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STABLE ISOTOPE ANALYSES OF TOOTH ANNULI REVEAL TEMPORAL DIETARY RECORDS: AN EXAMPLE USING STELLER SEA LIONS

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ABSTRACT

Stable isotope analysis of teeth of marine mammals can provide valuable information on trophic level and source of feeding. However, the isotopic analysis of whole teeth presents only an average dietary estimate for individuals across the period of growth of that tooth. While such analyses can be valuable, particularly in the case of fossil material, in contrast, isotopic analysis of individual annuli of teeth can provide dietary information for each year of tooth growth, in some cases representing the whole of the animal's life. We measured stable-carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) in the inorganic (hydroxyapatite) and stable-nitrogen isotope ratios ($^{15}\text{N}/^{14}\text{N}$) in the organic (primarily collagenous) components of individual tooth annuli of 18 male Steller sea lions (*Eumetopias jubatus*) obtained from archived collections from the Bering Sea and Gulf of Alaska and from single northern fur seals (*Callorhinus ursinus*) and northern elephant seals (*Mirounga angustirostris*) from the central Aleutian Islands and eastern Gulf of Alaska, respectively. In several individuals, we detected considerable variation in stable isotope values among annuli, up to 6.1‰ for $\delta^{15}\text{N}$ and 5.1‰ for $\delta^{13}\text{C}$ values. Enrichment in $\delta^{15}\text{N}$ and depletion of $\delta^{13}\text{C}$ values in the first annulus may correspond to dietary inputs from mother's milk during the period of suckling. Other variations among years may be caused by dietary changes or movements of individuals between regions differing in isotopic signatures of foodweb primary production. Our study indicates that the isotopic analysis of individual tooth annuli represents a fine-scale tool for dietary reconstructions involving marine mammals, and cautions against the use of whole-tooth material averaged over several annuli.

Key words: stable isotopes, hydroxyapatite, teeth, collagen, Steller sea lion, *Eumetopias jubatus*, northern fur seal, *Callorhinus ursinus*, northern elephant seal, *Mirounga angustirostris*.

The measurement of naturally occurring stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) in animal and plant materials is now a well-established technique to infer diet and trophic relationships in both terrestrial and marine foodwebs (reviewed by Peterson and Fry 1987, Michener and Schell 1994). While applications to marine mammal studies have been few, there is an obvious potential to combine conventional dietary investigations with isotope studies to gain insight into the ecology of several species (e.g., Schell *et al.* 1989, Ostrom *et al.* 1992, Abend and Smith 1995, Hobson *et al.* 1997). The recent investigation of isotopic fractionation or change between diet and tissues of seals raised in captivity on a known diet (Hobson *et al.* 1996) has also advanced our understanding of how several tissues are potentially available for isotopic analysis, including those involving non-destructive sampling or the use of archived museum material. Teeth can also be used in isotopic investigations, since they contain both inorganic (hydroxyapatite) and organic (collagenous) fractions that are ultimately derived from diet (Kreuger and Sullivan 1984, Ambrose and Norr 1993). In addition, teeth preserve well and have been used extensively in paleodietary reconstructions (Koch *et al.* 1989, Bocherens *et al.* 1995). Teeth represent a valuable material for dietary studies involving marine mammals, and there is significant potential for using marine mammal teeth to infer diet. Stable-carbon and nitrogen isotope values in the organic fraction of teeth should reflect those of the animal's diet, and historical dietary information could be obtained from the measurement of teeth from museum collections. However, previous isotope studies have used *whole* teeth. Investigation of diet using individual tooth annuli has not been attempted previously.

Teeth are composed primarily of dentin and enamel. Enamel forms the hard outer coating and contains only a small amount of protein. Dentin, on the other hand, is composed of an inorganic hydroxyapatite matrix infused with an organic, primarily collagenous fraction. Within dentin, both dietary and environmental information can be obtained from the measurement of stable-carbon and oxygen isotope ratios in hydroxyapatite (Koch *et al.* 1989, Lee-Thorp *et al.* 1989) or the stable-carbon and nitrogen isotope analysis of the collagenous fraction (Bada *et al.* 1990). Isotopic examination of the dentin obtained from individual tooth annuli is expected to provide dietary information averaged over that year of growth, since both the proteins and calcified tissues are apparently metabolically inert following formation (Bada 1984, Bada *et al.* 1990). There is potential, then, to obtain individual dietary records spanning the lifespan of individuals and, more importantly, to detect dietary shifts related to different age classes, environmental conditions, and migratory or movement patterns. As part of our ongoing isotopic studies involving Steller sea lions (*Eumetopias jubatus*) in the North Pacific (Hobson *et al.* 1997), we investigated patterns of stable-carbon and nitrogen isotope ratios in the inorganic and organic components of dentin from the annuli of individuals of this species. Our objectives were to demonstrate the utility of this approach to marine mammal dietary reconstructions and to investigate the range of variation in stable-isotope values across annuli.

