



MARINE MAMMAL SCIENCE, 26(2): 430–442 (April 2010)

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DOI: 10.1111/j.1748-7692.2009.00347.x

## Evidence of demersal foraging from stable isotope analysis of juvenile elephant seals from Patagonia

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Southern elephant seals (*Mirounga leonina*) are wide-ranging, deep-diving, generalist predators. Knowledge of their diet has come from analysis of stomach contents and feces and more recently from fatty acid and stable isotope analysis (Brown *et al.* 1999, Bradshaw *et al.* 2003, Lewis *et al.* 2006, Cherel *et al.* 2008, Ducatez *et al.* 2008). Elephant seal stomachs usually contain only a few indigestible food items, and the seals are difficult to sample during their long foraging trips (Biuw *et al.* 2007, Campagna *et al.* 2007). Most studies suggest that cephalopods are the dominant prey (75%) with fish comprising much of remainder (Rodhouse *et al.* 1991, van den Hoff *et al.* 2002). Yet the species is truly a generalist predator, with reported prey including cephalopods, fish, crustaceans, bivalves, and gastropods (Clarke and MacLeod 1982, Green and Williams 1986, Rodhouse *et al.* 1991, Daneri *et al.* 2000, Daneri and Carlini 2002, Bradshaw *et al.* 2003, Field *et al.* 2007). Laws (1956) suggested that southern elephant seals fed largely on fish close to shore but on squid in other areas. Stomach contents of animals at Heard and Kerguelen Islands (250,000 km<sup>2</sup> of continental shelf) had about twice the fish remains as those from animals at Macquarie Island (over 1,000 km<sup>2</sup> of sea floor <1,000 m deep), and the fish taken at Heard Island were pelagic, bentho-pelagic, and benthic, whereas those taken at Macquarie Island were pelagic (Green and Burton 1993). Fatty acid profiles revealed that seals from Macquarie Island had a fish-dominated diet when they spent more

time on the Antarctic continental shelf (Bradshaw *et al.* 2003). Extensive continental shelves clearly offer a greater opportunity for demersal foraging. Because squid beaks are much less digestible than fish bones and otoliths, the relative importance of these foods in fecal and stomach content analyses is influenced by the distance between foraging areas and breeding/molting sites where samples are typically collected (Green and Williams 1986, Daneri and Carlini 2002, Bradshaw *et al.* 2003).

Measurement of stable carbon and nitrogen isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively) values of consumers is a complement to traditional methods of dietary analysis, and one of the few alternatives for wide-ranging and deep-diving marine animals (Ducatez *et al.* 2008). Isotopic data shed light on many aspects of trophic ecology, such as feeding habits and trophic position (Burns *et al.* 1998) and foraging areas (Cherel and Hobson 2007). Stable isotope values of both elements in tissues of consumers reflect those of assimilated foods and experience a stepwise enrichment in the heavier isotope relative to prey (Kelly 2000). This increase is more pronounced in  $\delta^{15}\text{N}$  values (3‰–5‰), which consequently are a very useful indicator of trophic level (TL). Trophic enrichment in  $^{13}\text{C}$  is smaller. As a consequence, animal  $\delta^{13}\text{C}$  values are useful to identify consumption of prey with different  $\delta^{13}\text{C}$  values at a local scale, as well as foraging areas at larger geographic scales (10s to 100s km). In the southern hemisphere,  $\delta^{13}\text{C}$  values of plankton and particulate organic matter are higher in warm subtropical waters than in cold Antarctic waters (Cherel and Hobson 2007). In addition, coastal/inshore or benthic habitats have higher food web  $\delta^{13}\text{C}$  values than offshore or pelagic food webs (reviewed in Koch 2007).

The diet of southern elephant seals from the rookery on Península Valdés (Patagonia, Argentina) is poorly known. At present our understanding is based largely on stable isotope analysis of the whiskers of adult females and subadult males (Lewis *et al.* 2006). Some males seem to include relatively high TL prey in their diets (such as adult pelagic fish), whereas other males and the females may take more invertebrate prey, including cephalopods.

