Oecologia (2001) 129:461–472
DOI 10.1007/s004420100745

Mark T. Clementz · Paul L. Koch

Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel

Received: 2 November 2000 / Accepted: 10 May 2001 / Published online: 21 July 2001

Abstract We analyzed the carbon and oxygen isotope composition of tooth enamel from mammals inhabiting marine and terrestrial ecosystems to determine whether these stable isotopes were robust indicators of foraging and habitat preferences. Consumers were separated into six habitats (offshore, nearshore, kelp beds, estuarine, freshwater, terrestrial). Consumer $\delta^{13}C$ values were correlated with the $\delta^{13}C$ values of primary producers within each habitat, suggesting that $\delta^{13}C$ values of tooth enamel are a viable proxy for foraging zones. Offshore and terrestrial consumer $\delta^{13}C$ values were not significantly different, however, indicating that carbon isotope analysis alone is not sufficient to distinguish foraging within these two ecosystems. We propose that oxygen isotopes can be used along with $\delta^{13}C$ values to further clarify habitat use. Oxygen isotopes were assessed as an indicator of habitat use. Consumers were grouped into four categories: aquatic-marine, aquatic-estuarine, aquatic-freshwater, and terrestrial. Populations of aquatic taxa had significantly lower standard deviations for $\delta^{18}O$ values than those of terrestrial taxa. Mean $\delta^{18}O$ values of aquatic taxa were significantly different among groups, but surprisingly, the mean values for freshwater taxa were higher than those for marine taxa. We conclude that variation in $\delta^{18}O$ values of mammalian populations is a valid indicator of aquatic habits, but that mean $\delta^{18}O$ values should be utilized with caution when trying to discriminate between marine and freshwater habitat use. Together, $\delta^{13}C$ and $\delta^{18}O$ values serve as valuable tools for identifying foraging and habitat preferences in modern marine and terrestrial ecosystems, and may provide similar information on ancient ecosystems.

Keywords Isotopes · Enamel · Mammal · Diet · Habitat

M.T. Clementz (✉) · P.L. Koch
Department of Earth Sciences, University of California,
Santa Cruz, CA 95064, USA
e-mail: clementz@es.ucsc.edu
Tel.: +1-831-4595088

Introduction

Modern coastal systems are productive habitats that support a variety of aquatic and terrestrial organisms, serving as an important point of contact between marine and terrestrial ecosystems. Disentangling interactions among organisms and quantifying use of different ecological zones can be difficult when relying solely on field observations. To address this problem, ecologists have turned to analysis of stable isotope ratios, which serve as natural labels of the food webs in which animals feed and provide valuable monitors of the foraging and habitat preferences of extant mammals (Kelly 2000).

Stable isotope analysis is even more vital when considering problems in historical ecology. To evaluate the impact of human activities on contemporary ecosystems, baseline knowledge of the ecological dynamics of these systems prior to human influence is essential. For example, human hunting exterminated at least one large coastal zone mammal, the Steller's sea cow (*Hydrodamalis gigas*), and it has been implicated in changes in the breeding, foraging, and abundance of pinnipeds, cetaceans, and otters (Hoelzel et al. 1993; Anderson 1995; Estes et al. 1998). Assessing the dynamics of ecosystems prior to human activities requires methods like stable isotope analysis to gather ecological information from the fossil and sub-fossil remains of ancient populations.

Stable isotope analysis can also offer insight into the ecology of extinct animals that lived millions of years ago. For example, the coastal zone is the probable evolutionary spawning grounds for cetaceans, pinnipeds, and sirenians (Berta and Sumich 2000). Studies of secondary adaptation to aquatic life typically focus on functional and structural changes associated with locomotion, while studies of feeding ecology and habitat use in transitional forms have typically relied upon morphological features or inferences from depositional setting (Berta and Sumich 2000). Chemical evaluation of early marine mammal ecology (e.g., Thewissen et al. 1996) could reveal the selective forces acting in these transitions, as well as the relationship between evolutionary shifts in behavior and morphology.

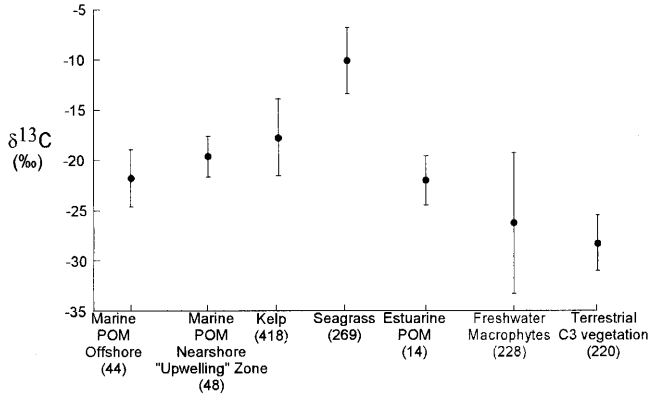

Fig. 1 Mean $\delta^{13}C$ values ($\pm 1\ \sigma$) for primary producers along a transect from offshore marine ecosystems to terrestrial C3 ecosystems. For three ecosystems, primary producer values were approximated with data for POM. Data sources: Fry and Sherr (1984), Simenstad and Wissmar (1985), Hemminga and Mateo (1996), Benner et al. (1997), Cerling and Harris (1999), and Rau et al. (in press). Sample size for each taxon is given in parentheses

The literature on isotopes as monitors of diet and habitat for either marine or terrestrial animals is substantial, but there is less work that synthesizes data from both settings (Kelly 2000). Little of this work has been conducted on materials likely to be preserved in museum collections or the fossil record (i.e., bone or tooth mineral and protein). Here, we evaluate whether the foraging zones of marine and terrestrial mammals can be distinguished via carbon isotope analysis of tooth enamel. We then describe a new method for discerning mammalian habitats (i.e. marine, freshwater, or terrestrial) using oxygen isotope analysis of enamel. We examine these points by analyzing a suite of marine, fresh water, and terrestrial mammals from coastal ecosystems restricted geographically to the northeastern Pacific.

Carbon isotopes and foraging zones

Carbon isotope values ($\delta^{13}C$) of tissues reflect an animal's diet, with a slight offset due to biological fractionation of isotopes that is dependent upon both tissue type (e.g., bone collagen, muscle, enamel) and diet (Sullivan and Krueger 1981). Also, when comparing whole body or tissue-specific $\delta^{13}C$ values, there is an ~1‰ enrichment in ^{13}C with each trophic step. Thus, dietary studies should consistently sample one tissue type, and interpretations must include assessment of trophic level effects.

Carbon isotope differences among animals largely reflect differences in the $\delta^{13}C$ of primary (1°) producers at the base of the food web. Trends in the $\delta^{13}C$ of 1° producers (or POM, which is likely derived mostly from 1° producers) are shown in Fig. 1. Ecosystem level differences are apparent, reflecting differences in environmental conditions and physiology among 1° producers in each ecosystem.

In marine ecosystems, 1° producers show strong spatial and temporal gradients in $\delta^{13}C$ (Fry and Wainright 1991; Rau et al. 1992; Hemminga and Mateo 1996), with values typically increasing from offshore to nearshore ecosystems, peaking in macrophytic ecosystems (i.e., kelp and seagrass beds). Differences in productivity, dissolved CO_2 concentration, and bicarbonate utilization have been suggested as possible causes for these differences. In estuarine and freshwater ecosystems, mean $\delta^{13}C$ values are typically lower than for marine 1° producers, but variations in the mixing of atmospheric and respired CO_2 under different flow conditions results in more variable primary producer $\delta^{13}C$ values (Osmond et al. 1981; Fry and Sherr 1984; MacLeod and Barton 1998). For terrestrial 1° producers, photosynthetic pathway (i.e., C3, C4, CAM) is the most critical factor for determining the $\delta^{13}C$ value of vegetation (Farquhar et al 1989). For our study area along the Pacific coast, C3 plants are the dominant 1° producers (Collatz et al. 1998).

Use of these gradients to study vertebrate foraging has mainly targeted terrestrial mammals from the coast, attempting to quantify the contribution of marine resources to diet (Kelly 2000). More synoptic analyses might find that isotopic segregation was lacking. For example, offshore-foragers might resemble land animals from C3 ecosystems, whereas $\delta^{13}C$ values from animals in marine macrophyte systems may overlap those for land animals in C4 ecosystems. This situation may not pose a problem in modern studies, where field observations can aid interpretation, but for historical studies, other methods are required to distinguish between marine and terrestrial habitat use before correct interpretations of foraging zone can be derived from $\delta^{13}C$ data.