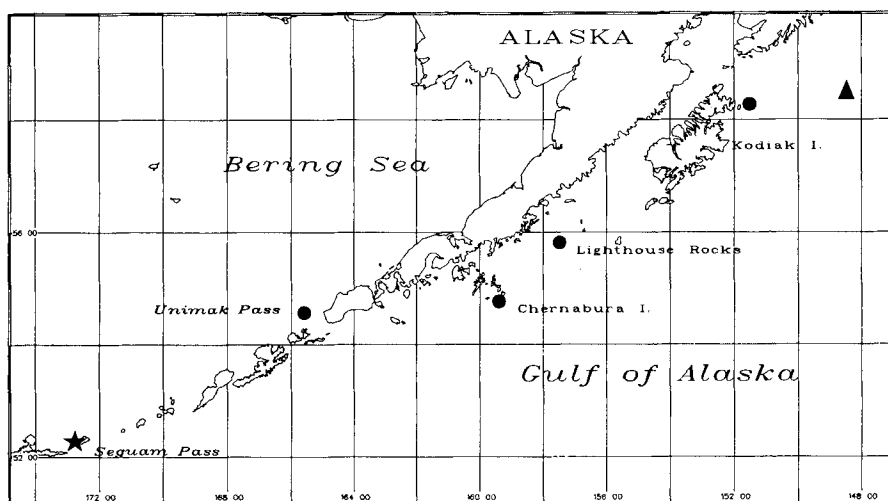


Figure 1. Locations where specimens were obtained.

METHODS

Steller sea lion teeth were obtained from the collections housed at the National Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle. We selected teeth from individual animals spanning a range of ages and covering a time period of several decades. Six samples were from sea lions taken at Chernabura Island in 1958 (Fig. 1). Two were from sea lions collected by the NMFS Pelagic Fur Seal Investigations in 1960: one from the Shumagin Islands (about 50 km northeast of Chernabura Island) and one from near Afognak Island. Ten samples were from sea lions collected by observers in the Alaska groundfish fisheries from 1978 through 1994. Of these, seven were from within 50 km of Unimak Pass in the eastern Aleutian Islands, two were from the eastern Bering Sea 200–250 km north of Unimak Pass, and one was from the vicinity of Lighthouse Rock. For the purpose of comparison, we also opportunistically sampled teeth from a northern fur seal (*Callorhinus ursinus*) collected in Seguam Pass in the central Aleutian Islands and a northern elephant seal (*Mirounga angustirostris*) collected from the central Gulf of Alaska about 200 km northeast of Kodiak Island. The fur seal and elephant seal each were collected by groundfish observers. All animals were males, ranging in age from 3 to 15 yr at the time of collection.

All teeth used in this study were non-decalcified upper canines that had been sawn in half longitudinally to determine age. However, among sea lion samples, eight (94-02, 93-05, 90-09, 88-21, 78-31, 78-32, 78-36, SS24) surfaces had been etched lightly in 5% formic acid to emphasize annuli. We assumed that such treatment did not influence $\delta^{13}\text{C}$ values or our interpretations of the dentin we examined, since dentin was taken from well within the annuli (*vs.* the small etched surface portion) and all annuli were treated similarly. The remaining sea lion samples (90-03, 3703, 3707, 78-34, 78-35,

SS-39, SS-34, SS-4, SS-55, SS-41) and the northern fur seal (87-11-CU) and northern elephant seal (93-06-MA) samples were polished but not etched. We used a hand-held drill to excavate approximately 20 mg of dentin from individual annuli. For Steller sea lions and the northern elephant seal, one-half of one tooth provided sufficient dentin. We used both upper canines from the fur seal; these teeth were about half the size of sea lion canines, and one-half of each tooth was effectively destroyed by the saw kerf.

The protein component of dentin was analyzed for stable-nitrogen isotope ratios by loading dentin samples into tin cups and combusting at approximately 1,800°C, using continuous-flow isotope ratio mass spectrometry involving a Europa 20:20 IRMS interfaced with a Robo Prep combustion system. Because we did not extract collagen *per se*, our $\delta^{15}\text{N}$ values were of whole protein composed primarily of collagen. The stable-carbon isotope ratios of the inorganic fraction were obtained by reacting powdered dentin samples with concentrated (100%) phosphoric acid in evacuated vacutainer tubes. The evolved CO_2 was sampled using either a breath sampler interfaced with a VG OPTIMA dual inlet or Europa 20:20 continuous-flow mass spectrometer. Isotope ratios are expressed in delta (δ) notation relative to the PeeDee Belemnite or AIR standards for carbon and nitrogen respectively (see Hobson *et al.* 1997). Using replicate measurements on albumin (N) and calcium carbonate (C) standards, we estimated analytical error to be $\pm 0.3\text{‰}$ for nitrogen and $\pm 0.1\text{‰}$ for carbon. By convention, the choice of the above international standards results in $\delta^{13}\text{C}$ values typically being negative and $\delta^{15}\text{N}$ values typically positive.

