You are what you eat: describing the foraging ecology of southern elephant seals (*Mirounga leonina*) using blubber fatty acids

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Understanding the trophodynamics of marine ecosystems requires data on the temporal and spatial variation in predator diet but, particularly for wide-ranging species, these data are often unavailable. The southern elephant seal (*Mirounga leonina*) consumes large quantities of fish and squid prey in the Southern Ocean relative to other marine mammals; however, how diet varies relative to seasonal and spatial foraging behaviour is unknown. We used fatty acid (FA) signature analysis of 63 blubber cores from adult female *M. leonina* over three seasons (winter 1999, summer 2000 and winter 2001) to determine diet structure. We detected significant differences between seasons and between the main foraging regions (Antarctic continental shelf versus pelagic). We used the FA profiles from 53 fish, squid and krill species to construct a discriminant function that would classify each seal, from its blubber sample as having a fish- or squid-FA profile. We determined that a higher proportion of *M. leonina* had fish-dominated diets during the winter and when foraging around the Antarctic continental shelf, and the majority had more squid-dominated diets during the summer when foraging pelagically. Thus, we were able to measure the coarse-scale diet structure of a major marine predator using FA profiles, and estimate its associated seasonal and temporal variation.

Keywords: fatty acid signature analysis; foraging; diet; spatial variation; seasonal variation

1. INTRODUCTION

Understanding the foraging ecology of predators within an ecosystem is an important step towards modelling energy flow and predator–prey interactions (Woodward & Hildrew 2002). Part of this process requires information on both the spatial and the temporal aspects of predator diet (Brown *et al.* 1999; Shurin 2001), and this is particularly important for wide-ranging species that occupy vastly different ecological zones during the course of their regular movements (Hyrenbach 2001). In the case of wide-ranging top-level marine predators, such as whales, seals and seabirds, there is scant information on diet structure with respect to individual, geographical and temporal variation (Iverson *et al.* 1997b; Hindell *et al.* 2003). This can lead to inaccurate predictions arising from numerical models used to predict consumption rates as part of the management of marine resources such as commercial fisheries (Thompson *et al.* 2000; Bjørge *et al.* 2002).

Many of the difficulties encountered in the quantification of diet stem from the assumptions made when using traditional techniques to investigate diet in marine mammals (e.g. stomach lavage, faecal analysis). These methods are often representative of the last meal eaten, and are influenced by the rate of passage of food (Green &

Williams 1986; Fea & Harcourt 1997) and other factors (Staniland 2002). A more recently developed method of diet analysis is the use of fatty acids (FA) as dietary tracers (Iverson 1993). FA signature analysis can theoretically be used to determine diet composition and also to provide a long-term indication of diet history (Iverson *et al.* 1997a,b). Recent research using FA analysis to quantify diet in top-level marine predators has shown promise (Iverson *et al.* 1997b; Raclot *et al.* 1998; Brown *et al.* 1999; Hooker *et al.* 2001), although others have been less optimistic (Grahl-Nielsen 1999). Differences in FA signatures among populations, geographical regions and seasons have all been identified (Iverson *et al.* 1997a; Walton *et al.* 2000; Lea *et al.* 2002; Walton & Pomeroy 2003), demonstrating that the technique can be used to detect changes in diet. However, only Iverson *et al.* (1997b) and Hooker *et al.* (2001) have been able to attribute some of these differences to specific prey. Further, no study has determined the spatial and temporal variation in diet structure of individuals relative to foraging regions. For this approach to be meaningful, a large sample of prey species and a realistic assessment of the minimum taxonomic resolution detectable are required (Iverson 1993).

The southern elephant seal (*Mirounga leonina*) is a large top-level predator that forages throughout most of the Southern Ocean, with a total world population estimated at 664 000 individuals (Laws 1994). Their capacity to ingest large quantities of prey (fishes and squid) and the

considerable size of the world population make them important consumers of Antarctic marine resources (Boyd *et al.* 1994; Santos *et al.* 2001; Hindell *et al.* 2003). Santos *et al.* (2001) estimated that the total annual consumption by *M. leonina* is *ca.* 4.5 million tonnes of prey (primarily squid), and this represents 19–36% of the total Antarctic consumption of cephalopods by sperm whales, beaked whales, seals and seabirds combined (Clarke 1983). However, these estimates were based on incomplete assessments of diet in all of these predators.