Although the specifics of prey selection are not well known, tracking data identified areas where animals forage. The Patagonian continental shelf is one of the largest ( $\sim 1 \times 10^6 \text{ km}^2$ ), shallowest (<150 m), and most productive ocean platforms in the world (Croxall and Wood 2002, Acha *et al.* 2004, Forero *et al.* 2004). For adult females, the shelf appears to be a required leg on a path to more distant foraging areas in water deeper than 200 m. Adult males concentrate foraging along the continental slope (Campagna *et al.* 2007). Juvenile tracks, in contrast, indicate wide dispersion and use several oceanographic regions (Fig. 1). Although juveniles are capable of long-distance travel and deep diving, some remain in shallow waters on the Patagonian shelf or along the shelf break (Campagna *et al.* 2007). Others forage in the open ocean, where the dominant currents are the southward flowing Brazilian Current (warm, oligotrophic, subtropical water) and the northward flowing Malvinas Current (cold, nutrient-rich, subpolar water). Some juveniles from Patagonia visit coastal and offshore waters south of the Antarctic Polar Front, as do seals from other subantarctic rookeries (Biuw *et al.* 2007).

Here we examine isotopic data from satellite-tracked juveniles to understand their diet in relation to their spatial foraging patterns. Whiskers of 11 juveniles (2–3 yr

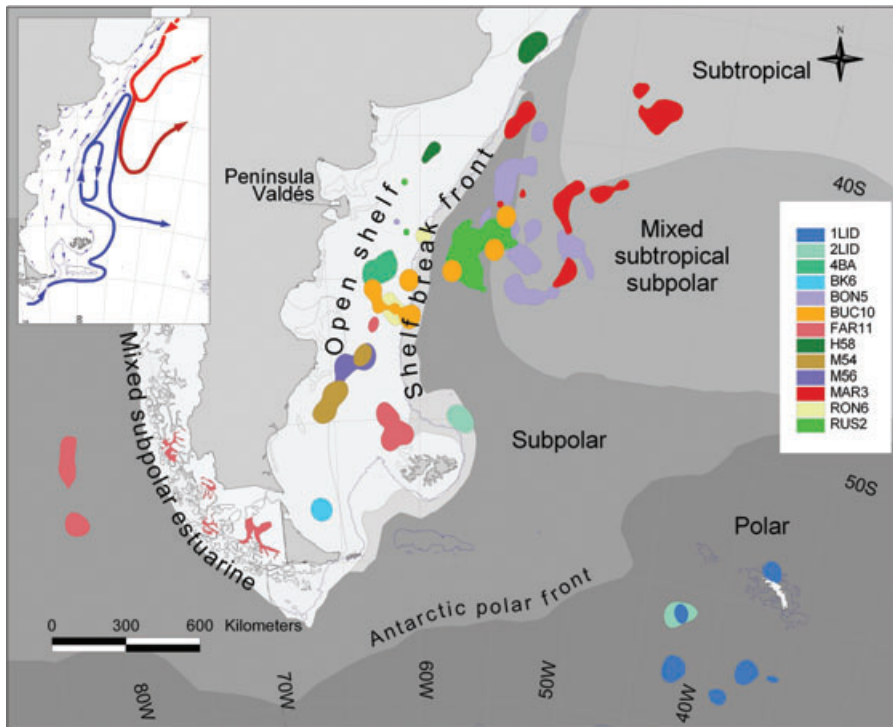


Figure 1. Foraging areas described by satellite tracking of juvenile elephant seals from Península Valdés. Use frequency estimated by Kernel technique (contours representing 75% of the satellite localizations). On the left superior corner, a scheme of the circulation of the Brazilian Current (red) and the Malvinas Current (blue).

