible by

conventional fecal analysis. To achieve this aim, milk FA signatures will be compared with FA profiles of a selection of possible prey items (see Lea et al. 2002b).

MATERIALS AND METHODS

Study site. The diet of female Antarctic fur seals breeding at Cap Noir, Îles Kerguelen (49° 07′ S, 70° 45′ E) was examined during February 1998, 1999 and 2000. The colony on the NE coast of the Courbet Peninsula comprised approximately 800 breeding female seals, which typically arrive at the colony in late November and usually give birth to a single pup, which they then suckle until weaning in late March or early April. The female's time ashore is interspersed with trips to sea of several days' duration to forage (Fig. 1).

Fecal analyses. Fecal samples of lactating fur seals were collected daily within the colony from areas used by adult females as well as from known seals upon their return to the colony whenever possible. Individual samples were frozen (–20°C) on site and returned to the laboratory for sorting and prey identification. Samples were elutriated overnight and subsequently sieved through a 1 mm and 500 µm mesh. The frequency of occurrence (FO) of fish (otoliths and bones), squid (beaks and eye lenses), invertebrates (amphipods, isopods, nematodes and annelids) and other miscellaneous items in feces was noted. Percentage FO is expressed as a percentage of the number of feces containing prey items. Otoliths (*sagitta*, *asteriscus* and *lapillus*) and squid beaks were sorted and identified to species level if possible, using the descriptions in Clarke (1986), Williams & Mc-Eldowney (1990), Reid (1996) and our own reference collection at the CEBC (France). Subsequently, otolith length was measured from sagittal otoliths showing little or no sign of erosion. Standard length and biomass of fish species were calculated from the conversion of otolith length (mm) using allometric equations (Adams & Klages

1987, Williams & McEldowney 1990, Cherel et al. 1997, Olsson & North 1997, Y. Cherel unpubl. data) for the majority of species. The conversion of lower rostral length to mantle length and squid body mass was achieved using allometric equations from Clarke (1986), Rodhouse et al. (1990) and Jackson (1995). In reconstructing the estimated fish biomass consumed by fur seals from scats, each otolith was considered to represent 1 fish, as there is little chance of all fish and therefore otoliths consumed by the fur seal being present in a particular scat.

Dietary energy value. The mean energetic value of the prey in each scat for the 3 yr was estimated using the calorific value of prey items (kJ g^{-1} wet mass). An estimate of the calorific content of the 8 major species of fish prey from the Kerguelen Plateau was available from Lea et al. (2002b), and for other species of myctophid from Cherel & Ridoux (1992) and Tierney et al. (2002). In instances where the calorific value of a particular species was unknown, an estimate was used. A value of 5.4 kJ g^{-1}, that of *Champsocephalus gunnari* from the Kerguelen Plateau, was assigned to other non-myctophid fish prey in the absence of further data. The calorific content of *Gonatus antarcticus* (3.78 kJ g^{-1}) was taken from Clarke et al. (1985), and a value of 2.31 kJ g^{-1} was used for ammoniac squids and 4.25 kJ g^{-1} for muscular squids (Clarke et al. 1985).

FA analyses. Milk samples were collected from breeding female fur seals captured for the deployment or retrieval of time-depth recorders in February 1999 and 2000 (see Lea et al. 2002a), usually within 24 h of the female's arrival in the colony. The seals were injected with 1 ml of 10 IU Oxytocin (Herriot Agvet) intramuscularly upon capture. The milk was then manually extracted into two 2 ml vials and frozen immediately at –20°C. In the laboratory, the milk samples were thawed, mixed and weighed.

The lipid was quantitatively extracted overnight by a modified (Bligh & Dyer 1959) 1-phase methanol/chloroform/water extraction (2/1/0.8, v/v/v). The phases were separated the following day by the addition of chloroform, water and sodium chloride (1/1, v/v). Concentration of the total solvent extract was obtained by *in vacuo* rotary evaporation at 40°C. A subsample of the extracted lipid was made up to a known concentration (typically around 0.01 g ml^{-1}) by the addition of chloroform and stored in the freezer (–20°C). Lipid class analyses were conducted immediately; samples were stored for no more than 3 d in a known volume of chloroform. The quantity of lipid extracted per sample was used to calculate percentage lipid values.

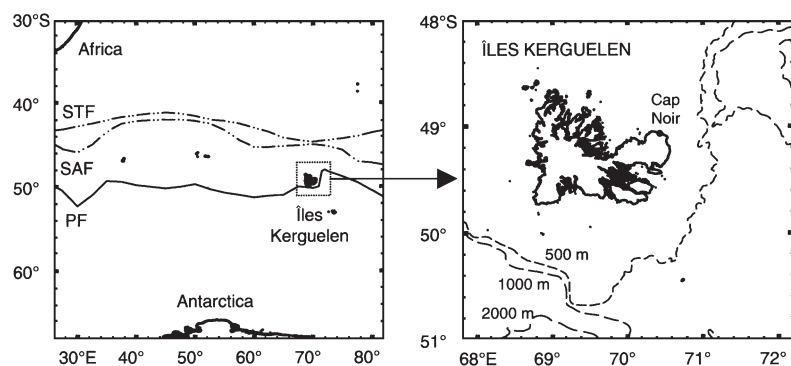An aliquot of the total lipid was analyzed using an Iatroscan MK V TH10 thin layer

Fig. 1. Îles Kerguelen and oceanographic fronts of Southern Ocean. STF, sub-tropical front; SAF, sub-Antarctic front; PF, Polar Front

chromatography flame ionization detector (TLC–FID) analyzer (Iatron Laboratories) to determine the abundance of individual lipid classes (Volkman & Nichols 1991). Peaks were quantified on an IBM-compatible computer using DAPA software (Dapa Scientific). Iatroscan results are generally reproducible to ±10% (Volkman & Nichols 1991).

An aliquot of the total lipid was treated with methanol/ hydrochloric acid/chloroform (10:1:1 v/v/v; 80°C, 2 h). The FA methyl ester (FAME) products were extracted into hexane/chloroform (4:1 v/v; 3×1.5 ml) and after reduction under a stream of nitrogen, the FAME mixture was treated with N,O-bis-(trimethyl-silyl)-trifluoroacetamide (BSTFA; 50 µl, 60°C, 1 h) to convert sterols to their corresponding TMSi (trimethyl-silyl) ethers. Gas chromatographic (GC) analyses of FAME were performed with a Hewlett Packard 5890A GC equipped with an HP-5 cross-linked methyl sili-cone fused silica capillary column (50 m × 0.32 mm in diameter), an FID, a split/splitless injector and an HP 7673A auto sampler; hydrogen was the carrier gas. Following the addition of methyl nonadecanoate and methyl tricosanoate internal standards, samples were injected in splitless mode at an oven temperature of 50°C. After 1 min, the oven temperature was raised to 150°C at 30°C min^{-1}, then to 250°C at 2°C min^{-1} and finally to 300°C at 5°C min^{-1}.

Peaks were quantified with Waters Millennium software. Individual components were identified using mass spectral data and by comparing retention time data with those obtained for authentic and laboratory standards. GC results are subject to an error of ±5% of individual component abundance.

Statistical analyses. All parametric statistical tests were performed using SYSTAT 9.0 (SYSTAT). Inter-annual comparisons of fish prey abundance identified from fecal analyses were conducted by Discriminant Function Analysis (DFA) of log+1-transformed abundance data. Otoliths not identified to species due to erosion were excluded. A backwards-stepwise DFA (α-level of 0.05 to remove) identified those species most influential in distinguishing the fish diet between years.