RESULTS

For Steller sea lions we determined that both $\delta^{13}\text{C}$ values for the inorganic fraction and $\delta^{15}\text{N}$ values for the organic fraction of individual teeth often showed considerable variation among annuli (Fig. 2). In several of the animals examined, $\delta^{15}\text{N}$ values were more enriched and $\delta^{13}\text{C}$ values more depleted in year 1 compared with year 2 and often subsequent years. However, for $\delta^{15}\text{N}$, this pattern was not evident in SS39, 88-21, 78-32, 78-36, and 90-09. In some individuals we also observed rather dramatic isotopic shifts for a single annulus compared with others (*e.g.*, SS41, 78-31, 90-09) or substantial changes over several annuli (*e.g.*, SS55, 93-005). For the single northern fur seal (87-11-CU), we also found that the first tooth annulus had the highest $\delta^{15}\text{N}$ compared with subsequent annuli, but we did not observe noticeable changes in $\delta^{13}\text{C}$ values. A similar, although less dramatic, pattern was found for the single northern elephant seal (93-06-MA). However, here we found it difficult to keep annuli separate due to their thinness, and material from adjacent annuli was undoubtedly combined.

In an attempt to facilitate broad isotopic comparisons between individual Steller sea lions over time, we present both the isotopic values of the first annulus and the mean isotope values corresponding to all subsequent annuli (Table 1). Considering only the mean isotope values for individuals based on all years after year 1, we observed that average $\delta^{15}\text{N}$ tooth values for individuals showed a significant enrichment after the 1960s compared with animals collected earlier