old) and one subadult male (5–6 yr old), as well as an eyebrow from a juvenile were sampled at Península Valdés after the feeding trip that precedes the molting season (Table 1; for details on animal handling see Campagna *et al.* 2006, 2007). The whiskers and eyebrow were washed in methanol in an ultrasonic cleaner, then dried. A 0.5 mg sample was collected every 0.5 cm along the length of each whisker ( $17.9 \pm 4.6$  samples per whisker; total  $n = 233$ ). Each sample was sealed in a tin boat. The remaining sections of each whisker were marked to indicate growth direction, labeled, and stored. Isotopic analysis was conducted using an elemental analyzer coupled with a Finnigan Delta plus XL isotope ratio mass spectrometer (Stable Isotope Lab., University of California, Santa Cruz, CA). Isotopic data for each whisker were averaged and results are expressed with the standard  $\delta$  notation in parts per thousand (‰) relative to Vienna PDB (V-PDB) for  $\delta^{13}\text{C}$  or atmospheric  $\text{N}_2$  for  $\delta^{15}\text{N}$ . The standard deviation for a gelatin standard analyzed during the sessions ( $n = 18$ ) with the elephant seals was 0.1‰ for  $\delta^{13}\text{C}$  and 0.12‰ for  $\delta^{15}\text{N}$  values.

Mean isotopic values of juveniles ranged from  $-18.8\text{‰}$  to  $-14.9\text{‰}$  for  $\delta^{13}\text{C}$  and from  $12.2\text{‰}$  to  $18.5\text{‰}$  for  $\delta^{15}\text{N}$  (Table 2). To compare to prey, the isotopic values of seals were adjusted for trophic fractionation using values determined for pinniped

Table 1. Satellite tracked seals included in the study.

Individual (sex)	Date of sampling (season)	Duration of trip (d)	Max distance from PV (km)	Duration of return trip (d)	Foraging area
M54 (M)	5 November 2004 (Spring)	108	778	11	Shelf
M56 (M)	6 November 2004 (Spring)	107	694	8	Shelf
BK6 (M)	12 November 2005 (Spring)	94	1,150	14	Shelf
RON6 (M)	18 March 2006 (Fall)	87	521	12	Shelf
H58 (F)	18 November 2004 (Spring)	106	1,058	14	Shelf/shelf-break
4BA (M)	28 June 2007 (Winter)	148	314	3	Shelf
Mean (SD)		108.3 (21.2)	752.5 (316.6)	10.3 (4.2)	
BUC10 (F)	20 June 2006 (Fall)	171	682	13	Shelf/offshore
FAR11 (F)	11 August 2006 (Winter)	218	3,017	103	Shelf/offshore
MAR3 (F)	19 November 2005 (Spring)	110	1,462	14	Offshore mid latitude
BON5 (F)	10 November 2005 (Spring)	100	1,084	8	Offshore mid latitude
RUS2 (F)	28 February 2006 (Summer)	75	742	10	Offshore mid latitude
1LID (M)	5 September 2007 (Winter)	247	2,769	48	Offshore high latitude
2LID (M)	28 June 2007 (Winter)	171	2,274	15	Offshore high latitude
Mean (SD)		156 (63.8)	1,718.6 (965.6)	30.1 (34.9)	

Foraging area is based on the percentage of the total time (days) at sea in core locations. Duration of return trip is the time that each seal took to come back to the rocky, considered from the last time that seals were foraging (denoted by areas at sea where density of satellite locations estimated by Kernel technique were 75%; for details see Campagna *et al.* 2006, 2007). All seals were juveniles except the subadult "4BA." Sex category is male (M) or female (F). PV: Peninsula Valdés.

Table 2. Mean isotopic values (‰ ± SD) of whiskers of juvenile elephant seals from Patagonia.