An analysis of covariance (ANCOVA) was performed on arcsine-transformed monounsaturated (MUFA) and polyunsaturated (PUFA) proportions for 1999 and 2000. Data were weighted according to MUFA proportions to account for the correlation between variables. Otherwise, the percentages of FAs identified in milk samples were compared inter-annually by *t*-test after arcsine transformation of the data, and a Bonferroni correction (Zar 1996) was applied to the significance level (p < 0.0014) to account for multiple comparisons and the possibility of significance occurring by chance. Those FAs identified as significantly different between years were then incor-

porated in a backwards-stepwise DFA on arcsine-transformed proportion data to identify those FAs most important in differentiating between milk samples from different years. FA profiles of milk samples were compared with profiles of 12 possible prey species from the literature. We selected species present in the diet of fur seals at Îles Kerguelen, which were sampled from the Kerguelen Plateau region where possible, to compare inter-annual variation in diet between the 2 techniques. All values are reported as ±SEM.

RESULTS

A total of 131 scats were collected in February over the 3 yr study, 60 in 1998, 24 in 1999 and 47 in 2000. Of those 131 scats, 83.2% contained fish otoliths (55 in 1998, 21 in 1999 and 33 in 2000). Fish comprised the majority of the diet in terms of FO in all 3 years (Table 1) with FO ranging from 90.9 to 94.9% of samples. Squid, while present in lower absolute numbers, were also found in the majority of scat samples (62.5 to 72.9%). The presence of several species of crustaceans such as the amphipod *Themisto gaudichaudii* was evident from exoskeletons found in the fecal remains (Table 1). Nematodes were also common in samples, while small quantities of plastic were also present in 9.1% of scats sampled in 2000.

Fish prey

In total, 3608 sagittal otoliths were found during the study averaging 38 ± 33 otoliths per scat (range 1 to 215). Otoliths from 25 fish species were identified in the scats over the 3 years (1998 to 2000), 16 of which were Myc-tophidae. *Gymnoscopelus piabilis*, *Electrona subaspera* and *G. nicholsi* accounted for 54.7% by number of the fish prey species identified in the mean diet of the fur seals (Table 2). A further 20.3% of otoliths were from the genus *Gymnoscopelus* or the family Myctophidae and were too eroded to reliably identify. Myctophids repre-sented an average of 90.4% of prey hard parts identified in scats. Other species of fish accounted for 7.5% of prey items by number with *Champsocephalus gunnari*, the mackerel icefish, being the most numerous of these (4.4%). *Harpagifer spinosus*, *Scopelosaurus hamiltoni* and the southern driftfish *Icichthys australis* followed in numerical abundance, all at less than 1%.

Cephalopod prey

Six species of squid were found in the diet, with squid remains occurring in 67.7% of scat samples

Table 1. Frequency of occurrence by number and percentage of prey items recorded in Antarctic fur seal scats at Cap Noir. Number of scats sampled and the number containing prey items are in parentheses

Prey type	1998 (60/59)		1999 (24/24)		2000 (48/44)		Total (132/127)	
	n	%	n	%	n	%	n	%
Fish	56	94.9	22	91.7	40	90.9	118	92.9
Otoliths	55	93.2	21	87.5	33	75.0	109	85.8
Eye lenses	52	88.1	18	75.0	31	70.5	101	79.5
Bones	48	81.4	20	83.3	37	84.1	105	82.7
Vertebrae	49	83.1	16	66.7	26	59.1	91	71.7
Myctophids (scales or jaw bones)	39	66.1	17	70.8	34	77.3	90	70.9
Channichthyids (jaw bones or opercles)	13	22.0	1	4.2	0	0	14	11.0
Nototheniids (jaw bones)	7	11.9	1	4.2	6	13.6	14	11.0
Paradiplospinus gracilis (teeth or vertebrae)	4	6.8	1	4.2	0	0	5	3.9
Harpagifer spinosus (opercles)	1	1.7	0	0.0	1	2.3	2	1.6
Cephalopods	43	72.9	15	62.5	28	63.6	86	67.7
Beaks	36	61.0	14	58.3	25	56.8	75	59.1
Eye lenses	30	50.9	8	33.3	20	45.5	58	45.7
Gladii	22	37.3	8	33.3	17	38.6	47	37.0
Radulae	13	22.0	9	37.5	11	25.0	33	26.0
Crustaceans	25	42.4	13	54.2	11	25.0	49	38.6
Themisto gaudichaudii	18	30.5	5	20.8	5	11.4	28	22.1
Other amphipods	9	15.3	6	25.0	0	0.0	15	11.8
Isopods	2	3.4	1	4.2	1	2.3	4	3.2
Euphausiacae	1	1.7	0	0.0	0	0.0	1	0.8
Others								
Nematodes	33	55.9	18	75.0	27	61.4	78	61.4
Pebbles	18	30.5	16	66.7	23	52.3	57	44.9
Mollusk shells	11	18.6	12	50.0	4	9.1	27	21.3
Plastic	1	1.7	1	4.2	4	9.1	6	4.7
Annelids	4	6.8	0	0.0	0	0.0	4	3.2
Feathers (penguin)	1	1.7	0	0.0	0	0.0	1	0.8

(Table 2). The ommastrephid squid *Martialia hyadesi* and *Brachioteuthis ?riisei* occurred most commonly, whilst *Gonatus antarcticus*, *Moroteuthis ingens*, *M. knipovitchi* and *?Mastigoteuthis A* (Clarke) were also present in lower numbers (Table 2). The squid component of the diet comprised on average only 2.1% of the diet by number.

Inter-annual variation in number and size of prey

The number of fish and squid species identified in the diet of seals was highest in 1998 at 33 species, with 21 and 22 species identified in 1999 and 2000 respectively. A prey diversity index was calculated on an individual scat basis (number of fish and squid species groups per scat) and averaged for each year. The prey index did not vary significantly between years (5.4 ± 0.3, n = 110, range 1 to 13) for those scats containing diagnostic hard parts (1-way ANOVA, $F_{107, 2}$ = 2.037, p = 0.135). However, if the prey indices for all scats were used, i.e. including those scats with no prey, the index was significantly lower in 2000 (3.2 ± 0.5, 1-way ANOVA, $F_{129, 2}$ = 6.027, p < 0.05) than in 1998 and 1999 (4.9 ± 0.4

and 5.8 ± 0.8, respectively). The high proportion of empty scats in 2000 (31.3%) as opposed to other years (both 8.3%), explains this finding.

Fish—Lanternfish comprised 85.6, 97.8 and 97.6% of the fish component of the diet in each of the 3 years respectively ($\bar{x}$ = 93.7%). G*ymnoscopelus piabilis* was the main prey species consumed in all years. Similar proportions of the 3 most common fish prey species (*G. piabilis*, *G. nicholsi* and *Electrona subaspera*) were consumed by seals in all years, although *G. nicholsi* was more prevalent in 2000 than in 1998 and 1999. The importance of some of the minor prey species varied considerably between years (Table 2). The mackerel icefish *Champsocephalus gunnari* was of variable importance in the diet, only being present in 1998 where it represented approximately 10% by number (Table 2). *E. carlsbergi* also occurred only in 1998, while *Protomyctophum choriodon* and *P. tenisoni* were present in higher numbers in 1999. The mean number of otoliths per scat (33.4 ± 3.65) did not vary significantly between years (1-way ANOVA, $F_{105, 2}$ = 2.123, p = 0.125) with considerable variation occurring in numbers of otoliths between scats (0 to 215).

