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# Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds

**Abstract** We investigated the impact of foraging location (nearshore vs offshore) and foraging latitude (high vs middle) on the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope compositions of bone collagen of northern fur seals (*Callorhinus ursinus*), harbor seals (*Phoca vitulina*), California sea lions (*Zalophus californianus*), and northern elephant seals (*Mirounga angustirostris*). Nearshore-foraging harbor seals from California had $\delta^{13}C$ values 2.0‰ higher than female northern elephant seals foraging offshore at similar latitudes. Likewise, nearshore-foraging harbor seals from Alaska had values 1.7‰ higher than male northern fur seals, which forage offshore at high latitudes. Middle-latitude pinnipeds foraging in either the nearshore or offshore were $^{13}C$ enriched by ~1.0‰ over similar populations from high latitudes. Male northern elephant seals migrate between middle and high latitudes, but they had $\delta^{13}C$ values similar to high-latitude, nearshore foragers. Female northern fur seal $\delta^{13}C$ values were intermediate between those of high- and middle-latitude offshore foragers, reflecting their migration between high- and middle-latitude waters. The $\delta^{13}C$ values of California sea lions were intermediate between nearshore- and offshore-foraging pinnipeds at middle latitudes, yet there was no observational support for the suggestion that they use offshore food webs. We suggest that their "intermediate" values reflect migration between highly productive and less-productive, nearshore ecosystems on the Pacific coasts of California and Mexico. The relative uniformity among all of these pinnipeds in $\delta^{15}N$ values, which are strongly sensitive to trophic level, reveals that the carbon isotope patterns result from differences in the $\delta^{13}C$ of organic carbon at the base of the food web, rather than differences in trophic structure, among these regions. Finally, the magnitude and direction of the observed nearshore-offshore and high-to middle-latitude differences in $\delta^{13}C$ values suggest that these gradients may chiefly reflect differences in rates and magnitudes of phytoplankton production as well as the $\delta^{13}C$ value of inorganic carbon available for photosynthesis, rather than the input of $^{13}C$-enriched macroalgal carbon to nearshore food webs.

## Introduction

The development and application of new technologies, including time-depth recorders and satellite geolocation, have substantially increased our knowledge of the habits of marine mammals at sea (Costa 1993; LeBoeuf et al. 1993; Gentry 1998). While these studies have revealed remarkable aspects of pinniped movements and diving capabilities, they do not directly address feeding habits. Analyses of prey remains from fecal samples, stomach lavage, or gastrointestinal dissection provide insights into the diets of marine mammals (Antonelis et al. 1987; Lowry et al. 1990; Sinclair et al. 1994), yet they may not reveal long-term diet, the use of patchily distributed, locally abundant food resources, or the relative importance of particular prey species to an animal's diet. The stable-isotope composition of animal tissues reflects the isotopic composition of their diet, and isotopic studies have revealed new details concerning the foraging ecology of marine vertebrates, such as trophic position, reliance on nearshore or offshore food sources, the relative importance of different prey species, and interspecific or intraspecific resource partitioning (Rau et al. 1983, 1992a; Dunton et al. 1989; Sholto-Douglas et al. 1991; Hobson and Welch 1992; Hobson 1993; Ostrom et al. 1993; Thomas and Cahoon 1993; Hobson et al. 1997). Pinnipeds are among the top consumers in marine

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systems worldwide, and they are important indicators of the "health" of marine ecosystems. Understanding the relationship between isotope composition and the foraging and behavioral ecology of modern pinnipeds will allow comparison of modern populations to those of the past and will be important for discerning if observed changes in modern pinniped populations (National Marine Fisheries Service 1994) are related to human influence on marine ecosystems or are a response to longer-term oceanographic or climatic changes.