Seal ID	<i>n</i>	δ <sup>13</sup> C	δ <sup>15</sup> N
1LID	16	−18.8 ± 1.4	12.2 ± 1.9
2LID	10	−18.1 ± 0.7	13.8 ± 1.1
BON5	16	−18.0 ± 0.5	12.3 ± 1.1
MAR3	16	−17.8 ± 0.4	13.2 ± 1.1
BUC10	19	−17.7 ± 0.2	13.2 ± 1.0
M54	24	−18.0 ± 0.7	13.0 ± 1.3
M56	20	−17.6 ± 0.4	13.2 ± 0.9
FAR11	22	−17.3 ± 0.6	14.0 ± 1.4
RUS2	17	−16.9 ± 0.2	11.7 ± 1.1
H58	25	−16.1 ± 0.7	15.4 ± 1.0
RON6	13	−15.1 ± 0.4	16.7 ± 0.9
4BA	13	−15.1 ± 0.4	17.8 ± 0.8
BK6	22	−15.1 ± 0.4	18.5 ± 1.0

*n* = number of pieces analyzed for each whisker.

whiskers: +2.8 for δ<sup>15</sup>N and +3.2 for δ<sup>13</sup>C (Hobson *et al.* 1996). Isotopic data for potential prey from the seals’ foraging areas were derived from prior publications. Approximately 65 species were considered, including teleost fish, skates, sharks, octopodids, squids, bivalves, gastropods, crabs, small crustaceans, and ctenophores, from benthic, demersal, and pelagic habits. Most potential prey were neritic species from the Patagonian shelf (Forero *et al.* 2004, Lewis *et al.* 2006, Ciancio *et al.* 2008), but many had distributions extending past the shelf break. Some pelagic species were obtained from offshore mid-latitude and high-latitude regions (Wada *et al.* 1987, Kaheler *et al.* 2000, Takai *et al.* 2000). Some prey stable isotope values are for lipid-extracted tissues; others are for untreated tissues (mostly muscle). Variation in <sup>13</sup>C-depleted lipid content is a common source of variability in δ<sup>13</sup>C values, therefore lipids are often removed prior to isotopic analysis, or δ<sup>13</sup>C data are corrected using empirical relationships between the C:N ratio and δ<sup>13</sup>C value. Unfortunately, lipid extraction may also affect δ<sup>15</sup>N values (Zhao *et al.* 2006, Mintenbeck *et al.* 2008), and the efficacy of the empirical relationships used to correct for lipid content is debated (Mintenbeck *et al.* 2008). A comparison of data compiled from a variety of animals showed differences between lipid-extracted and untreated tissue values, yet these differences were smaller than the standard deviation for most samples (Kelly 2000).

TL of elephant seals foraging on neritic waters and all species from the Patagonian shelf were estimated following Ciancio *et al.* (2008), considering euphasids to feed entirely on phytoplankton and to have the lowest TL of all animal groups (supported by their lowest δ<sup>15</sup>N values), assigning a TL value of 2 to this group, and using the following formula:

$$TL_{consumer} = 2 + \left[ \frac{\delta^{15}N_{consumer} - \delta^{15}N_{euphasids}}{TEF} \right].$$

TEF is the mean trophic  $^{15}\text{N}$ -enrichment factor for marine community members (3.4‰) (Ciancio *et al.* 2008), except for southern elephant seals, for which TEF value was the mean tissue-specific value for pinnipeds whiskers (2.8‰). TL of elephant seals foraging offshore at high latitude and prey sampled there were estimated using the  $\delta^{15}\text{N}$  value of euphasids from that latitude. To estimate TL of seals foraging offshore at middle latitude and prey sampled there, we used a  $\delta^{15}\text{N}$  value for euphasids averaged between Patagonian and high-latitude data.