Table 2. Mean abundance by number of fish (otoliths) and squid prey (lower beaks) in the diet of female Antarctic fur seals at Îles Kerguelen

| | 1998 (60/55) | | | 1999 (24/21) | | | 2000 (47/33) | | | Total (131/109) | | |
| | Number | | % | Number | | % | Number | | % | Number | | % |
	n	%	fish	n	%	fish	n	%	fish	n	%	fish
Myctophidae												
Gymnoscopelus piabilis	461	28.5	29.2	219	21.3	21.6	280	26.8	27.6	960	26.0	26.6
Electrona subaspera	269	16.6	17.1	194	18.9	19.1	192	18.4	18.9	655	17.8	18.2
G. nicholsi	152	9.4	9.6	92	9.0	9.1	159	15.2	15.6	403	10.9	11.2
G. fraseri	61	3.8	3.9	42	4.1	4.1	53	5.1	5.2	156	4.2	4.3
Protomyctophum bolini	46	2.8	2.9	16	1.6	1.6	19	1.8	1.9	81	2.2	2.2
P. choriodon	39	2.4	2.5	57	5.6	5.6	18	1.7	1.8	114	3.1	3.2
E. carlsbergi	26	1.6	1.6	0		0		26	0.7	0.7		
Krefftichthys anderssoni	24	1.5	1.5	20	1.9	2.0	3	0.3	0.3	47	1.3	1.3
E. antarctica	19	1.2	1.2	62	6.0	6.1	11	1.1	1.1	92	2.5	2.5
Gymnoscopelus sp.	131	8.1	8.3	130	12.7	12.8	197	18.9	19.4	458	12.4	12.7
Myctophidae (eroded)	97	6.0	6.2	137	13.4	13.5	42	4.0	4.1	276	7.5	7.6
Metelectrona ventralis	11	0.7	0.7	0		1	0.1	0.1	12	0.3	0.3	
P. tenisoni	9	0.6	0.6	20	1.9	2.0	3	0.3	0.3	32	0.9	0.9
G. braueri	1	0.1	0.1	0		0	0	1	0.0	0.0		
P. andriashevi	1	0.1	0.1	1	0.1	0.1			2	0.1	0.1	
G. bolini	2	0.1	0.1	2	0.2	0.2	13	1.2	1.3	17	0.5	0.5
Other fish												
Champsocephalus gunnari	161	10.0	10.2	0		0	2	161	4.4	4.5		
Harpagifer spinosus	23	1.4	1.5	2	0.2	0.2	0	0.2	0.2	27	0.7	0.7
Icichthys australis	10	0.6	0.6	7	0.7	0.7	0		17	0.5	0.5	
?Nansenia antarctica	7	0.4	0.4	3	0.3	0.3	0		10	0.3	0.3	
Scopelosaurus hamiltoni	7	0.4	0.4	8	0.8	0.8	5	0.5	0.5	20	0.5	0.6
Osteichthyes sp., (eroded)	7	0.4	0.4			4	0.4	0.4	11	0.3	0.3	
Paradiplospinus gracilis	3	0.2	0.2	3	0.3	0.3	0		6	0.2	0.2	
Gobionotothen acuta	4	0.2	0.3	0		13	1.2	1.3	17	0.5	0.5	
Paralepididae sp.	1	0.1	0.1	0		0		1	0.0	0.0		
Muraenolepis marmoratus	2	0.1	0.1	0		0		2	0.1	0.1		
Melanostigma gelatinosum	2	0.1	0.1	0		0		2	0.1	0.1		
Notothenia cyanobrancha	1	0.1	0.1	0		1	0.1	0.1	2	0.1	0.1	
Total otoliths	1577	97.5	100	1015	99.0	100	1016	97.3	100	3608	97.9	100
Squid												
Martialia hyadesi	23	1.4		1	0.05		15	1.4		39	1.1	
Brachioteuthis ?riisei	11	0.7		9	0.9		11	1.1		31	0.8	
Gonatus antarcticus	3	0.2		1	0.05		0		4	0.1		
Moroteuthis ingens	1	0.1		0		0		1	0.0			
M. knipovitchi	1	0.1		0		1	0.1	1	2	0.1		
?Mastigoteuthis A (Clarke)	0		0		1	0.1		1	0.0			
Total squid beaks	39	2.5		11	1.0		28	2.7		78	2.1	
TOTAL	1616	100		1026	100		1044	100		3686	100	

An inter-annual difference in dietary composition was detected by a complete linear DFA of log-transformed abundance data (Wilks' Lambda = 0.452, $F_{162,48}$ = ca. 1.646, p = 0.012). A plot of the canonical scores is illustrated in Fig. 2, indicating a high degree of overlap between years, particularly in 2000. A backwards-stepwise DFA conducted on the same data indicated that 2 species, *Protomyctophum tenisoni* and *Champsocephalus gunnari*, were largely responsible for the distinction in diet between years (Wilks' Lambda = 0.794, $F_{206,4}$ = ca. 6.292, p = 0.001). Using these 2 species as discriminators, an average 44% of scats were correctly assigned to the year by the Jackknife classification matrix (Table 3). The fact that 90% of samples collected in 2000 were correctly assigned, in comparison to the lower percentages for 1998 (22%) and 1999 (33%), indicates that although differences between years were evident, a core diet was present in all years and comprised the majority of the diet in 2000 (Fig. 2).

Otolith sizes of the 3 most common species of fish prey (Fig. 3) were compared between years by 1-way ANOVA. *Gymnoscopelus nicholsi* were smaller in 1999 than in 1998 and 2000 ($F_{145,2}$ = 13.104, p < 0.001), *Electrona subaspera* were larger in 1999 than in 2000, while fish consumed in 1998 were intermediate ($F_{117,2}$ = 7.549, p = 0.001). *G. piabilis* were similar in size in all years (Table 4), although the distribution of fish sizes in 1998 was skewed more toward fish of greater than 120 mm length. The majority of myctophid fish preyed upon by *Arctocephalus gazella* were juveniles excepting *G. piabilis* in all years, and *E. antarctica* and *Protomyctophum tenisoni* in 2000.

Champsocephalus gunnari consumed in 1998 ranged in size from 175.3 to 210.1 mm (mean 192.9 ±

Table 3. Discriminant function analysis stepwise (SCM) and Jackknife (JCM) classification matrices of fish abundance by number in 1998, 1999 and 2000

		1998	1999	2000	% correct
SCM	1998	13	5	37	24
	1999	0	7	14	33
	2000	0	3	28	90
	Total	13	15	79	45
JCM	1998	12	6	37	22
	1999	0	7	14	33
	2000	0	3	28	90
	Total	12	16	79	44

9.8 mm) indicative of fish at age 1+ from the September 1996 cohort (G. Duhamel pers. comm.).

Cephalopods—The overall abundance of squid was generally low, however of the 2 more prevalent species, *Martialia hyadesi* occurred in 1998 and 2000 in similar proportions (1.4%), whilst *Brachioteuthis ?riisei* was present in all years at 0.7 to 1.1% of the diet.

Lower rostral lengths (LRL) of *Martialia hyadesi* squid beaks were compared between 1998 (3.74 ± 0.4 mm) and 2000 (4.33 ± 0.5 mm) by Student's *t*-test as only 1 individual was present in 1999. Beaks of *M. hyadesi* were significantly larger in 2000 than those consumed in 1998 ($t_{0.05[36]}$ = 2.042, p < 0.001). The LRL of *Brachioteuthis ?riisei* were compared in all 3 years by ANOVA, with squid in 1998 (LRL = 2.43 ± 0.5 mm) being significantly larger than those in 2000 (LRL = 1.8 ± 0.5 mm; $F_{2,30}$ = 5.109, p < 0.05), while the length of *B. ?riisei* taken in 1999 was intermediate (LRL = 2.02 ± 0.4 mm; Table 4).
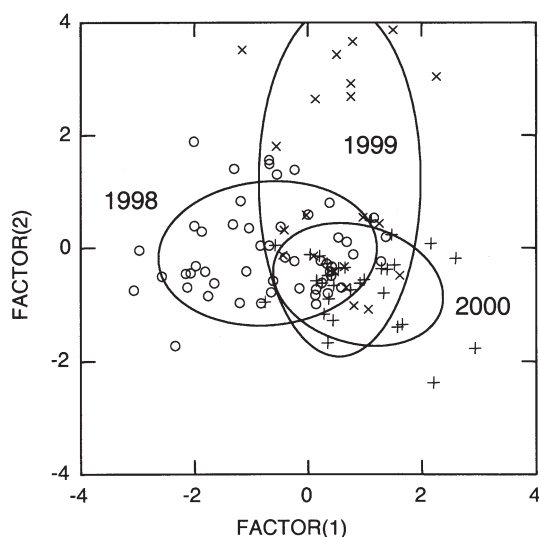
Reconstituted mass and calorific value of prey

Myctophids also dominated the diet in terms of reconstituted mass, accounting for 54, 74 and 82% of biomass in 1998, 1999 and 2000, respectively. In total, the 3 most commonly occurring species (*Gymnoscopelus piabilis*, *G. nicholsi* and *Electrona subaspera*) represented 42 to 51% of the reconstituted mass, whilst *G. piabilis* alone consistently represented approximately 30% of biomass (Table 4). Some species accounted for a considerably higher proportion of the diet in terms of reconstituted mass than by number, such as the mackerel icefish (17% cf. 10%) and the Southern driftfish *Icichthys australis* in 1999 (22% cf. 0.7%) owing to their large size (mean mass 620 g).