A number of studies have suggested that variations in carbon isotope composition among marine animals may be explained, in part, by differences in the isotope composition of marine plants between nearshore and offshore ecosystems (Thomas and Cahoon 1993; Michener and Schell 1994; Hobson et al. 1997). Factors contributing to nearshore-offshore differences in the isotopic composition of organic carbon at the base of marine food webs include differences in (1) the isotopic composition and concentration of dissolved $CO_2$ (Rau et al. 1992b; Goericke and Fry 1994; Hinga et al. 1994), (2) the species composition and rate of growth of phytoplankton (Fry and Wainright 1991; Pancost et al. 1997), and (3) the input of carbon from benthic macrophytes, which are significantly enriched in $^{13}C$ relative to phytoplankton (Michener and Schell 1994; France 1995). In areas of coastal upwelling, these factors lead to the production of relatively $^{13}C$ enriched organic carbon at the base of the food web. In offshore regions, where nutrients are more limited, phytoplankton growth rates are lower, and macrophytes are absent, organic carbon at the base of the food web is more enriched in $^{12}C$. If nearshore-offshore carbon isotope gradients are generated chiefly by the effects of differential growth rates of phytoplankton, then differences of 2–3‰ would be expected. Isotopic gradients supported by high nearshore production of benthic macrophytes could be much larger, perhaps 5–6‰ (France 1995).

While current data supply some evidence for the influence of nearshore-offshore differences at the base of the food web on the carbon isotope composition of marine consumers, this interpretation is complicated by trophic-level effects and long-distance migration across latitudinal zones. Whole-body isotope compositions are $^{13}C$ enriched by ∼1.0‰ relative to diet with each trophic step (see review by Michener and Schell 1994). Different tissue types (e.g., lipid, collagen, hair, muscle) show different absolute fractionations relative to diet (DeNiro and Epstein 1978; Tieszen et al. 1983; Hobson et al. 1996), but enrichments of ∼1‰ are also observed when single tissue types are examined at different trophic levels (Rau et al. 1983). If food webs are longer nearshore than in the open ocean, then upper-level consumers should have higher carbon isotope values in the nearshore, even if the carbon isotope composition at the base of the food web is identical in nearshore and offshore ecosystems.

Particulate organic carbon in high-latitude surface water is $^{13}C$ depleted relative to that in surface water from lower latitudes (Rau et al. 1982; Goericke and Fry 1994), suggesting that high-latitude primary producers are $^{13}C$ depleted as well (Schell et al. 1998). Hobson et al. (1997) reported $^{13}C$-depleted values for pinnipeds from Alaska relative to those from Washington, and these latitudinal isotopic differences were as large as those that have been interpreted as indicating foraging position relative to shore in other studies. Some pinnipeds migrate over large distances across latitudinal zones; therefore, these latitudinal differences at the base of the food web must be considered when interpreting the isotopic results in terms of nearshore versus offshore foraging.

The most direct approach to dissecting the effects of foraging location (nearshore vs offshore), trophic level, and latitude on the isotopic composition of these pinnipeds would be to compare pinniped carbon isotope compositions to those from phytoplankton as well as key pinniped prey species. While the isotopic chemistry of high-latitude, nearshore food webs of the north Pacific has been characterized (Dunton and Schell 1987; Dunton et al. 1989; Goering et al. 1990; Schell et al. 1998), comparable data from the offshore regions and middle-latitude, nearshore regions are limited.

Consequently, our approach is to establish carbon isotope gradients among these marine ecosystems by analyzing the carbon isotope composition of migratory and non-migratory pinnipeds that are known to forage within either nearshore or offshore waters. We then evaluate the potential influence of trophic-level differences on these gradients using nitrogen isotopes. Field studies of invertebrate and vertebrate food webs suggest an average diet-to-animal $^{15}N$ enrichment of ∼3.0‰ per trophic step (Schoeninger and DeNiro 1984; Michener and Schell 1994). Because the trophic-level effect on nitrogen isotope compositions is so large, trophic-level differences among species that might contribute to carbon isotope gradients should be conspicuous.

The difference in carbon isotope composition between nearshore and offshore regions will be assessed in the middle latitudes through comparison of harbor seals (*Phoca vitulina*) to female northern elephant seals (*Mirounga angustirostris*) from California. In the northeastern Pacific, harbor seals are relatively sedentary, living along rocky coasts and calm brackish sloughs from Baja California to the Aleutian Islands (Fig. 1a). They typically undertake short, shallow dives and feed nearshore (Bigg 1981; Stewart et al. 1989; Boness et al. 1994). Northern elephant seals arrive at rookeries along the central coast of California in December, where they give birth in January and February to pups conceived at the rookery during the previous year (LeBoeuf et al. 1972; LeBoeuf 1974). Northern elephant seals then undertake a double migration, first after breeding, and then after their return to shore to molt (Stewart and DeLong 1995). Upon leaving the rookeries, adult females from central California migrate to feed in middle-latitude waters (30–50°N), ranging from several hundred to several thousand kilometers offshore (LeBoeuf et al. 1993) (Fig. 1b).

