Polar Biol (1998) 19: 272–282

ORIGINAL PAPER

J.M. Burns · S.J. Trumble · M.A. Castellini
J.W. Testa

The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis

Received: 10 June 1997 / Accepted: 8 November 1997

Abstract The diet of adult and juvenile Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica, was determined from both scat and stable isotope analyses, to ascertain if foraging behavior varied with age, season, or diving pattern. Scats were collected over 6 years and recovered hard parts identified. Stable carbon and nitrogen isotope values were determined for seal blood samples and potential prey items and used to identify primary prey species and assess trophic interactions. *Pleuragramma antarcticum* remains were recovered from between 70 and 100% of the scats, and there was little evidence for inter-annual or age-specific variation in foraging behavior. However, stable isotope and dive data analyses indicated that while most seals foraged predominantly on pelagic fish and squid, some juveniles concentrated on shallow benthic *Trematomus* spp. Combining these three methods permitted firm conclusions about diet and foraging behavior to be drawn.

Introduction

The diet of Weddell seals (*Leptonychotes weddellii*) in Antarctica has been well studied, and is generally thought to consist mainly of nototheniid fishes, cephalopods, prawns, and other small invertebrates (Lindsey 1937; Bertram 1940; Dearborn 1965; Clarke and MacLeod 1982; Testa et al. 1985; Plötz 1986; Green and Burton 1987; Plötz et al. 1991; Castellini et al. 1992). Differences in diet due to location, season, and age of seal have been documented in Weddell seal populations outside McMurdo Sound, as well as in many other marine mammal species (Lindsey 1937; Bertram 1940; Sergeant 1973; Laws 1984; Green and Burton 1987, 1993; Croxall et al. 1988; Haug et al. 1991; Plötz et al. 1991; Boyd et al. 1994; Slip 1995). In general, the prey species consumed by marine mammals that are not specialist foragers vary seasonally, with foraging location, or with animal age. Within McMurdo Sound, little is known about dietary variation among individuals or by season, but given the large shifts in population structure and environmental conditions that occur through the year, such variation is likely to exist (Testa et al. 1985, 1991; Castellini et al. 1992). Other factors that may affect foraging behavior are sea-ice extent, air temperature, El Niño-Southern Oscillation index, and fluctuations in prey abundance (Laws 1984; Bengtson and Laws 1985; Croxall et al. 1988; Testa et al. 1991).

Most studies on the foraging behavior of Weddell seals and other marine mammals have determined diet from scats, vomitus, or stomach contents (for review, see Croxall 1993). These techniques rely on the identification of the remains of prey item hard parts, and are associated with unavoidable errors due to the nature of the collection methods. All of these samples are single “snapshots” of the most recent diet and, therefore, may not be representative of the overall diet. In addition, recovered prey parts are often too far digested to permit identification, and the contribution of soft-bodied prey to the diet can be significantly underestimated. Technical and logistical difficulties associated with collecting a sufficiently large and representative sample can also constrain the interpretation of the data (Pitcher 1980; daSilva and Neilson 1985; Murie and Lavigne 1985, 1986; Harvey 1989; Gales and Cheal 1992; Croxall 1993; Tollit et al. 1997). To avoid some of these difficulties, researchers have made inferences about marine mammal diets based on diving

J.M. Burns (✉)[1] · S.J. Trumble · M.A. Castellini
Institute of Marine Science, University of Alaska,
Fairbanks, Fairbanks, AK 99775, USA

J.W. Testa
Alaska Department of Fish and Game,
333 Raspberry Rd., Anchorage, AK 99518, USA

Present address:
[1] Department of Biology, EMS 316A,
University of California,
Santa Cruz, CA 95064, USA
Fax: (408) 459-4882; e-mail: bume@biology.ucsc.edu

patterns and the presumed foraging location and behavior of potential prey items. However, this method also suffers from errors and biases because the actual purpose of dives is not known. Furthermore, as marine mammals may forage selectively, without observations of prey capture, it is difficult to determine if dives to certain depths or regions actually represent foraging activity (Kooyman 1968; Hindell et al. 1991; Bengtson and Stewart 1992; Le Boeuf et al. 1992; Testa 1994; Schreer and Testa 1996; Burns et al. 1997).

Analysis of stable isotope ratios in animal tissues has recently emerged as a powerful technique for determining the trophic level at which foraging occurs, and the importance of different prey items in the diet (Owens 1987; Wada et al. 1987, 1991; Rau et al. 1991a; Hobson and Welch 1992; Hobson et al. 1997). Tropho-dynamic research using stable isotopes generally focuses on carbon and nitrogen, since the isotopic ratio of these elements varies in relation to the diet, trophic level, and foraging location (Owens 1987; Hobson and Welch 1992). The carbon and nitrogen isotope values ($\delta^{13}C$ and $\delta^{15}N$) differ between organisms and their diets because of the slight selective retention of the heavy isotope and excretion of the light isotope. Fractionation occurs because the lighter isotope has a lower activation energy for bond breakage, reacts more often, and is therefore more likely to be excreted. As a result, organisms tend to retain the heavier isotope, become enriched, and have a higher δ value than their diet (Owens 1987). Because this is a long-term process, stable isotope ratios in tissue reflect the diet over the past weeks to months (Tieszen et al. 1983; Hobson et al. 1997; A. Hirons, unpublished work).