Although reconstituted biomass and energy content of the diet are not quantitative measures, particularly when calculated from fecal remains, inter-annual comparisons of these measures are of interest. Prey bio-
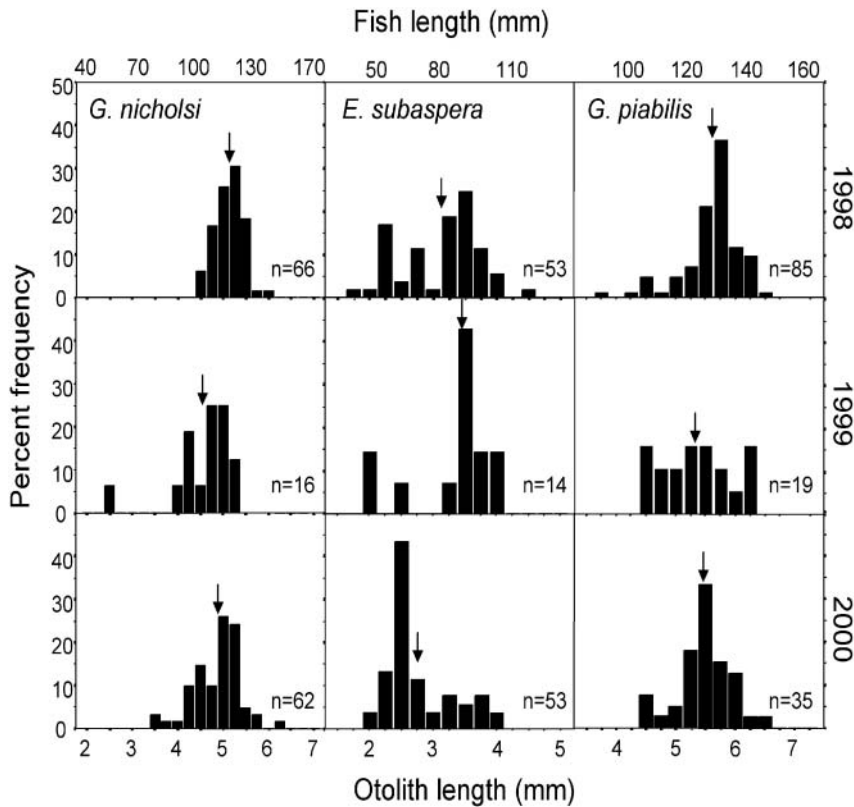

Fig. 2. Prey composition canonical scores plot by number in 1998 (○), 1999 (×) and 2000 (+)

Fig. 3. Percent frequency histograms of otolith and total fish length for *Gymno-scopelus piabilis*, *G. nicholsi* and *Electrona subaspera.* Arrows denote mean otolith or fish length

of a minimum 99% triacylglycerides (TAGs) and small amounts of polar lipid and sterols. The major FAs in Antarctic fur seal milk were 18:1ω9 (25 to 38%), 16:0 (15 to 23%), 20:1ω9 (6 to 11%), 22:6ω3 (1 to 10%), 16:1ω7 (5 to 8%), 20:5ω3 (1 to 8%) and 18:1ω7 (4 to 7%). Monounsaturated FAs (MUFAs; 50 to 63%) were more prevalent than either polyunsaturated FAs (PUFAs; 6 to 24%) and saturated FAs (22 to 33%).

Intra-individual variation in milk lipid composition

To evaluate the possibility of short-term temporal variation in milk FA composition, the FA profiles of milk samples collected before and after 1 or 2 foraging trips for 13 females were compared. A Pearson's correlation coefficient (PCC) was calculated for each pair of milk samples and regressed against the number of days between milk samples (Fig. 4a,b). The correlation between FA composition of pre- and post-foraging trip milk samples was high (mean PCC = 0.995 ± 0.005). However, no relationship was apparent between the number of days between samples, which ranged between 7.8 and 18.9 d (r^2 = 0.035, p > 0.05) and the r correlation co-efficient. Thus, it would appear that there is little intra-individual variation in milk FA composition over a 1 to 3 wk time span.

mass per scat (763 ± 77 g) did not differ between years when compared by 1-way ANOVA ($F_{105, 2}$ = 0.382, p = 0.683). Prey energy value per scat was similar between years (1-way ANOVA, $F_{105, 2}$ = 0.368, p = 0.693) at 5070 ± 522 kJ, with much variation evident between scats (33 to 33 674 kJ). Energy value per scat was positively related to the reconstituted mass per scat for all 3 years (r^2 = 0.901 to 991, p < 0.05). The slopes of the relationship were tested for year effects by ANCOVA. Scats in 1998 constituted less energy per g of reconstituted prey biomass than those from 1999 and 2000 ($F_{104, 2}$ = 2.910, p = 0.059).

Milk lipid and FA analyses

Antarctic fur seal milk is generally rich in lipid content, ranging from 28.1 to 68.7% of wet mass. The mean lipid content of milk sampled during late lactation 1999 (43.3 ± 7.1%, n = 22) was significantly lower than the 53.2 ± 6.8% recorded in 2000 (n = 16, $t_{36[0.05]}$ = –4.361 pooled variance, p < 0.001). Lipid class analyses of 20 milk samples indicated that milk was comprised

Inter-annual variation in milk FA profiles

The FA profiles of seal milk in February-March 1999 (n = 22) and 2000 (n = 16) were variable both within and between years (Table 5). The relationship between MUFA and PUFA levels in the 2 years was significantly different (ANCOVA, $F_{35, 1}$ = 22.354, p < 0.05), with milk samples being higher in PUFAs in 1999 (21.4%), while in 2000 milk was more variable in composition with several seals having a particularly high occurrence of MUFAs (Fig. 5). In 1999, relative proportions of 22:6ω3 (DHA) overall PUFA levels were higher than in 2000 (see Table 5 for test-results), whilst the abundance of saturated FA and 16:1ω7, 18:1ω7 and 20:1ω9 was greater in 2000 (Table 5). The ratio of essential ω6 to ω3 FA (6.1 ± 0.6) was significantly lower in 2000 than in 1999 (7.9 ± 0.4; $t_{36, [0.05]}$ = 2.63, p < 0.05).

Table 4. Size, reconstituted mass and energy value of the major fish and squid prey items in the diet of Antarctic fur seals. Length (L) = standard L for fish and mantle L for squid