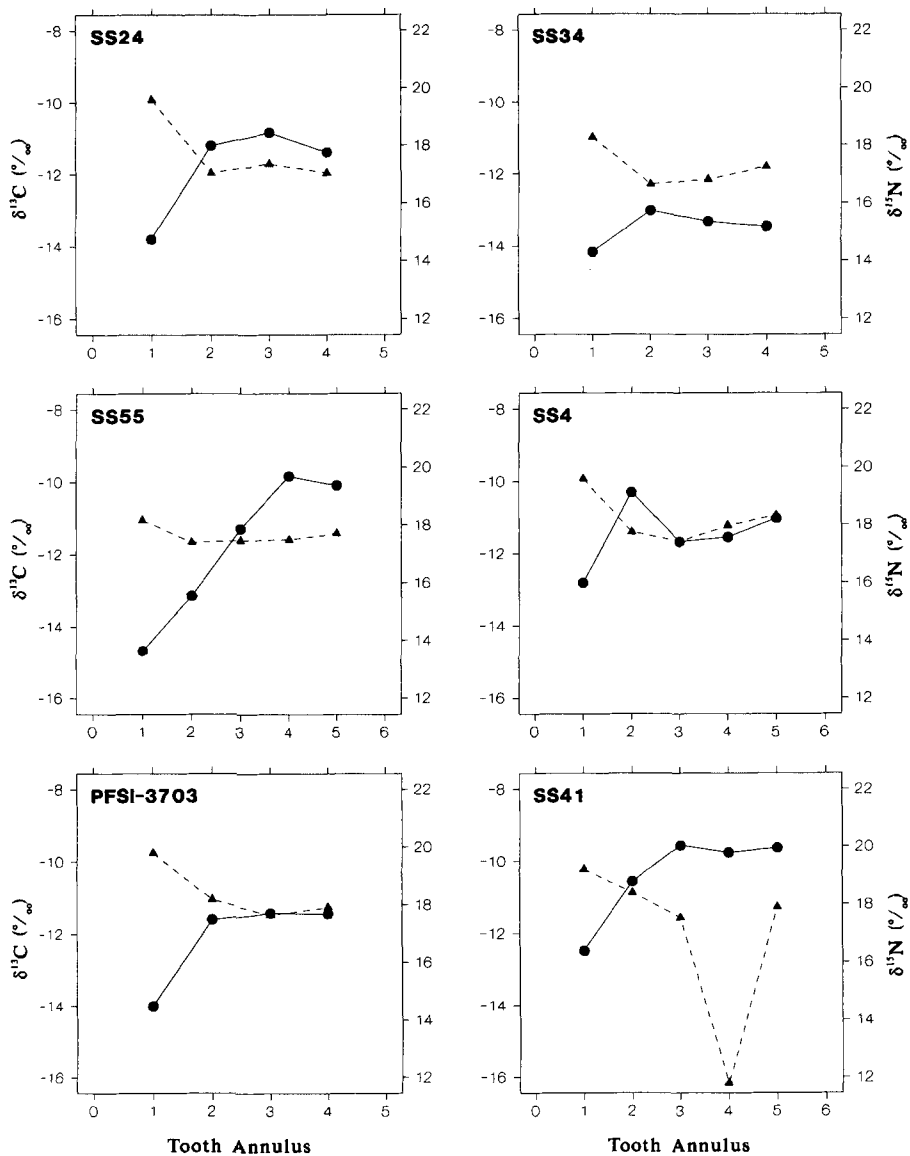


Figure 2. Patterns of $\delta^{13}\text{C}$ (●) and $\delta^{15}\text{N}$ (▲) values for individual annuli. See Table 1 for an explanation of codes.

(pre-1960 mean $\delta^{15}\text{N} = 17.1 \pm 0.9\%$, post-1960 mean $\delta^{15}\text{N} = 18.7 \pm 0.9\%$, 2-tailed t -test, $t = 3.72$, $P = 0.0021$). While there was a tendency for mean $\delta^{13}\text{C}$ values of the inorganic fraction of teeth to become more depleted between the same periods, no significant differences were found (pre-1960 mean $\delta^{13}\text{C} = -11.7 \pm 0.5\%$, $n = 8$; post-1960 mean $\delta^{13}\text{C} = -12.3 \pm 1.6\%$, $n = 9$; two-tailed t -test with unequal variance, $t = 0.733$, $P = 0.453$).

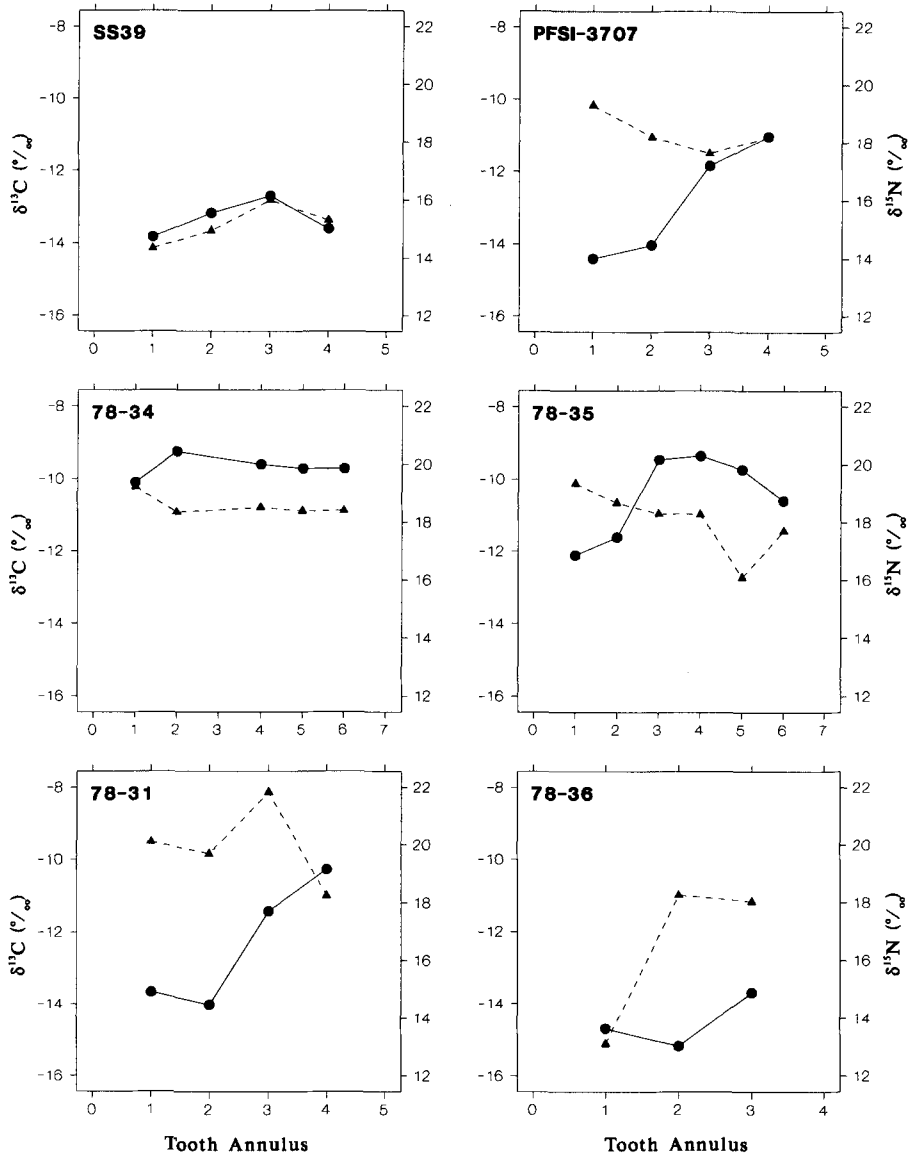


Figure 2. Continued.