Analyses of stomach contents collected at haul-out sites have identified a suite of fish and cephalopod prey eaten by *M. leonina* (Macquarie Island; Green & Burton 1993; Heard Island; Green & Burton 1993; Slip 1995; East Antarctica; van den Hoff *et al.* 2003; King George Island; Daneri *et al.* 2000; Daneri & Carlini 2002; Piatkowski *et al.* 2002; I. C. Field, unpublished data). The difficulties encountered in the quantification of diet in marine mammals using traditional techniques are exemplified in *M. leonina* owing to its predominantly marine existence (spending *ca.* 80% of its life cycle at sea; Hindell *et al.* 1991) and the pronounced spatial separation between its haul-out and foraging regions (Hindell *et al.* 2003). Estimates of the ratio of squid to fishes in the diet range between 55 : 45 (Slip 1997) and 75 : 25 (Boyd *et al.* 1994); however, the true ratio, and its associated temporal and spatial variance, are still unknown. For example, it is unknown whether diet composition differs significantly between the post-lactation (or summer; October–January) foraging phase and the post-moult (or winter; February–September) phase. In this paper, we determine whether FA from the blubber of adult female *M. leonina* can indicate spatial and temporal variation in diet between individuals. Different ecological zones in the Southern Ocean are likely to support different prey communities (Knox 1994); wide-ranging species, such as elephant seals, that forage within these different geographical zones should therefore be exploiting different prey. As such, elephant seals are a good test species for the application of FA signature analysis to determine diet structure (Brown *et al.* 1999). If even coarse-scale differences are not detectable, then the approach is unlikely to contribute much to the understanding of the variation in the diet of top predators in this, or other, marine ecosystems. To investigate this, we combine detailed data on the foraging locations of elephant seals over 3 years with an extensive library of FA profiles isolated from known and probable prey species.

2. MATERIAL AND METHODS

(a) *Data*

Blubber samples were collected from adult female southern elephant seals ($n = 63$ samples; $n = 24$ unique individuals) from Macquarie Island (54°30′ S, 158°50′ E) over 3 years. All animal handling procedures were reviewed and approved by the Antarctic Science Advisory Committee (ASAC 1171). The study population consisted of known-age animals born in 1993 (and branded after weaning; McMahon *et al.* 2000) to minimize the confounding effects of age and cohort in the analyses. Blubber samples were obtained in: (i) October 1999 ($n = 27$) immediately post-parturition; (ii) January 2000 ($n = 25$) as the animals returned from the post-lactation trip to moult; and (iii) October 2001 ($n = 11$) immediately post-parturition (see Field *et al.*

(2002) for capture, sedation and measurement details). The blubber samples therefore represented fat accumulated largely during the previous foraging trips: (i) winter 1999; (ii) summer 2000; and (iii) winter 2001. However, the proportion of blubber containing lipids accumulated during earlier trips depends on energy expenditure while onshore (Fedak *et al.* 1994; Carlini *et al.* 1999), and this may reduce the power to detect temporal differences.

Twenty-five out of the 63 samples had associated geographical data collected using time–depth recorder (TDR) archival tags (Wildlife Computers, WA, USA) fitted to the seals (two from winter 1999, 14 from summer 2000 and nine from winter 2001). The TDRs sampled time, depth, light level and temperature every 30 s for the duration of each foraging trip (Bradshaw *et al.* 2002). Because individuals from this cohort have demonstrated high fidelity to foraging regions between foraging trips (e.g. average of 62% overlap from summer 1999 to summer 2000; range of 44–86%; $n = 8$; C. Bradshaw and M. Hindell, unpublished data), individuals that were known to forage in a particular region in a specific season, but for which no geographical data were available, were assumed to use the same region on all trips.

The biopsy site was located by measuring 5–7 cm laterally from a site on the posterior dorsal surface of the seal (Best *et al.* 2003). A 2 cm × 2 cm square area was shaved and disinfected with an alcohol swab. A 1 cm anterior–posterior line was cut through the skin, and the biopsy corer (6 mm in diameter) was inserted into this incision. Biopsies contained 'whole' cores of blubber from the skin to the muscle layer. No suturing of the incision was required. Each core was placed into a vial containing a solvent mixture of 2 : 1 v/v chloroform and methanol, and 0.05% by weight of the anti-oxidizing agent, butylated hydroxytoluene. Samples were maintained at −20 °C until lipid analysis.

Lipids were extracted following Best *et al.* (2003). Briefly, we used a modified version of the Bligh & Dyer (1959) one-phase methanol–chloroform–water extraction (ratio modified to 2 : 1 : 0.8 by volume). Chloroform and saline water were added to separate the phases following overnight extraction (final solvent ratio of 1 : 1 : 0.9 by volume). Solvents were removed using rotary evaporation (40 °C), and the total lipid (TL) extracted (greater than 98%) was dissolved in chloroform and an aliquot treated with methanol–hydrochloric acid–chloroform (10 : 1 : 1 v/v/v; 80 °C; 2 h). TL samples were vortexed two to four times during that time to maximize conversion to FA methyl esters (FAME). The FAME were extracted three times into hexane–chloroform (4 : 1 v/v, 3 ml × 1.8 ml; +1 ml water) and subjected to gas chromatographic analyses using a Hewlett Packard 5890A GC (Avondale, PA, USA). Peaks were quantified with Waters Millennium software (Milford, MA, USA). Individual components were identified by comparing retention-time data with authentic and laboratory standards. Integrated chromatograms were normalized by expressing the FA components as percentages of the total FA. FA components that occurred at less than 0.5% were not included in the statistical analyses, as the precision of their determination is low (Walton & Pomeroy 2003). Total saturated FA (SFA), monounsaturated FA (MUFA), short-chain MUFA (SC-MUFA), long-chain MUFA (LC-MUFA) and polyunsaturated FA (PUFA) were also calculated (Best *et al.* 2003).