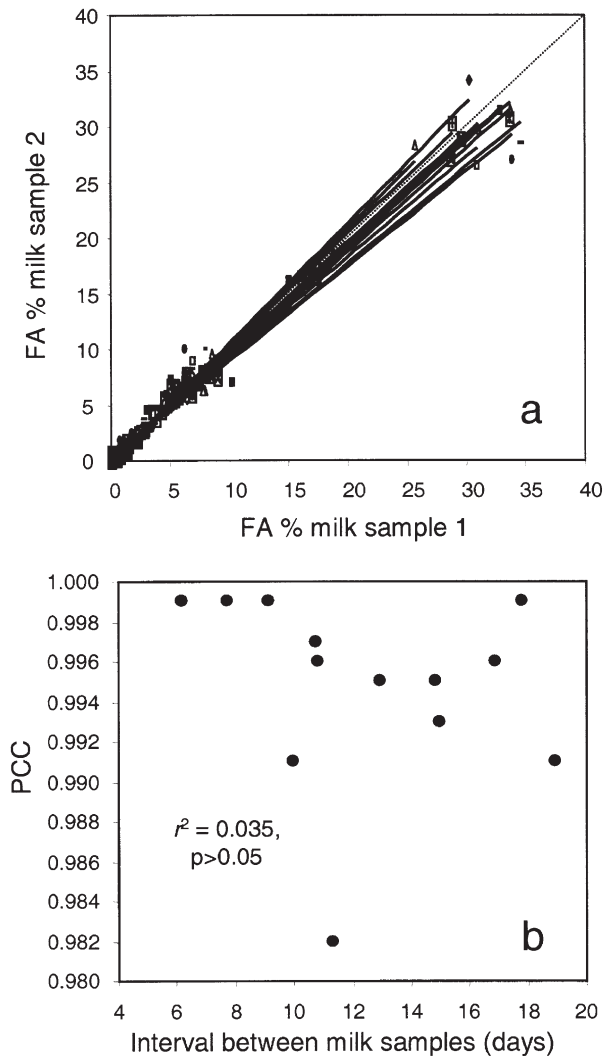| Taxon	1998 Mean length (mm)	1998 Mean mass (g)	1998 Total biomass (g)	1998 (%)	1998 Energy content (kJ)	1998 (%)	1999 Mean length (mm)	1999 Mean mass (g)	1999 Total biomass (g)	1999 (%)	1999 Energy content (kJ)	1999 (%)	2000 Mean length (mm)	2000 Mean mass (g)	2000 Total biomass (g)	2000 (%)	2000 Energy content (kJ)	2000 (%)
Myctophidae																		
Electrona antarctica	65.3	4.7	89	0.2	1181	0.4	51.9	2.1	127	0.7	1693	1.3	73.3	5.6	62	0.3	827	0.5
E. carlsbergi	80.2	7.8	202	0.5	1737	0.6	–	–	–	–	–	–	–	–	–	–	–	–
E. subaspera	77.9	10.2	2743	6.4	20295	7.4	83.7	12.5	2425	12.7	17945	13.7	67.5	6.5	1248	5.7	9235	6.0
Gymnoscopelus fraseri	75.7	5.0	305	0.7	3113	1.1	74.7	4.9	206	1.1	2105	1.6	78.1	5.6	295	1.4	3013	2.0
G. nicholsi	122.0	20.4	3107	7.2	30445	11.1	103.9	13.7	1264	6.6	12384	9.5	115.9	17.9	2844	12.9	27868	18.1
G. piabilis	129.7	26.4	12170	28.3	83976	30.6	124.2	23.4	5125	26.9	35360	27.1	127.4	25.0	7000	32.0	48300	31.4
G. bolini	186.7	71.8	144	0.3	1292	0.5	177.5	64.4	129	0.7	1160	0.9	190.8	78.5	1020	4.7	9182	6.0
G. braueri	95.9	7.9	8	0.02	71	0.03	–	–	–	–	–	–	–	–	–	–	–	–
Gymnoscopelus sp.	128.3	25.6	3354	7.8	23145	8.4	128.3	25.6	3329	17.5	22969	17.6	128.3	25.6	5044	23.0	34806	22.6
Krefftichthys anderssoni	34.0	0.4	10	0.02	78	0.03	32.5	0.3	6	0.03	49	0.04	39.0	0.7	2	0.01	17	0.01
Myctophidae (eroded)	74.0	8.8	858	2.0	6349	2.3	74.0	8.8	1212	6.4	8967	6.9	74.0	8.8	371	1.7	2749	1.8
Metelectrona ventralis	69.0	5.3	58	0.1	769	0.3	–	–	–	–	–	–	69.0	5.3	5	0.02	70	0.05
Protomyctophum bolini	40.7	0.9	43	0.1	245	0.1	40.3	0.9	15	0.1	83	0.06	38.8	0.8	16	0.07	89	0.06
P. andriashevi	51.2	8.4	8	0.02	51	0.02	51.2	8.4	8	0.04	51	0.04	–	–	–	–	–	–
P. choriodon	67.8	4.3	170	0.4	1034	0.4	68.5	4.7	268	1.4	1632	1.3	64.2	3.6	65	0.3	394	0.3
P. tenisoni	42.6	0.8	7	0.02	42	0.02	35.0	0.4	8	0.04	51	0.04	47.1	1.1	3	0.01	19	0.01
Total Myctophidae				54.1		63.3				74.1		79.9				82.1		88.8
Champsocephalus gunnari	129.9	47.5	7648	17.8	41297	15.0	–	–	–	–	–	–	–	–	–	–	–	–
Icichthys australis	318.1	620.9	6209	14.4	33527	12.2	318.1	620.9	4346	22.8	23469	18.0	–	–	–	–	–	–
Other fish	–	–	1618	3.8	8736	3.2	–	–	358	1.9	1935	1.4	–	–	659	3.0	3560	2.3
Squid																		
Martialia hyadesi	212.1	158.8	3652	8.5	15523	5.7	220.5	182.1	182	1.0	774	0.6	229.5	213.7	3206	14.6	13623	8.9
Brachioteuthis ?riisei	65.3	6.1	67	0.2	155	0.1	57.1	4.7	42	0.2	98	0.1	52.9	4.1	45	0.2	104	0.1
Gonatus antarcticus	143.9	71.6	215	0.5	812	0.3	27.0	0.6	1	0.0	2	0.0	–	–	–	–	–	–
Moroteuthis ingens	164.5	140.5	141	0.3	325	0.1	–	–	–	–	–	–	–	–	–	–	–	–
M. knipovitchi	91.8	163.0	163	0.4	377	0.1	–	–	–	–	–	–	.	1.9	2	0.01	4	0.0
?Mastigoteuthis A (Clarke)	–	–	–	–	–	–	–	–	–	–	–	–	76.5	14.4	14	0.07	26	0.02
TOTAL			42987	100	274572	100			19051	100	130726	100			21902	100	153888	100
Biomass or energy per scat			772 ± 102		4799 ± 674				865 ± 221		5942 ± 1549				673 ± 120		4712 ± 838	

Fig. 4. (a) Correlation between paired milk samples from 13 Antarctic fur seals. Dotted line denotes a 1:1 slope; (b) regression of Pearson's correlation co-efficient (PCC) against sampling interval between milk sample collections

Dietary implications of FA analysis

The proportional abundance of 19 FAs in the milk samples differed significantly between years (Table 5). Of those 19 FAs, 9 were identified by a backwards-stepwise DFA (i15:0, 15:0, 16:1ω5, 18:1ω7, 20:1ω9, 20:1ω7, c21PUFA, 22:5ω6 [DPA6] and 22:6ω3) as contributing to a significant inter-annual difference between milk samples (Wilks' Lambda = 0.1174, $F_{9, 28}$ = ca. 23.40, p < 0.01). Samples from the different years were correctly re-assigned to year in 100% of cases using both a standard classification matrix and a Jackknife classification matrix.

The relative abundance of the 9 influential FAs identified by DFA were compared between the 12 potential

prey items, which included 3 species of squid from the Southern Plateau (SP) and Heard Island (HI): *Martialia hyadesi* (SP), *Moroteuthis knipovitchi* (HI) and *Gonatus antarcticus* (HI) (K. Phillips only unpubl. data); 7 species of myctophid (*Electrona carlsbergi*, *E. subaspera*, *Gymnoscopelus piabilis*, *G. fraseri*, *G. nicholsi*; *Protomyctophum tenisoni*) and *Champsocephalus gunnari* from the Kerguelen Plateau (Lea et al. 2002b), and the crustacean *Themisto gaudichaudii* (Phleger et al. 1998) from the Elephant Island region, Antarctica. The relative proportions of 6 of the FAs were higher in milk samples in 2000 (Table 6). The FA i15:0, for which the highest *t*-value was recorded in inter-annual comparisons of milk samples, was highest in 2 of the common fish prey species (*G. piabilis* and *E. subaspera*) in addition to *G. fraseri* and *P. tenisoni* (Lea et al. 2002b); however, it was present only at very low levels (<0.5%) in milk samples (Table 2). The monounsaturated 18:1ω7 FA was unique in that the only prey item with high levels of this FA was *G. nicholsi*, which was more common in the diet of seals in 2000 (13.3%), in terms of prey biomass, than in 1999 (6.6%). Both 20:1ω9 and 20:1ω7 were also indicative of *G. nicholsi* to a lesser extent.