**Fig. 1a–d** Location and distribution of pinniped populations from which specimens were sampled. **a** Non-migratory harbor seals from Alaska and California. **b** Northern elephant seals, which migrate between breeding sites at Año Nuevo Island (*AN*) and middle-latitude offshore locations (*females*), and high-latitude nearshore locations (*males*). **c** Northern fur seals, which migrate between breeding sites on the Pribilof Islands (*PI*) and high-latitude offshore locations (*males*), and middle-latitude offshore locations (*females*). **d** California sea lions, which migrate between breeding sites off southern California and Baja California and northern waters along the coastal western United States
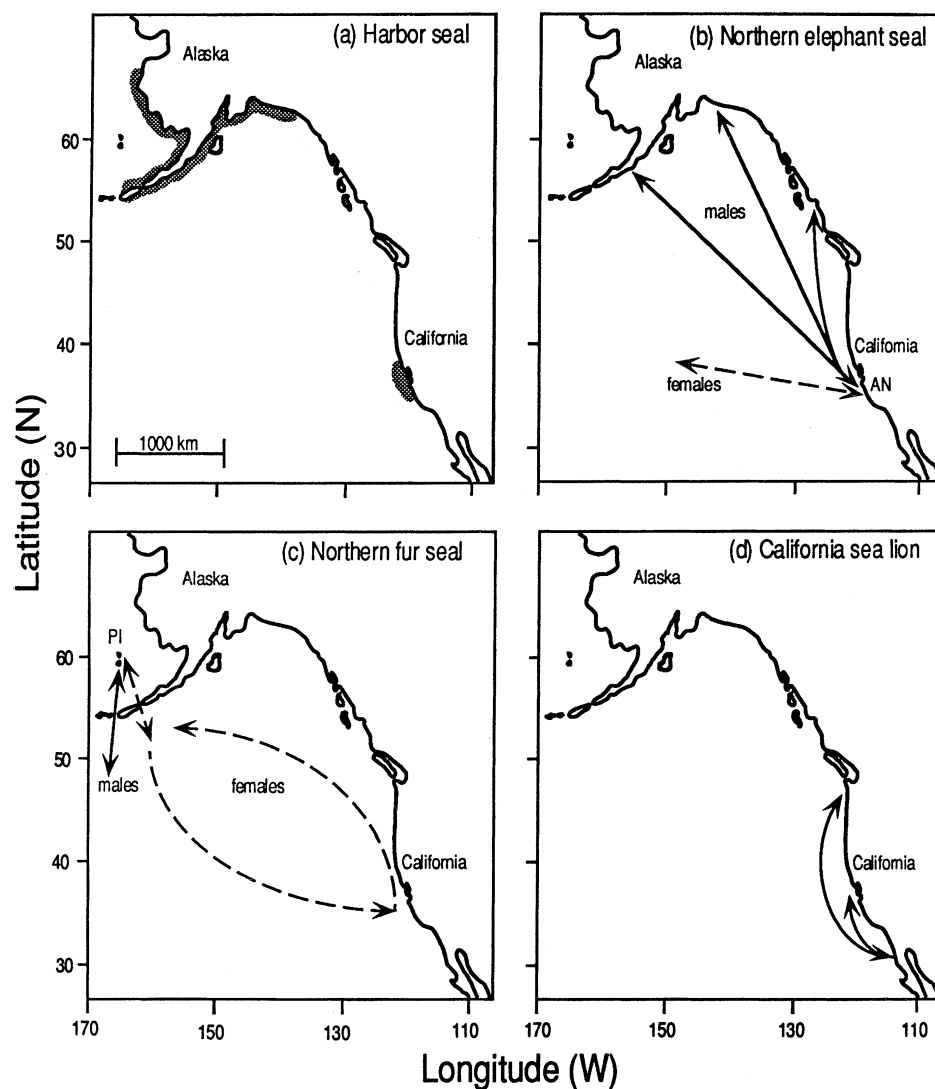


Harbor seals and adult male northern fur seals from Alaska provide a similar comparison between nearshore and offshore foraging at high northern latitudes. Northern fur seals (*Callorhinus ursinus*) breed only on the Pribilof Islands, Alaska, a few islands in the Bering and Okhotsk Seas, and, since 1965, on San Miguel Island, California (Peterson 1969; Gentry 1998). While on the Alaskan rookeries, fur seals typically forage in offshore waters west of the Pribilof Islands (Loughlin et al. 1987; Goebel et al. 1991). Following the breeding season, the adult males move offshore, yet remain in the northern portion of the species range (Gentry 1998; Fig. 1c).

