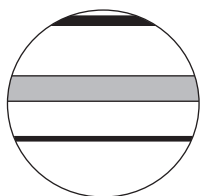


Changes in northeast Pacific marine ecosystems over the last 4500 years: evidence from stable isotope analysis of bone collagen from archeological middens

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Abstract: Changes in food web dynamics and ocean productivity over the past 4500 years are investigated using stable isotope analysis of nitrogen and carbon in collagen from animal bones preserved in coastal archeological middens on Sanak Island, along the eastern edge of the Aleutian archipelago. Samples included Steller sea lions, Harbor seals, Northern fur seals, sea otters, Pacific cod and sockeye salmon. Sea otters had the highest $\delta^{13}\text{C}$ ($-11.9 \pm 0.7\text{‰}$) and lowest $\delta^{15}\text{N}$ values ($14.5 \pm 1.4\text{‰}$), Northern fur seals had the lowest $\delta^{13}\text{C}$ values ($-13.6 \pm 1.4\text{‰}$), and Steller sea lions had the highest $\delta^{15}\text{N}$ values ($18.4 \pm 1.4\text{‰}$) of the marine mammals. Cod isotope values were consistent with those of demersal organisms from near shore habitats ($-12.5 \pm 0.9\text{‰}$ $\delta^{13}\text{C}$, $16.1 \pm 1.4\text{‰}$ $\delta^{15}\text{N}$), while salmon values were consistent with those of organisms existing in an open ocean habitat and at a lower trophic level ($-15.2 \pm 1.4\text{‰}$ $\delta^{13}\text{C}$, $11.5 \pm 1.7\text{‰}$ $\delta^{15}\text{N}$). When comparing six different prehistoric time periods, two time periods had significantly different $\delta^{13}\text{C}$ for salmon. Otters had significantly different $\delta^{15}\text{N}$ values in two out of the six prehistoric time periods but no differences in $\delta^{13}\text{C}$. The mean $\delta^{13}\text{C}$, corrected for the oceanic Suess Effect, of modern specimens of all species (except Northern fur seals) were significantly lower than prehistoric animals. Several hypotheses are explored to explain these differences including a reduction in productivity during the twentieth century in this region of the Gulf of Alaska. If true, this suggests that North Pacific climate regimes experienced during the twentieth century may not be good analogs of North Pacific marine ecosystems during the late Holocene.

Key words: Marine ecosystem, food webs, ocean productivity, stable isotopes, carbon, nitrogen, middens, bone collagen, North Pacific, late Holocene.

Introduction

Historical changes in both pelagic and anadromous fish abundance have been linked to North Pacific climate variability (Ware and Thomson, 1991; Hollowed and Wooster, 1992; Beamish and Bouillon, 1993; Francis and Hare, 1994; Hare and Francis, 1995; Roemmich and McGowan, 1995; Welch *et al.*, 1998; Mantua, 2004).

These climatic changes also affected other aspects of marine ecosystems, such as species composition, abundance and geographic distribution of shellfish, fish and sea mammals (Venrick *et al.*, 1987; Ware, 1995; Anderson and Piatt, 1999; Hare and Mantua, 2000; Hirons *et al.*, 2001; Benson and Trites, 2002; Trites *et al.*, 2007a). We conducted stable isotope (carbon and nitrogen) analysis of collagen from bones of six marine species that inhabited the North Pacific over the last 4500 years. Our resulting stable isotope data were interpreted based on current knowledge of the

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marine system in this region, stable isotope relationships to ecosystem changes, and climatic changes. We adopted a multitaxa approach to determine if there are consistent patterns of change and if any such patterns can be explained by broader-scale drivers, such as changes in the Pacific Decadal Oscillation (PDO), large-scale climate change such as the 'Little Ice Age' (LIA), or human-forced top-down processes.

Recent change in North Pacific climate and marine ecosystems

The PDO has characterized the climatic states of the North Pacific for most of the last century and has alternated between two ocean-climate modes, often referred to as regimes, every ~20–30 years (Mantua and Hare, 2002). Alternate states (positive or negative) of the PDO are defined by characteristic sea surface temperature (SST) patterns and are related to a number of other environmental characteristics (eg, sea level pressure (SLP) and the strength of the Aleutian Low (AL)) (Overland *et al.*, 1999). Changes in environmental characteristics such as wind strength, storm intensity, mixed layer depth and ocean current patterns have an influence on every trophic level in marine ecosystems of the North Pacific (Brodeur and Ware, 1992; Sugimoto and Tadokoro, 1998; Hare and Mantua, 2000; Overland and Stabeno, 2004). Warm coastal PDO phases appear to favor salmon production in the Gulf of Alaska (GOA), the Aleutian Islands and Bering Sea, but are detrimental to salmon production in the California Current system on the Northwest Coast (Beamish and Bouillon, 1993; Francis and Hare, 1994; Beamish *et al.*, 1999; Hare *et al.*, 1999; Mueter and Norcross, 2002). Moreover, gadids and other flatfish seem to increase in numbers in the GOA and Bering Sea during these years while shrimp and capelin decrease (Beamish, 1993; Botsford *et al.*, 1997; Anderson and Piatt, 1999). Pinnipeds, including Steller sea lions (*Eumetopias jubata*, SSL), Harbor seals (*Phoca vitulina*, HS), and Northern fur seals (*Callorhinus ursinus*, NFS), have declined in the western GOA and the Bering Sea since the 1980s (Gentry, 1998; Wynne and Foy, 2002; Stabeno *et al.*, 2005). Arguments for top-down (including anthropogenic) causes versus bottom-up causes for these declines have been recently debated in the literature. The most high profile debates include predation on some of these species by killer whales, nutritional stress caused by regime shifts or stressors from increased commercial fishing (Alverson, 1992; National Research Council, 2003; Springer *et al.*, 2003; Maniscalco *et al.*, 2007; Trites *et al.*, 2007a, b; Wade *et al.*, 2007; Atkinson *et al.*, 2008; Springer *et al.*, 2008).

Studies of past marine ecosystems and their responses to environmental changes in the North Pacific have primarily been based on historical data, which generally cover less than 100 years, and have focused mainly on decadal-scale regime shifts. Only a few researchers have investigated past, long-term changes in these ecosystems employing various sets of proxy data (eg, Finney *et al.*, 2000, 2002; Maschner, 2000; Burton *et al.*, 2002; Causey *et al.*, 2005; Trites *et al.*, 2007b), including stable isotope analyses.

Stable isotopes and marine ecosystems

In general, stable isotopic variations between organisms reflect different feeding ecologies, trophic positions and the isotopic composition of a food web's base (DeNiro and Epstein, 1981; Fry and Sherr, 1984; Schoeninger and DeNiro, 1984; Wada *et al.*, 1991; Michener and Schell, 1994; Doucet *et al.*, 1996; Hobson *et al.*, 1996, 1997; Post, 2002). $\delta^{15}\text{N}$ values increase in marine food webs by ~3‰ per trophic level while $\delta^{13}\text{C}$ increases by ~2‰ from primary to secondary producers and from between ~0.5 and 1‰ in higher trophic levels (Post, 2002). Dietary information on past ecosystems can be recorded in the stable isotope composition of bones (Schoeninger and DeNiro, 1984). Bone is often well preserved in archeological middens, permitting

researchers to compare isotopic signatures over hundreds to thousands of years, and is well suited for this type of study as it has a slower turnover rate relative to muscle tissue, organs and blood (Ambrose and Norr, 1993; Lambert and Grupe, 1993), allowing researchers to compare organisms' overall trophic status (Schoeninger and DeNiro, 1984). If an organism switches trophic level it can be detected by a change in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Variations in $\delta^{13}\text{C}$ can also be related to geography (Schell *et al.*, 1998), possible fluctuations in primary productivity (Hirons *et al.*, 2001) that are linked to climate shifts (Francis and Hare, 1994), and to changing carbon sources linked to events unrelated to productivity (McRoy *et al.*, 2004).