A total of 53 known and possible southern elephant seal prey species (36 fishes, 15 squid and two euphausiids (krill)) were identified, and their FA profiles were obtained from various published and unpublished sources (Nichols *et al.* 1994; Bakes *et al.* 1997; Phleger *et al.* 1999a,b, 2002; Phillips *et al.* 2002; Lea *et*
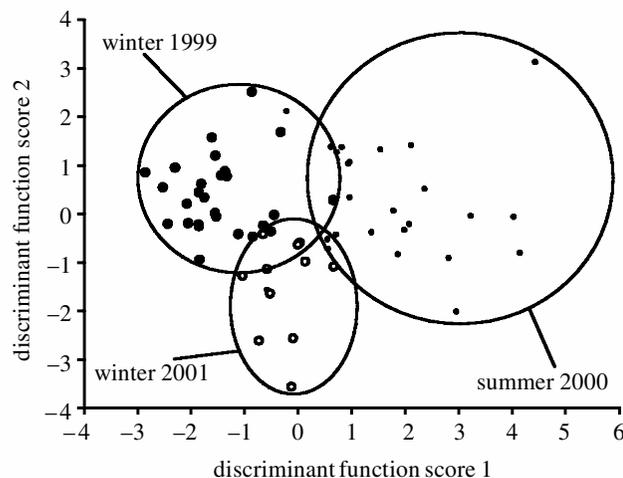
Figure 1. Seasonal separation of blubber FA profiles identified for southern elephant seals using linear discriminant scores. Large black circles, winter 1999; small black circles, summer 2000; open circles, winter 2001.

al. 2002; K. Phillips and G. Wilson, unpublished data). We endeavoured to include as many species as possible for which FA profiles exist and which are found within the foraging ranges of southern elephant seals.

(b) Statistical analysis

All FA proportions were arcsine–square-root transformed to reduce the heterogeneity of variances among test groups (Sokal & Rohlf 1981). We adopted a simple robust statistical technique (stepwise linear discriminant function analysis (DFA) using cross-validation) to identify distinct groups based on FA profiles. Separate functions were estimated to predict the group membership of the seal-blubber samples for seasonal classification (winter 1999, summer 2000 and winter 2001; e.g. figure 1).

Four main foraging regions were identified from the TDR geolocation data, based on the majority of time spent by an individual in a particular region: (i) southwest of Macquarie Island around the Antarctic continental shelf (SW); (ii) southeast of Macquarie Island and into the Ross Sea (SE); (iii) east of Macquarie Island in the vicinity of the Antarctic Polar Front (APF) (E-APF) (Hindell et al. 2003); and (iv) west of Macquarie Island in the vicinity of the APF (W-APF) (figure 2). The DFA was repeated for a regional breakdown based on whether the animals had foraged mainly over the Antarctic continental shelf (SW) or pelagically (SE, E-APF, W-APF) during their foraging trip. A more detailed examination of the possible interactions between season and foraging region was not possible because there were an insufficient number of seals with known or assumed foraging regions and only one summer season was sampled.

For the prey data, we first identified the lowest taxonomic level that provided clear separations using DFA. For example, we examined whether the prey data could be assigned clear membership based on family (e.g. nototheniid and myctophid fishes, or onychoteuthid squid); however, the lowest taxonomic resolution found was to divide the sample into fishes, squid and krill. We then applied the resulting predictive function for the prey groups to the blubber FA data from the elephant seals to classify them into one of these three prey groups. No seals were classified as belonging to the euphausiid group (see § 3d), so we repeated the DFA using only two prey groups: fishes and squid.

3. RESULTS

(a) Blubber FA composition
A total of 18 FAs present in greater-than-trace amounts (more than 0.5%) were identified from the blubber of the 63 southern elephant seals. These accounted for 93–96% of the total FA. Total percentages of SFA, PUFA, SC-MUFA and LC-MUFA for elephant seals in each season and for the prey groups are presented in table 1.

(b) Seasonal differences
DFA using the three seasons as the classification variable provided a correct assignment of 84% of blubber samples into their respective seasons. A biplot of the discriminant scores indicates a clear separation between seasons (figure 1). Most misclassifications (six out of 10) were either summer samples classed as 'winter' or winter samples classed as 'summer' (i.e. four out of 10 misclassifications were between the two winters).

(c) Regional differences
For the 33 individual seals with known or assumed foraging locations, there were four (12%) individuals identified with foraging trips in the SW region, 11 (33%) in the SE region, 13 (40%) in the E-APF region and five (15%) in the W-APF region. There were insufficient foraging trips within each region to estimate a four-class discriminant function (DF), so we grouped the regions into more southerly (SW and SE) and more northerly (E-APF and W-APF) regions for a two-class DF. DFA using these two regions as the classification variable provided a correct assignment of 76% of blubber samples into their respective regions (Wilks' Lambda = 15.18, d.f. = 1,31, $p < 0.001$). Five out of the eight overlapping classifications (63%) were northern foraging trips classified as southern foraging trips.

