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Temporal records of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in North Pacific pinnipeds: inferences regarding environmental change and diet

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Abstract Sea lion and seal populations in Alaskan waters underwent various degrees of decline during the latter half of the twentieth century and the cause(s) for the declines remain uncertain. The stable carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) isotope ratios in bone collagen from wild Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*) and harbor seals (*Phoca vitulina*) from the Bering Sea and Gulf of Alaska were measured for the period 1951–1997 to test the hypothesis that a change in trophic level may have occurred during this interval and contributed to the population declines. A significant change in $\delta^{15}\text{N}$ in pinniped tissues over time would imply a marked change in trophic level. No significant change in bone collagen $\delta^{15}\text{N}$ was found for any of the three species during the past 47 years in either the Bering Sea or the Gulf of Alaska. However, the ^{15}N in the Steller sea lion collagen was significantly higher than both northern fur seals and harbor seals. A significant decline in $\delta^{13}\text{C}$ (almost 2 ‰ over the 47 years) was evident in Steller sea lions, while a declining trend, though not significant, was evident in harbor seals and northern fur seals. Changes in foraging location, in combination with a trophic shift, may offer one possible explanation. Nevertheless, a decrease in $\delta^{13}\text{C}$ over time with no accompanying change in $\delta^{15}\text{N}$ suggests an environmental change affecting the base of the foodweb rather than a trophic level change due to prey switching. A decline in the seasonal primary production in the region, possibly resulting from decreased phytoplankton growth rates, would exhibit itself as a decline in $\delta^{13}\text{C}$. Declining production could be an indication of a reduced carrying capacity in the North Pacific Ocean. Sufficient quantities of optimal prey species may have fallen below threshold sustaining densities for these pinnipeds, particularly for yearlings and subadults who have not yet developed adequate foraging skills.

Keywords Stable isotope analysis · Steller sea lions · Northern fur seals · Harbor seals · Bone collagen

Introduction

Populations of Steller sea lions, northern fur seals and harbor seals have drastically declined for more than two decades, particularly in the western Gulf of Alaska and Bering Sea (Pitcher 1990; Loughlin 1993; ADFG 1996; Strick et al. 1997). These pinnipeds are generally found in coastal waters and along the continental shelf throughout the North Pacific Ocean, including the Bering Sea and the Gulf of Alaska (NRC 1996). Food limitation has been hypothesized as a likely cause behind the declines in the pinniped populations, potentially resulting from decreases in clupeid fishes and increases in gadid fishes (Merrick et al. 1987, 1997; Alverson 1991; Trites 1992; Alaska Sea Grant 1993; Merrick 1995; Anderson et al. 1997). In this paper we explore how the changes in physical and biological characteristics of this region may have impacted these animals.

Physical and biological changes in the Northeast Pacific Ocean and Bering Sea

An abrupt climatic change occurred in the Pacific Ocean in the mid-1970s and a new “regime” continued through the 1980s (Hare and Mantua 2000). This change in atmospheric circulation altered wind patterns and intensity, mixed layer depth, sea surface temperatures, ice extent and depth of ocean current patterns (Royer 1989; Trenberth and Hurrell 1994; Freeland et al. 1997). However, little is known on how the effects of the changing environmental conditions influenced pinnipeds in the North Pacific Ocean.

The biological responses to these physical changes have manifested themselves in fluctuating phytoplankton abundance, changing zooplankton production and shifting migration patterns and biomass of commercial

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and non-commercial organisms (Venrick et al. 1987; Ebbesmeyer et al. 1991; Brodeur and Ware 1992; Francis and Hare 1994; Polovina et al. 1994, 1995; Hollowed and Wooster 1995; Quinn and Niebauer 1995; Anderson et al. 1997; Anderson and Piatt 1999). Sugimoto and Tadokoro (1997) reported declining chlorophyll concentrations and zooplankton biomass during the mid-1970s and late 1980s in the eastern Pacific and Bering Sea, while peaks in both chlorophyll and zooplankton occurred in the late 1960s and continued to decline after that point in the Central Pacific.

Many forage fish stocks have dramatically increased while others have declined in the Gulf of Alaska and Bering Sea since the mid-1970s. The forage species composition for the region has shifted from an environment dominated by clupeid fishes and panaeid shrimp to one currently dominated by gadids and pleuronectids (Anderson et al. 1997; Anderson and Piatt 1998). In 1951 and 1964, samples from Steller sea lion stomachs from the Bering Sea showed that walleye pollock was the fourth most prevalent prey species (Fiscus and Baines 1966), but by 1976 pollock was the dominant prey (Lowry 1982; Lowry et al. 1989). Stomach content analyses of Pribilof Island fur seals in the early 1980s showed a predominance of juvenile walleye pollock and squid. Pacific herring and capelin, previously considered important prey, were absent (Sinclair et al. 1994). Kenyon (1965) noted that harbor seals from Amchitka Island in the Aleutian Archipelago had remains of octopus and Atka mackerel in their stomachs, whereas harbor seals sampled in 1979 from the Alaska Peninsula had primarily walleye pollock and octopus in their stomachs (Pitcher 1980).