Generally, there is an enrichment of approximately 3.0‰ in nitrogen and 0.8‰ in carbon per trophic level (DeNiro and Epstein 1978, 1981; Fry and Sherr 1984; Minagawa and Wada 1984; Owens 1987; Wada et al. 1991). Differences in nitrogen isotope ratios are frequently used to predict trophic level, and in cases where the isotopic ratios of different prey items are known, actual diet (DeNiro and Epstein 1981; Minagawa and Wada 1984; Schroeninger and DeNiro 1984; Wada et al. 1991). However, because carbon isotope ratios differ more between terrestrial versus marine, inshore versus offshore, and pelagic versus benthic food webs than by trophic level, carbon has more often been used to assess foraging location (DeNiro and Epstein 1978; Fry and Sherr 1984; Schroeninger and DeNiro 1984; Schell et al. 1989; France 1995). In the Antarctic, the carbon isotope signature of particulate organic matter is also characterized by effects of sea ice and a strong latitudinal gradient (Rau et al. 1991b,c). The interpretation of $\delta^{13}C$ values may also be complicated by the strong correlation between $\delta^{13}C$ and tissue C:N ratio and the inverse relationship between tissue lipid content and C:N ratio. To control for these effects, $\delta^{13}C$ values are often adjusted to reflect a standard C:N ratio, in which case they are referred to as lipid-corrected $\delta^{13}C$ values (McConnaughey and McRoy 1979; Tieszen et al. 1983; Rau et al. 1991a, 1992; Hobson and Welch 1992). While differences in $\delta^{15}N$ and $\delta^{13}C$ among organisms and tissues can arise from a variety of factors, when all are taken into consideration, stable isotope methods have proven to be powerful tools for understanding animal diet. This is especially true when stable isotope techniques have been combined with the more traditional dietary analysis methods (Hobson et al. 1997).

By using a combination of scat and stable isotope analysis in this study, our aim was to determine if the diet of Weddell seals in McMurdo Sound varied with age, sex, season, or diving pattern. Weddell seals in McMurdo Sound provide a unique opportunity to test the relationship between the diet as determined by scat and stable isotope analysis, and as indicated from foraging and diving behavior. This is possible because the prey within McMurdo Sound has been well studied. One family, the nototheniids, dominates the ecosystem, with one species, *Pleuragramma antarcticum*, making up more than 90% of the fish biomass (Eastman 1985; Everson 1985; Macdonald et al. 1987). In addition, scat and tissue collection are relatively simple, and the diving behavior of adults and juveniles has been previously documented (Kooyman 1968; Kooyman et al. 1983; Testa et al. 1985; Castellini et al. 1992; Testa 1994; Schreer and Testa 1996; Burns 1997; Burns and Testa 1997; Burns et al. 1997). It should therefore be possible to construct, and then compare, the diet of adults and juveniles using the different available methods.

Materials and methods

Scat collection and analysis

All identifiable seal scats within a 0.25 km^2 area at Cape Evans, Ross Island, Antarctica (77.63°S, 166.40°E) were collected once yearly between 1989 and 1993. Collected scats were placed into individually labeled Whirl-pak bags, and kept frozen until cleaning and analysis. In addition to these samples, scats were opportunistically collected from individuals of known age within the Erebus Bay region between 1992 and 1994.

Hard part remains were separated from the scats by two methods. Samples collected in 1989, 1990, and 1992 were processed using a series of progressive sieves (4.0, 2.0, and 0.8 mm), while samples collected in 1991, 1993, and 1994 were processed using an elutriator system that separated fecal material from hard parts using a running water/density gradient (Murie and Lavigne 1985; Croxall 1993). All hard parts recovered from the scats were sorted under a dissecting microscope. The following parts were separated and identified: teleost sagittal otoliths, cephalopod beaks, fish bones, eye lenses, crustacean fragments, and other invertebrate remains. Vertebrae of the Antarctic silverfish, *Pleuragramma antarcticum*, were separately identified and recorded based on the unique and large central lumen and the general fragility of the bones (Eastman and DeVries 1982; Macdonald et al. 1987; Castellini et al. 1992). Unless too badly eroded, all sagittal otoliths and cephalopod beaks were keyed to the lowest taxon possible, and sagittal otoliths were measured to the nearest 0.1 mm (Clarke 1980; Fischer and Hureau 1985; Okutani and Clarke 1985; Hecht 1987). Several scats contained small, badly eroded cephalopod beaks, tentatively identified as the small *Brachioteuthiid* squid, *Brachioteuthis picta* (W. Walker, personal communication). In addition, all identifiable invertebrate fragments found in the 1989 scat samples were classified to the family level.

The percent frequency of occurrence of prey items in Weddell seal scats was determined for each year and seal age class individually. For *P. antarcticum*, fish length was estimated using regression equations that related otolith diameter to fish length (Kock et al. 1985; Hecht 1987; Hubold and Tomo 1989). All *Trematomus* spp. otoliths were treated as if they had come from *T. bernacchii*, and the fish lengths were estimated using equations from Hecht (1987). Fish mass was not estimated because different equations in the literature produced values that differed by more than 100% (Kock et al. 1985; Hecht 1987; Hubold and Tomo 1989; Radtke et al. 1993). Before calculating fish lengths, otolith diameters were first corrected to account for erosion in the digestive process using the factor of 1.275 determined for small fishes by Harvey (1989) (see also daSilva and Neilson 1985; Murie and Lavigne 1986; Tollit et al. 1997). Comparison between years in the mean size of *P. antarcticum* eaten was performed using one-way ANOVA techniques with significance assumed at $P < 0.05$. Tukey HSD post-hoc comparison of means was used to identify groups (overall $P < 0.05$). We did not estimate the size of squid eaten by Weddell seals because, for most species, few beaks were retrieved. The size of *B. picta* eaten by seals could not be accurately estimated because beak rostral lengths were <2 mm and beaks were extremely eroded.

Stable isotope analyses

Blood samples were collected between 1992 and 1994 from known age pups ($n = 16$), yearlings ($n = 14$), and adults ($n = 12$). The blood collection and handling techniques have been described by Rea (1995), and plasma samples were kept frozen at −80°C until analyzed. Four species of nototheniid fishes, *P. antarcticum*, *Dissostichus mawsoni*, *Pagothenia borchgrevinki*, and *T. loennbergii*, as well as the eelpout, *Rhigophilia dearborni*, were collected opportunistically in the field and stored frozen until analysis. Stable isotope values for *T. bernacchii*, determined by Wada et al. (1987), were also used in the analyses of foraging behavior.