Of the 3 FAs occurring in higher proportions in milk samples in 1999, two—DPA6 (22:5ω6) and DHA (22:6ω3)—occurred in highest proportions in the ommastrephid squid *Martialia hyadesi*. Abundance of this species was much reduced in scats from 1999 (Table 2); however, total FO of squid remains was similar between years at approximately 63%. Thus, the relatively high proportions of both these FAs in 1999 may indicate the presence of *M. hyadesi* in the diet over a longer time span than scat analysis is capable of detecting. However, 22:6ω3 is also present in reasonable quantities in the amphipod *Themisto gaudichaudii* and *Protomyctophum tenisoni*, both of which were more common in the diet in 1999 and are rich in PUFA.

DISCUSSION

Limitations and assumptions of dietary techniques

There are many assumptions for all methods used to quantify the diet of a predator feeding at sea. Several studies have highlighted the errors associated with differential rates of digestion in relation to the hard parts of prey, particularly otoliths and squid beaks (Jobling & Breiby 1986, Pierce & Boyle 1991, Gales & Cheal 1992). Recent diet studies of sub-Antarctic fur seals *Arctocephalus tropicalis* at Marion Island have found that scat analysis indicated a diet rich in myctiophids (Klages & Bester 1998), whilst analyses of stomach contents for the same species at Marion (Ferreira & Bester 1999) and

Gough Islands (Bester & Laycock 1985) revealed a predominance of squid in the diet. Unfortunately, it is very difficult to account for many of these problems when studying free-ranging marine predators without the lethal take of individuals. However, as our primary aims were to identify variability in the diet over several years, many of the elements that make dietary quantification difficult, as mentioned above, should remain constant over time, thereby enabling a comparative study such as ours to draw conclusions about relative change with some confidence. By utilizing 2 techniques of dietary assessment, we have shown that whilst female Antarctic fur seals prey primarily on myctophids at Cap Noir, Îles Kerguelen, species composition of their diet varies significantly between years most probably in response to changes in prey availability affected by inter-annual shifts in the positioning of oceanic frontal structures and associated marine productivity.

Diet composition

The importance of fish, particularly myctophids, as the main prey items of Antarctic fur seals at the Kerguelen Archipelago was confirmed by fecal analyses and supports the previous findings of Cherel et al. (1997) and Guinet et al. (2001). Myctophids, which inhabit the Antarctic PFZ (Duhamel et al. 2000), dominated the diet in February in all 3 years, both by number and reconstitu-ted mass. *Gymnoscopelus piabilis* was consistently the most common species present in the diet. This species is also present in the diet of conspecifics at Macquarie Island and Marion Island (Goldsworthy et al. 1997, Klages & Bester 1998, Robinson et al. in press) and king penguins at the Crozet Archipelago (Cherel et al. 1996), and has even been reported in the diet of New Zealand fur seals in the temperate waters of southern Tasmania (Lake 1997). In addition to *G. piabilis*, *Electrona subaspera* and *G. nicholsi* were consistently important in the diet. These species are mesopelagic/epibenthic (Hulley 1990) and are present in the upper part of the mesopelagic fish community of the PFZ, being absent in daytime trawls at 300 m and abundant at the surface at night (Duhamel et al. 2000). The behavior of female Antarctic fur seals foraging nearby Îles Kerguelen is apparently determined by the diurnal movements of their prey. Antarctic fur seals typi-cally dive nocturnally, commencing at considerable depth, with dives gene-rally becoming progressively shallower throughout the night in conjunction with what is assumed to be the simultaneous migration of prey (Lea et al. 2002).

Gymnoscopelus piabilis is large in comparison to other myctophids and high in calorific value (Raclot et al. 1998), and may therefore be an advantageous species in terms of efficient energy consumption during lactation for Antarctic fur seals. The diet of Antarctic fur

Table 5. Fatty acid (FA) composition (% contribution of total FA content) of Antarctic fur seal milk in late lactation for 1999 and 2000. MUFA, monounsaturated FAs; PUFA, polyunsaturated FAs; SAT, saturated FAs. Values are mean ± SE

FAs	1999	2000	t	p
14:0	3.69 ± 0.11	4.56 ± 0.20	4.156	0.0001
15:0	0.33 ± 0.01	0.38 ± 0.02	3.458	0.001
16:0	16.53 ± 0.10	18.63 ± 0.52	4.639	0.0001
18:0	2.79 ± 0.04	3.35 ± 0.11	5.517	0.0001
20:0	0.14 ± 0.00	0.17 ± 0.01	3.594	0.001
i15:0	0.18 ± 0.00	0.26 ± 0.01	6.476	0.0001
a15:0	0.05 ± 0.00	0.07 ± 0.01	4.049	0.0001
4,8,12TMTD	0.07 ± 0.00	0.10 ± 0.01	3.756	0.001
SAT total	(23.79 ± 0.17)	(27.52 ± 0.84)	−5.038	0.0001
14:1ω5	0.15 ± 0.05	0.19 ± 0.01		
16:1ω9	0.43 ± 0.03	0.41 ± 0.02		
16:1ω7	5.98 ± 0.10	6.67 ± 0.16	3.818	0.0001
16:1ω5	0.25 ± 0.00	0.33 ± 0.01	5.529	0.0001
17:1	0.40 ± 0.01	0.37 ± 0.01		
18:1ω9	29.79 ± 0.57	27.96 ± 0.77		
18:1ω7	5.12 ± 0.12	5.96 ± 0.11	4.895	0.0001
18:1ω5	0.58 ± 0.01	0.64 ± 0.02	3.677	0.001
20:1ω9	8.47 ± 0.23	9.60 ± 0.22	3.504	0.001
20:1ω7	0.50 ± 0.01	0.60 ± 0.02	5.269	0.0001
22:1ω11	1.21 ± 0.07	1.56 ± 0.12		
22:1ω9	0.92 ± 0.04	1.06 ± 0.05		
22:1ω7	0.11 ± 0.01	0.17 ± 0.01	4.048	0.0001
24:1	0.58 ± 0.01	0.84 ± 0.07		
MUFA total	(54.92[a] ± 0.49)	(56.37 ± 0.92)		
C_{16}PUFA	0.28 ± 0.02	0.33 ± 0.01		
18:3ω6	0.07 ± 0.00	0.16 ± 0.03	3.973	0.0001
18:4ω3	1.04 ± 0.05	0.85 ± 0.04		
18:2ω6	1.12 ± 0.07	1.00 ± 0.06		
20:4ω6	0.63 ± 0.02	0.50 ± 0.05		
20:3ω6	0.19 ± 0.00	0.17 ± 0.01		
20:4ω3	0.97 ± 0.03	1.20 ± 0.08		
20:5ω3	6.39 ± 0.17	4.67 ± 0.58		
20:2ω6	0.28 ± 0.01	0.29 ± 0.01		
22:5ω6	0.10 ± 0.00	0.06 ± 0.01	3.614	0.001
C_{21}PUFA	0.46 ± 0.02	0.35 ± 0.03	4.490	0.0001
22:6ω3	7.80 ± 0.34	4.97 ± 0.73	3.895	0.0001
22:5ω3	2.07 ± 0.07	1.57 ± 0.19		
PUFA total	(21.37 ± 0.55)	(16.11 ± 1.52)	3.632	0.001
∑ ω3	(18.26 ± 0.56)	(13.25 ± 1.48)		
∑ ω6	(2.38 ± 0.08)	(2.18 ± 0.10)		
Ratio ω3:ω6	(7.92 ± 0.40)	(6.05 ± 0.63)	2.632	0.012