Isotope ratios in food webs

The isotopic ratios of animal tissues, particularly in marine organisms, are slightly more enriched in ^{13}C (0.5–1‰) and ^{15}N (3–5‰) than those found in their diet (Hobson and Welch 1992; France and Peters 1997). Isotopic variations observed in organisms throughout the marine environment are believed to result from differences that can originate at the base of food webs and metabolic pathways in the organisms (DeNiro and Epstein 1978, 1981; McConnaughey and McRoy 1979; Rau et al. 1983; Fry and Sherr 1984; Minigawa and Wada 1984; Sholto-Douglas et al. 1991; Hobson and Welch 1992; France and Peters 1997). Herbivorous zooplankton, consisting primarily of calanoid copepods and euphausiids in the North Pacific Ocean, are first-order consumers. Any changes affecting the stable isotope ratios within the phytoplankton, such as carbon and nutrient sources and their growth rate, would be carried through the food web and be reflected in foraging pinnipeds. Recent studies have shown a close correlation between cellular growth rates and carbon isotope ratios ($\delta^{13}\text{C}$) in phytoplankton. Rapid growth rates in phytoplankton result in reduced fractionation of the carbon being utilized and result in

higher $\delta^{13}\text{C}$ values if other factors (CO_2 , nutrients) remain constant. Laws et al. (1995) have shown a strong relationship between diatom growth rates and isotopic fractionation in the laboratory. Bidigare et al. (1997) confirmed these findings in laboratory studies of cultures of haptophyte algae and in phytoplankton sampled from various world ocean environments; increased growth rate and productivity in both the diatoms and haptophytes were correlated with increased $\delta^{13}\text{C}$ values.

Bone collagen is a tissue that has a relatively slow turnover rate, as much as 10 years in large adult mammals. Depending on the age of the animal (≤ 10 years), the stable isotope ratios in the collagen is likely integrated over much of its life (Hobson and Clark 1992; Ambrose and Norr 1993). This tissue acts as a long-term integrator of isotope ratios and moderator of sporadic isotopic fluctuations, a factor that is useful when comparing isotope ratios of many individuals over long periods of time (Schoeninger and DeNiro 1984; Lee-Thorp et al. 1989). Episodic or short-term changes in dietary isotope ratios are dampened in the collagen record, leaving only changes in the long-term trends as an indicator of the organism's trophic status in its environment.

Stable isotope analysis of archived samples of bone collagen is a potential tool that may reveal processes associated with the recent declines in pinniped populations. Herring and capelin, once dominant in the diets of these pinnipeds, are generally of a lower trophic level than the walleye pollock currently being eaten by these seals and sea lions (Hirons 2001). Thus, we hypothesize that this dietary change should be reflected as changes in bone $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. In addition, if changes in physical parameters altered primary production, this may be reflected in bone $\delta^{13}\text{C}$ values. As primary production regulates the carrying capacity for the entire food web, such changes could have important implications for top consumers such as seals and sea lions. If prey availability falls below threshold densities, recruitment would be greatly reduced.

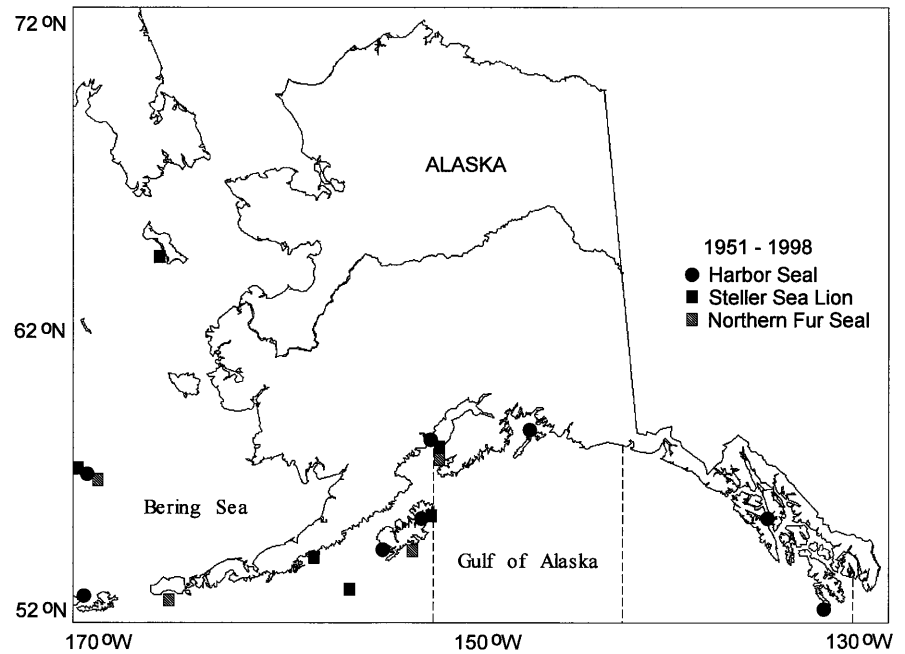
Materials and methods

Pinniped samples

Seal and sea lion bone samples were obtained from native-harvested animals and museum skeletal collections at the University of Alaska Museum and the Kodiak Historical Society. A total of 31 Steller sea lions, 13 northern fur seals and 63 harbor seals from regions throughout the Gulf of Alaska and the Bering Sea were analyzed. The specimens span the period 1951–1997 and range from coastal areas of southeast Alaska westward through the Gulf of Alaska and into the central Bering Sea (Fig. 1). The Gulf of Alaska was separated into three regions, based on distinct pinniped populations, for statistical analyses (SYSTAT 1997). The western Gulf of Alaska is defined as the area between 152°W and 175°W , the central Gulf of Alaska is the area between 144°W and 152°W and the southeastern Gulf of Alaska is the area between 130°W and 144°W .