DISCUSSION

Causes of Variation Across Annuli

Our study has demonstrated that $\delta^{13}\text{C}$ values of the inorganic and $\delta^{15}\text{N}$ values of the organic matrix of tooth dentin can show considerable variation across individual tooth annuli. These findings suggest that, depending on the life history of the marine mammal being studied, it may be inappropriate to

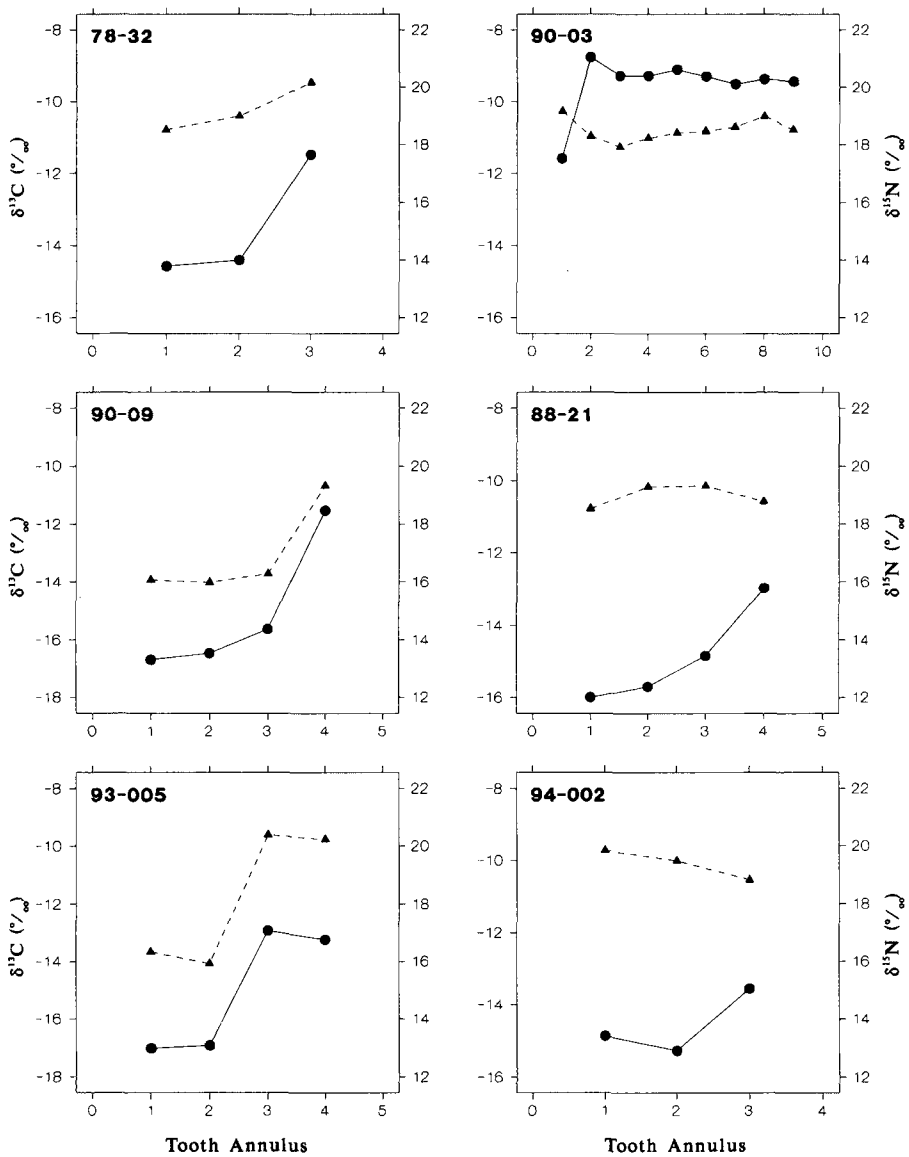


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use average isotopic values based on whole-tooth samples. This appears to be the case for Steller sea lions, since stable isotope values of the first and occasionally subsequent tooth annuli often differed by several parts per thousand compared with neighboring annuli. In such cases the use of an average isotope value based on dentin from the whole tooth may be biased considerably by the individual's diet in a given year. This effect is expected to be particularly significant for young animals in which dentin from the first tooth annulus