Stable isotopes and oceanography in the northeast Pacific

Phytoplankton discriminate against heavier isotopes during nutrient uptake and photosynthesis, but at lower rates when carbon and nitrogen are less available. The offshore pelagic region of the GOA is a HNLC (high nitrate–low chlorophyll) body of water where productivity is limited by Fe. Therefore nitrate concentrations are high and theoretically $\delta^{15}\text{N}$ values would be low as phytoplankton would discriminate against heavier isotopes. Data from 42°–59°N along four longitudinal transects of 128°, 132°, 134° and 145°W (Satterfield, 2000) does show lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in the GOA gyre versus the shelf (see Figure 4). Mean coastal copepods averaged $9.8\text{‰} \pm 1.1$ $\delta^{15}\text{N}$ and $-19.9\text{‰} \pm 2.0$ $\delta^{13}\text{C}$, while mean open ocean copepods averaged $6.1\text{‰} \pm 0.9$ $\delta^{15}\text{N}$ and $-26.9\text{‰} \pm 1.3$ $\delta^{13}\text{C}$. El-Sabaawi (2008) found similar copepod values with 7 to 9‰ $\delta^{15}\text{N}$ and -24 to -26‰ $\delta^{13}\text{C}$ at Ocean Station Papa (50°N and 145°W) while copepods in the coastal Strait of Georgia had values of 10 to 14‰ $\delta^{15}\text{N}$ and -16 to -19‰ $\delta^{13}\text{C}$.

Historically, change in the strength of the AL is the main climate driver effecting broad-scale physical conditions in the northeast Pacific. For example, in present times, when the AL is particularly strong it affects the GOA gyre with increased upwelling and Ekman transport and decreased SST (Overland *et al.*, 1999; Hare and Mantua, 2000). The water column is less stable, which could lead to reduced primary productivity if Fe inputs are unchanged. Therefore, both ^{15}N and ^{13}C might be expected to be depleted in phytoplankton. It should be noted however, that detailed studies are currently lacking in the gyre region to assess the effects of climate change on primary productivity and isotope fractionation.

If shelf productivity draws down the nutrients in the system faster than they are replenished, then both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ would be expected to increase under higher productivity conditions. Gargett (1997) hypothesized that the presence of an 'optimal stability window' could exist where mixing and stratification are balanced to create high primary productivity. Therefore, both climate and local oceanographic conditions can influence $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values over time in an ecosystem. During times when the AL is strong, GOA shelf waters experience increased vertical mixing in the winter (thought to determine spring nutrient levels) and increased SSTs. Increased precipitation and runoff leads to decreased surface salinity, which increases stability of stratification following wintertime mixing and tends to favor larger phytoplankton blooms in this region (Ware and Thompson, 1991; Gargett, 1997; Childers *et al.*, 2005; Stabeno *et al.*, 2005). Under these conditions, nitrate concentrations may not be drawn down, as it is not limiting in coastal GOA waters (Childers *et al.*, 2005; Strom *et al.*, 2006). However, if the water stability increased enough to limit nitrogen, or if a bloom was large enough to draw nutrients down, then both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ would be expected to increase in phytoplankton. In summary, for downwelling GOA shelf environments it seems likely that climatic conditions which result in higher productivity will lead to higher $\delta^{13}\text{C}$, though current studies are lacking to assess effects on $\delta^{15}\text{N}$.

Modern ecology of marine species

We analyzed the stable isotope composition of SSL, HS, NFS, sea otters (*Enhydra lutris*, SO), Pacific cod (*Gadus macrocephalus*, cod) and sockeye salmon (*Oncorhynchus nerka*, salmon). SO are known to forage throughout their habitat on sea urchin, abalone, crab, mussels, clams, octopus, tunicates, shrimp species and kelp-forest fish (Kenyon, 1969; Kvitck and Oliver, 1992; Watt *et al.*, 2000; Estes *et al.*, 2003; Bodkin *et al.*, 2004). Therefore SO are expected to have stable isotope ratios that reflect near shore/benthic values and to hold a higher trophic position in the kelp-forest community.

SSL are wide-ranging animals but do return to rookeries to pup and breed (Call and Loughlin, 2005; Fadley *et al.*, 2005). Today, SSL diet includes species such as walleye pollock, Atka mackerel, salmon, Pacific cod, arrowtooth flounder, herring, sandlance, Irish lord, squid and octopus (Sinclair and Zeppelin, 2002). Therefore SSL isotope ratios are expected to reflect a higher trophic position in a pelagic ecosystem.

NFS spend much of the year at sea, traveling from breeding grounds in the Bering Sea south to foraging grounds on the western coasts of the USA and Canada (Gentry, 1998). NFS are opportunistic feeders and as such have a wide variety of prey including small schooling fish (10–20 cm in size) and squid (York, 1995; Gentry, 1998). Therefore NFS are expected to have a slightly lower trophic level than SSL in a pelagic ecosystem.

HS are believed to stay closer (within ~50 km) to their coastal haulout (Iverson *et al.*, 1997; Frost *et al.*, 1999), although some studies have shown that they can range more widely, migrating hundreds of miles along coasts and through open ocean (Gentry, 1998). Prey items include large and small herring and pollock, cephalopods, sandlance, capelin, flatfish, cod, salmon and shrimp (Iverson *et al.*, 1997; Pitcher, 1980a,b). There is evidence from Prince William Sound that HS have localized feeding patterns based on prey availability in specific habitats (mostly near shore) (Iverson *et al.*, 1997). Therefore HS are expected to have isotope ratios that reflect a more nearshore food web than HS and SSL.

Cod along the coastal shelf of the lower Alaska Peninsula that are smaller than 60 cm prey mostly on invertebrates such as Tanner crabs, polychaetes and crangonid shrimp, while fish species such as walleye pollock were important parts of diets only of cod larger than 60 cm (Yang, 2004). Following the 1976/77 regime shift, however, pandalid shrimp and capelin were the main food species of Pacific cod in Pavlof Bay on the Alaska Peninsula (Albers and Anderson, 1985). Cod isotope ratios should therefore reflect upper trophic levels in an epi-benthic ecosystem.

Pacific salmon are opportunistic feeders and their diets range from copepods, euphausiids, squid, ctenophores and jellies to small fish (Burgner, 1991; Welch and Parsons, 1993). It appears from observational, stomach-content and stable isotope analyses that adult pink, chum and sockeye salmon feed primarily in more open ocean habitats on a diet of zooplankton and squid (Satterfield and Finney, 2002) and isotope ratios are expected to reflect lower trophic levels in offshore waters.

Study site

Sanak Island (54°25'07"N, 162°41'02"W, Figure 1) is located at the eastern most part of the Aleutian chain, 40 km south of the Alaska Peninsula in the North Pacific and is situated on the outer continental shelf, which is fairly broad in this region. Cool summers and mild winters with high winds and rain characterize the climate in this region (Hunt and Stabeno, 2005; Rodionov *et al.*, 2005). Climatologically, the area is dominated in the winter by the AL, a weather cell of extremely low pressure, which affects the eastern North Pacific, the Bering Sea and Sea of Okhotsk (Rodionov *et al.*, 2005). The primary ocean currents in the area are the ACC and the Alaska Stream (AS). The ACC carries fresher, warmer water from the coastal areas of the GOA down the coast of the Peninsula and along the eastern most islands of the chain, as opposed to the AS, which flows along the shelf break and carries colder, more saline and nutrient-rich waters from the subarctic gyre in the Gulf (Hunt and Stabeno, 2005; Ladd *et al.*, 2005; Logerwell *et al.* 2005).