In general, seals spent more time in the southern regions of their foraging range (e.g. northern Ross Sea and Antarctic continental shelf) during the winter than during the summer (see also Hindell et al. 2003). Following the hypothesis that elephant seals foraging mainly in the vicinity of the Antarctic continental shelf (SW region) were likely to encounter different prey communities from the more pelagic foragers (SE, E-APF and W-APF), we applied a second DFA using this distinction as the classification variable. This provided a correct assignment of 81% of blubber samples (Wilks' lambda = 16.22, d.f. = 1,30, $p < 0.001$). One (25%) out of the four shelf foragers was classified as a pelagic forager. The five remaining incorrect classifications were pelagic foraging trips classified as shelf foraging trips.

(d) Prey and seal blubber classification
DF classification using the three main prey groups—fishes, squid and krill—produced a correct assignment of 89% of all prey species. The FAs identified as adequate predictors of group membership using the stepwise procedure were 16 : 1ω7, 18 : 1ω9, 20 : 1ω7, 22 : 1ω11, 24 : 1ω9/11, 20 : 4ω3, 20 : 4ω6, 22 : 5ω3 and 22 : 6ω3 (Wilks' Lambda = 50.63, d.f. = 18,84, $p < 0.001$). A biplot of the discriminant scores indicated a clear separation between prey groups (figure 3). Only six out of the 53 species were classified incorrectly. These were the fishes
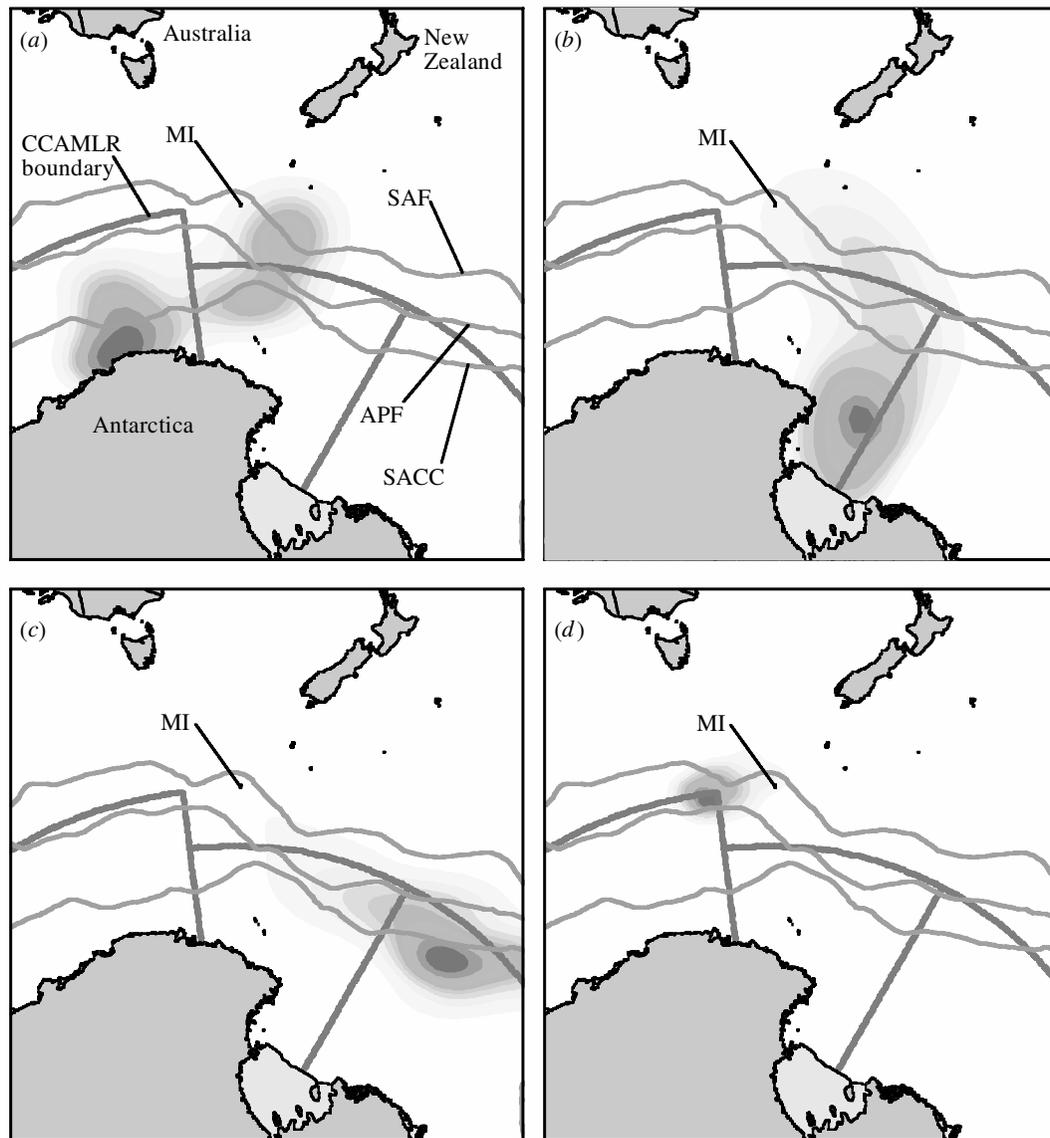
Figure 2. Examples of foraging regions estimated using TDR geolocations from female southern elephant seals, *Mirounga leonina*, from Macquarie Island (MI) during 1999 to 2001 (kernel home ranges; M. A. Hindell and C. J. A. Bradshaw, unpublished data). The mean positions of the major oceanic fronts, the Subantarctic Front (SAF), the APF and the southern boundary of the Antarctic circumpolar current (SACC), and the boundaries for the CCAMLR statistical subareas south of Macquarie Island are shown. Four main foraging regions were identified: (*a*) SW, (*b*) SE, (*c*) E-APF and (*d*) W-APF.