Oxygen isotopes and habitat use

Bocherens et al. (1996) and Thewissen et al. (1996) have argued that oxygen isotope analysis of the mineral apatite in bones and teeth can reveal whether an animal frequents an aquatic or a terrestrial habitat. The oxygen isotope composition ($\delta^{18}O$) of biogenic apatite is strongly correlated with that of body water, offset by a temperature-dependent fractionation that is constant in homeothermic mammals (Longinelli 1984; Luz et al. 1984; Huertas et al. 1995). Aquatic and terrestrial mammal body water $\delta^{18}O$ values should differ because of physiological differences, and differences in the $\delta^{18}O$ of ambient water between aquatic and terrestrial habitats.

Physiology influences the $\delta^{18}O$ of body water by altering the magnitude of fluxes of oxygen into and out of the body, as well as fractionations associated with transport and/or transformation of oxygen-bearing compounds (reviewed by Luz and Kolodny 1985; Bryant and Froelich 1995). Major oxygen fluxes into terrestrial mammals include ingested water (>50%), which is not fractionated during uptake, and inhalation of atmospheric O_2 (~25%) and water vapor (~15%), which undergo isotopic fractionation during diffusion across the lung lining. Metabolic water, or water formed from food dur-

ing digestion, is generally a minor flux (<10%) when external sources of water are readily available, but can be a significant flux for species, such as marine mammals, where freshwater resources are limited (Costa 1982; Condit 1984; Fadely 1989). Fluxes of oxygen out of the body include respired CO_2 (~25%), water and organic matter in feces and urine (~40%), and water lost during sweating and panting (~35%). Respired CO_2 and water lost by panting or transcutaneous evaporation are fractionated relative to body water. In aquatic mammals, in contrast, ~98% of the oxygen flux into and out of the animal may come from diffusion of water across the skin (Hui 1981; Andersen and Nielsen 1983).

External sources of oxygen (e.g., atmospheric O_2, surface water, plant water) provide the baseline from which mammal body water $\delta^{18}O$ deviates. Regional and temporal variations in these sources range from exceptionally high for meteoric water, atmospheric water vapor, surface water, and plant water (Flanagan et al. 1991; Rozanski et al. 1993; Gat 1996) to relatively low for atmospheric O_2 and sea water (Craig and Gordon 1965; Kroopnik and Craig 1972). Source differences can contribute to body water and tooth enamel $\delta^{18}O$ variability at the individual, population and species levels.

We predict that terrestrial and aquatic mammals should exhibit strong differences in the magnitude of $\delta^{18}O$ variability within populations. For terrestrial mammals, because both the $\delta^{18}O$ of oxygen sources and the physiological response of animals may be highly variable in space and time, we expect body water and tooth enamel $\delta^{18}O$ values to differ substantially among individuals in a population. For aquatic mammals, we expect variability due to differences in oxygen sources and physiological processes to be greatly reduced, and that the $\delta^{18}O$ of body water should closely reflect that of the water in which the animal lives. For animals that inhabit water with a relatively constant isotopic composition, such as the ocean or large lakes and rivers, we expect low $\delta^{18}O$ variability among individuals in a population for both body water and tooth enamel.

Materials and methods

Stable isotope analyses were conducted on carbonate in tooth enamel apatite. We chose this substrate for two reasons. First, the $\delta^{13}C$ of carbonate in apatite is correlated with that of bulk diet (Ambrose and Norr 1993; Tieszen and Fagre 1993). Second, we intend to apply our results to studies of extinct animals, and tooth enamel is more resistant to post-mortem alteration than other potential substrates (Wang and Cerling 1994; Koch et al. 1997). Because harbor porpoise teeth have a thin enamel coating, we had to analyze both enamel and dentin for this species. As the mineral phase in dentin and enamel is the same, and both materials grow by accretion, we expect similar mean values and levels of variability.

Table 1 $\delta^{13}C$ and $\delta^{18}O$ for enamel carbonate from mammals sampled along the eastern Pacific coast. (*OS* offshore, *NS* nearshore, *KB* kelp bed, *E* estuary, *FW* freshwater, *T* terrestrial)

Order	Species	Locality	*n*	Feeding zone	% Aquatic[a]	$\delta^{13}C$ Mean± SD (range)	$\delta^{18}O$ Mean± SD (range)
Pinnipedia	*Mirounga angustirostris* Northern elephant seal (female)	Central California	10	OS	>50%	–14.1±1.7 (–17.7to –11.5)	26.6±0.4 (25.7 to 27.2)
	Callorhinus ursinus Northern fur seal	Southern California	3	OS	>50%	–12.9±0.9 (–13.6 to –11.9)	25.8±0.5 (25.3 to 26.2)
	Zalophus californianus California sea lion	Southern California	6	NS	>50%	–11.3±1.0 (–12.8 to –10.1)	26.1±0.3 (25.7 to 26.5)
	Phoca vitulina Harbor seal	Central California	11	NS	>50%	–9.2±1.6 (–12.0 to –7.1)	26.5±0.3 (25.9 to 26.9)
Cetacea	*Globicephala macrorhynchus* Pilot whale	Southern California	7	NS	100%	–9.7±1.2 (–11.0 to –8.3)	28.1±0.2 (27.8 to 28.6)
	Phocoena phocoena Harbor porpoise	Central California	11[b]	NS	100%	–9.9±0.4 (–10.4 to –9.3)	28.5±0.2 (27.9 to 28.9)
	Tursiops truncatus Bottlenose dolphin	Southern California	9	NS	100%	–10.1±0.6 (–10.7 to –9.0)	27.8±0.2 (27.5 to 27.9)
Carnivora	*Enhydra lutris* Sea otter	Central California	5	KB	>50%	–6.1±0.9 (–7.1 to –5.2)	27.3±0.6 (26.4 to 27.8)
	Lutra canadiensis River otters	Washington	10	E	~33%	–8.1±3.0 (–15.9 to –6.0)	25.8±0.9 (24.2 to 27.2)
	Lutra canadiensis River otters	Oregon	7	FW	~33%	–17.3±4.3 (–21.5 to –11.5)	23.0±0.3 (22.8 to 23.4)
	Canis latrans Coyote	Central California	5	T	<5%	–10.4±3.4 (–14.5 to –6.0)	27.4±3.4 (26.3 to 32.6)
	Lynx rufus Bobcat	Central California	4	T	<5%	–13.5±1.1 (–14.5 to –12.1)	29.1±1.2 (27.7 to 30.8)
Artiodactyla	*Odocoileus hemonius* Black-tailed deer	Central California	47	T	<5%	–11.8±1.7 (–17.2 to –9.0)	29.8±1.3 (26.5 to 32.7)

[a] Estimate of the percentage of time per day that each taxa spends in the water
[b] Sampled dentin for analyses

Samples were obtained from the California Academy of Sciences, Long Marine Laboratory, Moss Landing Marine Laboratory, the University of California Santa Cruz Archaeological Collections, the U.S. Geological Survey, the Los Angeles County Natural History Museum, and the California Department of Fish and Game. Locality information and the number of individuals analyzed are reported in Table 1. For terrestrial mammals, specimens were restricted to populations found within 50 km of the coast, principally along central California (Fig. 2). Marine mammals were limited to specimens from central and southern California. River otters were obtained from Washington and Oregon. Specimen numbers, locality information, date of collection, and isotopic values for all individuals are available online at the UCSC paleobiology laboratory website (http://www.es.ucsc.edu/personnel/Koch/).

Fig. 2 Map of the Pacific coast of the United States. *Black dots* mark locations and surrounding areas from which modern samples were obtained. Terrestrial and marine taxa were obtained from locations within California, whereas river otters were collected from Washington and Oregon

For reasons described below, we set our minimum population sample size at 5 individuals, but attempted to collect 10 individuals if possible. For two taxa (bobcats and northern fur seals), we were unable to obtain this minimum sample size. We analyzed third molars and canines for terrestrial mammals and all otters because they record post-weaning body composition (Moore et al. 1995; Rue III 1997; Pilipili et al. 1998). For pinnipeds and cetaceans, enamel on most permanent teeth begins to form prior to birth, and teeth erupt shortly after weaning (Perrin and Myrick 1980; Modig et al. 1997; Stewart et al. 1998). Thus, enamel records the isotopic composition of the mother's diet and body water, plus any fractionations associated with diffusion across the placenta, nursing, and rapid growth of the young animal. We sampled canines in pinnipeds and proximal teeth in cetaceans to maintain sample consistency.