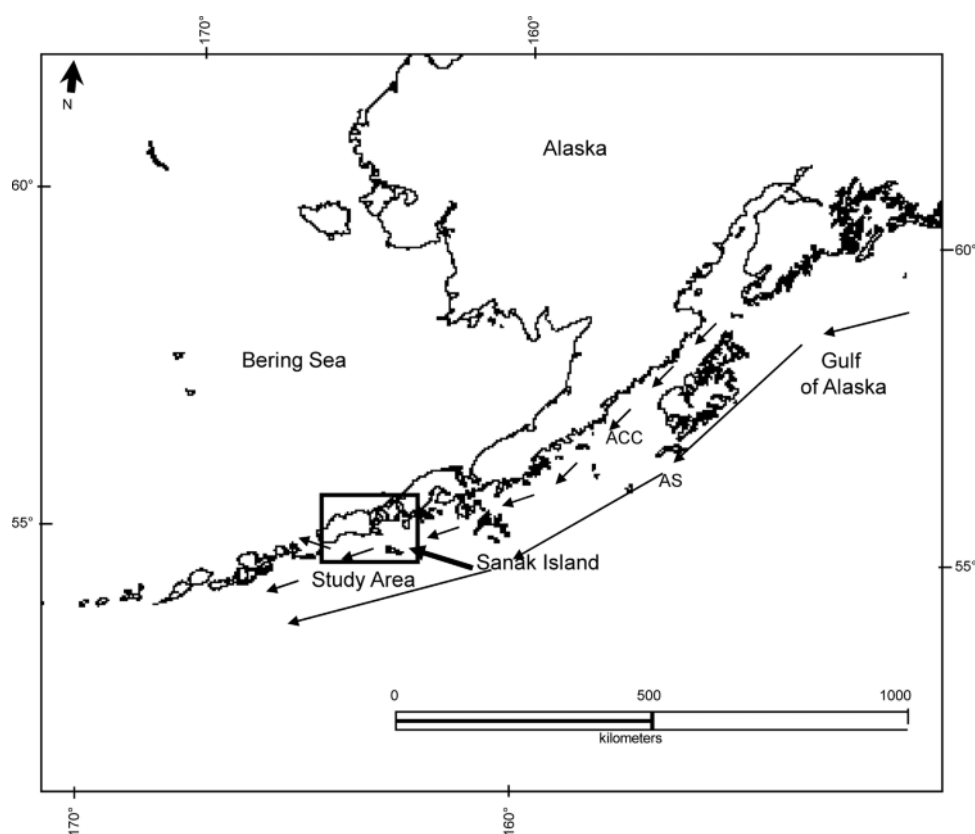


Figure 1 Location of study area in the Gulf of Alaska

Materials and methods

Sample collection and chronology

Samples were collected in 2004 from 24 archeological middens spanning the past 4500 cal. yr BP on Sanak Island, Alaska. All bone was identified to species at Idaho State University (Tews, 2005) and corroborated using comparison collections provided by University of Alaska's Anthropology Department and the Mammal Collection at the University of Alaska Museum of the North. All identifiable elements of marine mammals from each site were separated by element, with the largest number of lefts/rights used to assign individuals of each species (Grayson, 1984). Additional information on age was used to define five age categories; infant, juvenile, subadult, adult and adult + as described in Misarti (2007).

The samples used in this study are drawn from bulk samples from well-stratified shell midden deposits. These deposits, which are uniformly associated with winter village occupations of the island, are high resolution temporal records of changing subsistence regimes and have been left undisturbed by rodents, humans or geomorphic processes (Betts *et al.*, 2009a; Lech *et al.*, 2009; Maschner *et al.*, 2009a, b). All radiocarbon dates were analyzed by either Beta Analytic (BETA) or the Center for Accelerator Mass Spectrometry at Lawrence Livermore Laboratory (CAMS) and were calibrated using Calib 5.0.2 (Reimer *et al.*, 2004). The specific midden samples used in this analysis are from contexts where one or more dated charcoal sample could be directly associated with particular samples of faunal remains.

Prehistoric samples included bones of SSL (minimum number of individuals (MNI)=15), HS (MNI=27), NFS (MNI=21), SO (MNI=88), cod (number of identifiable specimens (NISP)=101) and salmon (NISP=91). We chose to integrate fish samples as vertebrae were used for analysis and there is no assurance that each vertebra represents a different individual. Therefore, each sample represents an average isotope ratio for cod or salmon from five vertebrae from each site. The number of samples (NS) used for salmon and cod were thus reduced to 34 and 35, respectively.

Pink and sockeye salmon are the most abundant species currently spawning in Sanak streams and lakes (Willis and Ball, 1930; Alaska Department of Fish and Game (ADFG), 2006) although a small number of chum salmon were collected in beach

seines from 1912 to 1927 (Willis and Ball, 1930). Satterfield and Finney (2002) found similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for all of these three salmon species in the GOA, which can be attributed to similar feeding locations and prey items. Therefore, despite difficulty associated with identifying vertebrae to a single species, we provisionally refer to these salmon as sockeye salmon, based on historical abundance and distribution data.

Six different time periods based on radiocarbon dates (Figure 2, Table 1), were defined by discontinuity in the recovered archeological record (ie, years the Sanak Island archipelago was either uninhabited or no archeological sites with middens are known as yet), or when the oldest and youngest calibrated site dates did not overlap. SO, cod and salmon were found in numbers sufficient to assess temporal changes in the archeological record. For SO, sufficient samples were available to subdivide two periods, Period 1 and 3, into additional time frames (Periods 1a, 1b, 3a, and 3b; Figure 2). When possible, large, known climatological periods such as the Neoglacial, 'Medieval Warm Period' (AD 900–1200, MWP) and the

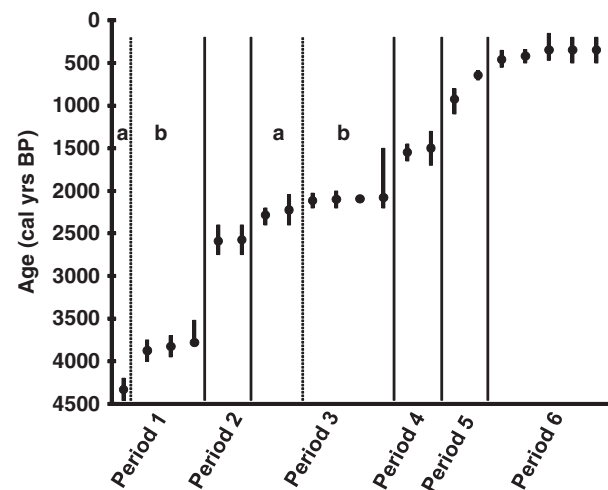


Figure 2 Calibrated radiocarbon ages of sites used for this study. Time periods were subdivided (vertical dashed lines) based on breaks in the radiocarbon age distribution

Table 1 Means and standard deviations of SO, salmon and cod for all six prehistoric time periods. SO is additionally separated into Periods 1a, 1b, 3a and 3b

Archeological time periods	<i>E. lutris</i> (SO)		<i>G. macrocephalus</i> (cod)		<i>O. nerka</i> (salmon)	
	Mean $\delta^{13}\text{C} \pm \text{S.D.}$	Mean $\delta^{15}\text{N} \pm \text{S.D.}$	Mean $\delta^{13}\text{C} \pm \text{S.D.}$	Mean $\delta^{15}\text{N} \pm \text{S.D.}$	Mean $\delta^{13}\text{C} \pm \text{S.D.}$	Mean $\delta^{15}\text{N} \pm \text{S.D.}$
Period 1 (4500–3700 BP)	-12.6 \pm 0.5	14.8 \pm 1.6	-12.8 \pm 0.4	16.2 \pm 0.6	-15.0 \pm 0.6	11.8 \pm 1.2
Period 1a (4500–4000 BP)	-12.4 \pm 0.2	13.9 \pm 0.8	n.a.	n.a.	n.a.	n.a.
Period 1b (4000–3700 BP)	-12.8 \pm 0.8	16.1 \pm 1.7	n.a.	n.a.	n.a.	n.a.
Period 2 (2700–2400 BP)	-11.7 \pm 0.7	13.9 \pm 1.3	-12.6 \pm 0.4	15.6 \pm 1.6	-17.6 \pm 2.0	9.7 \pm 0.9
Period 3 (2400–1900 BP)	-11.9 \pm 0.8	14.5 \pm 1.0	-12.5 \pm 1.6	15.9 \pm 1.6	-14.4 \pm 1.4	11.9 \pm 1.5
Period 3a (2200–2100)	-11.7 \pm 0.4	14.4 \pm 0.9	n.a.	n.a.	n.a.	n.a.
Period 3b (2100–2000 BP)	-12.1 \pm 1.0	14.6 \pm 1.0	n.a.	n.a.	n.a.	n.a.
Period 4 (1600–1500 BP)	-11.8 \pm 0.6	13.7 \pm 1.2	-12.7 \pm 0.3	15.9 \pm 0.5	-14.1 \pm 2.8	13.5 \pm 1.7
Period 5 (1100–600 BP)	-11.9 \pm 0.7	14.5 \pm 1.5	-11.9 \pm 0.3	16.3 \pm 0.5	-15.1 \pm 0.1	10.0 \pm 0.1
Period 6 (550–150 BP)	-11.7 \pm 0.5	14.7 \pm 1.1	-12.2 \pm 0.5	16.2 \pm 1.4	-15.9 \pm 1.0	11.0 \pm 1.1

LIA (AD 1250–1850) were associated with time period descriptions. The Modern Period was defined as AD 1952 to 2000.