Sex and age of the animal were not recorded for most of the specimens, though one sea lion skeleton was suspected as being from a pup on the basis of its size and dentition. The remaining skeletons were either labeled as adults or subadults; age unknown,

Fig. 1 Collection locations of bone samples from Steller sea lions, northern fur seals and harbor seals, 1951–1997



or in some cases age group as estimated by dentition development. The data were not sufficient to test for age-related trophic differences. More than half of the sampled sea lions (61%) and northern fur seals (62%) came from the Bering Sea, and the remaining skeletal samples came from the western and central portions of the Gulf of Alaska. Harbor seal samples were evenly distributed among the Bering Sea, western, central and southeastern Gulf of Alaska. Samples for both the sea lions and the harbor seals were generally evenly distributed throughout the 47-year study period, but there were years when, at a minimum, no samples were available, and at a maximum, six samples were available. Overall, an average of two specimens were available per year for all species.

Collagen extraction

Bone samples were well preserved and free of humus and tissues. Collagen was extracted following the procedure described in detail in Matheus (1997). Approximately 1 g of bone was either cut as a solid piece or shaved from the mandible or the shaft of a long bone. Only cancellous bone was used for extraction due to the larger quantity of collagen it contains. The bone samples had lipids removed by a methanol/chloroform procedure described in Bligh and Dyer (1959) prior to demineralization. The bone was allowed to demineralize in 1 N HCl for approximately 7 days at 5°C; fresh acid was added to the samples every day. The remaining material was rinsed and then boiled in deionized water for approximately eight hours to dissolve the collagen and precipitate peptides. The solution was passed through a 0.45- μ m filter, and the filtrate was dried in an aluminum dish at 60°C for a minimum of 48 h.

Mass spectrometry

Subsamples of each tissue (1–1.5 mg) were combusted and analyzed for stable isotope ratios with a Europa 20/20 continuous flow isotope ratio mass spectrometer. All samples were analyzed in duplicate. Stable isotope ratios were expressed in the following standard notation:

$$\delta X (\text{‰}) = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1,000$$

where X is ^{13}C or ^{15}N and R_{sample} is the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ respectively. R_{standard} for ^{13}C is Pee Dee Belemnite; for ^{15}N it is atmo-

spheric N_2 (air). If the difference between replicates was greater than 0.5‰, samples were re-analyzed. Analytical error for samples was approximately $\pm 0.2\text{‰}$ for both carbon and nitrogen.

Results

Nitrogen isotope values for harbor seals ranged from 14.0‰ to 20.5‰ with a mean of $17.2 \pm 1.6\text{‰}$. The $\delta^{15}\text{N}$ for northern fur seals ranged from 15.2‰ to 20.1‰ with a mean of $17.2 \pm 1.5\text{‰}$ and the $\delta^{15}\text{N}$ for Steller sea lions ranged from 16.2‰ to 21.9‰ with a mean of $18.5 \pm 1.4\text{‰}$. Harbor seal collagen $\delta^{13}\text{C}$ values ranged from -12.0‰ to -16.4‰ with a mean of $-14.2 \pm 1.0\text{‰}$. The $\delta^{13}\text{C}$ of collagen from northern fur seals ranged from -13.0‰ to -16.7‰ with a mean of $-14.4 \pm 1.1\text{‰}$ and the Steller sea lion collagen $\delta^{13}\text{C}$ ranged from -12.5‰ to -15.8‰ with a mean of $-14.3 \pm 1.0\text{‰}$ (Table 1). The between-animal and interannual variability in the $\delta^{13}\text{C}$ of all three species ranged from less than 1‰ to as much as 5‰.

Analysis of joint distribution in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ revealed differences among the three pinniped species (MANOVA: Wilks Lambda $F_{4, 130} = 3.30$, $P = 0.013$). Two separate analysis of variance tests (ANOVA) were then conducted to determine if nitrogen or carbon isotopes differed amongst the species. Univariate tests revealed that the three species segregated isotopically for only $\delta^{15}\text{N}$ ($P = 0.002$). Bonferroni correction tests for $\delta^{15}\text{N}$ showed that Steller sea lions had higher mean nitrogen isotope ratios than harbor seals and northern fur seals ($P = 0.015$ and $P = 0.014$, respectively). No differences in either isotope were detected among the defined regions for any of the three species (MANOVA: Wilks Lambda $F_{6, 130} = 0.58$, $P = 0.750$).