Determination of sample size

To explore the effects of sample size on estimates of population mean and standard deviation, we sampled 42 black-tailed deer from a population in Monterey, Calif. As noted above, environmental $\delta^{13}C$ and $\delta^{18}O$ values are probably more variable in terrestrial systems than in marine or freshwater systems. Therefore, determination of the minimum number of samples needed to provide robust estimates of mean and standard deviation for terrestrial mammals should offer a conservative indication of the minimum sample size needed from marine and freshwater taxa.

We calculated the mean and standard deviation for 1,000 randomly generated sub-samples from this data set, ranging in size from n=3 to n=41, and calculated mean values and standard errors on the mean for these parameters at each sample size for both $\delta^{13}C$ and $\delta^{18}O$ (Fig. 3). For all estimates of mean and standard deviation, standard error on the estimate dropped significantly for sample sizes greater than 3. Standard error on the estimate of the mean $\delta^{13}C$ value of the population dropped to 0.01‰ at a sample size of 5, whereas the standard error on the estimate of the mean $\delta^{18}O$ value dropped to 0.01‰ at a sample size of 4 (Fig. 3a, c). Standard errors on estimates of the standard deviation for $\delta^{18}O$ and $\delta^{13}C$ dropped to 0.01‰ at n=5 (Fig. 3b, d). We set our minimum sample size at 5 individuals, but we collected more individuals when possible.

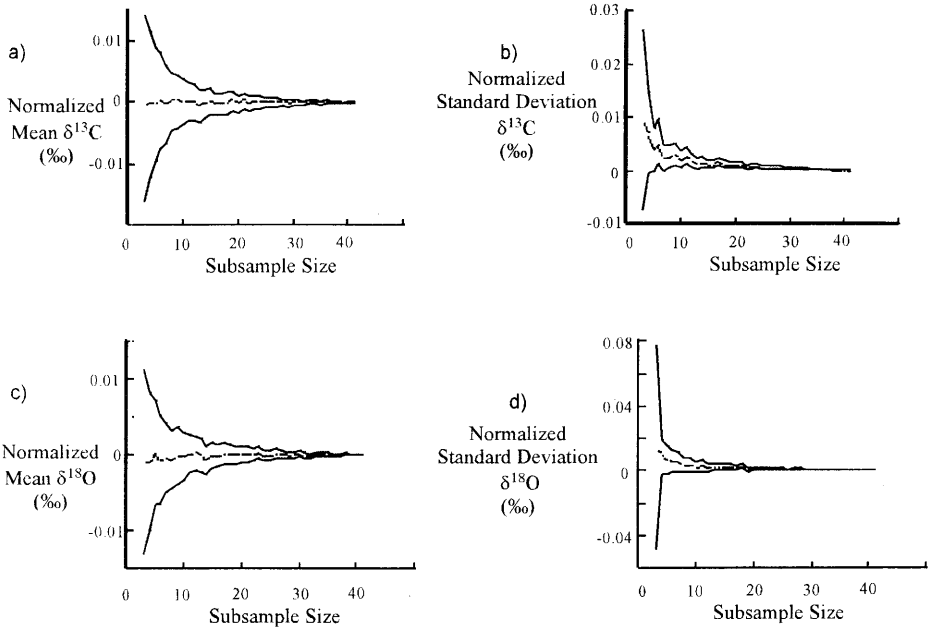

Fig. 3 Plots of the standard error for the estimated mean (**a**) and standard deviation (**b**) of $\delta^{13}C$ values, and the estimated mean (**c**) and standard deviation (**d**) of $\delta^{18}O$ values for 1,000 randomly selected subsamples of size n=3 to n=41 from a population of black tailed deer. *Dashed lines* represent the normalized mean for each sub-sample, and solid lines signify the standard error around the mean

We also performed statistical tests to assess the sample size needed to show that a difference in mean value of at least 1‰ was significant. A 1‰ difference was selected because that is the smallest difference in mean $\delta^{13}C$ and $\delta^{18}O$ values that is of interest to our study. We performed this test using representative $\delta^{13}C$ and $\delta^{18}O$ standard deviation values for aquatic (1σ=0.5) and terrestrial taxa (1σ>1.0). For all calculations, we assumed a level of significance (α) of 0.05 and a power level (1–β) of 0.2. Our tests revealed that comparisons of aquatic taxa would only require sample sizes of 4 individuals per group to demonstrate a significant difference in mean $\delta^{13}C$ and $\delta^{18}O$ values. For terrestrial taxa, required sample sizes are much larger, at least 16 individuals per group. Thus, our minimum sample size of 5 individuals is more than adequate for comparisons of $\delta^{13}C$ and $\delta^{18}O$ values among aquatic taxa, but insufficient for comparisons of small mean differences among terrestrial taxa. However, since our primary goal is to identify differences between aquatic and terrestrial taxa, our minimum sample size should be adequate.

Stable isotope analysis

Approximately 5–10 mg of powder were drilled from each tooth after the surface had been abraded to remove potential contaminants. Because of their small size, we ground entire harbor porpoise teeth using a mortar and pestle. Powders were soaked for 24 h in ~2% NaOCl to oxidize organic matter, rinsed 5 times with distilled water, soaked for 24 h in 1 M calcium acetate/acetic acid buffer to remove carbonate contaminants, rinsed 5 times with distilled water, and then freeze-dried (Koch et al. 1997).

Analyses involved ~1 mg of powder, using an ISOCARB carbonate preparation system linked to a Micromass Optima gas source mass spectrometer in the Departments of Earth and Ocean Sciences, University of California, Santa Cruz. Samples were dissolved in 100% phosphoric acid at 90°C with concurrent cryogenic trapping of CO_2 and H_2O. The CO_2 was then admitted to the mass spectrometer for analysis. We used Carrera Marble and NBS 19 as standards, and values are reported relative to V–PDB (for carbon) and V–SMOW (for oxygen). Precision, defined by repeated concurrent analysis (n=16) of a modern elephant enamel standard, was 1σ=±0.1‰ for $\delta^{13}C$ and 1σ=±0.3‰ for $\delta^{18}O$. Values are calculated using the formula $\delta^{13}C=[(^{13}C/^{12}C_{sample} \div {}^{13}C/^{12}C_{standard} -1\times1{,}000]$, where the standard is V–PDB. The same convention follows for $\delta^{18}O$, where the ratios are $^{18}O/^{16}O$ and the standard is SMOW. Units are reported in parts per thousand (‰).

Data analysis

Taxon-level differences within ecosystems were assessed using a one-factor analysis of variance (ANOVA), followed by a post-hoc pairwise comparison test (Bonferroni). Ecosystem differences amongst taxa were assessed using the same method. The relative significance of taxon or ecosystem level differences among our data was calculated using a Nested ANOVA. Comparisons of variance in $\delta^{18}O$ values among populations were conducted via a standard F-test. Statistical tests were calculated either manually or using the software program SYSTAT 9.0.

Unfortunately, two basic assumptions made when using an ANOVA were not met by some of the populations we sampled. The first assumption is that the populations are normally distributed; three of our sample populations were not normally distributed for either carbon or oxygen. A second assumption is homogeneous variance among populations. For comparisons of populations within ecosystems, variance was homogeneous. However, when taxa from different ecosystems were compared, variances were significantly different. Therefore, we conducted a non-parametric test, the Kruskal-Wallis one-way analysis of variance, to assess taxon-level and ecosystem-level differences. ANOVA results are reported in the Results section; Kruskal-Wallis results are reported only when they are in disagreement from ANOVA results.

Results

Comparisons among populations

Among marine mammals, pinniped mean $\delta^{13}C$ values (Table 1) differed significantly among taxa (one factor ANOVA, F=17.19, P<0.05). Pairwise comparisons found significant differences between harbor seals and elephant seals (Bonferroni test, P<0.05), harbor seals and northern fur seals (Bonferroni test, P<0.05), and California sea lions and northern elephant seals (Bonferroni test, P<0.05). Mean $\delta^{18}O$ values differed significantly among taxa (one-factor ANOVA, F=4.26, P<0.05; Kruskall-Wallis, P=0.061), but the only significant difference in pairwise comparisons was between northern elephant seals and northern fur seals (Bonferroni test, P<0.05).