Sample preparation and stable isotope analysis

All collagen samples were prepared following the bone collagen extraction procedures described by Matheus (1995, 1997). Slices of compact, cortical bone weighing between 0.1 and 1.0 g were cleaned in a sonicator. Lipids were removed from the bone using the methanol/chloroform procedure described by Bligh and Dyer (1959). The bones were then demineralized in 6N HCl and ultrapure water. Length of time needed to demineralize bone varied from sample to sample (ranging from 6 to 14 days). The remaining material was rinsed to neutral pH in ultrapure water, soaked in 5% KOH and 5 ml of ultrapure water for 8 h to eliminate contamination from surrounding humic soils, and rinsed to neutral pH again. Samples were gelatinized by adding 0.05 ml of 3N HCl to 5 ml of ultrapure water, heated to 65°C and agitated. The samples were filtered using Millex-HV 0.45µm filters and then placed in a freeze drier for 48 h. Stable carbon and nitrogen isotope analysis of these samples was completed in the Alaska Stable Isotope Facility, University of Alaska Fairbanks on a Finnigan Delta^{plus}XP IRMS. Stable isotope ratios are expressed using the standard delta notation:

$$\delta X (\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N and R_{sample} is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are expressed relative to Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 (air), respectively. Analytical precision (expressed as 1 standard deviation calculated from $n = 80$ peptone standards distributed throughout each run) was $\pm 0.2\text{‰}$ for both carbon and nitrogen.

Data analysis and display

All comparative modern salmon and cod muscle tissue (some samples analyzed by Satterfield, 2000 and Hiron, 2001) have been adjusted to reflect bone collagen values based on the isotopic fractionations determined for C and N between muscle tissue and bone collagen in these taxa for this region. These corrections are based on comparisons of cod and salmon ($n=20$ and 19, respectively) muscle tissue, lipid extracted muscle tissue and bone collagen (Misarti, 2007). The $\delta^{13}\text{C}$ of bone collagen of salmon is $\sim 2.5\text{‰}$ greater than lipid-extracted muscle tissue while $\delta^{15}\text{N}$ in bone collagen is $\sim 1.0\text{‰}$ less. Cod collagen $\delta^{13}\text{C}$ is $\sim 3.8\text{‰}$ greater than muscle and $\delta^{15}\text{N}$ is $\sim 0.8\text{‰}$ less.

Depletion in the $\delta^{13}\text{C}$ isotopic composition of dissolved inorganic carbon (DIC) in the worlds' oceans due to the increase in anthropogenic CO_2 released into the atmosphere (often referred to as the Oceanic Suess Effect) since the Industrial Revolution is estimated to be $-0.62 \pm 0.17\text{‰}$ as of 1991 in the eastern North Pacific (Ortiz *et al.*, 2000). Although this is a smaller estimate of change than published values for some oceanic regions, Schell (2001) noted that in areas where upwelling and winter deep mixing occur at higher latitudes, such as our study area, the effects of anthropogenic decreases of $\delta^{13}\text{C}$ are diminished. In the GOA and other areas of the North Pacific north of 50°, there has been a reduced accumulation of anthropogenic tracers such as $\delta^{13}\text{C}$ (Gruber *et al.*, 1999; Schell, 2001; Quay *et al.*, 2003; Guilderson *et al.*, 2006). All $\delta^{13}\text{C}$ of the Modern (ie, AD 1952–2000) samples used in this study have been adjusted for anthropogenic $\delta^{13}\text{C}$ effects according to year of sample using Equation (2) below, which was modified from Hilton *et al.* (2006) to allow comparisons between Modern and pre-historic values:

$$\text{Suess Effect Correction Factor} = a \cdot \exp(b \cdot 0.027) \quad (2)$$

where a is the maximum annual rate of $\delta^{13}\text{C}$ decrease in the North Pacific (in this case -0.014 derived from Quay *et al.* (1992), used in

our equation), which closely match water column data (Tanaka *et al.*, 2003), northeastern Pacific coral-based estimates (Williams *et al.*, 2007), and the global estimates of Gruber *et al.* (1999)); b is the year represented by the death of the animal minus 1850 (the start of the Industrial Revolution); and 0.027 describes the curve presented by Gruber *et al.* (1999) for change in the $\delta^{13}\text{C}$ of the worlds' oceans from 1945 to 1997. This equation yields a maximum $\delta^{13}\text{C}$ decrease from 1850 to 2007 of 0.97‰. Our corrected value for 1991 is 0.63‰, which is very similar to Ortiz *et al.*'s (2000) measured decrease of 0.62‰ in the North Pacific at this time.

In addition to the Oceanic Suess Effect, the increase in $\text{CO}_{2\text{aq}}$ in the ocean ($\text{CO}_{2\text{ocean}}$) due to increasing amounts of CO_2 released in the atmosphere ($\text{CO}_{2\text{atm}}$), and subsequent increasing discrimination by primary producers must also be taken into account since we assume that $\delta^{13}\text{C}$ values of consumers originate from the base of the food web (Laws *et al.*, 1995, 2002). Data on the increase in $\text{CO}_{2\text{atm}}$ from 1850 to present (286.8 to 377.43 ppm) were obtained from http://earthtrends.wri.org/searchable_db/index.cfm?theme=3 and compared with measurements along the Alaska Peninsula and Aleutian Islands in 1995 (Takahashi *et al.*, 2006). In the Pacific Ocean, net uptake is $\sim 41\%$ of $\text{CO}_{2\text{atm}}$ from 1970 to 1990 (Quay *et al.*, 1992) therefore we have estimated that maximum $\text{CO}_{2\text{ocean}} = \text{CO}_{2\text{atm}} \cdot 0.41$. Aqueous CO_2 in the ocean ($\text{CO}_{2\text{aq}}$) is affected by $\text{CO}_{2\text{ocean}}$ and the solubility of CO_2 (K_o) due to salinity and temperature (Weiss, 1974) or $\text{CO}_{2\text{aq}} = K_o \cdot \text{CO}_{2\text{ocean}}$, as modified from Hilton *et al.* (2006). We assumed a constant salinity of 32 psu (practical salinity units) (Coyle, 2005) and temperature was determined per year from 1854 to present (Smith and Reynolds, 2003; <http://nomads.ncdc.noaa.gov/#climatencdc>). The effect of phytoplankton $\delta^{13}\text{C}$ fractionation (ϵ_p) as a function of $\text{CO}_{2\text{aq}}$ was estimated using equation (9) from Laws *et al.* (2002) and modified from Hilton *et al.* (2006):

$$\epsilon_p = \epsilon_2 + \epsilon_1 - \epsilon_{-1} - 1/1 + \{ \text{CO}_{2\text{aq}} \cdot P / \mu C (1 + \beta) \} \cdot (\epsilon_2 - \epsilon_{-1}) / (\beta + 1) \quad (3)$$