The contribution of potential prey to the diets of seals was estimated using the IsoSource model (version 1.3.1, <http://www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm>). This method is useful when the number of sources is too large to permit unique solutions from stable isotope mixing models. It uses an iterative procedure to determine upper and lower limits for the contribution of each source to a mixture. All possible combinations of each source contribution are examined in small increments (1% in this case); combinations that sum to the observed mixture isotopic values within a small tolerance (0.01% in this case) are considered to be feasible solutions. The model assumes that the concentration and digestibility of C and N are the same in all food resources, which is reasonable when the foods are animal tissues (Phillips and Koch 2002).

A first analysis was conducted using five prey from the foraging regions that are reported in the diet of southern elephant seals from elsewhere (South Orkney Islands, South Georgia Islands, Stranger Point, King George Island, South Shetland Islands, and Macquarie Island). These are (1) the high-latitude, offshore squid *Kondakovia longimana* (60°S, 45°W, Wada *et al.* 1987); (2) the mid-latitude, offshore squid *Martialia hyadesi* (~47°S, 54°W, Takai *et al.* 2000); (3) myctophid fish and (4) notothenid fish *Dissostichus eleginoides* sampled on the Patagonian shelf; and (5) the mid-latitude, offshore notothenid *Lepidonotothen larseni* (47°S, 38°W, Kahler *et al.* 2000).

After correcting for trophic fractionation, mean isotopic values of juveniles from Península Valdés fell well inside the mixing polygon defined by the five prey (Fig. 2), yielding a general sense of the amounts of these potential prey in the diets of Patagonian elephant seals. Different juveniles were estimated to have quite different diets. For example, seal 1LID had a considerable and well defined amount of the high-latitude squid *K. longimana* in its diet (14%–55%); the squid was less constrained in the diets of seals 2LID, BON5, and M54 (Table 3). The mid-latitude squid, *M. hyadesi*, was estimated to make a small contribution to the diet of almost all seals, except 1LID, 2LID, M54, and M56. The offshore notothenid, *L. larseni*, contributed highly to the diets of seal BON5 and particularly RUS2 (70%–71%). The neritic toothfish, *D. eleginoides*, contributed to the diets of seals RON6 and H58 and was especially important for BK6 and subadult male 4BA (Table 3). The wide range of possible contributions of some prey types for some animals (Table 3) suggests that the diet of these seals could be accounted for, isotopically, by different sets of end members. Inspection of Figure 2 presents many feasible sets; the high number of potential combinations for some taxa (over 100 or 200) suggests this as well.

Mean isotopic values of juveniles and the subadult male identified animals that used similar foraging zones (Fig. 3). Cluster A contained animals that foraged exclusively