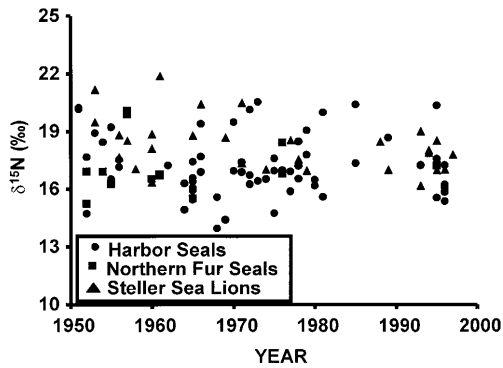
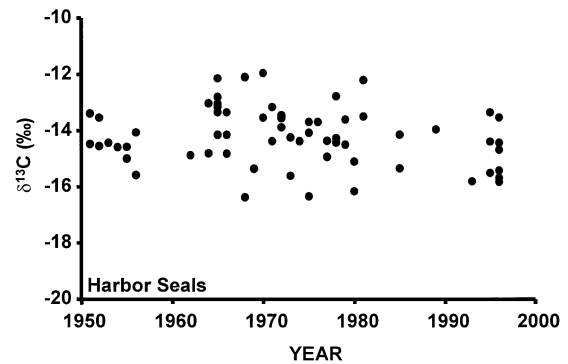
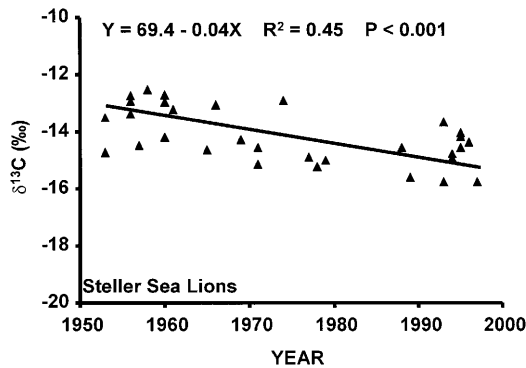
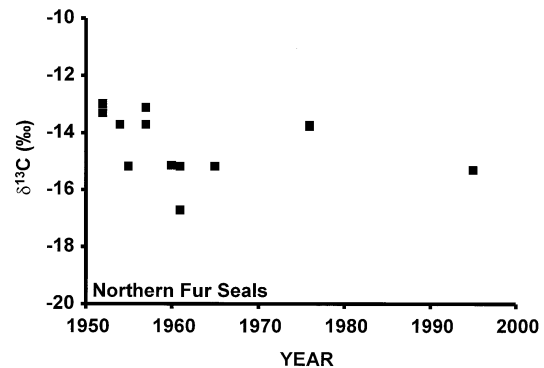
Analysis of joint distribution in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all years revealed only $\delta^{13}\text{C}$ differed significantly during

Table 1 Mean stable isotope ratios of bone collagen from harbor seals, northern fur seals and Steller sea lions. *SEGOA* Southeastern Gulf of Alaska, *CGOA* central Gulf of Alaska, *WGOA* western Gulf of Alaska, *BS* Bering Sea

Species	<i>n</i>	Year	Location	Mean $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$
Harbor seal	2	1951	CGOA	-13.9±0.5	20.2±0.0
	1	1952	CGOA	-13.6	17.7
	1	1952	WGOA	-14.6	14.7
	1	1953	BS	-14.4	18.9
	1	1954	WGOA	-14.6	18.4
	2	1955	CGOA	-14.8±0.2	17.9±1.4
	2	1956	CGOA	-14.8±0.8	17.3±0.2
	1	1962	CGOA	-14.9	17.2
	2	1964	WGOA	-13.9±0.9	16.1±0.2
	5	1965	SEGOA	-13.2±0.7	16.4±0.7
	1	1965	WGOA	-13.1	16.1
	1	1966	CGOA	-13.4	16.9
	1	1966	WGOA	-14.8	17.7
	1	1966	BS	-14.2	19.4
	2	1968	BS	-14.3±2.1	14.8±0.8
	1	1969	BS	-15.4	14.4
	1	1970	WGOA	-12.0	16.9
	1	1970	BS	-13.6	19.5
	1	1971	WGOA	-13.2	17.4
	1	1971	BS	-14.4	16.9
	1	1972	CGOA	-13.6	20.1
	2	1972	BS	-13.7±0.2	16.5±0.2
	1	1973	CGOA	-14.3	16.4
	1	1973	BS	-15.6	20.5
	1	1974	BS	-14.4	16.5
	3	1975	CGOA	-14.7±1.2	16.4±1.2
	1	1976	WGOA	-13.7	17.0
	2	1977	WGOA	-14.7±0.3	16.4±0.5
	2	1978	CGOA	-13.5±0.8	16.9±0.3
	1	1978	WGOA	-14.4	18.4
	2	1979	BS	-14.1±0.5	18.4±0.6
	2	1980	WGOA	-15.6±0.5	16.3±0.2
	1	1981	CGOA	-12.2	15.6
1	1981	BS	-13.5	20.0	
2	1985	WGOA	-14.8±0.6	18.9±1.5	
1	1989	CGOA	-14.0	18.7	
1	1993	CGOA	-15.8	17.2	
2	1995	SEGOA	-15.0±0.6	19.0±1.4	
1	1995	BS	-13.4	15.6	
1	1996	SEGOA	-14.4	15.8	
5	1996	CGOA	-15.0±0.9	16.2±0.6	
Northern fur seals	2	1952	BS	-13.2±0.2	16.1±0.8
	1	1954	WGOA	-13.7	16.9
	1	1955	BS	-15.2	16.3
	1	1957	CGOA	-13.1	20.1
	1	1957	WGOA	-13.7	19.9
	1	1960	BS	-15.2	16.5
Northern fur seals	1	1961	CGOA	-16.7	16.7
	1	1961	BS	-15.2	16.8
	1	1965	BS	-15.2	15.5
	1	1976	WGOA	-13.8	18.4
	1	1976	BS	-13.8	16.8
	1	1995	BS	-15.3	17.2
	2	1953	BS	-14.1±0.6	20.3±0.9
	3	1956	CGOA	-13.0±0.3	18.0±0.6
	1	1957	CGOA	-14.5	18.5
	1	1958	BS	-12.5	17.0
	2	1960	WGOA	-12.8±0.1	18.5±0.4
	1	1960	BS	-14.2	16.4
	1	1961	BS	-13.2	21.9
	1	1965	BS	-14.6	18.8
	1	1966	CGOA	-13.1	20.4
	1	1969	CGOA	-14.3	18.7
	2	1971	BS	-14.9±0.3	18.9±1.6
	1	1974	BS	-12.9	20.0
	1	1977	BS	-14.9	18.5
	1	1978	WGOA	-15.2	17.5
1	1979	BS	-15.0	17.0	