where ϵ_i is the isotopic discrimination associated with import into the cell (1‰ per Laws *et al.*, 2002); ϵ_{-1} is the isotopic discrimination associated with diffusion back into the water (1‰ per Laws *et al.*, 2002); ϵ_2 is the isotopic discrimination associated with carboxylation (in this case the median of Laws' *et al.* (2002) values or 26.5‰); C is the organic carbon content of the cell ($1.09 \cdot 10^{-9}$ gC/cell per Laws *et al.*, 2002); and P is the permeability of the plasmalemma to $\text{CO}_2 \times$ surface area of the cell ($4.57 \cdot 10^{-10}$ m/s \times m²/cell); and β is a constant equal to the ratio of net diffusional loss of CO_2 to carbon fixation (0.2 per Laws *et al.*, 2002). Both P and C were estimated using a cell radius of $1.5 \mu\text{m}$ (Hilton *et al.*, 2006). We held growth rate (μ) for our geographic area at a constant of 0.5/day (see Liu *et al.*, 2002) while $\text{CO}_{2\text{aq}}$ varied on a yearly basis as a function of $\text{CO}_{2\text{atm}}$ as discussed. The maximum correction factor for the period of AD 1850–2007 determined from these calculations is 0.19‰. This correction factor will vary in response to key parameters such as cell growth rate, surface area of cell, salinity and SST. For this study we have used values for each parameter that are derived from published data collected in our geographic area. The $\delta^{13}\text{C}$ of the modern samples used in this study have been additionally adjusted according to year of sample collection using this method. Note that although the premise for the equations in Hilton *et al.* (2006) was sound, modifications were made due to typesetting errors in equations and parameter value errors.

Results

The mean collagen C:N for bone samples analyzed is 3.2 ± 0.2 , which falls within the range of values (2.9–3.6) considered to be indicative of collagen that has not undergone diagenesis (Tuross *et al.*, 1988; Koch *et al.*, 1994; Hedges *et al.*, 2005). A summary of

the isotopic results of archeological specimens from Sanak Island (Table 2) shows that of the marine mammals sampled for this study SO had the lowest mean $\delta^{15}\text{N}$ and the highest mean $\delta^{13}\text{C}$ while NFS had the lowest $\delta^{13}\text{C}$, and SSL had the highest $\delta^{15}\text{N}$. Cod have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values compared with salmon (Table 2).

Most prehistoric species have higher mean $\delta^{13}\text{C}$ than their modern counterparts even after correcting for the Oceanic Suess Effect and CO_2 concentration (Table 2 and Figure 3). When compared with Modern collagen counterparts as analyzed by Hirons (2001), prehistoric SSL and HS had statistically higher $\delta^{13}\text{C}$ (*t*-test,

Table 2 Location, number, sample type and mean isotopic value of archaeological and modern specimens

Species	Location	No. of samples	Sample type	Mean $\delta^{13}\text{C} \pm \text{SD}$	Mean $\delta^{13}\text{C} \pm \text{SD}^a$	Mean $\delta^{15}\text{N} \pm \text{SD}$
Archaeological						
<i>E. lutris</i> (SO)	Sanak	88	bone	-11.9 ± 0.8	n.a.	14.5 ± 1.4
<i>C. ursinus</i> (NFS)	Sanak	27	bone	-13.6 ± 1.4	n.a.	16.1 ± 2.4
<i>P. vitulina</i> (HS)	Sanak	37	bone	-12.2 ± 0.8	n.a.	17.1 ± 1.7
<i>E. jubata</i> (SSL)	Sanak	15	bone	-13.1 ± 0.7	n.a.	18.4 ± 1.4
<i>G. macrocephalus</i> (cod)	Sanak	101	bone	-12.5 ± 1.0	n.a.	16.1 ± 1.2
<i>O. nerka</i> (salmon)	Sanak	91	bone	-15.2 ± 1.4	n.a.	11.5 ± 1.7
Modern						
<i>E. lutris</i> (SO)	GOA ^d	13	bone	-13.3 ± 0.9	-12.7 ± 0.9	11.3 ± 1.0
<i>C. ursinus</i> ^b (NFS)	GOA ^d	10	bone	-14.5 ± 0.8	-14.1 ± 0.8	17.2 ± 1.5
<i>P. vitulina</i> ^b (HS)	GOA ^d	48	bone	-14.3 ± 0.8	-13.8 ± 0.8	17.2 ± 1.6
<i>E. jubata</i> ^b (SSL)	GOA ^d	13	bone	-14.4 ± 0.9	-13.8 ± 0.9	18.5 ± 1.4
<i>G. macrocephalus</i> (cod)	Alaska Pen.	49	bone/muscle	-12.8 ± 0.6	-11.9 ± 0.6	15.6 ± 0.9
<i>O. nerka</i> ^c (salmon)	GOA ^d	34	bone/muscle ^e	-18.4 ± 0.8	-17.4 ± 0.8	9.9 ± 0.4

^aAll Modern carbon isotope values corrected to account for Suess Effect and discrimination changes in the eastern North Pacific (see methods).

^bSome modern data from Hirons (2001) and ^cSatterfield (2000).

^dGOA, Gulf of Alaska. All samples collected from Unimak Island to Kodiak Island and the western tip of the Kenai Peninsula.

^eAll modern salmon muscle tissue has been corrected for fractionation difference between bone and muscle (see methods; Misarti, 2007).

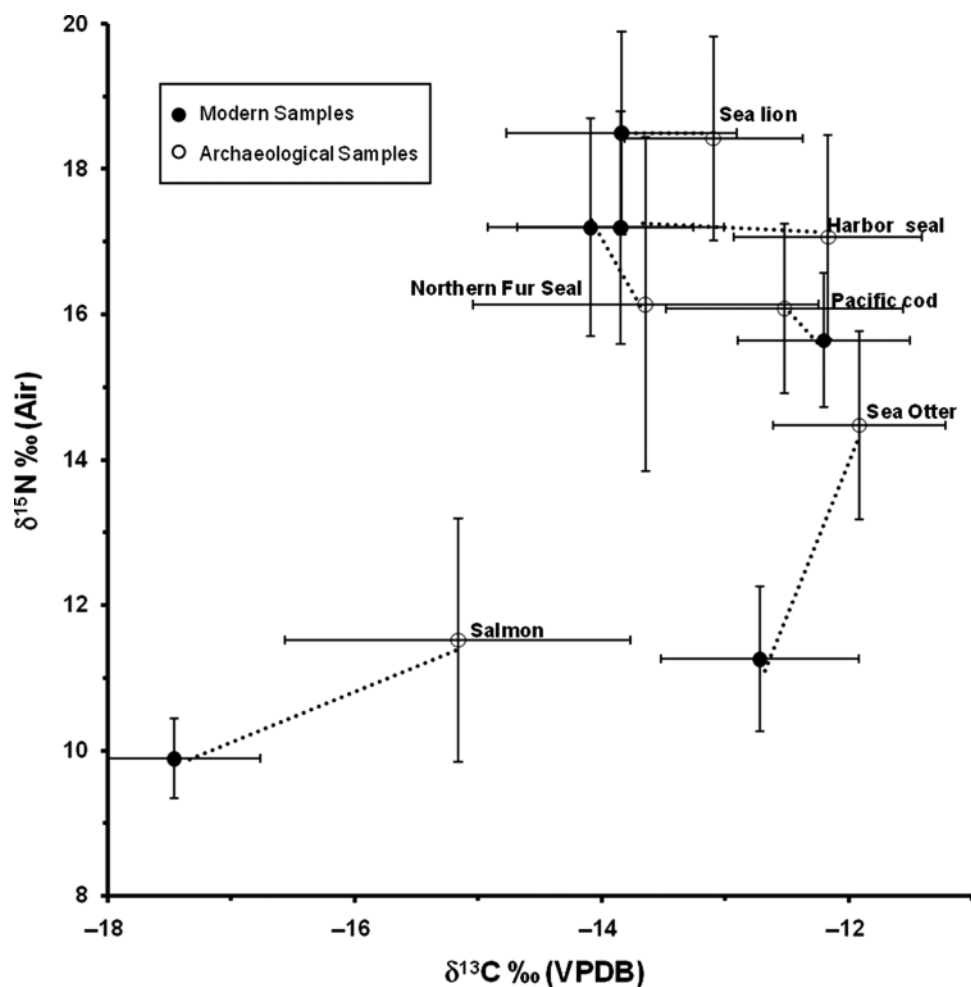


Figure 3 Means and one standard deviation of bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from both modern and archeological specimens. Modern data (~AD 1952–2000) from Satterfield (2000), Hirons (2001) have been corrected for the Suess Effect (see methods). Modern samples of cod and salmon are based on analysis of muscle and bone. All muscle has been adjusted to collagen values based on the fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between muscle and collagen (Misarti, 2007)