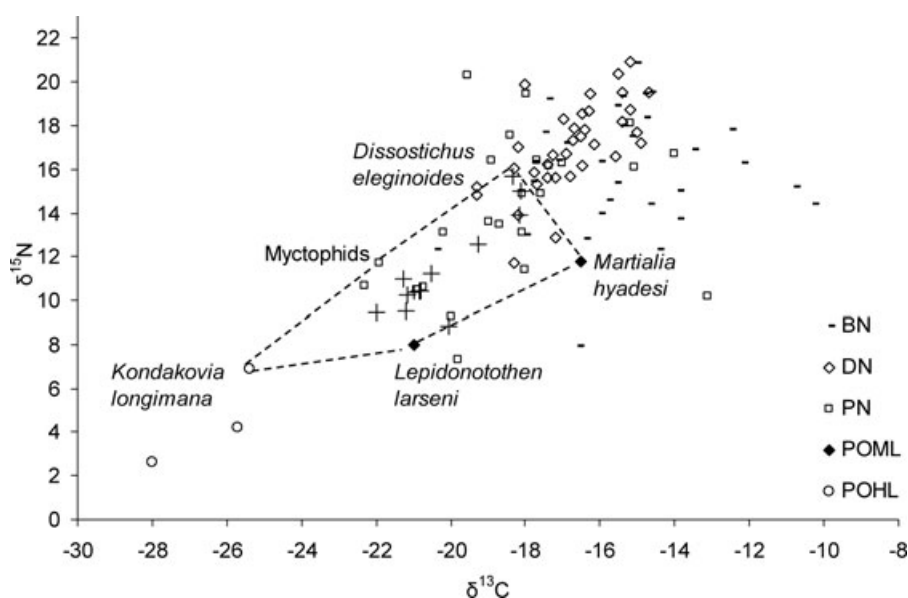


Figure 2. Mixing polygon for corrected  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  mean values of juveniles southern elephant seals from Península Valdés (+) and prey reported in the diet, sampled in Patagonian shelf (myctophids and *D. eleginoides* fish) and surrounding areas (*L. larseni* fish and the squids *M. hyadesi* and *K. longimana*). Potential prey from foraging areas are also plotted. All prey values were classified by their habits in the water column (BN: benthic neritic, DN: demersal neritic, PN: pelagic neritic, POML: pelagic oceanic mid latitude, POHL: pelagic oceanic high latitude).

over the Patagonian shelf (BK6, RON6, 4BA) or shelf break (H58) (Fig. 1). Cluster B included seals that used the shelf partially or just in transit toward more distant foraging areas, such as seals 1LID and 2LID, which moved offshore to high latitudes, and females MAR3, BON5, and RUS2, which foraged offshore at mid latitudes. Female BUC10 foraged at mid latitude over both the Patagonian shelf and offshore, whereas female FAR11 moved south over the shelf then foraged briefly near the Falkland Islands before moving offshore to the Pacific Ocean. Males M54 and M56 are the exception to the general pattern of cluster B; they foraged exclusively over the Patagonian shelf (Fig. 1).

The isotopic differences between the two clusters of animals foraging in different areas reflect, in part, differences in TL, which ranged from 4.9 to 6 for seals of the cluster A and from 3.5 to 4.4 for seals of the cluster B. In a principal components analysis performed with three variables ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , and TL values), seals and prey with high isotope values and TLs contrasted along the first principal component (x-axis, Fig. 4) to a group with lower values. The former group included mainly neritic prey (benthic and demersal elamosbranchs have the highest TL) and seals that foraged mainly on the Patagonian shelf. The latter group included only pelagic prey of low TL (high-latitude crustaceans are the lowest) and seals that foraged offshore and partially on the shelf. There was some overlap of lower TL neritic (myctophids, ctenophores,

Table 3. Contributions of prey reported in the diet of southern elephant seals (1‰–99‰).

Prey	1LID	2LID	BON5	MAR3	BUC10	M56	M54	RUS2	FAR11	H58	RON6	4BA	BK6
<i>Kondakovia longimana</i>	14–55	1–42	1–49	0–41	0–41	0–42	1–46	4–5	0–34	0–19	0–7	0–2	0–1
<i>Martialis byadesi</i>	0–29	0–20	2–41	2–34	3–36	0–37	0–33	24–25	1–31	9–34	28–36	18–20	6
<i>Lepidonotoben larveni</i>	0–44	0–29	3–60	0–47	0–48	1–55	0–48	70–71	0–44	0–35	0–10	0–4	0
Myctophids	0–40	0–70	0–35	0–50	0–48	0–46	0–49	0–1	0–59	0–41	0–15	0–5	1–3
<i>Dissostichus eleginoides</i>	0–20	0–40	0–19	0–30	0–30	0–28	0–29	0	0–39	22–52	49–60	75–78	91–92
Combinations	129	198	149	219	222	221	225	2	215	104	18	7	2



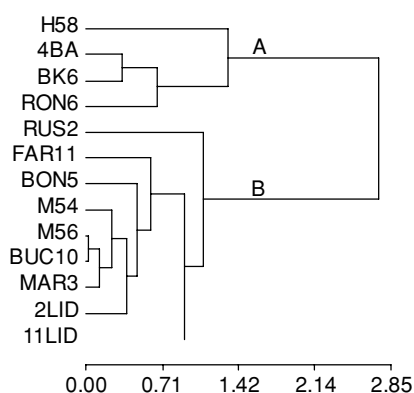


Figure 3. Cluster analysis (Euclidean distances, averaged method, cophenetic correlation factor: 0.909) using mean isotope values of whiskers of elephant seals from Península Valdés (after correction for trophic fractionation). Cluster A: seals that foraged exclusively on the shelf. Cluster B: seals that foraged mostly offshore.

and crustaceans) and offshore prey (notothenids, cephalopods, and crustaceans). This first principal component explained 91% of the variance.