Table 1 (continued)

Species	<i>n</i>	Year	Location	Mean $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$
Steller sea lions	1	1988	CGOA	-14.6	18.5
	1	1989	WGOA	-15.6	17.0
	2	1993	BS	-15.7 \pm 0.1	18.1 \pm 1.9
	2	1994	BS	-14.9 \pm 0.1	18.0 \pm 0.1
	3	1995	BS	-14.2 \pm 0.2	18.7 \pm 0.8
	1	1996	BS	-15.4	17.0
	1	1997	WGOA	-15.8	17.8

**Fig. 2** $\delta^{15}\text{N}$ values of bone collagen for Steller sea lions, northern fur seals and harbor seals from the Bering Sea and Gulf of Alaska, 1951–1997**Fig. 4** $\delta^{13}\text{C}$ values of bone collagen for harbor seals from the Bering Sea and Gulf of Alaska, 1951–1996**Fig. 3** $\delta^{13}\text{C}$ values of bone collagen for Steller sea lions for the Bering Sea and Gulf of Alaska, 1953–1997**Fig. 5** $\delta^{13}\text{C}$ values of bone collagen for northern fur seals from the Bering Sea and Gulf of Alaska, 1952–1995

the 47-year period (MANOVA: Wilks Lambda $F_{70,130} = 1.558$, $P = 0.015$). When two separate analysis of variance tests (ANOVA) were conducted for each isotope, Steller sea lions had a significant decline in $\delta^{13}\text{C}$ (Kruskal-Wallis $P = 0.004$). The declining trends in harbor seal and northern fur seal $\delta^{13}\text{C}$ were not statistically significant by this method ($P = 0.298$ and $P = 0.072$, respectively). Separate regressions of nitrogen and carbon isotope ratios were conducted against year for the combined and individual species. Regression analysis of $\delta^{15}\text{N}$ against year showed no significant relationship during the 47-year period either in combined or individual species (Fig. 2). Regression analysis of $\delta^{13}\text{C}$ showed a significant decline in the Steller sea lions ($P < 0.001$) (Fig. 3)

and a decrease, although not statistically significant at the $P = 0.05$ level, in both the harbor seals and northern fur seals ($P = 0.108$ and $P = 0.375$, respectively) (Figs. 4, 5). The sea lion $\delta^{13}\text{C}$ declined an average of 1.9‰ from 1953 through 1997. The lack of fur seal samples in recent years hinders the detection of any trends.

Discussion

The major features of the data suggest there have been no long-term changes in $\delta^{15}\text{N}$ over the approximately 47-year period for all three species. A significant decline in $\delta^{13}\text{C}$ of Steller sea lions occurred during this period.

This decline is also weakly suggested in data from the two species of seals. The trends, or lack thereof, appear to be uniform across regions. Three processes that may account for the changes in stable isotope ratios include temporal changes in diet/trophic position, foraging habits/location and isotopic composition of the base of the food web.

Diet/trophic variability

The present day diets of Steller sea lions, northern fur seals and harbor seals consist of a number of similar prey species but the composition may differ according to preferential prey and locally available species. Harbor seal diets appear to consist of mostly pelagic and semi-demersal fishes and benthic invertebrates, including herring, juvenile pollock and octopus (Pitcher 1980). The diet of northern fur seals appears to be largely composed of squid and juvenile pollock while Steller sea lions forage heavily on larger adult pollock, Pacific cod and flatfishes (Kajimura 1985; Sinclair 1997; Hirons 2001).

The $\delta^{15}\text{N}$ values obtained from the pinniped collagen suggest that Steller sea lions may feed at a slightly higher trophic level than the harbor seals and northern fur seals. Hobson et al. (1997) found similar results for Steller sea lions and northern fur seals from the Gulf of Alaska and concluded that the sea lions were consuming more large-size pollock, which were enriched in $\delta^{15}\text{N}$ relative to the juvenile pollock and squid that the fur seals were predominantly relying on. Perez and Bigg (1986) noted that northern fur seals in the eastern Aleutians and Gulf of Alaska between 1958 and 1974 fed largely on sandlance, capelin and herring. The diets of both the forage fish and juvenile pollock consist primarily of zooplankton and thus are at a similar trophic position consistent with similar $\delta^{15}\text{N}$ values. Pitcher (1980) noted that walleye pollock was the predominant prey in both the Steller sea lion and harbor seal diets in the Gulf of Alaska during the mid-1970s but that each species foraged on different sizes of pollock. Steller sea lions were eating pollock significantly larger than those eaten by harbor seals. These larger pollock are mainly piscivorous, often feeding on smaller pollock and forage fish, whereas the smaller pollock feed largely on zooplankton and juvenile forage fish. These trophic differences result in more enriched nitrogen isotope values in the large pollock by $\sim 2.5\text{‰}$ (DeNiro and Epstein 1981; Hirons 2001) and would result in higher $\delta^{15}\text{N}$ in the sea lions.