Table 3 Results of ANOVA and Bonferroni tests between all six prehistoric time periods and modern samples. Only Bonferroni results with significant differences are listed

Species	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$	
	Time periods	<i>P</i>	Time periods	<i>P</i>
<i>E. lutris</i> (SO)	All	<0.001	All	0.002
	1 and 2	0.026	2 and Modern	0.005
	1 and 4	0.016	3 and Modern	0.041
	1 and Modern	<0.001	4 and Modern	0.037
	2 and Modern	<0.001	6 and Modern	0.010
	3 and Modern	<0.001		
	4 and Modern	<0.001		
	5 and Modern	<0.001		
<i>O. nerka</i> (salmon)	All	<0.001	All	<0.001
	2 and 4	0.023	2 and 3	0.001
	1 and Modern	0.001	2 and 4	0.033
	3 and Modern	<0.001	1 and Modern	<0.001
	4 and Modern	0.001	3 and Modern	<0.001
			4 and Modern	0.001
<i>G. macrocephalus</i> (cod)	All	0.659	All	0.089
			6 and Modern	0.006

$p < 0.01$ and $p < 0.001$, respectively) while prehistoric NFS yielded no significant differences from modern samples for $\delta^{13}\text{C}$ (t -test, $p = 0.35$). Prehistoric $\delta^{13}\text{C}$ values were significantly higher than modern specimens for SO (t -test, $p < 0.01$), salmon (t -test, $p < 0.01$) and cod (t -test, $p = 0.003$). Salmon and SO also had significant differences in $\delta^{15}\text{N}$ between prehistoric and modern samples (t -test, $p < 0.001$). Comparisons of modern and prehistoric $\delta^{15}\text{N}$ for cod, SSL, NFS, and HS showed no significant differences (t -test, $p = 0.059, 0.992, 0.146, \text{ and } 0.457$, respectively).

SO were the only mammalian species with high enough sample numbers to allow comparisons between the six prehistoric time periods (Table 1). SO had a significant difference in $\delta^{13}\text{C}$ (single-factor ANOVA, $p = 0.002$) and in $\delta^{15}\text{N}$ (single-factor ANOVA, $p = 0.001$) between the six prehistoric time periods (Table 1, 3, see Figure 5). Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for cod between these same six time periods was not statistically significant (Table 1, 3, see Figure 5), while changes in $\delta^{13}\text{C}$ of salmon were statistically significant (single-factor ANOVA, $p = 0.028$) but no statistically significant changes were found for $\delta^{15}\text{N}$ (Table 1, 3, see Figure 5). A Bonferroni *post-hoc* test was used to further identify time periods that were significantly different. SO $\delta^{15}\text{N}$ was significantly different between Modern and all six prehistoric time periods, while Periods 1 and 2 and 1 and 4 were also significantly different (Table 3). SO $\delta^{13}\text{C}$ was significantly different between Modern and Periods 2, 3, 4 and 6 (Table 3). Salmon $\delta^{13}\text{C}$ differed significantly between Periods 2 and 3 and 2 and 4 as well as Modern and Periods 1, 3, 4 and 6 (Table 3). Salmon $\delta^{15}\text{N}$ differed significantly between Periods 2 and 4 and Modern and 1, 3 and 4 (Table 3).

Discussion

The elevated $\delta^{13}\text{C}$ signature (Figures 3 and 4) for SO reflects a benthic/nearshore diet of invertebrates that consume intertidal plants and macro-algae with elevated $\delta^{13}\text{C}$ in comparison with phytoplankton (Fry and Sherr, 1984) and prey items that include deposit-feeding bivalves (Hobson and Welch, 1992). Salmon, on the other hand, have isotopic signatures relatively depleted in ^{15}N and ^{13}C , indicating both lower trophic level foraging and an open-ocean habitat (Figures 3 and 4). In comparison, cod isotopic values reflect the enrichment of their shelf habitat and prey on some benthic species. SSL, HS and NFS stable isotope data show high, and generally similar, trophic positions. Prehistoric NFS have the

lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of all three prehistoric pinniped species, which more than likely reflects the species' mixed continental shelf/open ocean foraging patterns than absolute relative trophic position. SSL have the highest $\delta^{15}\text{N}$, which may simply reflect their ability to forage on larger fish than HS and NFS, while HS have the highest $\delta^{13}\text{C}$ values of all the pinniped species, reflecting a more near shore foraging pattern. Newsome *et al.* (2007b) found similar patterns when comparing prehistoric NFS and HS.

Changes between prehistoric time periods

Although the median $\delta^{15}\text{N}$ values of salmon changes over the six prehistoric time periods, suggesting changes in trophic level, prey or environment over time, there is statistically significant change only between Periods 2 and 4 (Table 3, Figure 5). Significant changes in $\delta^{13}\text{C}$ took place between Periods 2 and 3 and 2 and 4, with the median from each time period changing slightly more than 2%. Periods 3 and 4 have individual samples with the highest $\delta^{13}\text{C}$ after which the median drops slowly until Period 6. Based on sediment core data, salmon abundance in the Gulf of Alaska was relatively lower during Periods 1, 3 and 4 and higher during Periods 2 and 6 (Finney *et al.*, 2000, 2002, 2009; Misarti, 2007). Bottom-up hypotheses regarding salmon abundance suggest that ocean productivity, and thus $\delta^{13}\text{C}$, would be relatively higher during these periods (Brodeur and Ware, 1992; Beamish and Bouillon, 1993; Laws *et al.*, 1995). However, our data show that $\delta^{13}\text{C}$ is similar or lower at these times relative to the other periods (Figure 5, Table 1). It is possible that the fluctuations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for salmon during prehistoric time periods resulted primarily from changes in geographic areas salmon inhabited (per Schell *et al.*, 1998; Satterfield and Finney, 2002).

Cod $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ show no statistically significant changes over the last 4500 years (Table 3, Figure 5). This lack of change in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ over the six prehistoric time periods may be due to cod's broad semi-demersal feeding habits and a more limited geographic range of habitat, compared with salmon and some marine mammals. Despite changing climate and prey availability, it may be that the basic food web structure supporting cod did not change. For example, cod were documented to have switched some prey items following the 1976/77 regime shift (Yang 2004; Albers and Anderson, 1985), but not their foraging location. If the prey items before and after the regime shift held similar trophic positions, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of cod may not change.