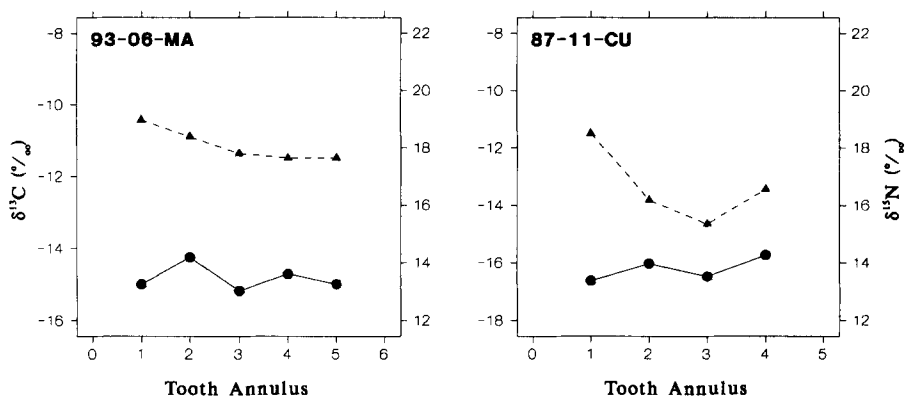


Figure 2. Continued.

comprises a considerable proportion of the whole sample, or for older individuals that may change trophic level or foraging location. This is not to suggest that the isotopic analysis of whole teeth cannot provide important information. For fossil material the analysis of individual annuli may be impossible, and several studies have demonstrated clearly the utility of isotopic data based on whole-tooth samples (reviewed by Koch *et al.* 1994). Rather, where possible, the isotopic analysis of individual tooth annuli from marine mammals will provide a finer-scale dietary resolution than the use of values averaged over the lifespan of individuals.

The enriched $\delta^{15}\text{N}$ values we observed in the first tooth annulus compared to subsequent annuli for several individual Steller sea lions may be related to the fact that a large portion of the diet of an animal during the first year of its life is derived from its mother. Milk derived from the tissues of lactating females is expected to be enriched in ^{15}N compared with the diet of adult females at that time, since milk is another female tissue whose protein is ultimately derived from diet. Stable-nitrogen isotope values enrich in a step-wise manner in marine foodwebs due to kinetic processes associated with amination and deamination of proteins derived from the diet (see Hobson and Welch 1992, Hobson *et al.* 1997). This effective trophic enrichment should be passed on to nursing pups. A similar effect has been observed for nursing polar bears (*Ursus maritimus*; Hobson, unpublished data). Bocherens *et al.* (1995) also suspected that higher $\delta^{15}\text{N}$ values of fossil deer and hyena tooth dentin compared with bone collagen was due to neonatal diets that included mother's milk. In almost all of the samples we examined, $\delta^{13}\text{C}$ of the inorganic fraction of tooth annuli was most depleted in Year 1 compared with subsequent years. Depleted $\delta^{13}\text{C}$ dentin values for the first annulus are likely associated with carbon being derived primarily from milk lipids during that period. Lipids are typically depleted in ^{13}C compared to other animal tissues (*e.g.*, Tieszen and Boutton 1988). Thus, the pup would be expected to depend on a diet that is much more depleted in ^{13}C prior to weaning than it would encounter at other times of its life. Bocherens *et al.* (1995) similarly attributed

Table 1. Results of stable-carbon and nitrogen isotope analyses (mean \pm SD) on inorganic and organic fractions, respectively, of teeth of Steller sea lions, elephant seal, and northern fur seal.