Changes in prey composition during the 1970s, as previously described, may have altered the isotope ratios in the pinnipeds. Adult and some juvenile pollock, which are currently predominant in the diets of many of these animals, generally have more enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the once prevalent clupeid fishes (herring, capelin) because they largely forage at a higher trophic level than the clupeids (Hobson et al. 1997; Merrick et al. 1997; Hirons 2001). If these pinnipeds shifted to forage at a higher trophic level, we would expect increases

in both the nitrogen and carbon isotope ratios (DeNiro and Epstein 1978, 1981; Rau et al. 1983). Although fish having high lipid content, i.e. clupeids, generally have more depleted ^{13}C than a fish naturally low in lipids, i.e. pollock and cod, only a trophic level change of $\sim 3\text{‰}$ was evident in ^{15}N (Tieszen et al. 1983; Hirons, unpublished data). However, the lack of co-variance between carbon and nitrogen isotopes does not support a prey-switching scenario for these pinnipeds.

Foraging habits/location

Harbor seals have strong site affinity and feed in nearby coastal locations in Bristol Bay, Bering Sea and coastally throughout the Northeastern Pacific Ocean (Pitcher 1980; Frost et al. 1999; Hirons 2001). Northern fur seals forage in the shelf break and offshore waters of the Bering Sea, the Gulf of Alaska and as far south as California during their annual migration to and from the Pribilof Islands in the Bering Sea (Kajimura 1984, 1985; Goebel et al. 1991; Loughlin 1993; Sinclair et al. 1994; Merrick 1995; NRC 1996). Steller sea lions spend their year foraging predominantly over the continental shelf and in offshore waters in the southern Bering Sea and Gulf of Alaska while traveling among rookeries and haul-out sites (Kenyon and Rice 1961; Merrick et al. 1997). Although the movements and life histories of our individual pinnipeds are unknown, and only generally known for each species, we assume the $\delta^{13}\text{C}$ values in the bone collagen represent prey from the northeastern Pacific and Bering Sea.

As discussed, these pinnipeds have heterogeneous diets that often include prey from different trophic levels and regions. Schell et al. (1998) noted the existence of isotopic gradients in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of zooplankton in 11 subregions from the Bering Sea and, recently, similar isotopic gradients were identified in the continental shelf waters of the Gulf of Alaska using the same taxa of zooplankton (Hirons 2001). Regions of high primary productivity, including the shelf break in the Bering Sea and continental shelf in the Gulf of Alaska, contain zooplankton with higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than areas further offshore. Thus variations in the year-to-year movement patterns of both pinnipeds and prey, as well as differences in prey availability, may cause fluctuations in the isotopic ratios among individual pinnipeds.

Pinnipeds may vary forage locations as they move to and from rookeries seasonally or as they follow potential prey and, all the while, the bone collagen is integrating these complex movements. The isotope ratios in harbor seals, which tend to have a strong site affinity, would represent the prey items in the seals' coastal feeding locations (Pitcher 1980). Such observations may help explain the high between-animal isotopic variability. The isotope ratios in the Steller sea lions likely reflect the prey often found in near- and offshore waters in the Bering Sea and in the Gulf of Alaska, whereas the isotopic ratios in northern fur seals could reflect prey consumed in the

Bering Sea, the Gulf of Alaska and as far south as the offshore waters of California as they migrate (Goebel et al. 1991; Loughlin 1993; Merrick 1995). Isotope data could reveal long-term changes in feeding location if these locations were isotopically distinctive in terms of their prey. If the zooplankton data (Schell et al. 1998; Hirons 2001) are indicative of regional patterns of changes in prey isotope composition, changes in foraging location should result in changes in both the carbon and nitrogen isotopes in the pinniped species examined. Thus, our data are not consistent with major changes in feeding location as the sole mechanism explaining these trends. The Steller sea lion data could be explained by a shift to offshore feeding (lowering $\delta^{13}\text{C}$) accompanied by a shift to a higher trophic level prey, i.e. offshore adult pollock which may have the same $\delta^{15}\text{N}$ as lower trophic level, inshore capelin (Hirons 2001). The isotope ratios of the higher trophic level pollock would be offset by the lighter isotope ratios at the base of food webs in pelagic waters.

A decrease in $\delta^{13}\text{C}$ in consumers can be due to a diet switch from isotopically enriched, benthic organisms to a more isotopically depleted, pelagic diet. Benthic organisms tend to be more enriched in ^{13}C due to an increase in the length of the food web by microorganisms, although no subsequent enrichment in ^{15}N was reported (Hobson and Welch 1992; France and Peters 1997). No historical or current data provide evidence of this happening with sea lions or fur seals but harbor seals currently eat a mix of pelagic and benthic prey (Hirons 2001). In summary, our data do not support the hypothesis of significant changes in trophic level of prey organisms for these mammals unless such effects were masked by simultaneous changes in factors such as feeding location or prey isotopic composition.

Environmental influences

A third process that could account for the observed trends is one in which the stable isotope composition at the base of the food web changes over time. Based on the Steller sea lion data, such a mechanism would require coherent trends over a large region spanning the Gulf of Alaska and Bering Sea. Further, such changes should be registered in much of the food web in this region. The declining $\delta^{13}\text{C}$ trends in the harbor seals and northern fur seals are consistent with this hypothesis, though are less significant than the sea lions. Steller sea lions were the only one of the three pinniped species to show significant long-term declines in their carbon isotope ratios. This may be due to the spatial variations in migration and habitat between the sea lions and the other two species. Harbor seals forage in productive coastal waters with prey enriched in ^{13}C while fur seals and sea lions often forage in less productive, offshore waters where the $\delta^{13}\text{C}$ values of prey are more depleted (Schell et al. 1998; Hirons 2001). The heterogeneous diets and localized habitats of harbor seals may have contributed

to large inter-animal variability hindering statistical detection. The available northern fur seal samples were too few to rigorously confirm this hypothesis. We conclude that our data at present cannot rule out isotopic variation due to forage location as a potential explanation.