Although we lack extensive data on offshore prey species, those available reveal large isotopic differences relative to prey from the continental shelf. These differences are in accordance to isotopic variations reported in the literature associated with latitude, and offshore/pelagic *vs.* coastal/benthic habits. Some of the isotopic distinctions among elephant seals reflect these differences at the base of the food web. For example, cluster A seals, which forage on the shelf, have higher  $\delta^{13}\text{C}$  values than cluster B seals, which include mostly animals that forage at least partially offshore. Among offshore foragers, animals at high latitudes (1LID and 2LID) had low  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, mostly likely because of low values at the base of the food web, as well as consumption of low TL prey. Sharp drops in  $\delta^{13}\text{C}$  values along the length of the whiskers of these animals matched the pattern expected for the transition to foraging in polar water, assuming that full replacement of the whisker takes about a year (Lewis *et al.* 2006). Unfortunately, whisker growth rate and details of the cycle of development and loss of whiskers are poorly known for elephant seals, so it is difficult to match movement between water masses with isotopic variations in whiskers in the other seals.

The inferred diets of southern elephant seals from Península Valdés do not depart much from those of animals from other colonies when the same food items are available. Potential food sources considered here fit well with a generalist and opportunistic predator. In our study based on assimilated food, seals that foraged exclusively on the shelf or shelf break had higher contributions of demersal fish in their diets (as noted in Green and Burton 1993 and Bradshaw *et al.* 2003) and are trophically closer to neritic prey than are offshore foragers, which most closely match isotopic data for pelagic oceanic fish. These differences are clearly a consequence of differences in the availability of such prey within the diving range of seals in the