The C:N ratio and the δ^{15}N and δ^{13}C stable isotope ratios in Weddell seal blood plasma and selected prey items were analyzed as follows. Plasma samples (1 ml) and prey muscle samples (1 g) were dried at 60°C, ground for homogeneity, and prepared for mass spectrometry (Schell et al. 1989; Schell and Hirons 1997). All carbon and nitrogen isotope ratios were determined in duplicate with a Europa 20/20 continuous flow mass spectrometer. Stable isotope ratios are expressed in del (δ) notation according to the following equation:

$$\delta X(‰) = (R_{\text{SAMPLE}}/R_{\text{STANDARD}} - 1) * 1000$$

where X is ^{13}C or ^{15}N and R is the ratio of ^{13}C:^{12}C or ^{15}N:^{14}N in the standard or sample. The standard for carbon was Pee Dee Belemnite and atmospheric N_2 was the standard for nitrogen (DeNiro and Epstein 1978, 1981). Analytical error for both carbon and nitrogen was ±0.1‰, and samples were reanalyzed if the difference between duplicates was greater than 0.5‰. The mass percent carbon and nitrogen in the samples were determined by the mass spectrometer, and the ratio (by mass) of total carbon to total nitrogen calculated. Analytical error in this C:N ratio was ±0.10.

The δ^{15}N, δ^{13}C, and C:N ratios were compared among seals of different age, sex, year, and foraging behavior using one-way ANOVA techniques. Significance was assumed at $P < 0.05$. The effect of collection year and sex on these ratios was tested within each age class (adult, yearling, or pup) and, if there was no significant difference in the δ^{15}N, δ^{13}C, or C:N ratio between years or sexes, groups were pooled. The effects of age and foraging behavior were subsequently tested. Yearlings were subdivided into three categories: shallow divers (mean dive depth < 100 m, $n = 4$), deep divers (mean dive depth > 100 m, $n = 6$), and yearlings with no dive records (NDR yearlings, mean dive depth unknown, $n = 4$). These categories were based on dive records collected from yearlings in McMurdo Sound that had previously been analyzed (Burns et al. 1997). The δ^{15}N, δ^{13}C, and C:N ratios were then compared among adults, pups, deep, shallow and NDR yearlings. Seal groups were pooled if there were no significant differences in any measured ratio. Finally, linear regression techniques were used to test for the effect of the C:N ratio on the δ^{13}C value determined for all seals. The regression was judged significant if $P < 0.05$ and the residuals were normally distributed.

Due to the small sample sizes for individual fish species, we did not test for inter- or intra-specific differences in the δ^{15}N and δ^{13}C stable isotope ratios. However, as the C:N ratio differed among species, linear regression techniques were used to test for the effect of the C:N ratio on the δ^{13}C values. As with the plasma samples, the regression was judged significant if $P < 0.05$ and the residuals were normally distributed. As this regression was significant, the δ^{13}C values of those fishes with elevated C:N values were adjusted to reflect a standard C:N ratio. These lipid-corrected δ^{13}C values were used for trophic level comparisons.

To better understand the foraging behavior of Weddell seals in McMurdo Sound, the isotopic values determined for the different groups of seals were compared to those of the prey items collected. As stable isotope ratios in blood plasma have been shown to be similar to those of other marine mammal tissues (with the exception of blubber and keratin), we assumed the blood values to be representative of the animal as a whole (DeNiro and Epstein 1978, 1981; Tieszen et al. 1983; A. Hirons personal communication). In constructing the food web, predators were assumed to be approximately 3‰ enriched in δ^{15}N over their prey. The δ^{13}C value was assumed to remain relatively constant across trophic levels, provided that habitats and C:N ratios were similar (Rau et al. 1992).

Results

Scat analysis

Between 1989 and 1993, 189 scats were collected from the sampling site at Cape Evans. Eight scats were collected between 1992 and 1994 from known age animals (one adult, five yearlings, two pups). Tables 1 and 2 show the number and types of prey hard parts identified from scats. The most common prey item, as determined by both numbers and frequency of occurrence, was *Pleuragramma antarcticum*. Other fishes identified from recovered otoliths were *T. bernacchii* and other *Trematomus* species. Identifiable remains from these fishes were found in only a few scats (2.7%), and did not appear to make up a significant proportion of the diet. However, as *Pleuragramma antarcticum* bones were found in 88.4% of the scats, and otoliths in only 10.6% of the scats, it is possible that the *Trematomus* species were under-represented in this Weddell seal diet sample because no other hard parts from these fishes were uniquely identifiable. Eleven percent of the recovered otoliths could not be identified due to breakage or severe erosion.

Forty-seven cephalopod beaks were recovered from the scats collected at Cape Evans from seals of unknown age, and another 765 from scats collected from 4 juveniles (1 pup and 3 yearlings). All identified beaks came from squid: three from an unidentified *Histioteuthiid* species, two from *Gonatus antarcticus*, two from *Kondakovia longimana*, and one from an unidentified *Mastigoteuthiid* species. The bulk of the beaks, 804, were

Table 1 Squid, fish, and invertebrate prey items identified in Weddell seal scat samples collected yearly from Cape Evans, McMurdo Sound, Antarctica. The 1989 collection was the first, and likely includes scats from more than 1 year. The age and species of the seals that deposited the scat were not known (*G.a. Gonatus antarcticus*; *M.sp. Mastigoteuthiid* spp.; *B.sp. Brachioteuthis picta* badly eroded; *H.sp. Histioteuthiid* spp.; *K.l. Koudakovia lougimana*; *P.a. Pleuragramma antarcticum*; *T.sp. Trematomus* spp.; *Unid.* Unidentified otoliths usually due to excessive erosion; *T.b. Trematomus bemacchii*; *P.a.* bones, *Pleuragramma antarcticum* vertebrae)

Year	Total # scats	# Beaks (# scats)	# Otoliths (# scats)	*P.a.* bones	Fish parts	Crustacean parts	Mollusc parts [a]
1989	75	G.a. 1 (1) M.sp. 1 (1)	P.a. 62 (16) T.sp. 1 (1) Unid. 6 (2)	75 100%	74 98.7%	70 93.3%	28 37.3%
1990	23	G.a. 1 (1)	P.a. 23 (1) T.sp. 1 (1) T.b. 1 (1)	18 78.3%	18 78.3%	2 8.7%	5 21.7%
1991	30	B.sp. 9 (3) H.sp. 1 (1)	P.a. 43 (4) Unid. 6 (4)	26 86.7%	21 70%	3 20%	2 20%
1992	30	B.sp. 6 (4) K.l. 2 (1)	P.a. 2 (2) T.sp. 1 (1) Unid. 1 (1)	21 70%	20 66.7%	6 20%	6 20%
1993	31	B.sp. 24 (3) H.sp. 2 (2)	P.a. 24 (7) T.sp. 2 (2) Unid. 7 (6)	27 87.1%	23 74.2%	2 6.5%	0
Total	189	B.sp. 39 (10) H.sp. 3 (3) G.a. 2 (2) K.l. 2 (1) M.sp. 1 (1)	P.a. 154 (30) T.sp. 5 (5) T.b. 1 (1) Unid. 20 (13)	167 88.4%	156 82.5%	83 43.9%	41 21.7%