Code	First annulus	Age	Location	Year 1 $\delta^{13}\text{C}$ (%)	Year 1 $\delta^{15}\text{N}$ (%)	No. annuli (> Year 1)	Mean $\delta^{13}\text{C}$ (%)	Mean $\delta^{15}\text{N}$ (%)
Steller sea lion:								
SS24	1943	15	Chernabura I.	-13.8	19.6	3	-11.1 \pm 0.3	17.2 \pm 0.2
SS34	1946	12	Chernabura I.	-14.2	18.3	3	-13.3 \pm 0.2	16.9 \pm 0.3
SS55	1947	11	Chernabura I.	-14.7	18.2	4	-11.1 \pm 1.5	17.5 \pm 0.1
SS4	1950	8	Chernabura I.	-12.8	19.6	4	-11.1 \pm 0.6	17.9 \pm 0.4
PFSI-3703	1951	9	Afognak I.	-14.0	19.8	3	-11.5 \pm 0.1	17.9 \pm 0.3
SS41	1953	5	Chernabura I.	-12.5	19.2	4	-9.9 \pm 0.5	16.4 \pm 3.1
SS39	1953	5	Chernabura I.	-13.8	14.3	3	-13.2 \pm 0.5	15.4 \pm 0.5
PFSI-3707	1956	4	Shumagin Is.	-14.4	19.8	3	-12.3 \pm 1.6	17.9 \pm 0.3
78-34	1972	6	Unimak Pass	-10.1	19.2	4	-9.6 \pm 0.2	18.4 \pm 0.1
78-35	1972	6	Unimak Pass	-12.1	19.4	5	-10.2 \pm 0.9	17.8 \pm 1.0
78-31	1973	5	Unimak Pass	-13.7	20.1	3	-11.9 \pm 1.9	19.9 \pm 1.8
78-36	1975	3	Unimak Pass	-14.7	13.1	2	-13.9	18.1
78-32	1975	3	Unimak Pass	-14.6	18.5	2	-12.9	19.5
90-03	1981	9	Lighthouse Rocks	-11.6	19.2	8	-9.26	18.4 \pm 0.3
90-09	1982	7	Unimak Pass	-16.7	16.1	3	-14.5 \pm 2.6	17.2 \pm 1.8
88-21	1984	4	Unimak Pass	-16.0	18.5	3	-14.5 \pm 1.4	19.1 \pm 0.3
93-005	1989	3	E. Bering Sea	-17.0	16.3	3	-14.3 \pm 2.2	18.8 \pm 2.5
94-002	1991	2	E. Bering Sea	-14.9	19.8	2	-14.4	19.2
Northern elephant seal:								
93-06-MA	1990	3	Central Gulf of Alaska	-15.0	19.0	4	-14.8 \pm 0.4	17.8 \pm 0.4
Northern fur seal:								
87-11-CU	1980	3	Central Aleutian Is.	-16.6	18.5	3	-16.1 \pm 0.4	16.1 \pm 0.6

more negative $\delta^{13}\text{C}$ values in carbonate hydroxyapatite in archaeological samples of carnivore *vs.* herbivore teeth to more lipids in the diets of carnivores. In future isotope investigations it should be possible, then, to elucidate the cause of the isotope enrichment effect we observed in the first tooth annulus of Steller sea lions by comparing marine mammals with different life-history strategies.

Steller sea lion females typically nurse their pups throughout the first year, and it is not unusual to see suckling animals older than one year (Pitcher and Calkins 1981). Females first return to the sea to forage when their pups are about 9 days old and continue to make foraging trips every 1–3 d thereafter (Gentry 1970, Sandegren 1970). This species is expected, then, to show a fairly pronounced maternal effect in the first tooth annulus. In contrast, northern fur seals are weaned at about 120 d of age, weaning is abrupt, and young do not suckle after the first year (Gentry and Holt 1986). As a result, northern fur seals are expected to show a less dramatic maternal effect, since only about a third of its first-year diet will be derived from mother's milk. We were able to examine the tooth of a single fur seal and determined a shift of 2‰ between $\delta^{15}\text{N}$ values for the first-year annulus compared with subsequent annuli. However, fur seals may travel considerable distances during their life cycle (Trites and Bigg 1996) and move between regions with foodwebs differing in isotopic signature (see below).

In northern elephant seals, pups are weaned abruptly after about four weeks, but the pup then undergoes a post-weaning fast of 8–12 wk (Reiter *et al.* 1978, Costa *et al.* 1986). Thus, as with fur seals, elephant seal pups may ultimately depend on food resources derived from their mothers for up to 16 wk. Fasting may also result in an enrichment of $\delta^{15}\text{N}$ as demonstrated by Hobson *et al.* (1993). For the single elephant seal examined in this study, we determined that the first annulus was enriched by about 1‰ compared to other years. Walrus calves suckle during the first year and then wean gradually during the second year (Fay 1982). While we did not examine this species, we predict that, like Steller sea lions, walruses should show a pronounced $\delta^{15}\text{N}$ enrichment and $\delta^{13}\text{C}$ depletion for the first and perhaps second tooth annulus compared with subsequent annuli.

An alternative explanation for the first-year effect we observed in tooth dentin may be that isotopic fractionation between dietary substrates and tooth dentin is different for the early growth period compared with later periods in the animal's life (see Tieszen and Boutton 1988). This question could be resolved by examining teeth from animals raised in captivity on constant diets (*e.g.*, Hobson *et al.* 1996). However, whatever the explanation for the first-year effect, it is likely to be the result of a combination of factors, since some animals did not show a pronounced enrichment in ^{15}N for the organic or depletion of ^{13}C for the inorganic components of the first-year annulus.