The $\delta^{13}\text{C}$ values in top trophic level marine organisms can be changed without modifying the animals' trophic position, as this value is set by the composition of phytoplankton in the food web. The isotopic composition of the phytoplankton is affected by the isotopic composition of dissolved inorganic carbon and the fractionation that occurs during the growth of plant cells. These isotopic differences are incorporated into all consumers in the food web.

Anthropogenic CO_2 from the burning of fossil fuel, which is depleted in ^{13}C , has resulted in a decrease in $\delta^{13}\text{C}$ of oceanic dissolved inorganic carbon (DIC), commonly referred to as the "oceanic Suess effect" (Kroopnick 1985). The degree of $\delta^{13}\text{C}$ change from the Suess effect varies spatially in the ocean due to processes such as ocean circulation and mixing. Smaller decreases have been observed in subpolar oceans ($< -0.15\text{‰}$ decade⁻¹). The high latitude zone of the Pacific Ocean, where these seals and sea lions reside, is subject to upwelling and deep water mixing in the winter. These events tend to reduce the Suess effect due to dilution from "old", deep water and the limited time for CO_2 equilibration to take place (Quay et al. 1992; Gruber et al. 1999; Sonnerup et al. 1999). Given the time period of this study, the Suess effect would account for a depletion of no more than 0.75‰ in $\delta^{13}\text{C}$ over five decades. The $\delta^{13}\text{C}$ decrease observed in the Steller sea lion bone collagen is too large and of a different temporal pattern to be explained simply by the increase in anthropogenic carbon during the past five decades.

Rapid use of CO_2 during photosynthesis can lead to an increase in the $\delta^{13}\text{C}$ of the plant cells if the rate of CO_2 replenishment is slower than usage (Goericke et al. 1994). Laws et al. (1995) and Popp et al. (1998) have empirically demonstrated strong, positive relationships between the $\delta^{13}\text{C}$ of a marine diatom and cell growth rates while Bidigare et al. (1997) showed a similar correlation among carbon isotope values and empirical haptophyte algal cell (coccolithophore) growth rate in natural marine settings. According to this process, the declining trends in bone collagen $\delta^{13}\text{C}$ imply a long-term decline in phytoplankton cell growth rates, and hence primary productivity, over this period.

The productivity hypothesis assumes that other factors controlling phytoplankton $\delta^{13}\text{C}$ ratios, such as $[\text{CO}_2]_{\text{aq}}$ and phytoplankton cell size (Rau et al. 1989), are relatively constant over this period. The offshore subarctic Pacific is dominated by small-sized phytoplankton whose populations stay relatively constant throughout the year (Martin et al. 1989). Phytoplankton growth is limited by photosynthetically active radiation (PAR) and nutrient availability though the subarctic Pacific Ocean is not nitrogen-limited. Studies conducted by Miller et al. (1991) in the subarctic Pacific indicate the phytoplankton are

dominated most of the year by small flagellates and that larger phytoplankton, particularly large diatoms, may be limited by iron availability. Iron input from land is proposed as being the reason large diatoms dominate over the continental shelf region during a portion of the year (Martin and Fitzwater 1988; Martin et al. 1989; Boyd et al. 1996). There is insufficient data to evaluate long-term changes in the phytoplankton community in this region and any subsequent effects on ecosystem $\delta^{13}\text{C}$. A seemingly uncommon occurrence of coccolithophorid blooms has occurred in the Bering Sea since 1997. These blooms are known to occur when a highly stratified water column in warm, calm seas hampers nutrient cycling (Sukhanova and Flint 1998; http://visibleearth.nasa.gov/Regions/Bering_Sea/index_3.html). However, this change is too recent to be strongly represented by our bone samples.

Physical factors affecting changes in wind intensity and mixed depth layers in the Northeast Pacific appear to have affected productivity in the region. Polovina et al. (1995) observed a shallowing of the winter mixed layer depth in the subarctic North Pacific from 1977 to 1988 and attributed the change to an intensification of the Aleutian Low Pressure System. Recent data presented by Freeland et al. (1997) and Mackas et al. (1998) for Station Papa (50°N 145°W) indicate that summer nitrate concentrations and mixed layer depths have decreased. The model used by Polovina et al. (1995) to test effects of changing mixed layer depths predicted potentially large changes in phytoplankton production and zooplankton stock in the northeastern Pacific.

Since 1976, northeastern Pacific and southern Bering Sea water temperatures have increased and the extent of sea ice cover in the Bering Sea has diminished (Niebauer 1988; Royer 1989). The timing of this change in thermal structure corresponds to shifts in species composition of fish and invertebrates (Ebbesmeyer et al. 1991; Anderson et al. 1997; Anderson and Piatt 1999). In the Gulf of Alaska, there has been a long-term trend of decreasing salinity due to increased runoff. The warmer temperatures and lower salinity would increase stability of the water column and that could impede the supply of nutrients to the surface waters in some environments. Data from the Bering Sea PROBES study demonstrated decreased primary production during times of the year when wind mixing diminished (Walsh and McRoy 1986). However, increased water column stability has been suggested as being favorable for phytoplankton growth in some settings (Gargett 1997).