Latitudinal differences in carbon isotopes will be assessed in the nearshore through comparison of harbor seals from California to those from Alaska, whereas the offshore comparison for latitudinal differences will be between female elephant seals and male northern fur seals. If the carbon isotope gradients we detect are due solely to trophic-level differences, then we would expect large changes in nitrogen isotope composition (up to 6 or 9‰) along these gradients as well.

Finally, we use the isotopic framework supplied by these groups that forage in relatively fixed regions to evaluate isotopic compositions among the groups that migrate across larger latitudinal distances. Adult male northern elephant seals, in contrast to the females, migrate from middle-latitude breeding grounds to feed in high-latitude nearshore waters along British Columbia, the Gulf of Alaska, and eastern Aleutian Islands (Stewart and DeLong 1995; LeBoeuf et al. in press; Fig. 1b). Adult female northern fur seals migrate in the opposite direction, from high-latitude breeding grounds to forage in middle-latitude offshore waters along the California coast as far south as the Mexican border (Kajimura 1980; Gentry 1998; Fig. 1c). California sea lions (*Zalophus californianus*) remain close to shore but they migrate from breeding sites on coastal islands, along southern California and Baja, into more northern waters. Males may occur as far north as Vancouver, while females generally remain closer to the breeding grounds (Odell 1981; Lowry et al. 1990; Fig. 1d).

## Materials and methods

We analyzed the carbon and nitrogen isotope compositions of 113 adult individuals (Table 1). All specimens were housed in museum collections in either California or Alaska. All of the individuals in the study died in this century, mostly in the last 30 years. Collection locations for pinnipeds sampled from Alaska were between 51° and 68°N, while those from California were between 36° and 38°N. Collection site, date collected, sex, and the isotopic compositions for all samples are available on the Spring-Verlag server (http://link.springer.de).

Stable-isotope analysis of marine vertebrates has typically been conducted on soft tissues (hair, muscle, fat), which limits the potential to compare modern and historical populations. Bone collagen also records the isotopic composition of diet, and provides a broader temporal average of dietary composition, due to the relatively slow turnover rate of collagen (Tieszen et al. 1983; Hobson and Clark 1992). Typical diet-to-collagen isotope fractionations for $\delta^{13}C$ and $\delta^{15}N$ are +5.0 and +3.0‰, respectively (see review by Koch et al. 1994).

A 200- to 300-mg fragment of the posterior portion of the ethmoid turbinals or cranium was sampled for isotopic analysis. Samples were cleaned of muscle and other surface tissues and demineralized by soaking for 48 h in 0.5 N HCl at 4°C. Lipids were extracted using a chloroform/methanol technique (Bligh and Dyer 1959). Samples were dried and placed in tin foil boats, then isotopic compositions were determined using a Carlo-Erba elemental analyzer interfaced with a Micromass Optima gas source mass spectrometer in the Department of Earth and Ocean Sciences, University of California, Santa Cruz. The standard deviation for repeated measurements of a gelatin standard was < 0.12‰ for both carbon and nitrogen. Results are expressed as:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[ (R_{sample}/R_{standard}) - 1 \right] \times 1000$$

where $R_{sample}$ and $R_{standard}$ are the ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for the sample and the standard, respectively. The standards are Pee Dee Belemnite limestone for carbon, and atmospheric $N_2$ for nitrogen, and the units are parts per thousand (‰).

## Results

Mean isotope values for males and females of each population are presented in Table 1. Mean $\delta^{13}C$ values for harbor seals did not differ between the sexes in either California or Alaska. Male California sea lions had a slightly higher mean value (~0.2‰) than females. Dif-

ferences between males and females were greater for northern elephant seals (0.8‰) and northern fur seals (0.6‰), but were not statistically significant ($t_{22} = 2.0$, $P = 0.056$ for elephant seals; $t_{17} = 1.6$, $P = 0.134$ for fur seals). Yet we know from previous observational studies that males and females of both species exhibit different foraging and migration patterns. Therefore we treat the sexes for northern elephant seals and northern fur seals as separate groups.