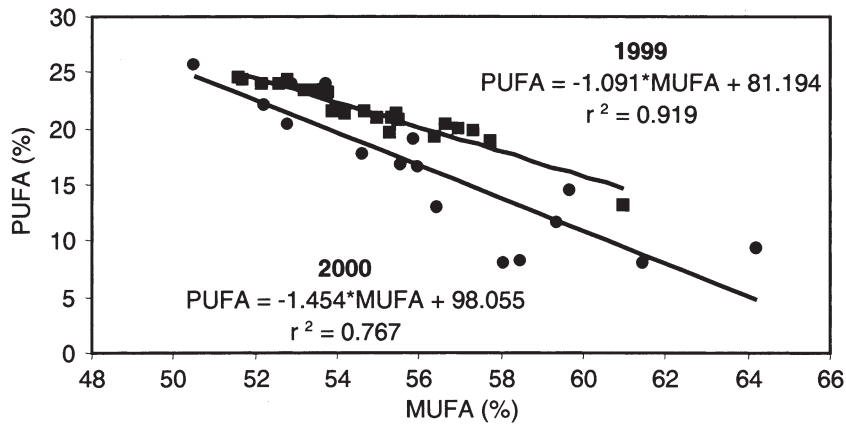[a]Includes minor proportions of other FAs (16:1ω7*t* and 18:1ω7*t*)

Fig. 5. Relationship between monounsaturated (MUFA) and polyunsaturated fatty acids (PUFA) in 1999 (■) and 2000 (●) milk samples. Predictive equations for the proportion of PUFAs in milk samples are included in the figure

1985), perhaps explaining the higher incidence of these species in scats in 1998. *T. gaudichaudii* is especially abundant in Kerguelen waters, where it plays a major trophic role in the pelagic ecosystem (Bocher et al. 2001). Icefish consumed by fur seals in 1998 were from the cohort age 1+ and averaged 193 mm in length, representing the largest of the fish species consumed in high numbers. It is possible that the heads of larger fish were not consumed, as is frequently the case with South African fur seals (*A. pusillus pusillus*; David 1987) and were thus not represented in scats. Icefish is not particularly high in calories at 5.4 kJ g^{-1} (Lea et al. 2002b) when compared to myctophids such as *Gymnoscopelus piabilis* or *G. nicholsi* (9.5 to 9.8 kJ g^{-1}); however, 1 icefish is equivalent in calorific value to several smaller and oilier myctophids, as a result of its larger size. Commercial trawlers conducting research trawls in the vicinity caught only larger, older fish of age 3+ measuring 310 mm (Claudet 2001). Thus, it would appear that female seals and trawl gear are generally capturing different-sized fish.

At other Antarctic fur seal breeding sites such as Bird Island, South Georgia and Heard Island, *Champsocephalus gunnari* is usually found in the diet of male fur seals (North et al. 1983, Reid 1995, North 1996, Green et al. 1997), although it is a relatively important dietary component of female fur seals in years of low krill

seals from Île de Croy to the NW of the archipelago in late lactation 1994 was also dominated by a *Gymnoscopelus* species, *G. nicholsi* (Cherel et al. 1997), a species often associated with the continental slope (Daneri 1996). This species is capable of forming dense concentrations (Kozlov 1995) and is 1 of the 4 most abundant myctophids in the Southern Ocean, the other 3 being *Electrona antarctica*, *E. carlsbergi* and *Krefftichthys anderssoni* (Kozlov & Tarverdiyeva 1989). *G. nicholsi* is also particularly oily (Lea et al. 2002b), although smaller than *G. piabilis*, and comprised a significant portion of the diet of seals from Cap Noir, particularly in 2000. Apart from *G. piabilis*, *G. fraseri* and some *E. antarctica* and *Protomyctophum tenisoni* in 2000, virtually all myctophids in the diet of Antarctic fur seals had not yet attained maturity (Hulley 1990).

While myctophids of the PFZ generally constituted the major dietary components of the fur seals, differences at the species level were evident between years, and in 1998 in particular, the consumption of other fish species represented 36% of prey biomass. The most common of these species (17%), the mackerel icefish *Champsocephalus gunnari*, is also trawled commercially at Îles Kerguelen (Duhamel 1991). This species usually occurs over shelf/upper-slope waters over depths of 150 to 300 m during the day, becoming more pelagic at night (Duhamel 1991). *C. gunnari* is known to forage on many of the smaller myctophid species also present in the scats of *Arctocephalus gazella*, such as *Krefftichthys anderssoni*, *Metelectrona ventralis*, *Protomyctophum andriashevi* and *P. choriodon* (Hulley 1990), some of which may be secondarily ingested from the stomachs of *C. gunnari* in 1998. The diet of *C. gunnari* at Kerguelen is, however, usually comprised of the amphipod *Themisto gaudichaudii* and the euphausiid *Euphausia vallentini* (Duhamel & Hureau

Table 6. Relationship between inter-annual differences in abundance of 9 fatty acids (FAs) in fur seal milk samples and the occurrence of FAs in prey items. PUFA, polyunsaturated FAs

FA	Year of highest abundance	Prey items
15:0	2000	Pt, Gp[a], Es[a]
i15:0	2000	Gp[a], Pt, Gf[a], Es[a]
16:1ω5	2000	Gf[a], Pt, Gp[a]
18:1ω7	2000	Gn[a]
20:1ω9	2000	Gn[a], Mk, Ga
20:1ω7	2000	Ea, Ga, Gn[a], Mk, Gf[a]
22:5ω6	1999	Mh
C$_{21}$PUFA	1999	Cg, Ga[a]
22:6ω3	1999	Mh, Tgaud[a], Pt[a], Cg

Mh, *Martialia hyadesi*; Mk, *Moroteuthis knipovitchi*; Ga, *Gonatus antarcticus*; Cg, *Champsocephalus gunnari*; Ec, *Electrona carlsbergi*; Es, *E. subaspera*; Gf, *Gymnoscopelus fraseri*; Gn, *G. nicholsi*; Gp, *G. piabilis*; Pt, *Protomyctophum tenisoni*; Tgaud, *Themisto gaudichaudii*

[a]Higher incidence of prey item confirmed by scat analyses

abundance around Bird Island (Reid & Arnould 1996). North (1996) observed 2 size classes of *C. gunnari* in the diet of fur seals over winter with the majority of those taken coinciding with the size classes trawled by the fishery (225 to 325 mm). At Heard Island, 2 peaks were detected at 195 and 225 mm in winter and summer, respectively (Green et al. 1997), coinciding with the size of fish taken by seals at Îles Kerguelen in 1998. *C. gunnari* was not present in the diet in either 1999 or 2000 at Îles Kerguelen, although research trawls caught low numbers of 244 and 313 mm sized fish in the 2 years, respectively (Claudet 2001). The consumption of icefish in 1998 may reflect either the reduced availability and/or catchability of myctophids close to the archipelago in this year, or more patchily distributed icefish in 1999 and 2000.

Cephalopod beaks were common in seal scats, although they occurred in low numbers when compared to the quantities fish prey consumed, accounting for only 2.1% of prey by number. At least 4 of the squid species taken by Antarctic fur seals are associated with waters of the PFZ and are known to feed on myctophids (Rodhouse & White 1995, González & Rodhouse 1998, Phillips et al. 2001). Only juvenile *Martialia hyadesi*, *M. ingens* and *M. knipovitchi* (Kubodera et al. 1998, Wormuth 1998) were taken by seals foraging in the Kerguelen region. Given the low numbers of squid present in the diet, it is probable that squid were either taken opportunistically as seals and squid fed on nocturnal myctophid aggregations, or the squid were patchier in their distribution than myctophids. Studies of Antarctic fur seals at other breeding sites confirm the relative paucity of cephalopods in the diet (Klages 1996, Goldsworthy et al. 1997, Daneri et al. 1999, Kirkman et al. 2000), contrary to studies of more temperate species such as the New Zealand and Australian fur seals (Gales et al. 1993, Fea & Harcourt 1997). In any event, the occurrence of cephalopods in the diet of Antarctic fur seals was low and never accounted for more than 2.1% of the diet by number, a figure that would be over-estimated by the preferential retention of squid beaks (see Klages & Bester 1998, Ferreira & Bester 1999). However, in years where squid were consumed, such as 1998 and 2000, the biomass and energy value of this prey was considerable, ranging from 10 to 15% of reconstituted biomass.