The variability in SO $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ over the last 4500 years may be explained by several hypotheses concerning environmental

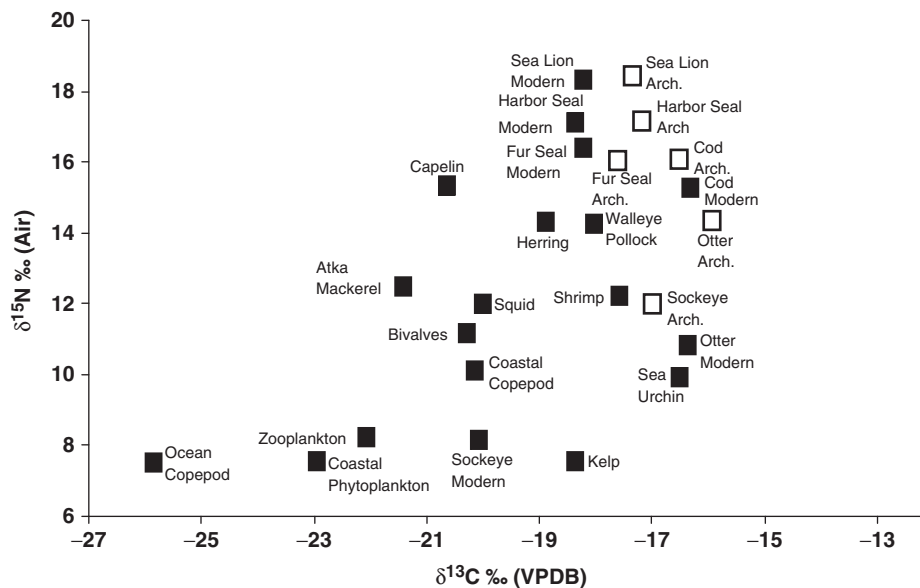


Figure 4 Trophic position of archeological mammals and fish with some selected modern prey species. All samples corrected for fractionation between muscle tissue and bone collagen. Prey data compiled from: Schoeninger and DeNiro (1984); Duggins *et al.* (1989); Hobson and Welch (1992); Hobson *et al.* (1997); Satterfield (2000); Hirons (2001). Nearshore, benthic prey species and kelp collected from Sanak Island in 2004 and 2006

change over time, as well as possible top-down effects of population size on foraging conditions. SO had a significant difference in $\delta^{15}\text{N}$ between Period 1 and 2 and 1 and 4 (Table 3). The stable isotope data suggest a change over time from a more mixed diet (including a greater emphasis on fish) in the earliest record for this study around Period 1a, to one based more on benthic invertebrates (while still including fish), Period 6. Top-down processes could have affected the isotopic signatures of SO, as they were an important subsistence resource for the Aleut. This would, of course, be a local phenomenon and our hypothesis is based on the understanding that the SO bones collected on Sanak Island represent a local Sanak SO community. During Period 1a, SO remains are frequent in the archeological record when compared with other sea mammals (Betts *et al.*, 2009b). Watt *et al.* (2000) compared diet studies from the 1950s and 1960s in the Aleutians when SO were at equilibrium density, with those from the 1990s when SO population had declined (Reisewitz *et al.*, 2006). They observed that fish were a much more important dietary item in the 1950s and 1960s than they were in the 1990s, when sea urchin were a greater percentage of the diet. If SO were at equilibrium density in Period 1a but were subsequently heavily exploited by the Aleut, causing a population decline, then a shift in diet similar to that recorded between the 1950s and the 1990s may have occurred. In fact, by Period 1b frequency of SO in the archeological record had declined drastically (Betts *et al.*, 2009b; Table 1), and perhaps reflects not only a change in Aleut subsistence to larger sea mammals but also a smaller SO population at a time when $\delta^{15}\text{N}$ was at its highest. By Period 2, after almost 2000 years of exploitation, SO $\delta^{15}\text{N}$ declined.

Differences in $\delta^{15}\text{N}$ between prehistoric and modern samples

SO are the only species in this study whose modern collagen samples have a significantly lower $\delta^{15}\text{N}$ compared with prehistoric samples as a group. Furthermore the modern data are significantly different from all separate prehistoric time periods (Table 3). The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ decrease is nearly 3:1, which represents a drop that might be expected if SO began feeding one trophic level lower. Although SO may have switched towards a more benthic foraging strategy by Period 2, our data suggest that SO diet changed further sometime in the past 250 years. This may be due partly to the near extinction of SO that began in the 1750s with Russian fur trading.

If, as SO numbers declined, urchin numbers increased, then overgrazing of kelp may have created urchin barrens (Simenstad *et al.*, 1978; Dayton, 1985; Duggins *et al.*, 1989; Estes and Duggins, 1995; Steneck *et al.*, 2002; Estes *et al.*, 2003), forcing drastic changes in the near shore ecosystem and food web. All 13 Modern SO samples came from the Aleutian Islands and the Alaska Peninsula, and were collected between 1960 and 2000. It is very possible that they were collected from areas with urchin barrens or newly recovering kelp forests, and therefore reflect a very different ecosystem than the prehistoric SO.

Differences in $\delta^{13}\text{C}$ between prehistoric and Modern samples

The most notable overall change in stable isotope signatures is the decrease of $\delta^{13}\text{C}$ in all species, except NFS, when comparing prehistoric as a group with Modern. This change occurred in both the fish and mammal species regardless of the ecosystem the species inhabits (eg, nearshore versus offshore) even after Modern values were corrected for the Oceanic Suess Effect and increasing phytoplankton discrimination due to increases in $\text{CO}_{2\text{aq}}$. SSL, HS and salmon reflect conditions in pelagic environments, due their feeding ecology. The mean $\delta^{13}\text{C}$ for these species from midden samples are 0.5–1.6‰ higher than their modern counterparts. Cod, whom we consider to reflect epi-benthic coastal realms, change by 0.6‰ when compared with their modern counterparts. SO, which represent nearshore benthic systems, have nearly a 1.0‰ decrease from prehistoric to Modern. There is a possibility that we underestimated the Suess Effect, which would likely have a unidirectional change in all habitats. However, our estimates correlate well with instrumentally based data in the NE Pacific. There are several other possible explanations/hypotheses for the observed differences.

One possible reason for a change in $\delta^{13}\text{C}$ of pelagic species is the recent reduction of ice in the Bering Sea (Niebauer, 1998; Parkinson and Cavalieri, 2002). Ice algae can have higher $\delta^{13}\text{C}$ than phytoplankton, and would have played a reduced role in the food web as winter ice area in the Bering Sea decreased, as might be expected between Modern and Neoglacial times (McRoy *et al.*, 2004). Sanak Island is close to Unimak and False passes and it is possible that SSL and HS captured near Sanak Island may also have fed in Bering Sea waters. However, reduced sea ice in the Bering Sea would not affect cod or SO that inhabit the GOA, as