Mean differences in $\delta^{13}C$ values among cetaceans were not significant (one factor ANOVA, F=1.631, P=0.217), but differences in mean $\delta^{18}O$ values were (one factor ANOVA, F=20.157, P<0.05). The harbor porpoise mean $\delta^{18}O$ value was significantly different from the mean $\delta^{18}O$ value for bottlenose dolphins. Cetaceans had the highest mean $\delta^{18}O$ values for marine mammals (averaging 28.1‰) and the lowest within-population $\delta^{18}O$ variability (mean 1σ=0.3‰).

Sea otters had mean $\delta^{13}C$ values higher than all other taxa, whether terrestrial, freshwater or marine (Table 1). The differences in mean isotopic values among pinnipeds, cetaceans, and sea otters were significant (one factor ANOVA, carbon: F=20.29, P<0.05; oxygen: F=117.73, P<0.05). Mean $\delta^{13}C$ values were statistically different for all pairwise comparisons, but only cetaceans and pinnipeds had significantly different mean $\delta^{18}O$ values (Bonferroni test, P<0.05). Within-population $\delta^{13}C$ variability for sea otters, at 0.9‰, was similar to that for cetaceans. Sea otters exhibited the highest within-population $\delta^{18}O$ variability among marine mammals (1σ= 0.6‰).

Differences in mean $\delta^{13}C$ values among terrestrial populations were not significant (one factor ANOVA, F=2.33, P=0.11). Within-population $\delta^{13}C$ variability was greater in black-tailed deer and coyotes than in bobcats. Black-tailed deer and bobcats had higher mean $\delta^{18}O$ values than any marine group, whereas coyotes had a mean value similar to sea otters. Differences in mean $\delta^{18}O$ values among terrestrial taxa were significant (one factor ANOVA, F=5.43, P<0.01). In pairwise comparisons, only black-tailed deer and coyotes were significantly different (Bonferroni test, P<0.01). All terrestrial mammal populations had 1σ values for $\delta^{18}O \geq 1.0$‰, averaging ~2.0‰ for the three populations.

We analyzed river otters from one freshwater (Willamette River, northwestern Oregon) and one estuarine population (Puget Sound, northwestern Washington). The mean $\delta^{13}C$ value for the Willamette River population (–17.7‰) was much lower than for any other group, whereas the estuarine population had a higher mean value (–8.1‰) than all other groups except sea ot-

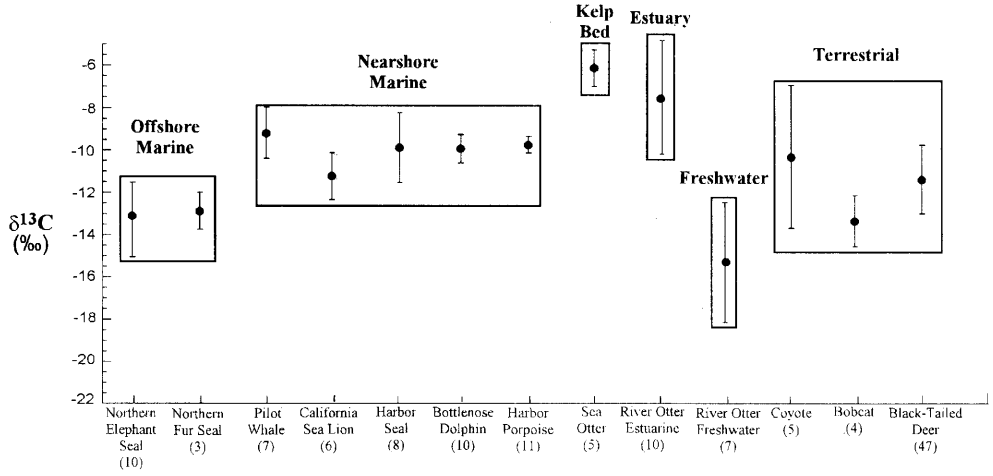

Fig. 4 Mean $\delta^{13}C$ values ($\pm 1\ \sigma$) of mammals from six foraging zones. Sample size for each taxon is given in parentheses

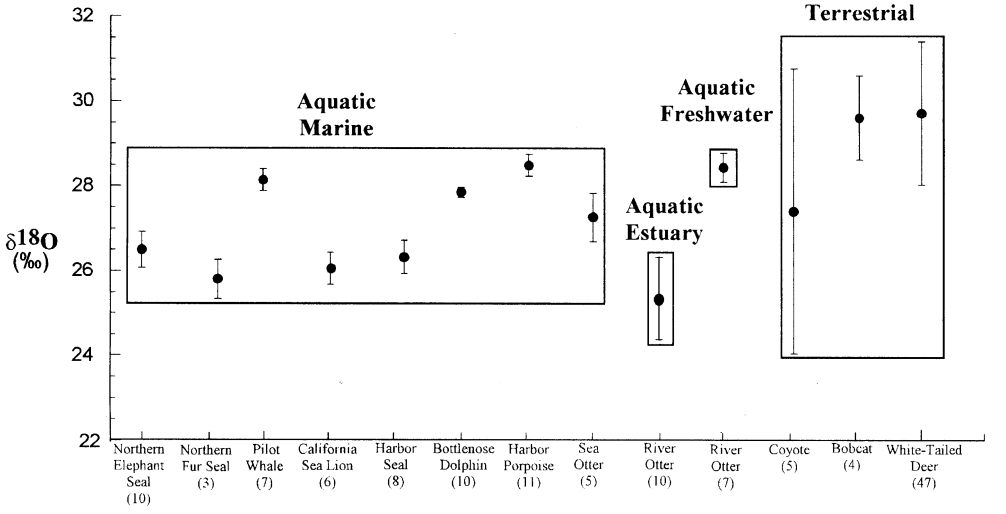

Fig. 5 Mean $\delta^{18}O$ values ($\pm 1\ \sigma$) for terrestrial and aquatic (marine, estuarine, and freshwater) mammals. *Boxes* are used to separate samples into specific habitats, and sample size for each taxon is given in parentheses

ters (Table 1). Within-population $\delta^{13}C$ variability for the Willamette River population was much higher than for any other population, and the 1σ value for the estuarine population was the third highest.

The mean $\delta^{18}O$ value for the Willamette River population was the lowest observed (23.0‰). This low mean may result, in part, from differences in the $\delta^{18}O$ of surface waters between California and Oregon. To evaluate this effect, we compared river $\delta^{18}O$ values between Oregon and central California using data from Coplen and Kendall (2000). The Willamette River has an average $\delta^{18}O$ value 5.9‰ lower than the mean value for three central California rivers (i.e., Pajaro, Salinas, and Napa rivers). If this 5.9‰ difference is used to normalize the Oregon otter $\delta^{18}O$ values to central California values, a mean of 28.9‰ is obtained, which is similar to the means for non-aquatic terrestrial mammals from California. Likewise, since the $\delta^{18}O$ value of estuarine water results from mixing of marine and freshwater sources, the lower mean $\delta^{18}O$ value for the estuarine population (25.8‰) may reflect differences in the $\delta^{18}O$ values of surface waters in California and Washington. However, the $\delta^{18}O$ value of the water in Puget Sound is likely to be highly variable, both spatially and temporally, so we will not attempt to correct for this in our study. Finally, the Willamette River population exhibited low within-population $\delta^{18}O$ variability (1σ=0.3‰), whereas the $1\ \sigma$ value for the estuarine population (0.9‰) was the highest for any aquatic group, whether marine or freshwater.