Differences in $\delta^{13}C$ values among offshore-foraging male northern fur seals and nearshore-foraging harbor seals from high latitudes, and offshore-foraging female northern elephant seals and nearshore-foraging harbor seals from middle latitudes were significant with regard to both foraging location (nearshore vs offshore) and latitude (high vs middle) (two-factor ANOVA, $P < 0.001$ for both factors). The $\delta^{13}C$ values for harbor seals from Alaska were, on average, 1.7‰ higher than those for male northern fur seals (Fig. 2a). Likewise the values for harbor seals from California were 2.0‰ higher than those for female elephant seals. With respect to latitudinal differences, the $\delta^{13}C$ values of harbor seals from California were about 1.3‰ higher than those for harbor seals from Alaska, while values for female northern elephant seals were about 1.0‰ higher than those for male northern fur seals (Fig. 2a).

Carbon isotope patterns among the animals that migrate long distances across latitudinal zones are intriguing (Fig. 2b). For example, offshore-foraging female northern fur seals had statistically unique $\delta^{13}C$ values intermediate between male northern fur seals and female northern elephant seals, the offshore foragers from high and middle latitudes, respectively (one-factor ANOVA, $P = 0.025$). In contrast, the $\delta^{13}C$ values of male northern elephant seals were not intermediate; they were indistinguishable from those of high-latitude, nearshore-foraging harbor seals. The $\delta^{13}C$ values of California sea lions varied statistically (one-factor ANOVA, $P < 0.001$) from nearshore-foraging California harbor seals and offshore-foraging female northern elephant seals, yet were closer to the values for female elephant

**Table 1** $\delta^{13}C$ and $\delta^{15}N$ of bone collagen from northeastern Pacific pinnipeds

| Group | n | Sex | Region collected | Foraging latitude | Foraging location | $\delta^{13}C$ (mean ± SD) (‰) | $\delta^{15}N$ (mean ± SD) (‰) |
|---|---|---|---|---|---|---|---|
| Groups that remain at middle latitudes | | | | | | | |
| Harbor seal | 5 | Female | California | Middle | Nearshore | −12.4 ± 0.9 | 18.3 ± 0.6 |
| Harbor seal | 13 | Male | California | Middle | Nearshore | −12.4 ± 0.6 | 18.9 ± 1.1 |
| Northern elephant seal | 14 | Female | California | Middle | Offshore | −14.4 ± 0.8 | 18.1 ± 1.3 |
| Groups that remain at high latitudes | | | | | | | |
| Harbor seal | 17 | Female | Alaska | High | Nearshore | −13.7 ± 1.0 | 16.7 ± 2.1 |
| Harbor seal | 20 | Male | Alaska | High | Nearshore | −13.7 ± 0.9 | 18.0 ± 1.2 |
| Northern fur seal | 9 | Male | Alaska | High | Offshore | −15.4 ± 0.9 | 17.4 ± 2.1 |
| Groups that migrate over broad latitudinal zones | | | | | | | |
| California sea lion | 4 | Female | California | Low ↔ middle | Nearshore | −13.9 ± 1.1 | 18.4 ± 0.9 |
| California sea lion | 11 | Male | California | Low ↔ middle | Nearshore | −13.7 ± 0.7 | 18.7 ± 1.0 |
| Northern elephant seal | 10 | Male | California | Middle ↔ high | Nearshore | −13.6 ± 1.1 | 18.2 ± 0.7 |
| Northern fur seal | 10 | Female | Alaska | High ↔ middle | Offshore | −14.8 ± 0.7 | 16.6 ± 1.4 |
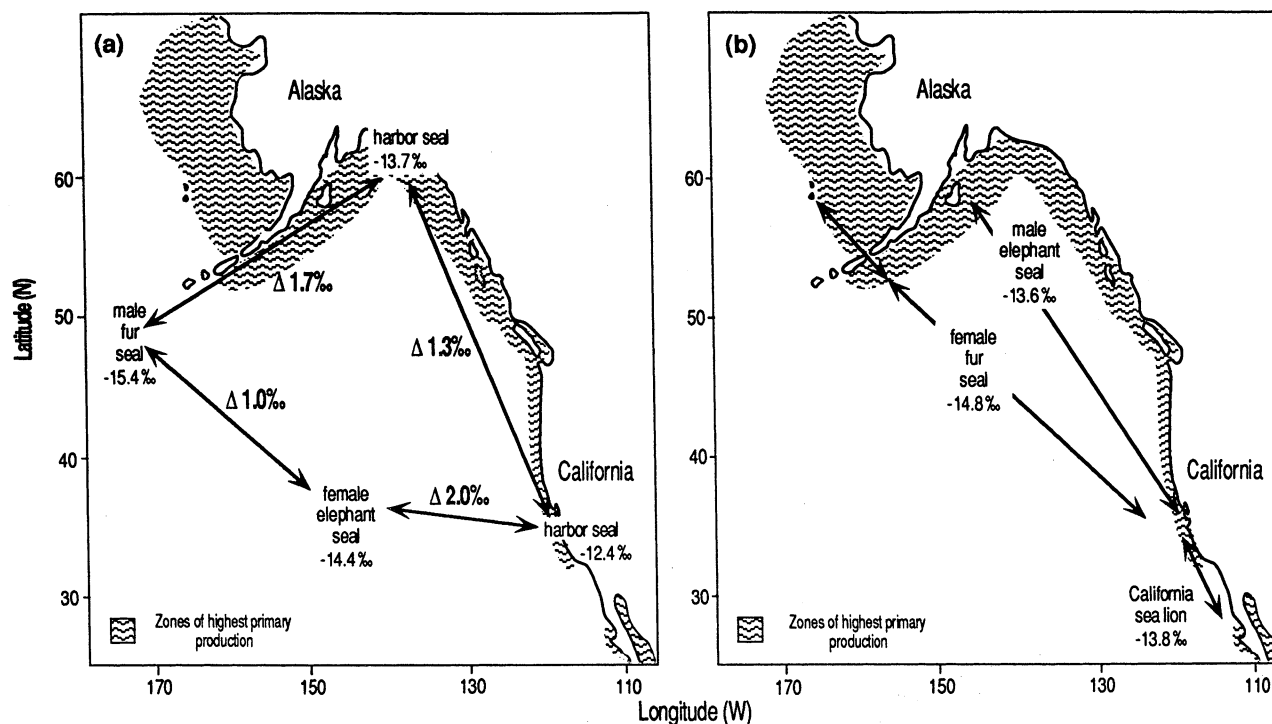
**Fig. 2 a** Variations in $\delta^{13}C$ values of pinnipeds foraging at high-latitude nearshore (harbor seal) or offshore (male northern fur seal) locations, and from middle-latitude nearshore (harbor seal) and offshore (female northern elephant seal) locations ($\Delta$ values are differences between mean $\delta^{13}C$ values). **b** Variations in $\delta^{13}C$ values of both nearshore- and offshore-foraging pinnipeds which migrate over broad latitudinal zones