Data on chlorophyll and zooplankton biomass may provide some evidence of past productivity fluctuations. Sugimoto and Tadokoro (1997) compiled estimates of zooplankton biomass and chlorophyll concentrations for the eastern Bering Sea spanning the years 1954–1994. These authors compiled a more limited data set for both variables for the northeastern Pacific Ocean. Values for both regions showed increases in both phytoplankton and zooplankton standing stocks during the mid-1960s and a general decline after that point. Carbon isotope values for organic matter in a sediment core from Skan-

Bay, Unalaska, in the Aleutian Islands of Alaska, revealed a decline of almost 1.5‰ between 1950 and 1998 (Finney, unpublished data).

The decline in the $\delta^{13}\text{C}$ of Steller sea lion bone collagen is similar to the pattern that Schell (2000) observed in bowhead whale baleen from the Bering Sea over the same period of time, 1947–1998. These baleen whales feed heavily on zooplankton stocks that have integrated the previous season's primary production and now serve as a proxy for the average annual productivity. The average carbon isotope ratios in bowhead whale baleen laid down in the Bering and Chukchi seas were used to estimate the relative interannual changes in primary production in the Bering Shelf ecosystem using relationships from Laws et al. (1995) and Bidigare et al. (1997). Assuming the correlation between the measured haptophyte algae growth rates and changes in $\delta^{13}\text{C}$ are similar to phytoplankton growth in the Bering Sea, the isotope ratios in baleen imply a decline of 30–40% in ecosystem productivity between 1966 and 1997.

Abundant evidence exists for environmental changes in the North Pacific Ocean and the Bering Sea in recent decades. However, changes within subregions may not always coincide with one another. The hypothesis that changes in primary productivity were coherent over this large region, a bottom-up mechanism, has been proposed by numerous researchers to explain changes in abundance of many different organisms in this region (Beamish and Boullion 1993; Francis and Hare 1994; Hare and Mantua 2000). Oceanographic and biological differences can result in a lack of concordance that has been illustrated by differences in salmon abundance, for example. Large increases in salmon catch in the Gulf of Alaska and Bristol Bay (southeast Bering Sea) occurred during this period. However, the salmon data are often interpreted as increasing productivity (Francis and Hare 1994) in contrast to the carbon isotope data.

A variety of physical and biological indices have provided evidence of rapid changes known as regime shifts around 1976 and 1989 (e.g. Ebbesmeyer et al. 1991; Brodeur and Ware 1992; Francis and Hare 1994; Polovina et al. 1995; Anderson et al. 1997; Beamish et al. 1997; Anderson and Piatt 1999; Hare and Mantua 2000). Evidence of declines in Steller sea lions, northern fur seals and harbor seals since the 1970s (Merrick et al. 1987; Pitcher 1990; Alaska Sea Grant 1993; Merrick et al. 1997) has prompted some researchers to try and link the declines to the reported regime shifts. As bone collagen has a relatively slow turnover rate that may be greater than 10 years, the isotope ratios present in the collagen would be an integrator of that period of their lifetime so that abrupt changes would be hard to detect.

Summary

An overwhelming amount of evidence suggests that the environment of the North Pacific Ocean and Bering Sea has changed during the past several decades. Further-

more, the changes in the physical environment may be associated with changes in the primary production in the region. The Committee on the Bering Sea Ecosystem assessed the likelihood of various potential causes on the declines of these three pinniped species and found that climate effects and environmental changes were likely factors affecting the fish community and food availability for these animals (NRC 1996). Reduction in food, which subsequently leads to population declines if depletion is great enough, seems to be supported for Steller sea lions (Trites 1992; Merrick 1995). Our $\delta^{15}\text{N}$ data show no major shift in trophic status for any of the three pinniped species during the past five decades even though changes in prey composition and feeding locations have likely occurred.

Temporal changes in the diets of these pinnipeds may have contributed to changes in the animals' isotope ratios but detection of these changes can be complicated by the ecology of each of these animals. Simultaneous changes in foraging locations, e.g. nearshore versus offshore, as well as foraging habits, e.g. switching from a benthic to pelagic diet, could alter the isotopic composition of the sea lions. Heterogeneity in diet and forage locations for these pinnipeds would likely prevent either of these mechanisms from completely explaining the decline in the carbon isotope ratios. Extensive changes in the physical environment have occurred in the northeastern Pacific Ocean and Bering Sea for decades but their impact on primary productivity can only be surmised. Our understanding of how pinnipeds are impacted by these events is impeded by the absence of detailed or adequate long-term monitoring of primary productivity in these regions. However, carbon isotope ratios may provide a means to measure the impact of environmental change in upper trophic level organisms.

Marine mammal populations can be expected to change with time in response to environmental perturbations. The large-scale declines seen in the Bering Sea and Gulf of Alaska pinnipeds are unusual because they appear to have happened in a short time whereas some populations of the same species have remained stable or increased in other areas of the North Pacific. Short-term environmental changes, such as El Niño events, would have only a limited impact on these pinniped populations by reducing food availability (Trillmich and Ono 1991). Short-term changes that could alter the carbon isotope ratios in the marine food webs would likely be tempered in the bone collagen records due to the relatively slow turnover rate of isotopes in this tissue. The magnitude of changes observed in the North Pacific seem to warrant further investigation of their impact on marine mammal populations, and the use of isotope ratios should enhance our understanding of these changes.

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