Comparisons among foraging zones and habitats

To test how well foraging zone is reflected in enamel $\delta^{13}C$ values, samples were grouped into six ecosystems/foraging zones (Fig. 4). Mean consumer $\delta^{13}C$ values correlated strongly with the $\delta^{13}C$ of 1° producers in their respective ecosystem (R=0.598, P<0.05). Also, $\delta^{13}C$ values differed significantly among ecosystems (Nested ANOVA, F=24.15, P=0.004), accounting for 63.5% of the variance, whereas species differences were not significant (Nested ANOVA, F=1.27, P=0.265). In marine systems, mean $\delta^{13}C$ values ($\pm 1\sigma$) were lowest for mammals from offshore ecosystems (–13.6±1.6‰), intermediate in nearshore ecosystems (–9.9±1.2‰), and highest in kelp ecosystems (–6.1±0.9‰). Onshore, mean

$\delta^{13}C$ values were highest in estuarine ecosystems (–8.2±2.8‰), intermediate in fully terrestrial ecosystems (–11.8±1.9‰) and lowest in freshwater ecosystems (–17.7±4.2‰). Pairwise comparison of the 6 ecosystems uncovered significant mean differences in all cases except estuaries versus kelp beds (Bonferroni test, P=0.709) and estuaries versus nearshore systems (Bonferroni test, P=0.200).

To investigate how well habitat use is reflected by $\delta^{18}O$ values, samples were grouped into four habitat types (Fig. 5). Mean values were highest for terrestrial mammals (29.6±1.7‰). Mean $\delta^{18}O$ values for aquatic mammals were highest in freshwater habitats (28.9±0.3‰), intermediate in marine (27.3±1.0‰), and lowest in estuarine habitats (25.9±0.9‰). Habitat and species differences were statistically significant (Nested ANOVA, Habitat: F=7.70, P=0.008; Species: F=7.20, P<0.001), accounting for 65.3% and 16.6% of the variance, respectively. Post-hoc tests using Bonferroni's method revealed that differences were significant (P<0.02) for all pairwise comparisons among habitats, except for fully terrestrial and freshwater habitats. F tests revealed that the high $\delta^{18}O$ variability for fully terrestrial mammals was significantly different when compared to the lower variability for marine (P<0.001), freshwater (P<0.001), or estuarine groups (P=0.003). Within aquatic groups, F tests showed statistically significant differences for $\delta^{18}O$ variability when the freshwater group was compared to estuarine (P=0.02) or marine groups (P=0.005).

Discussion

Reconstruction of preferred foraging zone

The $\delta^{13}C$ values of 1° producers are distinct among marine and terrestrial ecosystems, and mammals exhibit similar trends in $\delta^{13}C$ values. Still, interpretation of $\delta^{13}C$ differences among mammals may be complicated by (1) trophic level differences, (2) taxon-specific differences in metabolism, and (3) differences in the timing of formation and eruption of teeth. If the trends in $\delta^{13}C$ detected among mammals are controlled by ecosystem-level differences in the $\delta^{13}C$ value of 1° producers, then the isotopic offsets among consumers should be predictable.

To test this premise, we estimated the $\delta^{13}C$ of 1° producers at the base of the food web from the mean $\delta^{13}C$ value for each consumer, and compared our estimates with a compilation of measured primary producer $\delta^{13}C$ values (Table 2). The $\delta^{13}C$ value of 1° producers was estimated by first assessing the fractionation between diet and tooth enamel ($\Delta^{13}C_{diet\text{-}enamel}$) at the last trophic step. Unfortunately, the exact $\Delta^{13}C_{diet\text{-}enamel}$ have not been determined for most marine species, so we have assumed $\Delta^{13}C_{diet\text{-}enamel}$ was 14.0‰ for herbivores (Cerling and Harris 1999) and 9.0‰ for carnivores (Tieszen and Fagre 1993), based on controlled feeding experiments on terrestrial species. Next we determined the number of trophic levels separating each species from 1° producers at the base of the food web using the values presented in Pauly et al. (1998), which sets 1° producers at a trophic

Table 2 Estimated and measured $\delta^{13}C$ values of primary producers (mean±1σ) for each taxon and each habitat. For marine mammals, trophic level estimates were taken from Pauly et al. (1998), in which 1° producers are assigned a value of 1.0. Comparable estimates for estuarine, freshwater, and terrestrial mammals were based on dietary information obtained from Nowak and Paradiso (1983)

Feeding zone	Taxon	Trophic level	$\Delta^{13}C_{diet\text{-}enamel}$	Taxon-specific estimate of 1° producer $\delta^{13}C$ (Mean±1 σ)	Ecosystem estimate of 1° producer $\delta^{13}C$ (Mean±1 σ)	Measured 1° producer $\delta^{13}C$ (Mean±1 σ)
Offshore (marine)	N. Elephant seal (female)	4.3	9	–25.7±1.7**	–23.7±2.5**	–21.7±2.7
	N. fur seal	4.2	9	–24.4±0.9**		
Nearshore (marine)	California sea lion	3.4	9	–22.2±1.0**	–21.3±1.2**	–19.6±2.0
	Harbor seal	4.0	9	–20.6±1.6		
	Harbor porpoise	4.1	9	–21.4±0.4**		
	Bottlenose dolphin	4.2	9	–21.6±0.6**		
	Pilot whale	4.3	9	–21.6±0.6**		
Kelp Bed (marine)	Sea otter	3.4	9	–17.1±0.9	–17.1±0.9	–17.8±3.8
Estuarine	River otters	3.5	9	–19.1±3.0*	–19.1±3.0*	–22.1±2.1
Freshwater	River otters	3.5	9	–28.3±4.3	–28.3±4.3	–26.3±7.0
Terrestrial	Black-tailed deer	2.0	14	–26.6±1.7**	–26.2±2.2**	–28.2±2.6
	Coyote	3.0	9	–22.6±3.4[a]*		
	Bobcat	3.0	9	–25.5±1.2		

* Significant difference between estimated and measured $\delta^{13}C$ values of 1° producers (α=0.05)
** Significant difference between estimated and measured $\delta^{13}C$ values of 1° producers (α=0.01)
[a] Not included in calculation of ecosystem estimated 1° producer $\delta^{13}C$ values (see text)

level equal to 1. After subtracting 1 from this trophic level value to account for the step associated with diet-enamel fractionation, we multiplied the remainder by a whole organism trophic level fractionation of ~0.8‰ per level (Kendall et al. 2000). Both the diet-enamel fractionation and the trophic level fractionation from this calculation were then subtracted from the consumer value to yield an estimate of the $\delta^{13}C$ of 1° producers.

Estimated $\delta^{13}C$ values for 1° producers were roughly comparable to measured values for 1° producers in each habitat (Table 2), and were typically within 1 sigma of measured values. Mean measured and predicted values showed a significant correlation (R=0.596, P<0.05). This relationship was stronger than the relationship between mean consumer and measured 1° producer $\delta^{13}C$ values (R=0.598, P<0.05), suggesting that trophic effects were contributing to some but not all of the offsets we detected. Using our consumer data (excluding coyotes for reasons detailed below), we constructed an average $\delta^{13}C$ estimate for 1° producers in each ecosystem. *T*-tests of ecosystem $\delta^{13}C$ estimates versus measured values of 1° producers revealed significant differences for offshore (P=0.009), near shore (P<0.001), estuarine (P=0.020), and terrestrial systems (P<0.001). Comparisons of primary producer $\delta^{13}C$ values estimated from each taxon with measured primary producer $\delta^{13}C$ values were significant in all cases except for harbor seals, sea otters, freshwater river otters, and bobcats (Table 2).

The lack of detailed agreement between estimated and measured $\delta^{13}C$ values of 1° producers may have resulted from misdiagnosis of the trophic level, incorrect assumptions about $\Delta^{13}C_{diet\text{-}enamel}$ values, or incorrect assumptions about the magnitude of trophic level fractionation. However, a greater concern is our lack of 1° producer $\delta^{13}C$ values for all systems in the years when our study animals were alive. Temporal shifts in ecosystem $\delta^{13}C$ values may contribute to the mismatch. Finally, for several aquatic comparisons, POM $\delta^{13}C$ values were used as a proxy for 1° producers. Yet POM is a complex mixture of phytoplankton, bacteria, zooplankton and their decay products, so its use as a proxy may also complicate detailed isotopic comparisons.

We suspect that in several cases, however, the mismatch between estimated and measured 1° producer $\delta^{13}C$ values is an indication of an ecologically significant factor that was not considered in our simple calculations. For example, in nearshore systems, only harbor seals have values that are not significantly different from those expected. Harbor porpoises, bottlenose porpoises, and California sea lions have values that are lower than expected. Differences in foraging distance from the coast may explain these isotopic patterns. Mean $\delta^{13}C$ values of 1° producers drop sharply within a relatively short distance of the coast in Monterey Bay (~20 km) (Rau et al. in press). Among the nearshore foragers, only harbor seals are known to restrict their foraging to regions extremely close to shore. If California sea lions, bottlenose dolphins and harbor porpoises foraged further from the coast, for example near the mouth of Monterey Bay, they would encounter food webs fueled by 1° producers with values ~1–2‰ lower than nearshore phytoplankton (Rau et al. in press).