northern elephant seals had values intermediate between middle- and high-latitude pinnipeds, whereas female northern fur seals had values similar to high-latitude pinnipeds (Table 1). California sea lions had high $\delta^{15}N$ values, like other middle-latitude pinnipeds.

seals. A possible explanation for the apparent discrepancy between the carbon isotope data for sea lions, which seem to imply a mixed nearshore-offshore foraging strategy, and the observational data, which suggest nearly exclusive nearshore foraging, is discussed below.

For all the pinniped species and populations examined here, males consistently had higher $\delta^{15}N$ values than females (Table 1). For California sea lions and northern elephant seals, these differences were small (0.3‰ and 0.1‰, respectively), and not statistically significant. Harbor seals from California and northern fur seals exhibited greater differences between the sexes (0.6‰ and 0.8‰, respectively), but again, were not statistically significant. On the other hand, the relatively large difference (1.3‰) between male and female harbor seals from Alaska was significant ($t_{35}$ = 2.3, $P$ = 0.027).

Differences in $\delta^{15}N$ values among offshore-foraging male northern fur seals and nearshore-foraging harbor seals from high latitudes, and offshore-foraging female northern elephant seals and nearshore-foraging harbor seals from middle latitudes were significant for latitude (two-factor ANOVA, $P$ = 0.019), but not for foraging location ($P$ = 0.512). Among those groups, which do not migrate across great latitudinal distances, the pinnipeds from middle latitudes had higher $\delta^{15}N$ values than those from off Alaska (Table 1). Among the groups that do migrate across great latitudinal distances, male

## Discussion

Although comparable data are limited, the $\delta^{13}C$ and $\delta^{15}N$ values we obtained fall within the ranges expected for collagen from top-level marine consumers (Schoeninger and DeNiro 1984; Lee-Thorp et al. 1989; Ramsay and Hobson 1991). The mean $\delta^{15}N$ values of all of the groups we studied varied by about 2.3‰. Although there are differences in nitrogen isotope composition between species or populations feeding at middle versus high latitudes, and in some case between the sexes, all of these groups appear to be feeding on prey that span less than two trophic levels.