[a] Not including cephalopods

Table 2 The proportion of scats collected from known and unknown age individuals in McMurdo Sound Antarctica which contained *B. picta* beaks or fish otoliths. Mean otolith size (uncorrected) and *Pleuragramma antarcticum* (*P.a.*) standard length are indicated for each age group. Fish size was calculated following Hubold and Tomo (1989), and corrected otolith diameters (1.275*OD, Harvey 1989) were used

Age	# Scats	# *Brachioteuthis picta* beaks (% scats)	# *Trematomus* spp. otoliths (% scats)	% Scats with *P.a.* vertebrae	# *P.a.* otoliths (% scats)	Mean *P.a.* OD ± SD (mm)	Mean fish length ± SD (mm)
Adults	1	0		100	2 (100)	2.6 ± 0.1	249.8 ± 13.1
Yearlings	5	87 (60)	1 (20)	80	12 (40)	1.0 ± 0.1	99.9 ± 13.2
Pups	2	678 (50)	1 (50)	50	2 (50)	0.9 ± 0.0	89.5
Unknown	189	39 (21)	6 (3)	88	154 (16)	1.5 ± 0.4	143.2 ± 40.8

badly eroded lower beaks of the small *Brachioteuthiid* squid tentatively identified as *B. picta*.

While a wide variety of invertebrates were identified from the scats collected in 1989 (Table 3), the vast majority of these items were benthic invertebrates of less than 5 mm in size. Because of their small size, and the fact that these items form the bulk of the fish diet in McMurdo Sound, these items were thought to have been ingested secondarily. More than half of the scats collected in 1989 contained parasites, the majority of which were nematodes.

The mean size of the sagittal otoliths recovered from the scat samples, and the estimated length of the *Pleuragramma antarcticum* and *Trematomus* species consumed are shown in Table 4. There was significant inter-annual variation in the estimated mean length of *Pleuragramma antarcticum* eaten (Fig. 1) as otoliths collected in 1989 and 1990 were significantly larger than those collected from 1991 to 1994 (one way ANOVA $P = 0.000$, Tukey HSD post-hoc comparison of means, $P < 0.05$). While the number of fish otoliths per scat collected [mean of 0.9 ± 3.3 (SD) otoliths/scat] did not differ among years ($P = 0.49$), the fewest otoliths were recovered in 1992, and 1992 had the lowest proportion of scats with remains from *Pleuragramma antarcticum* and other fishes.

An examination of the percent frequency of occurrence of prey items from scats of known age animals to that of the whole sampled population (the Cape Evans scat collection) suggested that juveniles may have eaten more invertebrates and benthic fishes. Similarly, the mean *Pleuragramma antarcticum* otolith diameter and estimated fish length were smallest in the youngest animals (Table 2). However, these samples were too unbalanced to permit any statistical tests, and the conclusions are necessarily tentative.

Stable isotope analysis

The stable isotope ratios determined from the Weddell seal plasma samples are shown in Fig. 2. There were no significant differences in the $\delta^{15}N$, $\delta^{13}C$, and C:N ratios by collection year or sex within any group ($P > 0.05$ in all cases), so samples from males and females from all years were pooled for among-group comparisons. While there were no significant differences in the $\delta^{15}N$ ratio among adults and any group of yearlings, nursing pups did have a slightly elevated $\delta^{15}N$ value when compared to adult females (mean difference of 0.8‰). The mean $\delta^{15}N$, $\delta^{13}C$, and C:N ratios for all groups of seals are given in Table 5.

While the C:N ratio of seal blood was significantly correlated with its $\delta^{13}C$ value ($\delta^{13}C = -1.61^{*}$C:N ratio -19.06, $n = 42$, $P < 0.001$, $r^2 = 0.53$, Fig. 3a), there were no significant differences in the C:N ratio among adults and foraging yearlings. However, pups did have a slightly higher C:N value than all other seals (Table 5). Despite the similarity in $\delta^{15}N$ and C:N ratio, adults and all yearlings were not pooled because there were significant differences in their $\delta^{13}C$ values. Shallow-diving yearlings had significantly enriched $\delta^{13}C$ values relative to those of adults, deep-diving and NDR yearlings (Table 5).

Table 3 Invertebrates identified from 75 Weddell seal samples collected at Cape Evans, Ross Island, Antarctica, in October 1989

Group	Order	# Scats
Crustaceans	Isopods[a]	23
	Amphipods[b]	37
	Calanoid copepods	12
	Shrimps[c]	2
	Fragments	68
Parasites	Nematodes	48
	Acanthocephalans	8
	Cestodes	6
Benthic invertebrates	Hydrozoans	6
	Molluscs	10
	Gastropods	21
	Balanomorpha valves	3
	Polychaete setae/palaea[d]	8

[a] *Gnathiidae*, *Flabelliferidae*, *Idoteidae*, *Arcturidae*
[b] *Hyperiidae*, *Leucothoidae*
[c] *Euphausiidae*, *Pleocyemata*
[d] *Pectinaridae or Flabelligeridae*

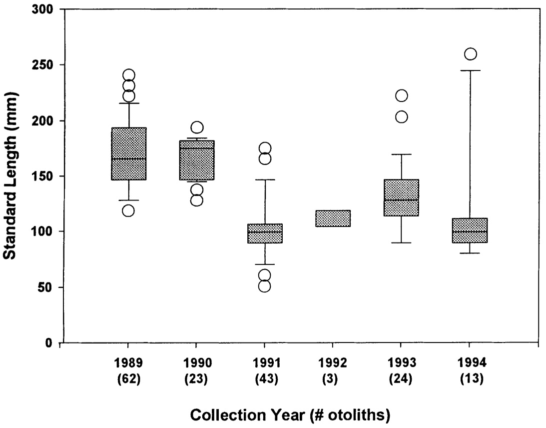

Fig. 1 Box and whisker plot of standard lengths of *Pleuragramma antarcticum* identified from otoliths (*n*) recovered from Weddell seal scats collected between 1989 and 1994 in McMurdo Sound, Antarctica. Fish length estimated following Hubold and Tomo (1989). *Box* shows median, lower and upper quartiles, whiskers cover 10th–90th percentile range, and *circles* are statistical outliers