Differences in dive depth may also contribute to differences among offshore foragers. Female northern elephant seals had the lowest mean $\delta^{13}C$ value of any marine group, and they were 1‰ lower than the other offshore forager in our sample, the northern fur seal. Northern elephant seals routinely forage at depths >300 m, with maximum dive depths of >1,000 m (Le Boeuf et al. 1999), whereas fur seals generally forage at depths of 200 m or less (Gentry et al. 1986). Food webs at depths >100 m may be partially fueled by POM with significantly lower $\delta^{13}C$ values than surface phytoplankton (Benner et al. 1997). Thus, elephant seals feeding at great depths might have lower values than expected from surface primary producer values.

Finally, even northern fur seals have lower enamel $\delta^{13}C$ values than expected for an animal foraging in an offshore food web; northern elephant seals merely present a more extreme example of this tendency. Burton and Koch (1999) analyzed bone collagen $\delta^{13}C$ values in many of these pinniped specimens, and did not detect unusually low values in fur seals or elephant seals. The $\delta^{13}C$ of collagen in a carnivore reflects chiefly the $\delta^{13}C$ of dietary protein, whereas enamel $\delta^{13}C$ values correlate with the $\delta^{13}C$ of bulk diet (protein + lipid). Differing results between collagen and enamel $\delta^{13}C$ could result from differences in the amount of protein versus lipid in the diet. Lipids have lower $\delta^{13}C$ values than other body tissues (DeNiro and Epstein 1978; Ambrose and Norr 1993; Tieszen and Fagre 1993). Offshore-foraging northern fur seals and female northern elephant seals are known to consume a large percentage of lipid-rich prey (Condit 1984; Antonelis et al 1990). In addition, they may preferentially forage on lipid-rich fish during gestation to ensure adequate body fat stores for milk production during their brief period of lactation. Since pinniped enamel is deposited in utero or during nursing and reflects the $\delta^{13}C$ of the mother's diet, increased lipid influx would likely impact the $\delta^{13}C$ of enamel.

Freshwater river otters had $\delta^{13}C$ values in the range expected for animals feeding in a freshwater food web, but river otters feeding in estuaries did not meet expectations. In fact, otters from Puget Sound were not significantly different from mammals living in nearshore systems, suggesting greater reliance on fully marine resources. Otters living along the Pacific coast are known to consume nearshore prey (Bowyer et al. 1995; Kruuk 1995; Ben-David et al. 1997, 1998), so this interpretation is reasonable.

On land, terrestrial vegetation $\delta^{13}C$ estimates derived from black-tailed deer most likely failed to match expectations because central California herbivores do not sample the full range of $\delta^{13}C$ in C3 vegetation. Still, mean $\delta^{13}C$ values for this taxon are wholly consistent with an exclusively C3 diet. In contrast, the high $\delta^{13}C$ values in coyotes require a ^{13}C-enriched food source. Since C4 plants are rare in this region, coyotes may be getting C4

carbon from anthropogenic sources (e.g., human garbage or predation on house pets). Alternatively, coyotes may be obtaining ^{13}C-enriched diets by hunting (or scavenging) seals, sea lions, otters, or marine-foraging birds (Rose and Polis 1998).

As expected from 1° producer $\delta^{13}C$ values, offshore-foraging marine mammals (e.g., northern elephant seals, northern fur seals) had mean $\delta^{13}C$ values similar to some fully terrestrial mammals (e.g., black-tailed deer, bobcats). Likewise, coyotes had mean $\delta^{13}C$ values similar to some nearshore-foraging marine mammals, though this similarity may indicate that both groups obtain nutrients from nearshore food webs. Still, coyote and dolphin ecology obviously differ, yet carbon isotope analysis alone fails to reveal these differences. Perhaps the difference in within-population $\delta^{13}C$ variability could be used as an ecological monitor, but these values do overlap between marine and terrestrial populations. Clearly, an independent monitor of habitat would greatly facilitate dietary reconstruction in this situation.

Identification of aquatic preferences

Thewissen et al. (1996) and Roe et al. (1998) proposed that the mean $\delta^{18}O$ of cetacean tooth enamel is diagnostic of the type of aquatic system animals inhabit. Roe et al. (1998) analyzed the $\delta^{18}O$ of phosphate in tooth enamel and bone, which is ~8.8‰ depleted in ^{18}O relative to carbonate in apatite (Bryant et al. 1996). Since we analyzed the $\delta^{18}O$ of enamel carbonate, we have converted the Roe et al. (1998) mean $\delta^{18}O$ phosphate values to carbonate values for comparison. River dolphins (*Inia, Lipotes, Platanista*) had consistently lower, and more variable, $\delta^{18}O$ values (23.0±1.7, n=5) than marine cetaceans (*Tursiops, Stenella, Sotalia, Physeter, Orcinus, Delphinus*) (27.8±0.5, n=10). This result is expected, because fresh water is typically ^{18}O-depleted relative to seawater, though the magnitude of depletion varies geographically and temporally. Mean $\delta^{18}O$ values for the marine cetaceans analyzed here fall within the marine range reported by Roe et al. (1998), with a total spread of just 1.4‰ for the nine cetacean species analyzed in both studies. In addition, our more data intensive analysis demonstrates that marine cetaceans exhibit remarkably little $\delta^{18}O$ variability within a population, consistent with our expectation that aquatic mammals in isotopically homogeneous bodies of water should show low variability. Pinnipeds, sea otters, and river otters exhibited low $\delta^{18}O$ variability as well, demonstrating that our conjecture holds for all aquatic mammals. Likewise, though the $\delta^{18}O$ variability calculated for the estuarine otters (1 σ=0.9‰) is higher than that of other aquatic taxa, it is still lower than that reported for terrestrial mammals (1 σ>1.0‰), and can be explained as evidence of a mixture of freshwater and marine isotope signals in animals that are frequenting both ecosystems (Kruuk 1995).

While marine pinnipeds and cetaceans exhibited low within-population $\delta^{18}O$ variability, mean values for pinnipeds were ~2‰ lower than those for cetaceans. If body water is largely controlled by the $\delta^{18}O$ of environmental water, we would expect marine cetaceans and pinnipeds to have identical mean $\delta^{18}O$ values. Assuming that seawater has a mean $\delta^{18}O$ of 0.0‰, the expected $\delta^{18}O$ of enamel carbonate in marine mammals is 26.4‰, which is based on a model of mammalian oxygen fluxes developed by Kohn (1996). This is close to the mean for pinnipeds (26.4±0.4‰), but differs significantly from the values for cetaceans (28.2±0.4‰) and sea otters (27.3±0.6‰). Some important aspect of physiology or diet must differ consistently between cetaceans, sea otters, and pinnipeds to explain this isotopic difference.

One obvious difference is that pinnipeds spend a considerable amount of time out of the water, especially during the breeding season. Evaporative effects could cause differences in the $\delta^{18}O$ of body water, but they should result in pinnipeds having higher $\delta^{18}O$ values than cetaceans. We detected the opposite pattern. Roe et al. (1998) suggested that cetacean teeth may form at a lower temperature than the body core due to the influx of cool water during feeding. Cooler formation temperature in cetaceans would yield higher enamel $\delta^{18}O$ values. However, cetacean tooth enamel forms prior to birth, so formation temperature should be constant at the value of the mother's body core, rendering this explanation unlikely. Also, prior studies of cetacean bone phosphate have shown that it, too, is ^{18}O-enriched relative to values expected for equilibrium with sea water (Yoshida and Miyazaki 1991; Barrick et al. 1992). Bone turns over throughout life, so explanations that attribute the ^{18}O-enrichment in cetaceans to physiological or growth phenomena specific to pre-natal or neonatal life are likely flawed. At present, we can offer no compelling explanation for the consistent ^{18}O-enrichment in cetaceans. It is an interesting feature that requires further work.