Icichthys australis, *Gymnoscopelus bolini*, *G. fraseri*, *G. nicholsi* and *Champsocephalus gunnari*, which were classified as squid, and the squid *Todarodes* sp. (Appendix A), which was classified as a fish. We also recalculated the DFA using only two prey groups, fishes and squid (because no seals were classified as belonging to the krill group, see below). This produced a correct classification of 89% of prey species. Only four FAs were required to provide group membership into these two prey groups: $16:1\omega7$, $20:1\omega9$, $22:1\omega11$ and $24:1\omega9/11$ (Wilks' lambda $= 15.62$, d.f. $= 4,46$, $p < 0.001$). Six out of the 53 species were classified incorrectly: these were the fishes *G. bolini*, *G. fraseri*, *Borostomias antarcticus* and *I. australis*, which were classified as squid, and the squid *Moroteuthis robsoni* and *Kondakovia longimana* (Appendix A), which were classified as fishes.

Using the first DF for the three-prey classification (fishes, squid, krill), we recalculated the DF by inserting the proportions of each of the nine FAs from the individ-

ual blubber samples. This produced a classification of a seal blubber sample as 'fish', 'squid' or 'krill'. None of the seals was identified as belonging to the krill group. Thus, we reanalysed the blubber FA data using only the two-prey (fishes, squid) DF.

Using the number of samples classed into each of these two groups, we calculated the proportion of seals in each group relative to season (table 2). A histogram of the discriminant scores for the prey data identified the values for which there was no overlap between fishes and squid (figure 4). By superimposing the scores derived using the seal data and the prey DF onto this histogram, we were able to classify each seal as having a fish-dominated diet if the value was more than 0.0, and as having a squid-dominated diet if the value was less than -3.5 (figure 4). The remaining seals were identified as having a mixed diet of fish and squid. This methodology assumes that there is little modification of the FA concentrations from prey to predator (Grahl-Nielsen & Mjaavatten 1991; Iverson

Table 1. Seasonal breakdown of the main FA groups isolated from elephant seals and prey.
(Prey data are averages and are not available seasonally.)

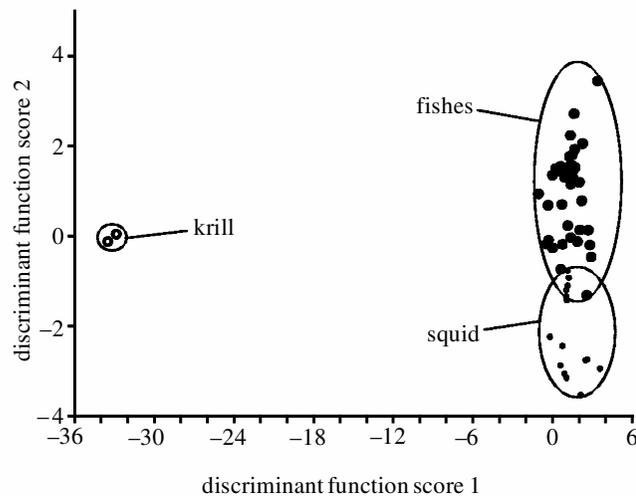| season	seals		fishes		squid		krill	
	mean (%)	s.d.	mean (%)	s.d.	mean (%)	s.d.	mean (%)	s.d.
winter 1999								
sum SFA	15.5	2.3	20.1	7.5	22.8	7.4	29.2	2.5
sum SC-MUFA	47.0	2.7	39.4	15.6	28.0	10.1	26.9	7.0
sum LC-MUFA	21.7	2.9	13.1	6.4	19.0	8.2	8.8	12.1
sum PUFA	15.8	1.9	25.7	13.3	29.9	12.8	34.4	17.5
summer 2000								
sum SFA	14.8	2.7	—	—	—	—	—	—
sum SC-MUFA	46.8	2.3	—	—	—	—	—	—
sum LC-MUFA	24.5	4.7	—	—	—	—	—	—
sum PUFA	13.9	2.7	—	—	—	—	—	—
winter 2001								
sum SFA	17.2	1.9	—	—	—	—	—	—
sum SC-MUFA	46.6	1.8	—	—	—	—	—	—
sum LC-MUFA	22.1	3.8	—	—	—	—	—	—
sum PUFA	14.2	1.7	—	—	—	—	—	—