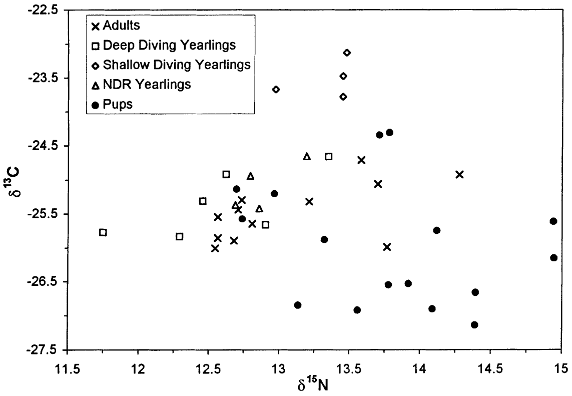

Fig. 2 The $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios in Weddell seal blood plasma. Dive patterns for yearlings determined from TDR records (Burns et al. in press). NDR Yearlings are those for which there were no dive records

The stable isotope and C:N ratios of Weddell seal prey items are shown in Table 6. There were clear differences in the isotopic ratios between prey items, with

Table 4 Diameter of sagittal otoliths (OD) recovered from Weddell seal scats collected from 1989 to 1994 in McMurdo Sound, Antarctica, and the estimated length of fish consumed. Corrected otolith diameters (1.275*OD, Harvey 1989) were used in the estimation of fish lengths

Species	*N*	Uncorrected OD mean ± SD (mm) (range)	Corrected OD mean ± SD (mm) (range)	Mean fish standard length ± SD (mm)	Range (mm)
Pleuragramma antarcticum[a]	168	1.4 ± 0.5 (0.5–2.7)	1.8 ± 0.6 (0.6–3.4)	140.7 ± 42.7	50.7–259.1
Trematomus species[b]	6	3.3 ± 1.2 (1.9–5.2)	4.2 ± 1.5 (2.4–6.6)	233.4 ± 78.9	127.3–341.0
T. bernacchii[b]	1	2.1	2.7	140.4	

[a] Standard length, following Hubold and Tomo 1989
[b] Total length, following Hecht 1987

Table 5 The $\delta^{13}C$, $\delta^{15}N$, and C:N ratios (mean ± SE) in the plasma of Weddell seals of known age. Diving patterns for deep-and shallow-diving yearlings were determined from time depth recorder records (Burns et al. in press)

Group	*n*	$\delta^{13}C$	$\delta^{15}N$	C:N
Adults	12	−25.5 ± 0.1	13.1 ± 0.2	3.82 ± 0.08
Deep-diving yearlings	6	−25.4 ± 0.2	12.6 ± 0.2	3.87 ± 0.05
NDR yearlings	4	−25.1 ± 0.2	12.9 ± 0.1	3.65 ± 0.11
Shallow-diving yearlings	4	−23.5 ± 0.1*	13.3 ± 0.1	3.68 ± 0.12
Pups	16	−26.0 ± 0.2	13.8 ± 0.1†	4.12 ± 0.16*

*Significantly different from all other groups ($P < 0.05$)

†Significantly different from adult females ($n = 6$, $P < 0.05$) and deep-diving yearlings

the large Antarctic cod, *Dissostichus mawsoni*, the most nitrogen enriched and carbon depleted. The C:N ratios also differed by prey, with the most $\delta^{13}C$ depleted species having the highest C:N ratio ($\delta^{13}C = -0.81$*C:N ratio-22.73, $n = 15$, $P < 0.001$, $r^2 = 0.79$, Fig. 3b). As a result, the $\delta^{13}C$ values for *Pleuragramma antarcticum* and *D. mawsoni* were adjusted to reflect a C:N ratio of 3.75 (the mean for foraging seals) using the regression equation above. The lipid-corrected $\delta^{13}C$ value for these species, −25.8‰, was similar to those of all seals except shallow-diving yearlings, as is shown in Fig. 4.

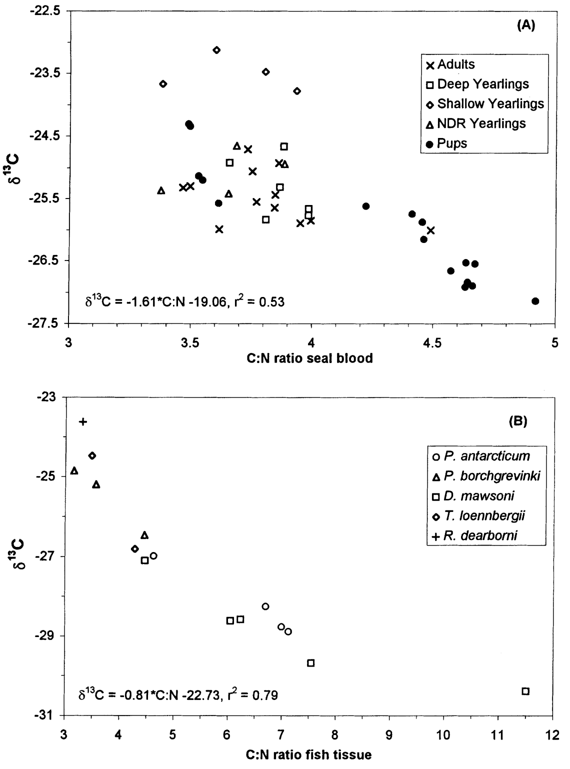

Fig. 3A,B The relationship between $\delta^{13}C$ and tissue C:N ratio for all seals (**A**) and fish (**B**) sampled. *Trematomus bernacchii* is not included in **B** because no C:N ratio was available ($\delta^{13}C$ value taken from Wada et al. 1987).