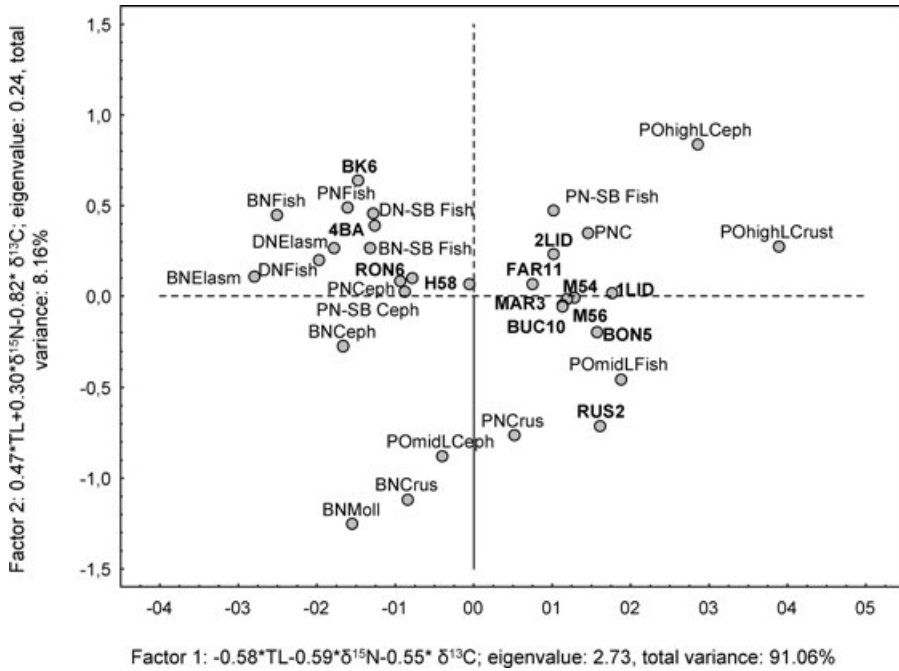


Figure 4. Principal component analysis. Ninety-one percent of the total variance is explained by Factor 1 (x-axis). Along this axis, high trophic level organisms (mainly neritic species and seals that foraged over the shelf) contrast to those of lower trophic level. BN-Fish: benthic neritic fish; BNElasm: benthic neritic elasmobranchs; BNCeph: benthic neritic cephalopods; BNMoll: benthic neritic mollusks; BNCrust: benthic neritic crustaceans; DNFish: demersal neritic fish; DNElasm: demersal neritic elasmobranchs; PNFish: pelagic neritic fish; PNCeph: pelagic neritic cephalopods; PNCrust: pelagic neritic crustaceans; PNC: pelagic neritic ctenophores; POhighLCeph: pelagic oceanic high-latitude cephalopods; POhighLCrust: pelagic oceanic high-latitude crustaceans; POmidLFish: pelagic oceanic mid-latitude fish; POmidLCeph: pelagic oceanic mid-latitude cephalopods. BN-SB Fish, DN-SB Fish, PN-SB Fish, and PN-SB Ceph, denote those benthic, demersal, and pelagic fish species and pelagic cephalopod species of the shelf that can also extend their distribution further from the shelf break.

different foraging areas. Thus, our isotopic data confirm what might have been suspected given the tracking data—different individuals from Península Valdés forage in very different habitats to exploit very different types of prey. Temporal and spatial segregation of foraging areas by age and sex, as well as sex-specific foraging strategies, have been reported for both northern and southern elephant seals (Le Boeuf *et al.* 2000, Campagna *et al.* 2007). Sexual segregation of foraging areas is related to a high sexual dimorphism and a strong polygamy structure observed in adults (Le Boeuf *et al.* 2000). These features are not apparent in juvenile seals, consequently spatial segregation by sex is not expected in this age class, though a small proportion of males from Patagonia (5 of 23 satellite-tracked animals) distributed in mid-shelf areas in contrast of females ( $n = 4$ ), which foraged close to the continental slope

(Campagna *et al.* 2007). Movements of juvenile elephant seals from Macquarie Island ( $n = 48$ ) showed spatial segregation by age (1–4 yr old), not by sex (Field *et al.* 2005). Our isotopic study of foraging did not provide evidence for a clear pattern of segregation by sex among juveniles, and the small number of animals and ages studied precluded comparisons between different age classes.

The information gathered to date suggests individualistic behavioral choices, as seen in some other marine mammal species when population densities rise and food become limiting (*e.g.*, Tinker *et al.* 2008). However, the reason why juvenile seals choose to forage offshore, or to take the prey available on the shelf when the benefit in terms of mass increase is similar between non-shelf foragers and shelf foragers (Campagna *et al.* 2007), is a subject for future research.

#### ACKNOWLEDGMENTS

We thank M. R. Marin for tracking data processing and for help in preparing the figures; M. Uhart, F. Pérez, V. Zavatieri, and R. Vera for field assistance during collection of seal whiskers; S. Kim for assistance in the laboratory during isotopic analysis, Centro Nacional Patagónico (CENPAT-CONICET) for logistical support; and University of California Santa Cruz for the Stable Isotope Laboratory. Three anonymous reviewers provided helpful comments on the paper. This work was funded by Proyecto de Cooperación Internacional CONICET-NSF Resolución 1542/06. The satellite tracking research was financed by Agencia Nacional de Promoción Científica y Tecnológica PICT 01-11749 and CONICET PIP 02462 Resolución 1123/03. This research was part of a Ph.D. program supported by the National Research Council of Argentina (CONICET).

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Received: 23 October 2008

Accepted: 14 July 2009