As for our primary conjecture regarding aquatic/terrestrial differences in oxygen isotopes, variability was indeed much higher in terrestrial mammals than in aquatic mammals. The combined effects of isotopically variable oxygen sources and more varied physiological responses to environmental fluctuations resulted in higher $\delta^{18}O$ variability among terrestrial individuals. Many factors also serve to enrich the body water of terrestrial mammals in ^{18}O. As a result, even though terrestrial mammals drank water that was more ^{18}O-depleted than seawater, mean $\delta^{18}O$ values for these mammals were as high as, or higher than, mean values for marine mammals (e.g., the mean for coyotes was identical to that for sea otters). Surprisingly, the normalized data for Willamette river otters imply that freshwater mammals may have higher mean $\delta^{18}O$ values than marine mammals, as well as values statistically indistinguishable from terrestrial mammals. Our results suggest that mean $\delta^{18}O$ values alone do not provide a robust signal of terrestrial vs freshwater vs marine habitat use among mammals (contra the arguments of Thewissen et al. 1996 and Roe et al. 1998). This conclusion is strongly contingent upon the normalized river otter data, however, and further study

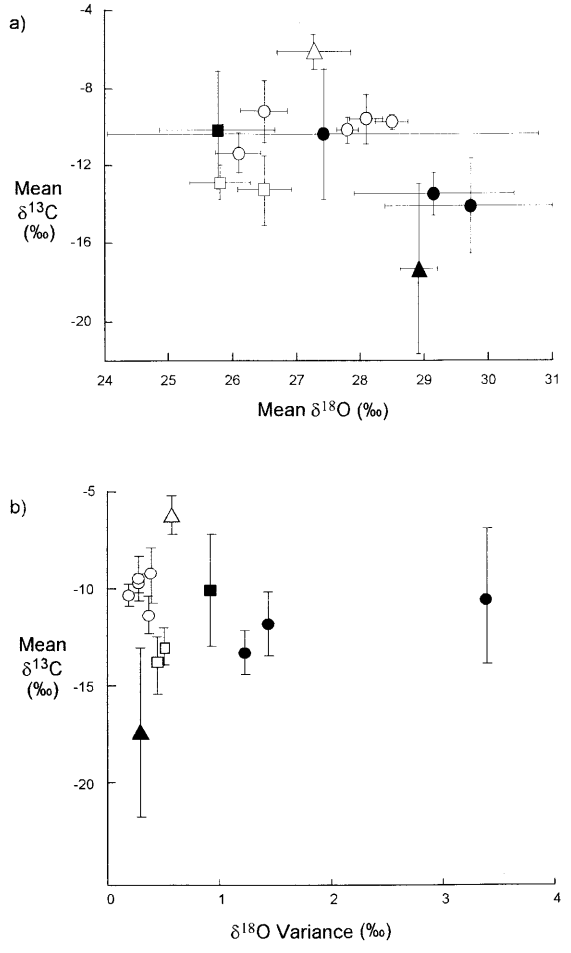

Fig. 6 Mean $\delta^{13}C$ value (±1 σ) of taxa plotted **a** versus corresponding mean $\delta^{18}O$ values (±1 σ) and **b** versus corresponding 1 σ for $\delta^{18}O$ values. Symbols used to represent the six different ecosystems are the same in both plots (offshore □, nearshore ○, kelp △, estuary ■, freshwater ▲, terrestrial ●). Note the clearer separation of ecosystems in **b** versus **a**

of terrestrial, marine, and freshwater aquatic species from the same region will be needed to establish the reliability of habitat assessments based on mean $\delta^{18}O$ values.

Overall, our analyses revealed that $\delta^{13}C$ and $\delta^{18}O$ values of mammalian enamel were statistically distinct amongst the ecosystems we studied. However, a comparison of mean $\delta^{13}C$ and $\delta^{18}O$ values does not yield clear separation among ecosystems (Fig. 6a), mainly because of the large variance within the terrestrial populations. Instead, comparison of mean $\delta^{13}C$ values with calculations of standard deviations of population $\delta^{18}O$ values generates distinct groupings among species (Fig. 6b). Terrestrial and aquatic species are identified based on differences in $\delta^{18}O$ variability, while foraging zone preferences among aquatic taxa are discriminated by the mean $\delta^{13}C$ values. Together, these parameters can be utilized to characterize foraging zone and habitat preferences of animals in areas where several distinct ecosystems come into contact, and have promise for providing ecological information for species when observational or even morphological information is lacking.

In conclusion, we have demonstrated that coupled carbon and oxygen isotope analysis of mammals provides useful information on animal ecology when other techniques may be costly, time-consuming, or not feasible. If the $\delta^{13}C$ values of 1° producers are well-constrained for an area, then the $\delta^{13}C$ of consumers can be used to infer the foraging zones of animals. In addition, we have shown that the variability in $\delta^{18}O$ values of mammal populations indicates the degree of utilization of aquatic habitats. Finally, we have confirmed that dietary and habitat information can be obtained from tooth enamel, an isotopic substrate that is rarely used in ecological studies of modern mammals, yet one that is readily available in museum collections. Finally, enamel has a high preservation potential, so the techniques outlined here can be applied to paleontological research, where information on habitat and foraging preferences will be crucial to evaluating ecological influences on lineages as they made the transition from life on land to life in an aquatic medium.

Acknowledgements We thank the following individuals and institutions for collection and access to specimens for analyses: Doug Long, California Academy of Sciences; John Heyning and David Janiger, Los Angeles Co. Natural History Museum; Dave Casper, Long Marine Lab.; Amanda Toperoff, Moss Landing Marine Lab.; Diane Gifford-Gonzalez and Richard Baldwin, Univ. of California, Santa Cruz Archaeological Collections, Charles Henny, the U.S. Geological Survey, and the California Dept. of Fish and Game. In addition, we thank Terrie Williams, Jim Estes, Don Croll, and Dan Costa for comments on earlier drafts of this paper, and Dave Fox for creation of the computer program used for calculating minimum sample size needed for analyses. M.T.C. was supported by a National Science Foundation Predoctoral Fellowship and Achievement Rewards for College Scientists Fellowship when much of this research was conducted. Analytical and travel costs were covered by NSF grants EAR 9725854 and 0087742, and a grant from the Dr. Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust Fund.

References

Ambrose SH, Norr L (1993) Experimental evidence for the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert JB, Grupe G (eds) Prehistoric human bone: archaeology at the molecular level. Springer, Berlin Heidelberg New York, pp 1–37

Andersen SH, Nielsen E (1983) Exchange of water between the harbor porpoise, *Phocoena phocoena*, and the environment. Experientia 39:52–53

Anderson PK (1995) Competition, predation, and the evolution and extinction of Steller's sea cow, *Hydrodamalis gigas*. Mar Mammal Sci 11:391–394

Antonelis GA, Stewart BS, Perryman WF (1990) Foraging characteristics of female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*). Can J Zool 68:150–158

Barrick RE, Fischer AG, Kolodny Y, Luz B, Bohaska D (1992) Cetacean bone oxygen isotopes as proxies for Miocene ocean composition and glaciation. Palaios 7:521–531

Ben-David M, Hanley TA, Klein DR, Schell DM (1997) Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. Can J Zool 75:803–811

Ben-David M, Bowyer RT, Duffy LK, Roby DD, Schell DM (1998) Social behavior and ecosystem processes: river otter latrines and nutrient dynamics of terrestrial vegetation. Ecology 79:2567–2571

Benner RB, Biddanda B, Black B, McCarthy M (1997) Abundance, size distribution, and stable carbon and nitrogen isotopic compositions of marine organic matter isolated by tangential-flow ultrafiltration. Mar Chem 57:243–263

Berta A, Sumich JL (1999) Marine mammals evolutionary biology. Academic Press, San Diego

Bocherens H, Koch PL, Mariotti A, Geraads D, Jaeger J (1996) Isotopic biogeochemistry ($\delta^{13}C$, $\delta^{18}O$) of mammalian enamel from African Pleistocene hominid sites. Palaios 11:306–318

Bowyer RT, Testa JW, Faro JB (1995) Habitat selection and home ranges on river otters in a marine environment : effects of the Exxon Valdez oil spill. J Mammal 76:1–11

Bryant JD, Froelich PN (1995) A model of oxygen isotope fractionation in body water of large mammals. Geochim Cosmochim Acta 59:4523–4537

Bryant JD, Koch PL, Froelich PN, Showers WJ, Genna BJ (1996) Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. Geochim Cosmochim Acta 60:5145–5148

Burton RK, Koch PL (1999) Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. Oecologia 119:578–585

Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120:347–363

Collatz GJ, Berry JA, Clark JS (1998) Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. Oecologia 114:441–454

Condit RS (1984) Feeding biology of the northern elephant seal. Phd thesis, University of California, Santa Cruz

Coplen TB, Kendall C (2000) Stable hydrogen and oxygen isotope ratios for selected sites of the U.S. Geological Survey's NASQAN and benchmark surface-water networks. Open-file report 00–160. U.S.G.S., Reston, Va.