Discussion

There was general agreement between the diet determined for Weddell seals by scat analysis and the diet and trophic level estimated from stable isotope analyses. In addition, the diet estimated by both techniques agreed with observed diving behavior and with previous studies on the diet of Weddell seals in McMurdo Sound (Dearborn 1965; Testa et al. 1985; Green and Burton

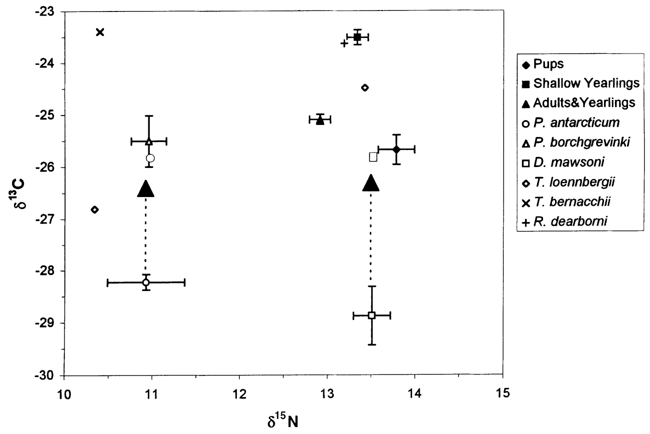

Fig. 4 The $\delta^{13}C$ and $\delta^{15}N$ stable isotope values for Weddell seals and fishes in McMurdo Sound. *Arrows* to second data points for *Pleuragramma antarcticum* and *Dissostichus mawsoni* indicate the $\delta^{13}C$ values corrected to account for their higher C:N ratios. The two *Trematomus loenbergii* samples are shown separately because of the large difference in values

Table 6 The $\delta^{13}C$, $\delta^{15}N$, and C:N ratios of fish collected in McMurdo Sound, Antarctica

Species	*n*	$\delta^{13}C$	$\delta^{15}N$	C:N
Dissostichus mawsoni	5	−28.9 ± 0.6	13.5 ± 0.2	7.17 ± 1.19
Pleuragramma antarcticum	4	−28.3 ± 0.4	10.9 ± 9.2	6.37 ± 0.58
Pagothenia borchgrevinki	3	−25.5 ± 0.5	11.0 ± 0.2	3.73 ± 0.39
Trematomus loennbergii[a]	2	−26.8	10.3	4.29
		−24.5	13.4	3.49
Trematomus bernacchii[b]	1	−23.4	10.4	–
Rhigophilia dearborni	1	−23.6	13.2	3.31

[a] Samples shown separately due to the large difference between individuals

[b] Values from Wada et al. 1989

1987; Castellini et al. 1992). While each technique had associated biases and uncertainties, by combining these methods it was possible to more completely characterize the diet of Weddell seals than would otherwise have been possible.

The scats collected at Cape Evans over 5 years indicated that there was remarkably little variation in the diet of Weddell seals. In all years, *Pleuragramma antarcticum* was the primary constituent of the diet, and remains were found in 70–100% of the collected scats. Otoliths from other nototheniids were rare, as were cephalopod remains. However, given the absence of *Pleuragramma antarcticum* otoliths from many of the scats in which vertebrae were found, and the extremely eroded condition of many of the otoliths and all of the small *B. picta* beaks, it is possible that both small fishes and squids were eaten more commonly than indicated by recovered remains. Crustacean and mollusc parts were found in approximately a quarter of the scats collected each year, but it is likely that the majority of the amphipods, mysid shrimps, molluscs, and polychaetes came from the stomachs of ingested fishes, as all nototheniids in McMurdo Sound are known to forage on these items (Bertram 1940; Dearborn 1965; Eastman 1985; Everson 1985). Euphausiids and prawns, which were more common than fishes in the stomachs of seals collected in Davis Sound (Green and Burton 1987), have never been identified as important food items for seals in McMurdo Sound, probably due to their absence in large numbers from this ecosystem (Eastman 1985; Everson 1985).

The mean size of *Pleuragramma antarcticum* otoliths recovered from the collected scats, 1.4 mm, was at the low end of the size range reported in other studies from throughout Antarctica (1.4–1.8 mm) (Plötz 1986; Green and Burton 1987; Castellini et al. 1992). However, the majority of otoliths recovered in these other studies came from stomach samples, and were probably less eroded than those we recovered from scats (Croxall 1993). Fish standard length calculated using the corrected otolith diameters indicated that, as in other areas of Antarctica, the mean size class of *Pleuragramma antarcticum* eaten was 141 mm (Plötz 1986; Green and Burton 1987; Castellini et al. 1992). While there was some variation in the size of fish eaten, differences between years were small. However, if the calculated fish sizes are correct, these small differences may be significant. *Pleuragramma antarcticum* reaches maturity at approximately 140 mm and the mean length of fish ingested in 1989 and 1990 indicated that most fish eaten were mature. However, otoliths collected between 1991 and 1994 suggested a tendency to take smaller fish that may have been immature (see Fig. 1). We do not know if this shift is indicative of changes in the ecosystem, circulation patterns, fish growth rates and availability, or if it is an artifact from the calculations of fish size. In any case, as *Pleuragramma antarcticum* larger than approximately 120 mm are generally found at depths greater than 200 m, it was not surprising that the mean depth of foraging dives for adults and most yearlings was greater than 200 m (Hubold 1984, 1985; Eastman 1985; Kellermann 1986; Hubold and Tomo 1989; Castellini et al. 1992; Radtke et al. 1993; Testa 1994; Schreer and Testa 1996; Burns et al. 1997).