Dietary Reconstructions

Patterns of isotopic fractionation between diet and tooth dentin have not been studied extensively, but Schoeninger and DeNiro (1984) suggested an

enrichment of +3‰ in $\delta^{15}\text{N}$ for bone and tooth collagen. This value can be applied to our data to estimate $\delta^{15}\text{N}$ values of prey. For Steller sea lions in the Gulf of Alaska (*i.e.*, from Chernabura Island east, Fig. 1), predicted average prey $\delta^{15}\text{N}$ after the year of birth ranged from 13.4‰ to 14.9‰. These values are intermediate between those $\delta^{15}\text{N}$ values we measured previously for large- and small-sized fishes and squid in this area and are consistent with dietary inferences made from bone collagen $\delta^{15}\text{N}$ values we measured for this species in Alaska (Hobson *et al.* 1997). We have not examined prey samples from the Bering Sea, but our isotope data suggest that, during the early 1990s, the two Steller sea lions examined from this area fed on prey with an average $\delta^{15}\text{N}$ value of about 16‰. Using the same approach, the single elephant seal from eastern Gulf of Alaska consumed prey with an average $\delta^{15}\text{N}$ value of about 14.8‰, and the northern fur seal from the Aleutians showed one of the lowest $\delta^{15}\text{N}$ dentin values with a predicted average diet of 13.1‰. The latter result is consistent with our earlier isotopic investigations indicating lower trophic level feeding in this species compared to Steller sea lions (Hobson *et al.* 1997).

Stable-carbon isotope values provide little trophic-level information in high-latitude marine systems (Hobson and Welch 1992) but can be associated with distinct oceanographic systems or inshore *vs.* offshore or pelagic sources of feeding (Schell *et al.* 1989, Hobson and Welch 1992, France 1995). In addition, $\delta^{13}\text{C}$ in marine systems in the northern hemisphere shows a general depletion with latitude (Rau *et al.* 1982, Hobson *et al.* 1997). For carnivores, stable-carbon isotopic fractionation between diet and carbonate in the mineral phase of bone and tooth is about +9‰ (Ambrose 1993). This suggests that mean dietary $\delta^{13}\text{C}$ for years following the birth year in Steller sea lions in the eastern Gulf of Alaska ranged from about -18.3‰ to -22.3‰. Predicted mean dietary $\delta^{13}\text{C}$ for sea lions from the Bering Sea averaged -23.3‰. The most negative average dietary $\delta^{13}\text{C}$ value was estimated for the single northern fur seal from the central Aleutian Islands (-24.1‰). While this value appears unusually negative, the pattern is consistent with a general depletion of $\delta^{13}\text{C}$ in the foodweb from east to west along the Gulf of Alaska (Hobson and Piatt, unpublished data).

Long-term Trends

The stable isotope analysis of archived marine mammal teeth allows investigation of dietary shifts through time. For contemporary samples, or those museum specimens collected directly from live or recently killed animals, no diagenetic alteration of proteins in teeth are expected. However, for fossil material such processes may result in isotopic changes in both the organic and inorganic phases (reviewed by Koch *et al.* 1994). Careful laboratory preparation of fossil material can ensure that only unaltered organic and inorganic components of fossil teeth are measured isotopically (Lee-Thorp and van der Merwe 1991). Our analysis of Steller sea lion teeth from the 1940s to the 1990s suggested that the mean $\delta^{15}\text{N}$ values for combined annuli after Year 1 may have increased since the 1960s, and this may correspond to a slight trophic-

level increase in this species. However, due to small sample sizes, we were unable to examine our sample for location as well as year effects. Geographical and temporal shifts or gradients in stable-carbon and nitrogen isotope ratios in marine foodwebs, in turn caused by changes in isotopic signatures of primary production, may confound interpretation of diets using isotope measurements, and $\delta^{15}\text{N}$ in the central Bering Sea foodweb may be enriched compared to neighboring regions. The mean $\delta^{15}\text{N}$ for combined annuli of Steller sea lion teeth from the Bering Sea was among the most enriched in our sample, but this may not necessarily correspond to higher trophic-level feeding among these animals. Future isotopic studies examining the possibility of dietary shifts in Steller sea lions and other marine mammals through time, particularly in response to changes in food supplies (see Hobson *et al.* 1996), will need to examine a time series of animals from several discrete locations. Our study further suggests that such studies should take into account the often considerable variation in isotope signatures among annuli and possibly standardize all measurements to a single annulus, corresponding in turn to a particular age. This approach will avoid influences of variable weaning dates and better associate migratory animals to a given geographic location.

ACKNOWLEDGMENTS

We thank all those individuals who assisted with the collection, storage, and ageing of tooth samples used in this study. Garth Parry of the Stable Isotope Laboratory, Department of Soil Science, University of Saskatchewan, provided important assistance with the isotopic analysis of samples. E. Ranta kindly allowed us the use of his dental drill and workspace, and additional laboratory facilities were provided by the Prairie and Northern Wildlife Research Center in Saskatoon. This research was funded by the Alaska Fisheries Science Center of the National Marine Fisheries Service. We thank L. Atwell for help with figures and H. Braham, T. Loughlin, R. L. Merrick, and two anonymous reviewers for helpful comments on an earlier draft of this paper.

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Received: 3 December 1996

Accepted: 5 February 1997