Costa DP (1982) Energy, nitrogen, and electrolyte flux and sea water drinking in the sea otter *Enhydra lutris*. Physiol Zool 55:35–44

Craig H, Gordon LI (1965). Deuterium and oxygen-18 variations in ocean and the marine atmosphere. In: Tongiorgi E (ed) Proceedings of a conference on stable isotopes in oceanographic studies and paleotemperatures. University of Rhode Island, Rhode Island, pp 277–374

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science 282:473–476

Fadely BS (1989) Investigations on the water balance and assimilation efficiency of the northern fur seal. M.S. thesis, University of California, Santa Cruz

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. In: Briggs WR (ed) Annual review of plant physiology and plant molecular biology, vol 40. Annual Reviews, Palo Alto, pp 503–538

Flanagan LB, Bain JF, Ehleringer JR (1991) Stable oxygen and hydrogen isotope composition of leaf water in C3 and C4 plant species under field conditions. Oecologia 88:394–400

Fry B, Sherr EB (1984) $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib Mar Sci 27:13–47

Fry B, Wainright SC (1991) Diatom sources of carbon-13 rich carbon in marine food webs. Mar Ecol Prog Ser 76:149–157

Gat JR (1996) Oxygen and hydrogen isotopes in the hydrologic cycle. Annu Rev Earth Planet Sci 24:225–262

Gentry RL, Kooyman GL, Goebel ME (1986) Feeding and diving behavior of northern fur seals. In: Gentry RL, Kooyman GL (eds) Fur seals, maternal strategies on land and at sea. Princeton University Press, Princeton, N.J., pp 66–77

Hemminga MA, Mateo MA (1996) Stable carbon isotopes in seagrasses: variability in ratios and use in ecological studies. Mar Ecol Prog Ser 140:285–298

Hoelzel AR, Halley J, O'Brien SJ, Campagna C, Arnbom T, Le Boeuf B, Ralls K, Dover GA (1993) Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. J Hered 84:443–449

Huertas AD, Iacumin P, Stenni B, Chillon BS, Longinelli A (1995) Oxygen isotope variations of phosphate in mammalian bone and tooth enamel. Geochim Cosmochim Acta 59:4299–4305

Hui CA (1981) Seawater consumption and water flux in the common dolphin *Delphinus delphis*. Physiol Zool 54:430–440

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78:1–27

Kendall C, Silva SR, Chang CCY, Dias RF (2000) Spatial changes in redox conditions and food web relations at low and high nutrient sites in the Everglades. Applications of stable isotope techniques to ecological studies: book of abstracts. Federal Agricultural Research Centre, Braunschweig, Germany

Koch PL, Tuross N, Fogel ML (1997) The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. J Archaeol Sci 24:417–429

Kohn MJ (1996) Predicting animal $\delta^{18}O$; accounting for diet and physiological adaptation. Geochim Cosmochim Acta 60:4811–4829

Kroopnick P, Craig H (1972) Atmospheric oxygen; isotopic composition and solubility fractionation. Science 175:54–55

Kruuk H (1995) Wild otters: predation and populations. Oxford University Press, Oxford

Le Boeuf BJ, Crocker DE, Costa DP, Blackwell SB, Webb PM, Houser DS (2000) Foraging ecology of northern elephant seals. Ecol Monogr 70:353–382

Longinelli A (1984) Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochim Cosmochim Acta 48:385–390

Luz B, Kolodny Y (1985) Oxygen isotope variations in phosphate of biogenic apatites. IV. Mammal teeth and bones. Earth Planet Sci Lett 75:29–36

Luz B, Kolodny Y, Horowitz M (1984) Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochim Cosmochim Acta 48:1689–1693

MacLeod NA, Barton DR (1998) Effects of light intensity, water velocity, and species composition on carbon and nitrogen stable isotope ratios in periphyton. Can J Fish Aquat Sci 55:1919–1925

Modig A, Engstrom H, Arnbom T (1997) Postweaning behaviour in pups of the southern elephant seal (*Mirounga leonina*) on South Georgia. Can J Zool 75:582–588

Moore NP, Cahill JP, Kelly PF, Hayden TJ (1995) An assessment of five methods of age determination in an enclosed population of fallow deer (*Dama dama*). Biol Environ 95B:27–34

Nowak RM, Paradiso JL (1983) Walker's mammals of the world, 4th edn. John Hopkins University Press, Baltimore

Osmond CB, Valaane N, Haslam SM, Uotila P, Roksandic Z (1981) Comparisons of $\delta^{13}C$ values in leaves of aquatic macrophytes from different habitats in Britain and Finland; some implications for photosynthetic processes in aquatic plants. Oecologia 50:117–124

Pauly D, Trites AW, Capuli E, Christensen V (1998) Diet composition and trophic levels of marine mammals. ICES J Mar Sci 55:467–481

Perrin WF, Myrick AC Jr (eds) (1980) Age determination of toothed whales and sirenians. Reports of the international whaling commission (Special Issue 3). Cambridge University Press, Cambridge

Pilipili CM, Goret-Nicaise M, Dhem A (1998) Microradiographic aspects of the growing mandibular body during permanent premolar eruption in the dog. Eur J Oral Sci 106:429–436

Rau GH, Chavez FP, Friederich GE (in press). Plankton $^{13}C/^{12}C$ variations in Monterey Bay, CA: evidence of non-diffusive inorganic carbon uptake by phytoplankton in an upwelling environment. Deep-Sea Res

Rau GH, Takahashi T, Des Marais DJ, Repeta DJ, Martin JH (1992) The relationship between $\delta^{13}C$ of organic matter and $[CO_{2(aq)}]$ in ocean surface water: data from a JGOFS site in the northeast Atlantic Ocean and a model. Geochim Cosmochim Acta 56:1413–1419

Roe LJ, Thewissen JGM, Quade J, O'Neil JR, Bajpai S, Sahmi A, Hussain ST (1998) Isotopic approaches to understanding the terrestrial-to-marine transition of the earliest cetaceans. In: Thewissen JGM (ed) The emergence of whales. Plenum Press, New York, pp 399–422

Rose MD, Polis GA (1997) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79:998–1007

Rozanski K, Araguas-Araguas L, Gonfiantini R (1993) Isotopic patterns in modern global precipitation. In: Swart PK (eds) Climate change in continental isotopic records, monograph 78. American Geophysical Union, Washington, D.C.

Rue L III (1997) The deer of North America. Lyons and Buford, New York

Simenstad CA, Wissmar RC (1985) $\delta^{13}C$ evidence of the origins and fates of organic carbon in estuarine and nearshore food webs. Mar Ecol Prog Ser 22:141–152

Stewart BE, Innes S, Stewart REA (1998) Mandibular dental ontogeny of ringed seals (*Phoca hispida*). Mar Mammal Sci 14:221–231

Sullivan CH, Krueger HW (1981) Carbon isotope analysis of separate chemical phases in modern and fossil bone. Nature 292:333–335

Thewissen JGM, Roe LJ, O'Neil JR, Hussain ST, Sahni A, Bajpal S (1996) Evolution of cetacean osmoregulation. Nature 381:379–380

Tieszen LL, Fagre T (1993) Effect of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite, and soft tissues. In: Lambert JB, Grupe G (eds) Prehistoric human bone: archaeology at the molecular level. Springer, Berlin Heidelberg New York, pp 121–155

Wang Y, Cerling TE, Bryant JD (1994) A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. In: MacFadden BJ (ed) Stable isotope and trace element geochemistry of vertebrate fossils. Elsevier, Amsterdam

Yoshida N, Miyazaki N (1991) Oxygen isotope correlation of cetacean bone phosphate with environmental water. J Geophys Res 96:815–820