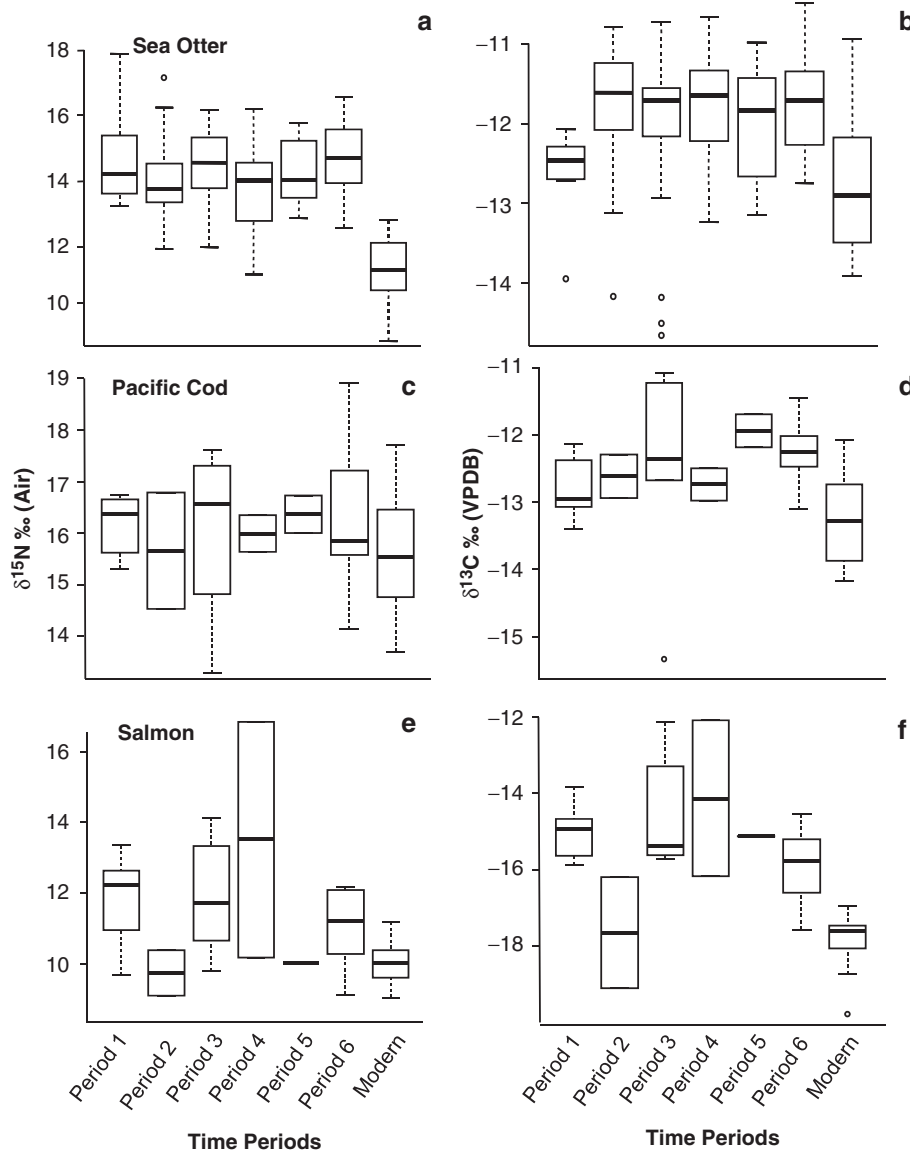


Figure 5 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ medians (denoted by central line), quartiles (outer hinges of box), non-outlier range (whiskers) and outliers (single points) of SO, cod and salmon over seven time periods discussed in the text. Modern data (~AD 1952–2000) from Satterfield (2000) and Hirons (2001) have been corrected for the Suess Effect and phytoplankton discrimination (see methods). Some modern samples of salmon are based on analysis of muscle and have been adjusted to collagen values based on the fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between muscle and collagen

neither of the species travel to the extent that the pinniped species analyzed here do.

A second hypothesis involves changes in the foraging locations of SSL and HS. Burton *et al.* (2001) proposed that differences in mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between archeological and Modern NFS are due to a difference in location of foraging from middle latitudes to higher latitudes. NFS are the only marine mammal in this study whose mean archeological $\delta^{15}\text{N}$ appears different (~1.1‰ lower) than the modern $\delta^{15}\text{N}$ mean, though they are not statistically different due to the high variance in the prehistoric data. Most of the prehistoric NFS in our study were juveniles while Modern specimens were of varying ages. Newsome *et al.* (2006) showed that $\delta^{15}\text{N}$ values from NFS between 6 and 20 months of age (after weaning) decreased dramatically and were lower than both pre-weaned and adult $\delta^{15}\text{N}$ values, while $\delta^{13}\text{C}$ did not change. The disproportionate number of juveniles in our study therefore makes it difficult to draw any conclusions about possible changes in $\delta^{15}\text{N}$ in comparison with the Modern data (see Newsome *et al.*, 2007a).

A study by Burton and Koch (1999) found that pinnipeds (including NFS and HS from Alaska and California) assumed to

be foraging in various locations (both nearshore and offshore), but at similar trophic levels, had similar $\delta^{15}\text{N}$ composition of bone collagen but widely ranging $\delta^{13}\text{C}$. However in the GOA, $\delta^{15}\text{N}$ values are significantly lower in the offshore, pelagic realm than on the continental shelf (Satterfield, 2000; El Sabaawi, 2008). Based solely on the $\delta^{13}\text{C}$ it is possible that the pinnipeds found in the archeological middens we investigated on Sanak Island spent a greater percentage of time foraging in nearshore waters while modern pinnipeds utilize more offshore waters. However, given that our $\delta^{15}\text{N}$ data remain relatively unchanged, an onshore versus offshore change in forage locations is not supported.

A final hypothesis to account for the lower $\delta^{13}\text{C}$ in modern pinnipeds and fish is that it reflects a decrease in primary productivity. Some researchers have suggested that the historical decreases in $\delta^{13}\text{C}$ reflect a decrease in ocean primary productivity in the GOA and the Bering Sea (Schell, 2000, 2001; Hirons *et al.*, 2001; Hobson *et al.*, 2004). The change we observe may have also resulted from productivity declines associated with a reorganization of the ocean/climate system of the northeast Pacific/southern

Bering Sea at the end of the LIA (AD 1850), a time which divides our Modern and archeological samples (Finney *et al.*, 2009).

As the Modern baseline we used spans the 1976-regime shift (averaging across two periods of extreme differences in mean AL strength and PDO indices), the prehistoric to historical decrease in $\delta^{13}\text{C}$ (-0.5 to -1.6‰) might suggest that prehistoric environmental conditions are different from the 'average' recent historical period. Such an hypothesis assumes we have correctly accounted for anthropogenic changes in the carbon system. In support of this hypothesis, a synthesis of available sedimentary records of Pacific pelagic fish abundance demonstrated a widespread shift in inter-species and fish-climate relationships prior to the twentieth century relative to modern observations (Finney *et al.*, 2009). A basin-wide reorganization of ocean-atmospheric circulation at the end of the LIA in the nineteenth century is suggested by several paleoclimatic records. For example, tree-ring chronologies show that strong positive PDO states are relatively rare over the past 1000 years, and evaluations of both tropical and high-latitude Pacific paleoclimatic records also suggest different prehistoric circulation patterns (Fisher *et al.*, 2004; MacDonald and Case, 2005; D'Arrigo *et al.*, 2005). Alternatively, long-term trends in oceanographic conditions may have also resulted in the crossing of ecological thresholds. For example, there has been an overall warming trend in SST in the northeast Pacific over the last 7000 years (Kim *et al.*, 2004). Warming ocean waters could have caused a decrease in mixed layer depth and increased stratification in summer months, thereby reducing available nutrients that can, in turn, reduce primary productivity. Perhaps the recent oceanic/climate patterns have resulted in stratification that exceeds the 'optimal' productivity window when compared with the last 4500 years. In summary, there is a growing body of evidence to suggest that conditions in the twentieth century may not be good analogs for previous Holocene environments, and could have resulted in different primary productivity regimes.

Conclusions

Our research illustrates that the stable isotope signatures of species foraging in different ecosystems in the northeast Pacific reacted in both similar and different ways to changes over the past 4500 years. Comparisons of shifts in the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of prehistoric salmon, cod and SO revealed different trajectories of change. Both top-down and bottom-up forcing mechanisms may explain these changes, depending on species and time period. SO and salmon had a significant change in $\delta^{15}\text{N}$ over the six prehistoric time periods investigated. In the case of SO, it is possible that bottom-up processes such as changes in sea level and climate change might have affected kelp bed communities and thus changed relative proportions of kelp-based versus pelagic fish diets. Top-down processes such as hunting pressure by humans may also have affected SO $\delta^{15}\text{N}$ through trophic cascades altering the kelp-forest community in which they foraged, or by altering the areas in which they foraged. In the case of salmon it is possible that foraging locations (ie, gyre versus shelf) or upwelling areas and mixed layer depth changed in response to climatic shifts that have not been documented in Modern stable isotope data.

Our multispecies, multiecosystem approach allowed us to put forward hypotheses based on broader-scale drivers for change in the GOA. Modern pinnipeds and fish (with the exception of NFS), regardless of habitat size, location and prey items, showed a significant decrease in $\delta^{13}\text{C}$ when compared with the prehistoric specimens we investigated. These changes are greater than can be reasonably attributed to the Suess Effect. A unifying hypothesis to explain this $\delta^{13}\text{C}$ data is declining primary productivity regimes in the pelagic realm. Two potentially interrelated mechanisms may

account for this surprising conclusion. Major climatic reorganization at the end of the LIA may have resulted in differing modes of oceanic variability and resultant productivity in historic vs. modern during much of the late Holocene. Alternatively, warming of ocean waters may have reached a threshold in the twentieth century whereby changes in physical conditions reduced primary productivity, and/or shifted upwelling and downwelling locations. All of these hypotheses point to a recent reorganization of the northeastern Pacific system when compared with much of the last 4500 years. Changes in ocean carrying capacity have significant implications for management of marine ecosystems, and further research to better understand ocean-climate variability and its influence on biological processes is of critical importance.

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