Figure 3. Separation of three prey groups (fishes, large black circles; squid, small black circles; and krill, open circles) based on linear discriminant scores derived from FA profiles of known and possible elephant seal prey species.
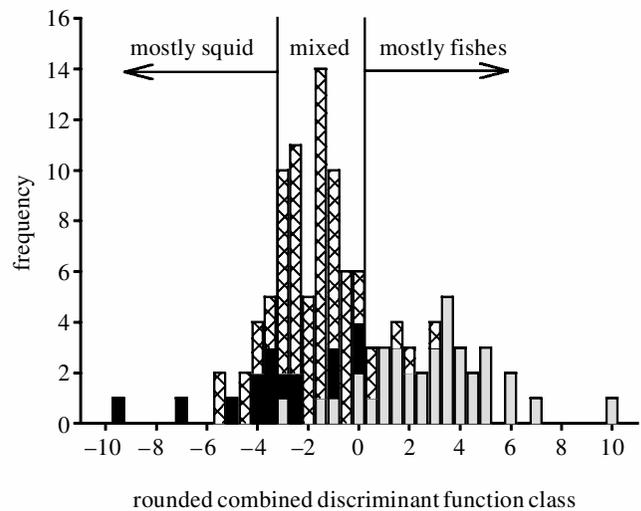

Figure 4. Histogram of linear discriminant scores derived from prey data by separating prey into two groups: fishes (grey bars) and squid (black bars). Elephant seal FA values (hatched bars) were applied to the discriminant function derived from the prey data to classify seals as having a fish-dominated diet, squid-dominated diet or a diet comprising a mixture of the two prey groups. Seals were classified into the three categories based on the overlap of discriminant scores between fishes and squid: when seal scores fell into the extreme ranges of the prey scores without overlap (score less than −3.5 for squid; more than 0.0 for fishes), we classified them accordingly.

1993; Grahl-Nielsen *et al.* 2000). The summary of these classifications is presented relative to season and geographical foraging region in table 3. In general, seals foraging over the Antarctic continental shelf had diets dominated by fish, whereas those feeding more pelagically had diets dominated by squid (table 3). This was also supported by the observation that during winter (when individuals foraged farther south, in the vicinity of the Antarctic continent) fish-dominated diets were more prevalent than in summer.

4. DISCUSSION

A common problem in ecological research is the difficulty of estimating prey consumption by a predator population in a spatial context, and this often limits a satisfactory understanding of trophodynamics in even simple ecosystems (Hyrenbach 2001; Shurin 2001; Woodward &

Hildrew 2002). Spatial variation in diet has rarely been assessed, especially for wide-ranging top predators such as marine mammals (Goldsworthy *et al.* 2001). We used the unique combination of FA signature analysis and tracking data to estimate diet structure in a wide-ranging pinniped, the southern elephant seal, and its temporal and spatial variation. There was a clear separation of diet between all three seasons examined based on FA profiles. Although the main separation was between the summer and the winters (figure 1), even the two winter groups were clearly

Table 2. *Seasonal summary of the numbers of seals identified as belonging to the 'fish' and 'squid' prey groups using linear DFA.*
(Percentages are also shown.)

	season				
prey type	all	summer	winter 1999	winter 2001	winter (both)
fishes (n)	7	1	4	2	6
squid (n)	56	24	23	9	32
fishes (%)	11	4	15	18	16
squid (%)	89	96	85	82	84

Table 3. *Seasonal and regional summary of the number of seals classified as having a fish-dominated, squid-dominated or mixed diet using discriminant scores derived from prey data.*
(Percentages for each season are shown in parentheses in the 'total' column. Abbreviation: Unk, unknown foraging region.)

		region					
season	prey type	Unk	SE	SW	E-APF	W-APF	total
summer	fish	1	—	—	—	—	1 (4)
	squid	4	—	—	3	1	8 (32)
	mix	6	—	2	5	3	16 (64)
summer total		11	0	2	8	4	25
winter	fish	1	1	1	1	—	4 (11)
	squid	—	—	—	—	—	0 (0)
	mix	18	10	1	4	1	34 (89)
winter total		19	11	2	5	1	38

different. Interannual fidelity to foraging areas (C. J. A. Bradshaw and M. A. Hindell, unpublished data) supports the conclusion that seasonal changes were indicative of diet changes, and interannual variation in prey distribution or abundance may result from regular fluctuations in oceanographic features such as the Antarctic Circumpolar Wave (White & Peterson 1996) that affect prey availability and may be detectable in the FA profiles of their predators. We also found a clear separation between seals foraging mainly over the Antarctic continental shelf and those feeding more in the open ocean. Pelagic feeders and those with more northerly foraging ranges had largely squid-dominated diets.