While we did not estimate the size of squid eaten, *B. picta*, the most common species identified, is not thought to reach sizes in excess of 15 cm (mantle length) (Fischer and Hureau 1985; W. Walker personal communication). In Antarctic waters, *B. picta* has been caught in trawls from the surface to the bottom (> 1000 m), but is thought to occur predominantly below 200 m during the day (Filippova 1972; Rodhouse 1989, 1990; Rodhouse and Piatkowski 1995). Commonly caught in research nets, *B. picta* has been seen in the diet of southern elephant seals (*Mirounga leonina*), Weddell seals, and sperm whales (*Physeter catodon*), and its absence in the diet of other Antarctic predators has been remarked upon (Clarke and MacLeod 1982; Rodhouse 1990; Rodhouse et al. 1992; Green and Burton 1993; Rodhouse and Piatkowski 1995; Slip 1995). While cephalopod beaks have generally been thought to be indigestible (Clarke and MacLeod 1982; Harvey 1989), heavily eroded beaks of the market squid, *Loligo opalescens*, have been found in the stomachs of emperor penguins (*Aptenodytes forsteri*, Pütz 1995), and "a fine gravel composed entirely of fragmented (squid) beaks" was found in Weddell seal stomachs by Bertram (1940). Seals may retain squid beaks for long periods of time (Pitcher 1980; Gales et al. 1993) and, if the beak fragments retrieved in this study are any indication, then perhaps the absence of *B. picta* from the estimated diet of many marine animals is due to erosion of these small beaks during the digestive process.

Inferences about seasonal variation in the diet of seals in McMurdo Sound rely on the assumption that scats collected from Cape Evans were deposited throughout the year, as has been supported by animal tracking and observational studies (Testa 1994; personal observation). If this assumption is valid, then there is little evidence for seasonal or annual variation in the diet. The contents of all collected scats were similar, and very few "unusual" scats were found. While comparable to other studies in McMurdo Sound, this differs from observed seasonal variation in the diet of Weddell seals from the Weddell Sea which foraged mainly on *Pleuragramma antarcticum* in the summer but concentrated on other species in the spring (Plötz 1986; Green and Burton 1987; Plötz et al. 1991; Castellini et al. 1992). It may be that seasonal variation is more common in lower Antarctic latitudes or in areas where the prey base is more diverse. In McMurdo Sound, *Pleuragramma antarcticum* makes up more than 90% of the fish biomass, and so it is not surprising that it is the major prey of the local Weddell seal population (Eastman 1985; Everson 1985).

Variation in the diet due to age was difficult to test because of the limited number of scats collected from known age animals. However, it appeared that younger animals may have been foraging on smaller fishes or more cephalopods than the population as a whole. Ontogenetic shifts in diet have been observed in some phocid species, and are generally apparent when juveniles are unable to efficiently capture the prey consumed by adults due to physiological constraints on dive depth and duration (Sergeant 1973; Haug et al. 1991; Lydersen et al. 1991; Slip 1995). Studies on the diving behavior of juvenile Weddell seals have suggested that young animals are capable of reaching the depths selected by foraging adults, but that dive durations are limited by smaller body size and immature physiological processes (Kooyman et al. 1983; Burns and Castellini 1996; Burns 1997; Burns and Testa 1997; Burns et al. 1997). To avoid direct competition with adults, juvenile Weddell seals may forage in different locations, but as yet, studies have been unable to determine if they concentrate their foraging on different prey (Burns and Testa 1997; Burns et al. 1997).

The diet of Weddell seals estimated based on the examination of the stable isotope ratios in seal blood and fish tissues was remarkably similar to that determined from scat samples. While there was a wide range in the δ^{15}N values among individuals, there were no significant differences due to animal age, sex, year of sample collection, or diving behavior. This similarity indicated that all seals in this study had been foraging at a similar trophic level during the previous 8 weeks. The slight enrichment in δ^{15}N between nursing pups and adult females was expected as pups were effectively "foraging" on their mothers (Hobson et al. 1997). When the mean δ^{15}N values for seals were compared to those of the potential prey items, it appeared that foraging Weddell seals of all ages were feeding primarily on *Pleuragramma antarcticum*, *Pagothenia borchgrevinki*, and/or *Trematomus* species. There was an approximate 2.5‰ enrichment in δ^{15}N between seals and these prey items, as expected for a single trophic level increase (Owens 1987; Wada et al. 1991; Rau et al. 1992; Hobson et al. 1997). *Dissostichys mawsoni* and *Rhigophilia dearborni* had δ^{15}N values similar to those of the seals, and therefore could not have contributed significantly to the seals' diet. Unfortunately, we did not have specimens or reported isotopic ratios for any cephalopods found in the diet, or for the five other *Trematomus* species known to occur within McMurdo Sound (Macdonald et al. 1987). Therefore, using only the δ^{15}N values, it was impossible to determine the relative importance of some of the prey items that appeared in scat samples, or to distinguish which of several small nototheniids were most important in the diet. This difficulty results from the dietary and trophic level overlap (and therefore similar δ^{15}N values) of most nototheniids in McMurdo Sound (Eastman 1985; Everson 1985).

In contrast to the nitrogen data, there was significant variation in the δ^{13}C and C:N values among the five fish species, fishes and seals, and seals with dissimilar diving patterns. These differences were helpful in determining the relative importance of individual prey species and foraging locations to Weddell seals feeding in McMurdo Sound. Because nototheniid fishes use lipid as a means for controlling buoyancy, the lipid content (and therefore δ^{13}C and C:N ratios) of different species is strongly correlated with their lifestyle, and this is reflected in their C:N ratios and δ^{13}C values (McConnaughey and McRoy 1979; Tieszen et al. 1983; Clarke et al. 1984; Eastman 1985; Reinhardt and Van Vleet 1986; Rau et al. 1991a, 1992; Hobson and Welch 1992). The high lipid content of the more active, pelagic fishes such as *Pleuragramma antarcticum* and *D. mawsoni* was reflected in their high C:N ratio and low δ^{13}C values. The cryopelagic lifestyle of *Pagothenia borchgrevinki* is indicated by their intermediate lipid levels, C:N, and δ^{13}C values. The more benthic and sedentary *Trematomus* species had the lowest lipid levels of all the nototheniids and also the lowest C:N and highest δ^{13}C values measured in this study (Clarke et al. 1984; Macdonald et al. 1987; Friedrich and Hagen 1994). As benthic habitats are carbon enriched relative to the pelagic system due to the different dynamics surrounding carbon uptake by benthic and pelagic algae (Fry and Sherr 1984; France 1995), the high δ^{13}C values seen in the *Trematomus* species probably resulted both from their lower lipid content and their benthic habitat.