Milk lipids as indicators of dietary variation

The dietary dependence of fur seals on myctophids during late lactation was further supported by the high levels of MUFAs present in the FA profiles of fur seal milk. Myctophidae generally have high levels of MUFAs (Seo et al. 1996, Raclot et al. 1998), which may

be transferred directly to predators, as shown by the close relationship between the FAs of king penguin subdermal fat and of their myctophid diet (Raclot et al. 1998). The percentage of MUFAs in fur seal milk (53 to 55%) more closely approximates that of TAG-rich myctophids rather than those species rich in wax esters, such as *Electrona antarctica* or *Gymnoscopelus braueri* (Phleger et al. 1999), thus supporting the findings of the fecal analyses. High levels of 18:1ω9, 20:1ω9 and 22:1ω11, apparent in fur seal milk samples, also tend to be characteristic of many teleost fish (Reinhardt & van Vleet 1986, Iverson et al. 1997).

Milk secreted later in lactation is thought to contain FAs representative of dietary intake, whilst FAs present in blubber stores during the peri-natal period may represent dietary intake over winter prior to parturition (Iverson 1993, Iverson et al. 1997). Mammalian milk composition varies according to lactation stage (Oftedal 1984). Consequently, milk samples for this study were collected in the same season for both years, in order to reduce the effect of any compositional differences related to lactation stage or season. Thus, the differences observed in the FAs composition of milk samples in 2 consecutive years in this study confirm the inter-annual shift in diet detected by fecal analysis.

The similarity of milk samples from the same seal collected up to 19 d apart suggests that seals may feed on similar prey during successive trips, therefore exhibiting little change in their milk FA profiles. Alternatively, milk FAs may be indicative of dietary intake over at least 19 d and FA profiles are therefore not particularly responsive to short-term changes in prey consumption. Little information is available on short-term dietary preferences, although Bonadonna et al. (2001) have recently shown that fur seals at Cap Noir often maintain the direction of travel used in the preceding trip, perhaps foraging on the same prey. However, in either scenario, it is probable that milk FA compositional profiles represent longer-term dietary intake, at least up to 3 wk, than fecal analyses.

Milk samples collected during late lactation 1999 were high in PUFAs (21.4% cf. 16.1%), whilst samples from 2000 where higher in saturated FAs and MUFAs. Nine FAs were identified by DFA as differentiating between milk samples from the 2 years. Of these FAs, 18:1ω7, indicative of *Gymnoscopelus nicholsi* consumption, was particularly useful in confirming the higher incidence of this species as shown by scat analyses. Also, the higher levels of PUFAs in 1999, particularly DHA (22:6ω3), could indicate a greater reliance on *Protomyctophum tenisoni,* which are relatively high in DHA (Lea et al. 2002b), because of the digestibility of their small otoliths.

The significance of such comparisons is undoubtedly influenced by both the number and site of origin of

potential prey items. Fish of the same species from different localities may vary considerably in FA composition. Fortunately, we could compare milk samples with FA profiles of 8 prey species collected in the foraging zone of fur seals (see Lea et al. 2002b). However, the FA profiles of many prey species, in particular *Protomyctophum* spp., are yet to be described at Îles Kerguelen, and in many regions of the Southern Ocean.

Previously, significant seasonal shifts in dietary intake of Antarctic fur seals at South Georgia have been identified by Iverson et al. (1997) using FA signature analysis, whilst Brown et al. (1999) could distinguish between the diet of Antarctic fur seals and Southern elephant seals from South Georgia by comparing the FA composition of milk samples to potential prey items. More recently, gray seals from different breeding sites have been differentiated on the basis of milk FA profiles alone, without reference to possible prey items (Walton et al. 2000). Thus, the usefulness of quantitative FA analysis in answering particular questions regarding prey group consumption or inter-site dietary differences is beyond doubt. Although it was possible to statistically discern between milk samples from 2 consecutive years on the basis of milk FA profiles at Îles Kerguelen, isolating those species attributing to the observed difference was less clear. Considerable debate regarding the statistical analysis and interpretation of dietary signature FA analysis has taken place in recent years (Grahl-Nielsen & Mjaavatten 1995, Iverson et al. 1997, Smith et al. 1997) and although this study provides support for the occurrence of dietary shifts using milk FA analysis, further developments in the analytical tools used to adequately interpret such data are still necessary.

Approximately 94% of the Antarctic fur seal diet (according to scat analysis) at Îles Kerguelen consists of myctophid fish. The variation in FA composition recorded between species of myctophids is minimal when compared to the larger-scale differences between fish, prey items of other trophic levels and milk profiles. Had milk samples been collected in 1998, a year of higher consumption of fish from other families such as *Champsocephalus gunnari*, differences in milk compositional profiles may have been more easily attributed to a particular prey family or species.

Interestingly, the proportion of lipid in milk samples also differed between years in addition to the FA profile differences. Percentage lipid was particularly high in year 2000's samples (53%), which were still within the range of values reported by Arnould & Boyd (1995) for conspecifics in late lactation at South Georgia and Robinson et al. (in press) at Macquarie Island. Lantern-fish of the genus *Gymnoscopelus*, and *Electrona antarctica* are particularly rich in lipids, with up to 18% of wet mass reported for *G. nicholsi* from the Kerguelen

region (Lea et al. 2002b). One hypothesis for the observed inter-annual variation in milk lipid content in 1999 and 2000 is the variability in the consumption of *Gymnoscopelus* spp. in the 2 seasons, which comprised approximately 54% of the dietary biomass in 1999 and 74% in 2000 (or 57 and 80% in terms of energy, respectively). Thus, it would appear that differences in diet between years may also affect the quality of milk stores delivered to pups.

Implications for foraging ecology and oceanic conditions

On a broad taxonomic scale, the composition of the diet between years was similar as myctophids consistently formed the majority of the diet both in number and in terms of biomass. In all years, *Gymnoscopelus piabilis* comprised between 27 and 32% of prey biomass. However, on a finer scale, the composition of prey species was highly variable with the occurrence of icefish *Champsocephalus gunnari* and *Electrona carlsbergi* in 1998, a greater proportion of *Protomyctophum* species in 1999, and perhaps squid as well as a considerably higher proportion of *G. nicholsi* and myctophids in general in 2000. Changes in oceanographic circulation appear to be responsible for fluctuations in prey abundance (Hunt 1991, McCafferty et al. 1999, Nel et al. 2001), and the position of oceanographic features such as the Antarctic PF may be affected seasonally by weather systems (Priddle et al. 1988). Reid & Arnould (1996) have suggested that periods of myctophid consumption by female Antarctic fur seals at South Georgia, which usually feed on Antarctic krill, coincide with oceanographic changes bringing concentrations of myctophids, associated with the APF, into the foraging range of the seals. Thus, it is reasonable to suggest that the position of the APF and oceanographic conditions at Kerguelen varied sufficiently within the foraging range of fur seals from 1998 to 2000 to change the species composition of prey available to fur seals.

Guinet et al. (2001) have recently demonstrated that in February 1998 female Antarctic fur seals at Îles Kerguelen tended to forage in the vicinity of the PF in areas of high fish abundance over the continental slope. In our study, 1998 was the year of least myctophid abundance in the diet in comparison to the other 2 years and was also the year that seals dived most deeply on average (Lea et al. 2002). Thus, it would appear that prey availability as measured by the diving behavior of the seals (Boyd et al. 1994, Boyd 1999) and confirmed by dietary analysis varied considerably between years. The higher incidence of scats devoid of otoliths and prey remains in 2000 also tends

to suggest that seals were foraging farther from the colony in this year. All these factors indicate that possible changes in oceanographic features in the vicinity of the Kerguelen Archipelago from 1998 to 2000 affected the dietary intake and foraging behavior of Antarctic fur seals considerably.

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