We were able to differentiate seals as having fish- or squid-dominated diets by using the simple but effective approach of classifying seal FA profiles as belonging to one of two main prey groups: fishes or squid. Of particular interest was the difference in the FA profiles describing more fish-dominated versus more squid-dominated diets relative to foraging region. There were more individuals with fish-dominated diets in the winter, when elephant seals from Macquarie Island are generally spending more time in the region of the Antarctic continental shelf (Hindell *et al.* 2003). No seals were identified as having a squid-dominated diet during the winter. Although the taxonomic resolution of the diet was coarse (i.e. fishes versus squid), the ability to make this distinction has important implications for the modelling of spatially and temporally explicit prey consumption rates by large marine predators (Thompson *et al.* 2000; Hindell *et al.* 2003). Understanding broad-scale diet structure and the associated variance will permit more precise estimates of prey

consumption within the Southern Ocean ecosystem and provide essential information regarding the ecological relationships between harvested, dependent and competing marine populations (Constable *et al.* 2000).

Our results are important for the management of Antarctic commercial fisheries by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Previous results from the adult female component of the southern elephant seal population of Macquarie Island indicate that they spend a significant proportion of their time foraging within regions managed by the CCAMLR, even during the summer months (Hindell *et al.* 2003). However, there is little evidence that the current levels of commercial fishing would be in direct competition with southern elephant seals at Macquarie Island (Burton & van den Hoff 2002; Hindell *et al.* 2003). Regardless, our results indicate that fish prey, including larger specimens such as some of the sub-adult and adult Nototheniidae and Moridae, are an important component of the winter diet of elephant seals. Many fish species within these taxa are also commercially important for fisheries operating within the Southern Ocean regions managed by the CCAMLR (Nichols *et al.* 1994).

The ability of FA profiles to reflect differences in diet structure depends on the degree of dietary specialization and the magnitude of geographical or temporal separation (Iverson *et al.* 1997*b*; Brown *et al.* 1999). For differences in diet between seals foraging in different zones to be detected by examining FA profiles, several scale-dependent conditions must be satisfied: (i) prey communities within these putatively distinct ecological zones must be measurably different from each other, with minimal over-

lap of prey species among zones; (ii) prey species within each geographical zone must possess distinct FA profiles; and (iii) the combined FA profile of a number of dietary items of the predators from each zone must retain sufficient individuality to allow distinction between the animals that forage in each region. Inferring regional differences in diet composition from different FA signatures requires the assumption that the diet of the prey items identified is constant between regions (i.e. top predators from different regions may have different FA signatures and still have similar diets if the prey themselves have different diets). Despite these restrictive prerequisites, our study and others have detected interpopulation and seasonal variation in FA profiles of marine predators such as seals (Iverson *et al.* 1997*b*; Walton *et al.* 2000; Walton & Pomeroy 2003). However, when a predator is known to eat a wide range of prey species within a comparatively limited foraging range, the ability to use FA signatures to detect such variation is limited (Dahl *et al.* 2000; Hooker *et al.* 2001). In reality, the diets of more generalist consumers are less restricted and include a larger range of prey items. The FA profile of the predator therefore would reflect a mixture of the FA profiles of all its prey.

Some of the overlapping classification in the different comparisons may be related to the lack of discreet boundaries between identified foraging regions. The boundary between the SE and E-APF regions was often unclear, and the circumpolar APF acts as a diffuse boundary between water bodies with different salinities, temperatures and nutrient concentrations (Orsi *et al.* 1995). Although different algal and animal communities populate the geographical zones to the north and south of the APF (Moore & Abbott 2002), this front is characterized by a high degree of short- and long-term latitudinal variation between 40° S and 60° S (Knox 1994). This latitudinal variation may blur the distinction of the assigned areas across seasons (Orsi *et al.* 1995). Misclassification may also have arisen from temporal and geographical variation in the FA profiles of the prey species themselves and the residual lipids accumulated in previous foraging trips still present in the blubber layer.

The annual cycle of southern elephant seals is characterized by changes in metabolic demands and the use of specific energy reserves (Boyd *et al.* 1993; Fedak *et al.* 1994). If *M. leonina* is differentially modifying the blubber composition (Best *et al.* 2003) in preparation for the two fasting periods (lactation and moult), then seasonal variation in FA profiles may incorporate this confounding factor. The effect of metabolism on the FA composition of blubber is unknown, and whether *M. leonina* selectively stores specific dietary FAs or actively biosynthesizes other FAs in preparation for the different fasting periods is uncertain (Grahl-Nielsen & Mjaavatten 1991; Grahl-Nielsen *et al.* 2000; Best *et al.* 2003). Although modification may occur, the difference between the two winter seasons supports the conclusion that the differences observed were caused, to a large extent, by shifts in diet composition.