Our study demonstrates that nearshore-offshore differences in carbon isotope composition among these pinnipeds do not merely reflect differences in the length of the food web. At middle latitudes, offshore-foraging female northern elephant seals have $\delta^{15}N$ values 0.5‰ lower than nearshore-foraging harbor seals, which can be viewed as evidence that they feed at a slightly lower trophic level. Yet, given typical stepwise trophic-level enrichments of ~1.0‰ for $\delta^{13}C$ and ~3.0‰ for $\delta^{15}N$, the minor trophic-level difference between female northern elephant seals and harbor seals inferred from nitrogen isotopes is much too small to explain the 2.0‰ difference in $\delta^{13}C$ values between these groups. At higher latitudes, comparison of nearshore-foraging harbor seals from

Alaska to offshore-foraging male northern fur seals reveals a similar pattern. The difference in $\delta^{15}N$ values between these two groups is too small to explain the 1.7‰ $^{13}C$ enrichment of harbor seals relative to male northern fur seals. We conclude, therefore, that variations in the $\delta^{13}C$ values of pinnipeds reflect the sources of organic carbon at the base of the food web.

France (1995) attributed differences in the carbon isotope compositions of marine consumers to the input of $^{13}C$-enriched carbon fixed by benthic macrophytes in the nearshore environment. Indeed, macroalgae from the north Pacific are typically $^{13}C$ enriched by 5.0–6.0‰ relative to open-ocean phytoplankton (Dunton and Schell 1987; Goering et al. 1990), and organisms that feed within these macroalgae beds do have higher $\delta^{13}C$ values than conspecifics feeding in nearshore ecosystems that lack macroalgae (Duggins et al. 1989). Yet nearshore food webs utilized by pinnipeds may extend 20 or 30 km from the coast. It is not clear that the contribution of organic carbon from macroalgae is great enough to cause detectable $^{13}C$ enrichments in nearshore food webs that are not intimately associated with macroalgae beds.

Nearshore food webs may also be $^{13}C$ enriched due to rapid phytoplankton blooms induced by the mixing of deep nutrient-rich waters into the surface layer (Schell et al. 1998). Over the course of such blooms, the $\delta^{13}C$ values of phytoplankton and zooplankton tend to shift by +2.0 to +3.0‰ as a result of the rapid sequestration of $^{12}C$ in photosynthetically fixed organic carbon and, perhaps, due to a reduced discrimination against $^{13}C$ during photosynthesis as aqueous $CO_2$ concentrations are drawn down (Goering et al. 1990; Rau et al. 1992b; Wainright and Fry 1994; Schell et al. 1998). In the open ocean, where the nutrient supply may be limited, microalgal production rates are too low to decrease aqueous $CO_2$ concentrations dramatically. Consequently, the $\delta^{13}C$ value of carbon fixed at the base of offshore food webs is low relative to carbon fixed by phytoplankton in the nearshore. The isotopic shift observed over the course of plankton blooms is similar in direction and magnitude to the $\delta^{13}C$ differences between nearshore- and offshore-foraging pinnipeds (Fig. 2a). Our results suggest that $\delta^{13}C$ differences in higher-trophic-level consumers, such as pinnipeds, may more closely reflect differences in phytoplankton photosynthesis than the influence of carbon fixed by macroalgae.

As suggested by Hobson et al. (1997), we found that the latitude at which animals forage also has an important effect on carbon isotope compositions. Overall, for both the nearshore- and offshore-foraging pinnipeds we studied, high-latitude pinnipeds have lower $\delta^{13}C$ values than middle-latitude residents (Fig. 2a). This pattern mirrors the trend seen in north Pacific phytoplankton, which have lower $\delta^{13}C$ values at high latitudes (e.g., −22.0‰ at 71°N) than at low latitudes (e.g., −20.3‰ at 28°N) (Rau et al. 1982; Goericke and Fry 1994). Lower temperatures, which increase the solubility and concentration of $CO_2$ in marine waters and decrease phytoplankton growth rates, may contribute to lower

$\delta^{13}C$ values at high latitudes (Goericke and Fry 1994; Michener and Schell 1994; Schell et al. 1998). In addition, Pacific deep water contains ~20% more $CO_2$ than surface water and is $^{13}C$ depleted by ~2.0‰ (Craig 1970; Kroopnick 1974). The more intense mixing of $CO_2$-rich, $^{13}C$-depleted deep water into the photic zone at high latitudes would also contribute to lower $\delta^{13}C$ values across all high-latitude food webs (Schell et al. 1998).