Unlike the fishes, there were differences in the seals' δ^{13}C values that were not clearly related to differences in their C:N ratios. All foraging seals (non-pups) had approximately the same C:N ratios, but the δ^{13}C values of shallow-diving yearlings were significantly enriched in comparison to adults and other yearlings. This suggested that shallow-diving yearlings were foraging on different prey, or in different locations, to other seals. For yearling Weddell seals diving in McMurdo Sound, dive records have demonstrated a clear dichotomy among individuals that concentrate their diving activity along the bottom in shallow waters, and those that dive predominantly in the deep-water pelagic zone (Burns et al. 1997). Because all animals in this study were captured in the same area, differences in foraging location probably resulted from shallow-diving yearlings concentrating their foraging in the more δ^{13}C-enriched benthic community (France 1995; Burns et al. 1997). In combination with observed diving behavior, these findings imply that differences in mean dive depths do indeed reflect differences in foraging behavior. As shallow-diving yearlings were larger and made longer dives (on average) than the deep-diving yearlings, differences in foraging behavior probably did not reflect physiological limitations, but instead were a result of behavioral preferences (Kooyman et al. 1983; Burns and Castellini 1996; Burns et al. 1997).

When the δ^{13}C values for both deep-and shallow-diving yearlings were compared to those of the prey items sampled, it was possible to estimate the prey types selected. The δ^{13}C values of many nototheniids were directly comparable to those of adults and most yearling seals, and even those of *Pleuragramma antarcticum* and *D. mawsoni* were similar once the lipid-corrected δ^{13}C values were determined. However, two of the three *Trematomus* samples (*T. bernacchii* and one *T. loennbergii* sample), were carbon enriched relative to other nototheniid fishes, and the $\delta^{13}C$ value of these samples came within 1.0‰ of that of the shallow-diving yearlings. Both of these fishes are benthic scavengers with relatively low lipid contents (Clarke et al. 1984; Friedrich and Hagen 1994). When combined with the nitrogen isotope data, these findings strongly suggested that most adults and juveniles were foraging primarily in the pelagic ecosystem on *Pleuragramma antarcticum* and perhaps *Pagothenia borchgrevinki*, and concentrating less on benthic species. In contrast, while the nitrogen data indicated that shallow-diving yearlings were foraging at the same trophic level as other seals, their enriched $\delta^{13}C$ values suggested they were foraging more frequently in the benthic ecosystem on species such as *T. bernacchii* and *T. loennbergii*. Fecal samples collected from three deep divers and one shallow diver seem to confirm this hypothesis. Scats from the deep-diving yearlings contained several *Pleuragramma antarcticum* otoliths, many vertebrae, and 83 *B. picta* beaks, but that from the shallow diver did not contain any *Pleuragramma antarcticum* otoliths, and few vertebrae.

When the food web constructed in this study is compared to that proposed by Rau et al. (1992) for vertebrates in the Weddell Sea, it is clear that Weddell seals in McMurdo Sound occupy a higher trophic level than other Antarctic pinnipeds. The average Weddell seal $\delta^{15}N$ value, 13.3 ± 0.1‰, places Weddell seals at the trophic level of an obligate fish or squid predator, a niche probably shared with southern elephant seals (*Mirounga leonina*), but apparently not occupied by Ross (*Ommatophoca rossii*), crabeater (*Lobodon carcinophagus*), leopard (*Hydrurga leptonyx*), or fur (*Arctocephalus gazella*) seals in the Weddell Sea (Hindell et al. 1991; Rau et al. 1992). Because fish in both areas have similar $\delta^{15}N$ values, the lower $\delta^{15}N$ values (highest value 9.4‰) for pinnipeds in the Weddell Sea probably reflect the larger role that euphausiids ($\delta^{15}N < 5‰$) play in their diet (Laws 1984; Green and Williams 1986; Lowry et al. 1988; Rau et al. 1991a, 1992). From this work, it appears that Weddell seals occupy a higher trophic level than most other phocids within the Antarctic ecosystem, at least in regions such as the Ross Sea where they concentrate their foraging primarily on nototheniid fish and cephalopods.

In conclusion, by combining scat collections with stable isotope analysis and diving behavior records, this study was able to more completely characterize the diet of Weddell seals in McMurdo Sound than would have been possible using any one of these methods singly. In the instance of deep and shallow divers, dietary differences suggested by diving behavior were unable to be verified by scat analysis, but were clearly identified by the analysis of predator and prey isotope ratios. Within the deep divers, the dietary specialization on *Pleuragramma antarcticum*, as indicated by the scat samples, could not have been determined from the isotope data alone because both *Pleuragramma antarcticum* and *T. bernacchii* had similar $\delta^{15}N$ values. Finally, all three methods were needed to conclusively determine that Weddell seal adults and most yearlings were foraging primarily in the pelagic ecosystem on *Pleuragramma antarcticum*, while the shallow-diving yearlings were foraging mainly on the benthic *Trematomus* species. Unfortunately, because isotopic values were not available for the squid species identified in scats, the contribution of cephalopods to the diet of benthic or pelagic foraging seals could not be determined in this study. Similarly, small sample sizes prevented definitive conclusions about age-related variation in the diet of Weddell seals in McMurdo Sound. However, now that these techniques have been proven effective in determining small-scale dietary differences, it would be a relatively simple matter to collect sufficient samples from predator and prey to quantify age and seasonal dietary shifts. Clearly, these three methods complement each other, and in combination are a powerful tool for better understanding the foraging behavior of marine mammals.

Acknowledgements This research was supported by grant OPP-9119885 from the National Science Foundation to J. Ward Testa and Michael Castellini and by a University of Alaska Fairbanks Chancellor's fellowship to J.M. Burns. Help with field collection of scats and tissues came from T. Zenteno-Savin, L. Rea, B. Fadely, J. Fadely, K. Hastings, and many others. We would particularly like to thank Max Hoberg, Amy Hirons, Norma Haubenstock, and Andrew Trites for help with the scat and stable isotope analyses. The comments of three anonymous reviewers significantly improved the final version. The research was carried out under permit # 801 of the Marine Mammal Protection Act. Experimental protocols for the studies were approved by the UAF Institutional Animal Care and Use Committee, and comply with the "Principles of animal care" publication No. 85-23 revised 1985 of the National Institute of Health, and the current laws of the United States of America.

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