The need to gain a better understanding of predator–prey interactions in the Southern Ocean is becoming more urgent. The full extent of overlap between the resources exploited by *M. leonina* and other predators and those exploited by commercial fisheries in the Southern Ocean is unclear. The exploitation of Antarctic marine resources is increasing because of the growing sophistication in fishing technology and increased market demands. *Mirounga leonina* is known to be an important consumer of squid (Boyd *et al.* 1994; Santos *et al.* 2001; Hindell *et al.* 2003), and many of the known squid species have rather small, but developing, fishing industries (Gonzalez *et al.* 1997). Most cephalopods have short life cycles and rapid growth rates, so they may be highly susceptible to overfishing, but also capable of rapid recovery (Pierce & Guerra 1994). In comparison, many fishes that have been exploited in recent times are characteristically long-lived animals that recover poorly from exploitation (e.g. the Patagonian toothfish, *Dissostichus eleginoides*; Williams & Lamb 2001). Given the fragile balance of effective natural resource management and the over-exploitation of some species, predators that are dependent on a small number of these commercially targeted species are vulnerable. Therefore, it is important to determine to what extent predators in the Southern Ocean are dependent on the available resources. To this end, our study has achieved a spatial and temporal summary of the broad-scale diet structure of a major marine predator, the southern elephant seal.

APPENDIX A

List of species used to identify prey groups in southern elephant seals. Items known to be a part of the elephant seal diet are indicated by the location of the stomach samples collected: mi, Macquarie Island; hi, Heard Island; kg, King George Island; vb, Vincennes Bay, Antarctica. Also indicated is the type of tissue analysed for each prey species to extract FAs.

species	family	diet	tissue
euphausiids (krill)			
Euphausia superba	Euphausiidae	hi	whole
Euphausia crystallorophias	Euphausiidae	?	whole

fishes

Arctozenus risso	Paralepididae	?	whole
Bathylagus antarcticus	Bathylagidae	hi,mi	whole
Borostomias antarcticus	Astronesthidae	?	whole
Champsocephalus gunnari	Channichthyidae	hi	whole
Chauliodus sloani	Stomiatidae	?	whole
Cyclothone sp.	Gonostomatidae	?	whole
Diplophos rebainsi	Gonostomatidae	?	whole
Dissostichus eleginoides	Nototheniidae	hi,mi	muscle
Dissostichus mawsoni	Nototheniidae	hi,mi	muscle
Echiodon cryomargarites	Carapidae	?	whole
Electrona antarctica	Myctophidae	hi,mi,kg	whole
Electrona carlsbergi	Myctophidae	hi,mi	whole
Electrona subaspera	Myctophidae	hi,mi	whole
Gymnoscopelus bolini	Myctophidae	mi	whole
Gymnoscopelus braueri	Myctophidae	mi	whole
Gymnoscopelus fraseri	Myctophidae	hi,mi	whole
Gymnoscopelus nicholsi	Myctophidae	hi,mi,kg	whole
Icichthys australis	Centrolophidae	mi	whole
Krefftichthyes anderssoni	Myctophidae	mi	flesh
Labichthys yanoi	Nemichthyidae	?	whole
Lampanyctus archirus	Myctophidae	hi,mi	whole
Melanostigma gelatinosum	Zoarcidae	?	whole
Pagothenia borchgrevinki	Nototheniidae	kg	flesh
Paradiplospinus gracilis	Gempylidae	mi	whole
Phosichthys argenteus	Phosichthyidae	mi	whole
Pleuragramma antarcticum	Nototheniidae	kg	flesh
Poromitra crassiceps	Melamphaidae	?	whole
Protomyctophum bolini	Myctophidae	?	whole
Salilota australis	Moridae	?	whole
Sternoptyx sp.	Sternoptychidae	?	whole
Stomias boa boa	Stomiatidae	hi,mi	whole
Stomias gracilis	Stomiatidae	?	whole
Trematomus bernacchi	Nototheniidae	kg	flesh
Trematomus hansoni	Nototheniidae	kg	flesh
Trematomus newnesi	Nototheniidae	kg	flesh
Trematomus pennellii	Nototheniidae	kg	flesh

squid

Brachioteuthis sp.	Brachioteuthidae	hi,mi	digestive gland
Galiteuthis glacialis	Cranchiidae	hi,mi	whole
Gonatus antarcticus	Gonatidae	hi,mi	whole
Histioteuthis eltaninae	Histioteuthidae	hi,mi	whole
Kondakovia longimana	Onychoteuthidae	hi,mi	whole
Loligo gahi	Loliginidae	?	whole
Martialia hyadesi	Ommastrephidae	hi,mi	digestive gland
Mastigoteuthis sp.	Mastigoteuthidae	hi,mi	whole
Mesonychoteuthis hamiltoni	Cranchiidae	hi,mi	digestive gland
Moroteuthis ingens	Onychoteuthidae	hi,mi	whole
Moroteuthis knipovitchi	Onychoteuthidae	hi,mi	digestive gland
Moroteuthis robsoni	Onychoteuthidae	hi,mi	digestive gland
Onychoteuthid sp.	Onychoteuthidae	?	digestive gland
Psychroteuthis glacialis	Psychroteuthidae	hi,mi,vb	digestive gland
Todarodes sp.	Ommastrephidae	hi,mi	digestive gland

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