We also found that isotope compositions may accurately reveal foraging location of groups that migrate across larger latitudinal distances. Time-depth records of dives and satellite tracking of movements indicate that adult male northern elephant seals migrate north from the central coast of California, crossing thousands of kilometers of open ocean to arrive in coastal waters off British Columbia and Alaska. While in transit, over a period of about 1 month, less than 10% of their dives appear to be foraging dives, while in high-latitude, nearshore waters, 80% of their dives are presumed to be benthic foraging dives (LeBoeuf et al. 1993, in press). The $\delta^{13}C$ values of male northern elephant seals are in agreement with these conclusions, as they are essentially identical to those of nearshore-foraging harbor seals from Alaska (Fig. 2). Likewise, the small difference in nitrogen isotope composition between male harbor seals from Alaska and male northern elephant seals implies a similar foraging strategy. Even though male elephant seals may travel great distances across the open ocean, they appear to be feeding chiefly within the highly productive nearshore regions that experience extensive upwelling off British Columbia and Alaska.

Female northern fur seals leave the Alaskan breeding sites in November, migrating to offshore waters along the California margin where they remain for 2 or 3 months. In March, females begin the migration northward, either along the continental margin or by crossing open ocean, returning to high-latitude rookeries the following June to give birth (Gentry 1998). The carbon isotope composition of female northern fur seals reflects their pattern of foraging in high-latitude offshore waters during the breeding season and in middle-latitude offshore waters during migration (Fig. 2b). Their $\delta^{13}C$ values are intermediate between resident offshore feeders from high latitudes (male northern fur seals) and those from middle latitudes (female northern elephant seals).

California sea lions are interesting in that they have $\delta^{13}C$ values intermediate between nearshore and offshore foragers (Fig. 2b). California sea lions may range as far north as southern British Columbia, and as far south as their breeding grounds on islands off southern California and Baja, yet they rarely venture more than 50 km offshore (Antonelis and Fiscus 1980). We suggest that the apparent discrepancy between isotopic and observational assessments of foraging location can be reconciled through consideration of the differences in primary production (as measured by phytoplankton pigment concentrations) between the nearshore ecosystems in which California sea lions forage. Phytoplankton pigment concentrations are relatively high along the

central coast of California, but are lower and much more similar to offshore concentrations from the Santa Barbara Basin to the south (Falkowski et al. 1998). Thus the intermediate $^{13}$C values for California sea lions may reflect their movement between the highly productive nearshore waters of the California Current and the less-productive nearshore waters of southern California and Baja, rather than a strategy of feeding in both nearshore and offshore food webs. Comparison of isotopic compositions of California sea lions residing exclusively in waters off Baja to those of sea lions migrating into northern waters will clarify our understanding of these patterns.

In summary, we suggest a conceptual model that links the carbon isotope composition of upper-trophic-level marine consumers to carbon isotope variations in phytoplankton at the base of the food web. Isotopic variations in phytoplankton are largely controlled by the rate of primary production and the isotopic composition of inorganic carbon available for photosynthesis. In regions of the northeastern Pacific where deep-water mixing is intense along the margin, we would expect higher $\delta^{13}$C values for animals foraging in the nearshore relative to those foraging offshore. The carbon isotope compositions of animals feeding in coastal regions where upwelling is less intense are expected to be more like those of offshore foragers. Latitudinal differences in the isotopic composition of inorganic carbon available for photosynthesis may be large, and these differences must be considered when comparing animals from different zones. Further study of the isotopic ecology of pinnipeds from low-latitude, northeastern Pacific sites and a more complete characterization of the isotopic chemistry of offshore food webs will clarify the source of these isotopic gradients and their utility as monitors of pinniped foraging and migratory behavior. Greater refinement of these isotopic proxies for animal foraging and migration is important, as these same techniques may be used to investigate historical changes in the productivity of ecosystems and the past response of pinnipeds to these perturbations.

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